Egg Attendance and Brooding by Males of the Giant Water Bug *Lethocerus medius* (Guerin) in the Field (Heteroptera: Belostomatidae)

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Males of the giant water bug Lethocerus medius *(Guerin) typify their monobasic subfamily, the Lethocerinae, in that they do not brood eggs attached to their backs as do males of all members of the subfamily Belostomatinae. Exclusive male parental investment as expressed in the Belostomatinae is extremely rare behavior among animals, and evolution of the trait is obscure.* Lethocerus me-dius *males apparently remain with their mates through oviposition and are consistently found in attendance of eggs after the female has departed. This behavior may enhance paternity assurance at no cost in opportunity for poly-gyny. Two double clutches of eggs were found, from which we infer the potential for polygynous matings and shared parental investment. Male* L. medius *brood attended egg clutches above the surface of the water, where they may moisten them, shade them, and defend them against predation. Egg attendance/brooding by* L. medius *and other* Lethocerus *species may represent a plesiomorphic state from which paternal back-brooding evolved in the Belostomatinae.*

INTRODUCTION

The giant water bug *Lethocerus medius* (Guerin) belongs to the monobasic subfamily Lethocerinae, sister group to the Horvathiniinae + Belostomatinae

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(Lauck and Menke, 1961; Popov, 1971; Mahner, 1992). The Belostomatinae, as currently envisaged (Mahner, 1992), contains five or six genera characterized by an apomorphic coenotrope: obligatory paternal care that takes the form of males brooding eggs attached to their backs by their mates (Slater, 1899; Torre Bueno, 1906; Voelker, 1966, 1968; Cullen, 1969; Böttger, 1974; Smith, 1975, 1976a, b, 1979a, b; Kopelke, 1981; Venkatesan, 1983; Jawale and Ranade, 1988; Kraus, 1989a, b; Kraus et al., 1989; Ichikawa, 1989b; Kruse, 1990).

The Belostomatinae is an extraordinary taxon that has been the focus of keen interest because it contains more than 95% of the insect species known to exhibit the rare phenomenon of exclusive postzygotic paternal care (see Ridley, 1978; Smith, 1980). Males in the Belostomatinae possess complex behavioral patterns associated with this exceptional reproductive behavior. For example, species representing three genera that have been studied all exhibit some shared and some unique brooding behavioral patterns. Additionally, several of these species have been noted to copulate repeatedly at regular intervals during the process of egg deposition (Böttger, 1974; Smith, 1976a, 1979a; Kopelke, 1981; Jawale and Ranade, 1988, Kraus et al., 1989; Ichikawa, 1989b), and Smith (1979b) has shown that this behavior nearly perfectly assures paternity of the brooding male despite most females holding sperm from previous matings.

Prior to 1989, only fragments of mating behavior had been observed for any Lethocerus spp. (Tawfik, 1969; Smith, 1975), but oviposition behavior could be inferred from several studies (Hoffman, 1924; Hungerford, 1925; Rankin, 1935; Tawfik, 1969; Cullen, 1969; Menke, 1979b). All species deposit their eggs in large, compact, single layer clusters, most on stems of stout emergent vegetation (i.e., cattails, papyrus, rushes and other aquatic graminoids) or on tree branches (dead or alive) that project into aquatic habitats (Menke, 1979b). Rarely, eggs are deposited on other objects (De Carlo, 1962), but always at least several centimeters above the surface of the water. Weed (1989) and Parker (both cited by Hoffman, 1924), in separate anecdotes, reported finding adult Lethocerus americanus (Leidy) associated with, and apparently "defending," their eggs. Also, a single specimen of L. americanus in the insect collection of the University of Michigan Biological Station at Douglas Lake bears the note: "guarding eggs, female?" The specimen in question was a male (Smith, personal observation). In spite of these anecdotes, Rankin (1935) collected 2118 eggs of L. americanus in 30 clutches and made no mention of egg-guarding behavior. Cullen (1969) provided data on 10 clutches of eggs laid by captive Lethocerus maximus De Carlo in concrete tanks and, likewise, did not report that he observed adult bugs in their attendance. Recently, Ichikawa (1988, 1989a, 1990) conducted laboratory studies on Lethocerus deyrollei Vuillefroy which show that males in that species brood their eggs at night. No previous work on any Lethocerus species has demonstrated consistent attendance of eggs by males in the field.

This paper provides several years' field observations on the habits of *L. medius* in southern Arizona and reports the results of an experiment designed to test the hypothesis that male bugs have a long-term (deposition to hatching) association with eggs which are deposited in their presence. We discuss our results (and the laboratory studies of Ichikawa) in light of past conjecture on characters and events that may have led to the evolution of male back-brooding in the Belostomatinae.

MATERIALS AND METHODS

Study Area

All work on *L. medius* was conducted in the Altar Valley region, southwest of Tucson, Arizona. The Altar is a broad alluvial out-wash basin bordered by the Coyote, Quinlan, and Baboquivari Mountains to the west and south and the Sierrita Mountains to the east. This locality is near the northernmost boundary for the distribution of *Lethocerus medius* and a narrow area in the southwestern United States devoid of any species of *Lethocerus*. Observations and a field survey experiment were conducted in the numerous stock tanks that pockmark the Altar Valley.

Stock tanks are natural or man-made depressions in the drainage physiography that act as runoff catchments. They are usually enhanced by earthen dams on rangeland to provide water storage for livestock (Fig. 1A). Most stock tanks in the Altar Valley are dry for at least part of the year. The "monsoon season"
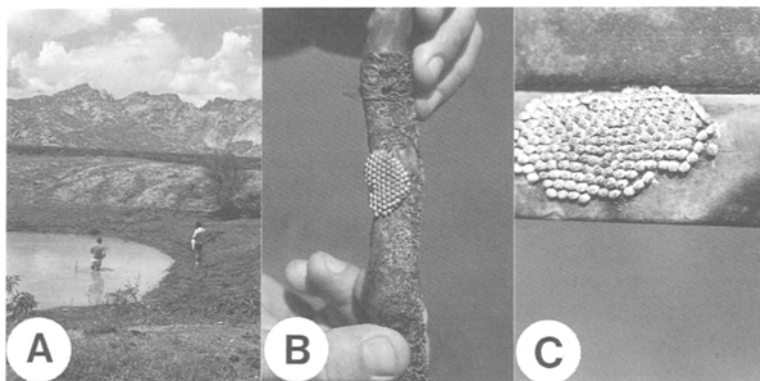
Fig. 1. Habitat and eggs of *Lethocerus medius*. (A) Placing laths in recently filled stock tank in the Altar Valley, Arizona. Mountains in background contain canyon rock pools (tanajas) which may serve as winter habitat for *L. medius*. (B) *Lethocerus medius* egg clutch laid on a dead mesquite branch. (C) *Lethocerus medius* egg clutch laid on a metal fence post (held horizontally).

in southern Arizona is a period characterized by frequent local afternoon thundershowers. The monsoons typically begin during the first 2 weeks of July. Virtually all stock tanks have collected water from these local rains within a month of their onset. Ponds rarely exceed 3 m in depth, and most are less than 2 m deep at their deepest point. Due to evaporation, infiltration, and repeated local showers, their depths may fluctuate substantially throughout the monsoon season.

Reconnaissance

During March through September of 1985 and July through September in 1986, we visited a number of tanks in the Altar Valley, where we made qualitative notes on ecology and seined the lateral margins for *L. medius*. In addition, we observed the above-surface activities of *L. medius* and examined a variety of naturally occurring substrate for eggs. In an effort to determine if oviposition substrate was limiting on *L. medius* reproduction in these ponds, we augmented normally occurring substrate by placing a number of roughsawn pointed laths (about 5 cm × 0.5 cm × 1 m) in several ponds. The pointed end of each lath was pushed into the mud bottoms of the tanks at a depth that submersed at least a 25-cm length such that at least 25 cm protruded vertically above the surface of the water. We irregularly surveyed these laths for egg clutches and removed each lath that contained eggs in order to count them. In the course of removing laths with egg clutches, we noted that most had an adult bug clasping just below the water's surface (Fig. 2A) and all of these individuals we captured were found to be males. This discovery prompted the design of an "egg-attendance" survey experiment as outlined below.

Egg-Attendance Survey Experiment

To investigate further the association of adult bugs and laths containing eggs, we conducted a field survey experiment in the summer and fall of 1987. Beginning in early August, about 200 laths were placed in 10 stock tanks (about 20 lathes/tank) in the Altar Valley. Laths were deployed as described previously, but with the added provision that each was placed not less than 3 m from its nearest neighbor. During the experiment, laths were moved and replaced as needed to compensate for loss or disturbance by cattle and fluctuating pond water levels. Laths that remained standing in water of at least 30 cm were monitored at least once each week over a 10-week period. Each lath was approached cautiously to avoid disturbing any resident bug(s). Upon reaching a lath, the observer then slowly dipped two rectangular (10 × 20-cm) aquarium nets into the water about 50 cm to either side of the lath. The nets were then brought together at the bottom of the lath and drawn rapidly upward along its wide surfaces to capture bugs resting along the submerged length. Data from
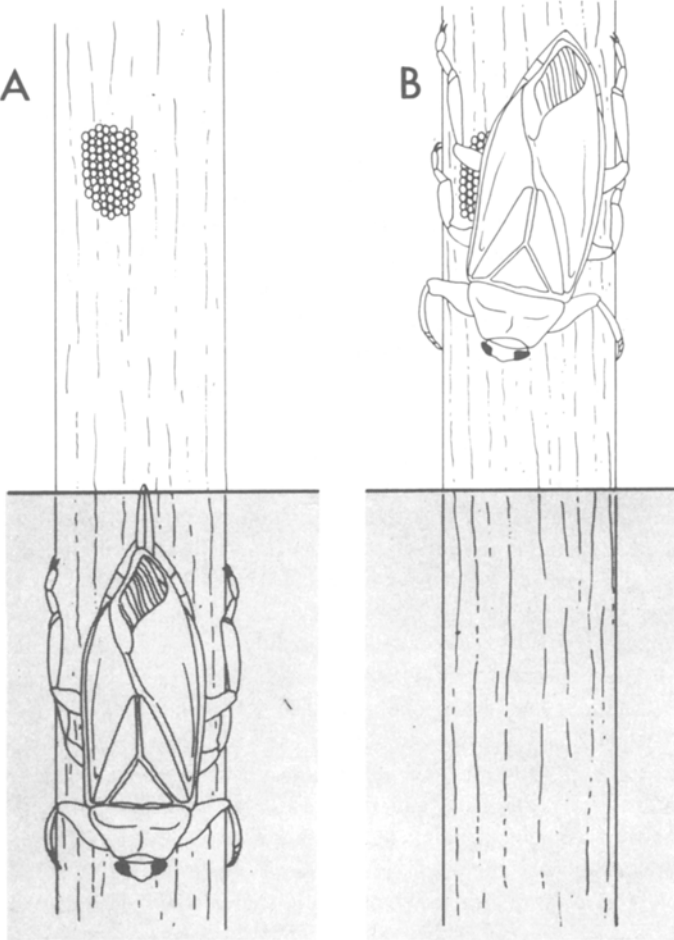
Fig. 2. Male *Lethocerus medius* attending a clutch of eggs. (A) Male sub-
mersed with air straps protruding at surface. (B) Male resting above surface
on egg clutch.

each observation consisted of a note on the presence or absence of eggs, presence
or absence of a bug(s), and if present, the sex of the bug, if an adult, or the
development stage, if a nymph. If the lath contained both a bug and eggs, we
noted from which side (egg side or other side) of the lath the bug was taken.
Adult bugs and clutches of eggs found on laths were collected, labeled, placed
on ice, and transported to the laboratory, where eggs were incubated by misting
with tap water until they hatched. Hatchlings and putative fathers were then
preserved by ultrafreezing for future paternity studies.

RESULTS

In the summers of 1985 and 1986 we observed that stock tanks were colonized by *L. medius* soon after the catchments accumulated enough water to produce persistent ponds. Before the stock tanks filled, we found *L. medius* in permanent ponds, small residual pools (inlet plunge basins) in some stock tanks and in rock pools (*tinajas*) associated with canyon streams in the surrounding mountains. We collected 77 adult bugs and no nymphs from these habitats in six visits to the Altar Valley area during March through May 1986.

Temporary ponds in the Altar Valley typically explode in algal bloom and rich hatches of cryptobiotic Eubranchiopoda (Anostraca, Notostraca, and Conchostraca) shortly after filling with water. The monsoon rains also break the hibernal-aestivation of bufonid (*Bufo* spp.) and spadefoot (*Scaphiopus* spp.) toads that dig out of their deep hibernacula and use the ponds for reproduction. Toad larvae utilize the flush of algae and phyllopods for food (Bragg, 1955; Pomeroy, 1981) and the population of *L. medius* adults is the prime beneficiary of the enormous prey base embodied in the standing crop of larger toad larvae. [Water scorpions (Heteroptera: Nepidae), dragonfly and damselfly nymphs (Odonata), and beetle (Coleoptera: Dytiscidae and Hydrophilidae) larvae and adults certainly take smaller anuran larvae, as do the hatchlings and early instars of *L. medius* and, great blue herons occasionally seen at the ponds may harvest tadpoles in large numbers.] Belostomatids are known to be the most important predators of anuran larvae (Brockelman, 1969; Heyer and Belin, 1973; Heyer *et al.*, 1975).

This prodigious food source is apparently important for *L. medius* reproduction in the Altar Valley. We noted that early season recent immigrant female water bugs were decidedly gaunt, but the majority (>75%) of the female bugs seined from ponds that contained anuran larvae from late July through August was heavily gravid (as determined by palpation, validated by dissection). Female bugs taken in late September through November, long after all toad larvae had metamorphosed, were again nongravid. The period of female gravidity was temporally coincident with our finding the largest number of lethocerine egg clutches. No eggs were observed before the second week in July or after August in 6 years of observation, and no immature bugs were ever collected until the last week of July.

The Altar Valley stock tanks produce no emergent vegetation of the kind normally used for oviposition by lethocerine water bugs. However, we did observe their egg clutches laid on the only available substrata, which included dead branches, usually of mesquite (*Prosopis* sp.: Fig. 1B), metal fence posts (Fig. 1C), and sometimes the dead stocks of thick stemmed terrestrial plants (*Xanthium* sp.) which had grown on the ponds' moist lateral margins and were inundated and killed by rising water. In 1985, we observed 4 egg clusters on

such substratum and in 1986 we encountered 14 clutches on objects other than the laths we used for substrate enhancement. Discrete egg clutches counted in 1986 contained a mean of 161.13 [±45.29 (SD); range, 111–265; n = 8] eggs. In 1987, we obtained 135.45 mean eggs/clutch (±36.27; range, 78–230; n = 21) taken entirely from laths. At no time did we observe eggs to be laid on the shore as had been reported for a South American species, *Lethocerus mazzai* De Carlo (De Carlo, 1962). Although we accumulated no precise data on egg viability, we estimate *L. medius* egg survivorship in this locality to be lower than 50%. All of the egg mortality we observed seemed attributable to two causes, drowning by submersion of eggs after heavy rains, and desiccation, which seemed to occur when the water levels receded, leaving egg clutches high above the water's surface and unattended by a male. Eggs killed by either cause were shriveled and hardened and were easily discernible from viable eggs. None of the nonviable eggs we examined showed evidence of their having been parasitized.

Laths (about 10/pond) placed in three ponds during the 1986 season accumulated a total of nine clutches of eggs. In 1987, about 200 laths placed in 10 ponds accumulated 21 clutches of viable eggs. In 1985 we found three adult bugs resident on substrate containing eggs and in 1986 we observed eight adult bugs associated with substrate to which egg clutches had been attached. Six of these eight bugs were captured and all were males.

In 1987, a total of 770 observations was taken under the egg-attendance field experiment. These data are presented in Table I. A total of 49 adult bugs and 12 nymphs was captured on laths. Of the adults, 34 were males and 15 were females. Nineteen males and no females were found on laths that contained eggs. All of the 19 males associated with egg-bearing laths were positioned head down near the air–water interface on the side of the laths to which the clutch

Table I. Egg/Male Association Survey Data, 780 Observations in Total

	Eggs present on lath	No eggs present on lath
Male present	19	15
Female present	0	15
Nymph present	0	12[a]
No bug present	1[b]	718

[a] Nymphs taken on lath consisted of 10 fourth instars, 1 fifth instar, and 1 third instar.

[b] Two adult bugs were lost from each of two laths that contained eggs, so their sex could not be determined. These lost data are not otherwise included in this table and were ignored in the chi-square analysis.

was attached (Fig. 2A). In one case where eggs had been attached to the narrow edge of a lath, the male bug in attendance was found grasping the narrow edge containing the eggs. One lath was found to contain two separate clutches of eggs, one of which was nonviable. Four additional laths were each found to contain a single inviable clutch of eggs. None of the four were attended by adult bugs. These four were not included in our data set. In August of 1990, Smith found a double clutch of viable eggs on natural substrate (Fig. 3A) attended by a single male. The clutches contained 135 and 137 eggs, respectively. The two were separated in the laboratory and incubated by misting with tap water. More than 75% of each clutch hatched. The resulting nymphs were recovered and frozen (along with the putative father) for future paternity studies. Although both clutches were treated identically, the onset of hatching occurred with a 2-day lag between the clutches, suggesting that the two had been deposited 2 days apart.

A log-likelihood ratio test (Sokal and Rohlf, 1981) was performed on a 2 × 3 contingency table (data from Table I) to test for independence of the presence of egg clutches and the presence or absence of adult bugs by sex. The null hypothesis asserting no association between egg clutches and adult bugs
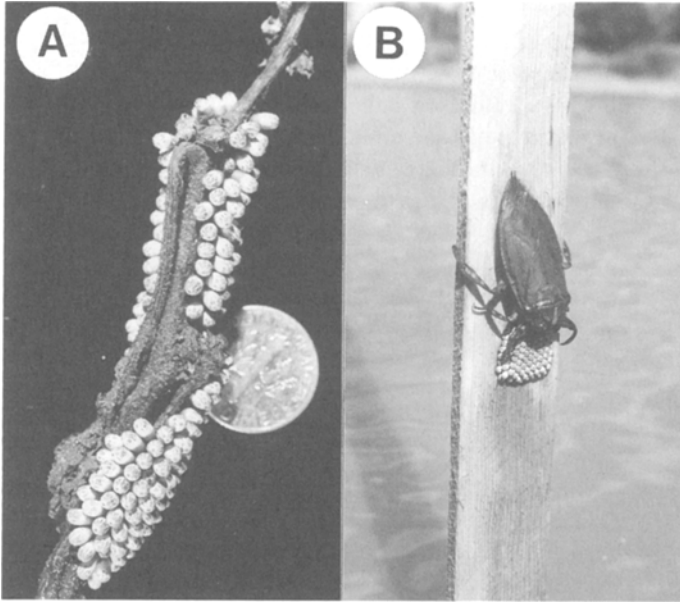
Fig. 3. (A) Double clutch of *Lethocerus medius* eggs on a single stem of *Xanthium* sp. (B) Male *Lethocerus medius* "watering" eggs (see text and Ichikawa, 1989).

was rejected ($G = 123.58$, df $= 2$, $P < 0.000005$). A second (2×2) contingency table excluding the "no bug present" cells was likewise tested for independence of presence of egg clutches and presence of adult bugs by sex. Again, the null hypothesis was rejected ($G = 18.78$, df $= 1$, $P < 0.0003$). We accept the alternative hypothesis that egg clutches and adult bugs are positively associated on laths, and we observed that males present on laths containing egg clutches, and females absent from same, overwhelmingly contributed to the G statistic. We concluded that males are present and females are not present on laths with egg clutches (19 males, 0 females) after a clutch has been laid. We further concluded that there is an equivalent probability of laths without eggs being occupied by adult bugs of either sex (15 males, 15 females).

Finally, in the course of 6 years, we have observed 12 instances of adult bugs standing over egg clutches out of the water (Fig. 2B). In four cases the bug was "startled" by an approaching investigator and immediately dropped into the water. In the remaining eight instances, bugs were observed standing head down, partially or completely covering the egg clutch with their bodies, or with the bug's head positioned over the top third of the egg clutch (Fig. 3B). We note that the latter is the posture employed by *L. deyrollei* to moisten eggs with water that drips from the bug's body via its beak (Ichikawa, 1988). Ichikawa has shown that this is essential care, without which, embryos of *L. deyrollei* fail to develop.

Bugs found brooding eggs remained with them for variable periods of time, often exceeding 5 min, before descending the lath into the water. All of these observations were made during the daylight hours, between 0900 and 1400. In four instances when the observer approached "guarding/brooding" bugs that remained in place on their egg clutches, each bug displayed aggressively by elevating its body and extending its raptorial forelegs toward the observer's hand when moved in the vicinity of the bug. This display, reminiscent of the aposomatic "alert" posture of polistine wasps disturbed on their nest, was impressive and unmistakably threatening. Ten of the 12 adult bugs were recovered after being observed brooding/defending eggs. All of these individuals were males.

It should be noted that all observations of brooding out of the water were serendipitous, no special effort having been made during this study to collect data on the behavior of males bugs associated with eggs. Also, we did not observe at night during the course of this study. Ongoing investigations by Smith will later detail patterns of male egg brooding behavior in *L. medius*.

DISCUSSION

The fieldwork on *Lethocerus medius* presented here complements the laboratory studies by Ichikawa (1988, 1989a) on *Lethocerus deyrollei* and corroborates most of his findings. The combined results of the investigations on these

two *Lethocerus* species coupled with some older anecdotes on a few other species establish unequivocally the existence of exclusive paternal brooding patterns in the stem group to the Belostomatinae. This information may provide a new foundation upon which to build an understanding of the evolution of the more remarkable patterns of paternal back-brooding and the adaptive radiation of the Belostomatinae.

Smith (1980) published a scheme for the evolution of back-brooding by members of the Belostomatinae innocent of the knowledge that male lethocerines brood. This account recognized several elements which seem to be reinforced by the recent work on *Lethocerus* spp. behavior, including this study.

Smith's scenario assumes that the Belostomatinae evolved from a common ancestor with the Lethocerinae, which had attained great size by selection to utilize large (vertebrate) prey. This current study suggests that *Lethocerus medius* in Arizona extensively exploits, and may require, toad larvae for reproduction. Smith (1980) further suggested that selection for large size inadvertently caused enlargement of eggs and a concomitant reduction in the surface to volume ratio of belostomatid ova. It is assumed that ancient lethocerine ancestors laid their eggs under water, in the tissues of submersed aquatic plants, or in mud as is characteristic of all the other extant, true aquatic Nepomorpha (Cobben, 1968; Menke, 1979a). The reduction in surface-to-volume ratio that accompanied egg enlargement eventually caused the embryonic metabolic demand to exceed the rate of oxygen diffusion through water. This then constrained any further enlargement of eggs and thus ultimately circumscribed the dimensions of adult bugs.

Clearly some adaptation to mitigate this physiological constraint would have to have been found in order for selection to affect further enlargement of adult bugs. Smith (1980) proposed that such an adaptation was created by a simple behavioral modification—the deposition of eggs out of the water on emergent vegetation. Smith (1980) previously assumed that eggs so laid would have survived unattended and that it would be a small step for females then to begin laying a few eggs on the backs of their mates. If these back-laid eggs survived as well as or better than those deposited on emergent vegetation, the male's back could then have become the preferred substrate, especially in habitats that lacked suitable vegetation which constituted the "traditional" ovipositional substrate. Speciation events could then have given rise to new taxa and the genesis of the subfamily Belostomatinae. Back-brooding released members of the belostomatine clade from dependence on habitats containing emergent vegetation for oviposition, and this in turn opened vast ecological opportunities into which members of the subfamily elaborated.

Smith asserted that the evolution of back brooding was entirely under female control and that its occurrence diminished male opportunities for polygyny because the area of the male back approximates the area required to accom-

modate the reproductive product of a single fully gravid female. It has been shown that male back space in an extant species can accommodate a fraction of an additional clutch, up to a full additional clutch in certain circumstances (see Kraus, 1989a; Kruse, 1990; Ichikawa, 1989b), but no mating takes place among females and males having no back space available for additional eggs. Therefore, the only remaining fitness improvement options available to males were to perfect paternity assurance and optimize brooding efficiency.

The new information provided in this paper and the work of Ichikawa do not invalidate the substance of this evolutionary scenario but only shift certain events back in the phylogeny to the stem species of the Belostomatidae.

It is now apparent that lethocerine eggs require brooding which at least involves their periodic hydration (Ichikawa, 1988), apparently because the eggs' chorion is incapable of conserving sufficient water to sustain development. Future work on additional species of *Lethocerus* will establish if brooding is ubiquitous in the genus and if male service to eggs may include their defense against predation and protection from solar insolation as suggested by casual observations reported here and also by the brooding behavior of *Lethocerus colossicus* Stål observed by Rogelio Macías-Ordóñez and R. Smith in the former's laboratory (Instituto de Ciencias del Mar y Limnologia, Puerto Morelos, Quintana Roo, Mexico). Also in need of further comparative study is the temporal patterning of brooding by male lethocerine bugs. Ichikawa (1988) reported that *L. deyrollei* broods only at night, but diurnal brooding was observed in *L. medius*, and one male *L. colossicus* spent most of its time above the water's surface, in contact with the eggs throughout every day until they hatched (Rogelio Macías-Ordóñez, personal communication).

Diminished prospects for polygyny presents the primary impediment to the evolution of paternal care in any animal species. Such forfeiture of future matings is affected by male costs in time and energy in current brood (Trivers, 1972). This study and older reports (Rankin, 1935) intimate that some modern and perhaps all ancient male lethocerines may not have sacrificed polygyny to care for eggs. This underscores the yet unproven implication that multiple clutches of eggs may share the care [see Wittenberger (1979) for discussion of sharable paternal investment] of a single male. In this current study, two double clutches of *L. medius* eggs were observed, and in one instance both clutches were viable and attended by a single male; and Rankin (1935) reported and presented photographs of numerous multiple clutches containing up to eight on a single stem.

High paternity assurance may be a requisite to the evolution of paternal care (Trivers, 1972; Xia, 1992). Smith (1975) first observed that *L. medius* engage in multiple copulations, and Ichikawa's more extensive laboratory observations have revealed this pattern in *L. deyrollei*. Multiple copulations alternating with oviposition is the putative mechanism that achieved nearly 100%

paternity assurance for a belostomatine, *Abedus herberti* Hidalgo, under conditions designed to create intense sperm competition (Smith, 1979b). It now seems possible that this paternity assurance mechanism first evolved in the stem species of the Belostomatidae and was then passed unaltered to the belostomatine clade. Maynard Smith's (1977; see also Zeh and Smith, 1985) game theory model suggests that parental care is more likely to evolve when future fitness is minimally affected by current investment. Therefore, the possibility that male lethocerines can obtain and brood several clutches of eggs may have abolished the primary impediment to evolution of paternal care.

Ichikawa, (1990) working in the laboratory, provided dramatic evidence of a phenomenon, foreshadowed by an anecdote (Cullen, 1964), which may undermine male opportunity for polygyny and shared paternal investment in some modern *Lethocerus* species. He found that females routinely cannibalize and otherwise destroy existing egg clutches while they are attended by males. Although Ichikawa observed that males initially defended these clutches against the females' onslaughts, defending males were never able to deter the assailant females and the nonfilial eggs were always cannibalized or otherwise destroyed and replaced by the eggs of each of the ovicidal females. This extraordinary behavior was not observed in *L. medius* and seems inconsistent with the double clutching of this species in the field, and the numerous multiple clutches (containing from two to eight clutches) reported and depicted by Rankin (1935) suggest that egg cannibalism does not occur in *L. americanus*. The paradox of nonfilial female egg cannibalism and the apparent potential for polygyny and shared paternal brooding in different species of *Lethocerus* is an issue in need of detailed comparative study. If female cannibalism on nonfilial eggs is a condition-dependent behavior found in all modern lethocerines, it could have limited male potential for polygyny early in the belostomatid clade and created intense selection for paternity assurance soon after paternal brooding evolved.

Despite some apparent behavioral differences among modern species, the association of mates through oviposition and the historical initiation of paternal brooding can now be displaced back in the Belostomatidae phylogeny to the stem species of the Belostomatidae, whose sister species is the common ancestor of the Nepidae. This new information also suggests a more gradual transition to back-brooding than had previously been posited and points to a probable earlier perfection of paternity assurance in the belostomatid clade before the divergence of the Belostomatinae.

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