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Temperature-Dependent Parental Investment in the Giant Waterbug Belostoma flumineum (Heteroptera: Belostomatidae)

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Temperature-Dependent Parental Investment in the Giant Waterbug *Belostoma flumineum* (Heteroptera: Belostomatidae)

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ABSTRACT We examined the effects of ambient temperature on the brooding behavior of male waterbugs, *Belostoma flumineum* Say. Male waterbugs are more likely to prematurely terminate care for small egg-pads than for larger egg-pads. Because embryogenesis and breeding season are both associated with ambient temperature, males in warmer environments may respond differently than those in cooler conditions. We studied the effects of temperature on male parental behavior by housing groups of completely and partially egg-encumbered males under different thermal regimes. Completely encumbered males rarely discarded egg-pads, regardless of ambient temperature. Partially encumbered males housed under warm ambient temperatures, however, were significantly more likely to discard the eggs than those housed under cooler conditions. These results are consistent with the hypothesis that cool ambient temperatures at the end of the breeding season elicit a terminal investment strategy.

KEY WORDS *Belostoma*, Belostomatidae, parental, behavior, waterbug, investment

ALTHOUGH THE BIOLOGY of parental investment and behavior has received much attention (reviewed by Krasnegor and Bridges 1990, Clutton-Brock 1991), few studies have investigated parental behavior among invertebrates. Insects offer a particularly valuable system for evolutionary studies because parental behavior is rare and has evolved independently in several distantly related taxa (reviewed by Tallamy 1984, Tallamy and Wood 1986).

Male giant waterbugs *Belostoma flumineum* Say brood eggs deposited as cohesive units (egg pads) upon their dorsal surfaces by females. Brooding involves remaining at the water surface, which exposes the eggs to atmospheric oxygen while simultaneously preventing desiccation (Smith 1976, 1997). Males also stroke the egg pad with their legs, presumably to increase aeration of eggs, prevent the establishment of fungi (Cullen 1969), and possibly to assess the status of egg development. Brooding continues until the eggs hatch, after which males remove and discard the pad of egg membranes with their legs. Caring for eggs is costly (Smith 1976, Kight et al. 1995) and males appear to make optimal investment decisions based on clutch size and time invested (Kight and Kruse 1992).

In this study, we investigate mechanisms associated with the termination of care. Investment in offspring is ultimately costly to parents because caring for 1 clutch generally delays the production of subsequent young (Trivers 1972). We may therefore expect the evolution of mechanisms to optimize the amount of time and energy invested per offspring. Male waterbugs occasionally remove egg pads with their legs before the eggs hatch. Our previous work with parental insects indicates that termination of care is released by cues associated with hatching of eggs (Kight and Kruse 1992, Kight 1997), the passage of time (Kight 1997), and ambient temperature (Kight and Cseke 1999).

Male waterbugs are more likely to terminate care prematurely for small egg-pads than for larger egg-pads (Kight and Kruse 1992). Natural selection has presumably favored this strategy to maximize the number of young directly benefitting from nondepreciable parental investment. In *B. flumineum* this maximum corresponds to the number of eggs a male can carry on his back. Because insects are poikilothermic ectotherms, development of eggs and the behavior of parents are both influenced by ambient temperature. Males in warmer environments, therefore, may respond differently than those in cooler climates. If cool temperatures serve as a cue indicating the end of a breeding season, males should increase parental investment (terminal investment, see Scott and Gladstein 1993). Males at higher temperatures, however, should be more likely to discard small egg-pads and seek larger replacement broods.

Materials and Methods

Capture and husbandry followed Kight and Kruse (1992). Giant waterbugs were captured as last instar nymphs or adults during August 1998 in temporary and permanent ponds (Morris County, NJ) using aquatic dip nets. Individuals were immediately transported to the laboratory in plastic coolers containing pond water and transferred to 40-liter aquaria filled with dechlorinated tap water at 27°C. Each aquarium contained ≈30 waterbugs at a sex ratio of 1:1 and plastic vege-

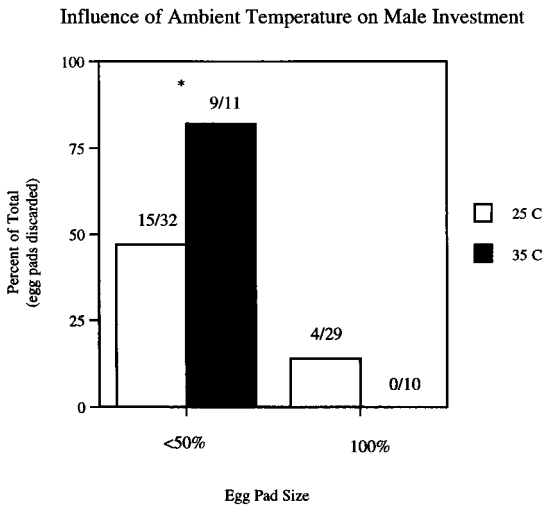

Fig. 1. Relationship of warm ambient temperature to the probability of male termination of care; frequency discarded/total above bars.

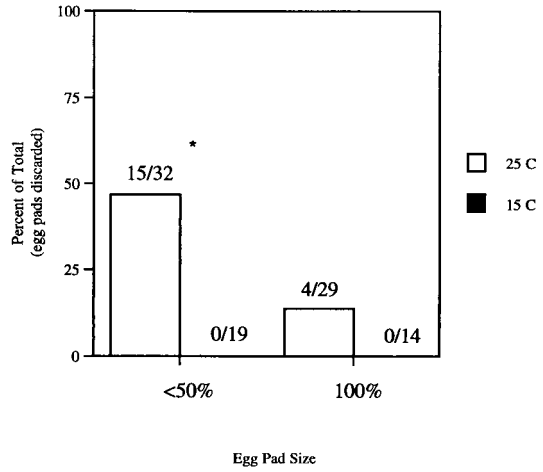

Fig. 2. Relationship of cool ambient temperature to the probability of male termination of care; frequency discarded/total above bars.

tation. Nymphs were allowed to molt in captivity. We maintained animals on a diet of crickets and dragonfly naiads administered ad libitum. We conducted all experiments in environmental chambers in which ambient temperature and photoperiod 14:10 (L:D) h could be controlled.

We studied the effects of temperature on parental investment by housing experimental groups at 3 different ambient temperatures: 15, 27, and 35°C. These experimental conditions are representative of seasonal variation in surface water temperature of the ponds from which specimens were collected (13–37°C, April–October; K. C. Kruse, unpublished data). Photoperiod was maintained at a photoperiod of 15:9 (L:D) h. Each experiment was conducted on 2 groups of males—males with 100% of backspace covered with eggs and males with 25–50% of backspace covered (the latter group were obtained by selecting males before completion of mating). Experimental insects were isolated in cylindrical 1-liter plastic containers containing 0.5 liters of dechlorinated tap water until either eggs hatched or the egg pad was removed from the back.

Data were analyzed using goodness-of-fit statistical procedures (Siegel and Castellan 1988) with $\alpha = 0.05$.

Results

Parental investment data for males housed at 27°C were obtained from previously published research (Kight and Kruse 1992). Males with egg pads covering 25–50% of backspace ($n = 32$) discarded unhatched pads significantly more often than males with larger egg pads ($n = 29$; $\chi^2 = 7.76$, $P = 0.0053$). Males housed at 35°C with small pads ($n = 11$) also discarded unhatched pads significantly more often than males with larger pads ($n = 10$; Fig. 1; Fisher exact test, $P = 0.0002$). No males in either treatment group under 15°C (small, $n = 19$; large, $n = 14$) discarded eggs (Fig. 2).

There were no statistical differences between males with 100% backspace covered under the 3 ambient temperatures studied (χ^2, $P > 0.15$ in all cases). There were, however, significant differences among males with small pads. Males with small pads housed at 15°C were significantly less likely to discard than males housed at 27°C ($\chi^2 = 12.62$, $P = 0.0004$). Males with small pads housed at 35°C, however, were significantly more likely to discard than males housed at 27°C ($\chi^2 = 4.05$, $P = 0.0441$). This difference was pronounced between males at the 2 extreme temperatures ($\chi^2 = 8.72$, $P = 0.0031$). The likelihood that a male will terminate investment in a small egg pad therefore increases at warmer ambient temperatures.

Discussion

A reliable mechanism regulating the termination of parental investment should facilitate reproductive success in male *B. flumineum.* Seasonal reproduction in North American populations occurs in 2 phases: a fall cycle and a spring cycle. Waterbugs breeding in the fall are young-of-the-year nulliparous individuals, whereas those breeding in the spring are overwintered adults. The current study examined nulliparous adults breeding in the fall, a season in which falling ambient temperatures are associated with the end of the breeding cycle. Because the length of embryogenesis is also thermally dependent, male *B. flumineum* should benefit by accounting for temperature in the regulation of paternal behavior.

We found that completely encumbered males rarely discarded egg-pads, regardless of ambient temperature. Partially encumbered males housed under warmer ambient temperatures, however, were significantly more likely to discard than those housed under

cooler conditions. This effect is consistent with theory predicting that parents with low residual reproductive success should increase investment in terminal broods. The cool temperatures at the end of the breeding season may therefore initiate a terminal investment strategy in male waterbugs. Warm temperatures, however, appear to amplify the strategy of discarding small broods of low reproductive value. Such a strategy would be advantageous in mid to late summer, when temperatures are high and sufficient time remains to obtain a replacement brood.

It is possible that thermal stress contributed to the high discard frequency of males with small pads at the constant experimental temperature of 35°C. Although daytime surface temperatures of the collection ponds can exceed 35°C during summer months (K. C. Kruse, unpublished data), water temperatures fall at night. In the current study, however, all completely encumbered males kept at 35°C retained successfully hatching egg pads, indicating that experimental conditions did not markedly stress adults or embryos. It should be noted that field-captured males with full complements of eggs often discard them following transport to the laboratory (unpublished data). General stress may therefore lead to termination of care, regardless of egg pad size.

Other insects appear to have evolved internal mechanisms governing the duration of parental care. For example, female burying beetles, *Necrophorus vespiloides* (Coleoptera: Silphidae), respond maternally to conspecific replacement larvae only during the anticipated hatching period of their own young (Müller and Eggert 1990). Females kill larvae presented either too early or too late, but larvae introduced at the time of hatching elicit maternal care.

Termination of care is associated with ambient temperature in female burrower bugs, *Sehirus cinctus* (Heteroptera: Cydnidae), which display increased maternal investment under cooler ambient temperatures. Unlike *B. flumineum,* North American populations of *S. cinctus* appear to breed only in the spring, and temperature-dependent maternal care may function to compensate for the effects of widely fluctuating daily ambient temperatures on embryogenesis (Kight and Cseke 1999).

Our results with partially-encumbered male waterbugs support the terminal-investment model developed by Scott and Gladstein (1993) for burying beetles, in which males terminate investment when there is sufficient probability of obtaining additional mates. Reproductive success in male waterbugs, however, is constrained by backspace availability (Kruse 1990) such that the terminal-investment model does not apply to males bearing the maximum number of eggs. This is consistent with our observation that completely encumbered males care for eggs until hatching, regardless of ambient temperature.

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