EVOLUTION OF EXCLUSIVE POSTCOPULATORY PATERNAL CARE IN THE INSECTS[1]

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Among the many thousands of insect species whose reproductive behavior is known, only about 100 have males that exclusively care for eggs and/or young, and all but a few of these are water bugs in the subfamily Belostomatinae. In fact, all recorded cases of exclusive postcopulatory paternal care are restricted to a few families in 1 order, the Hemiptera. These include the Belostomatidae, Gerridae, Reduviidae, Coreidae, and Aradidae (reviewed in Ridley 1978, Melber and Schmidt 1977, and see Appendix). Of these, only representatives of the Belostomatidae and the Reduviidae have been studied in sufficient detail to expose discernible pathways to the evolution of their paternal care. This paper will develop scenarios for giant water bugs and assassin bugs with the hope of revealing principles generally useful for understanding the evolution of paternal care in insects.

Several recent reviews and theoretical contributions (Trivers 1972, Parker 1970, Dawkins and Carlisle 1976, Thornhill 1976, Emlen and Oring 1977, Maynard Smith 1977, Melber and Schmidt 1977, Ridley 1978) make possible an elucidation of the general circumstances that have favored, and the preadaptations that have permitted, paternal care to evolve. A synthesis of these theories may predict where additional examples might likely be found and, conversely, explain why exclusive paternal care is so rare in the Class Insecta.

RESISTANCE TO THE EVOLUTION OF POSTCOPULATORY PATERNAL CARE IN THE INSECTS

Several factors have mitigated against the evolution of paternal care in insects. Insect eggs originally were selected to develop unattended on land. Embryogenesis takes place within a wide range of temperatures uncontrolled by parents. The chorion of the insect egg, recently recognized for its remarkably complex structure (Hinton 1970), permits the encapsulated embryo to breathe without desiccating, a spectacular achievement when one considers that oxygen molecules that must enter are larger than the water molecules that must be retained. Beyond this, the external chorionic microstructure of most insect eggs is capable of supporting a plastron (Thorpe 1950) when the egg is submersed in water. This gas film protects unattended eggs from drowning when they are temporarily covered with water (Hinton 1969). Because of these original adaptations to a terrestrial existence, the majority of insect ova are programmed to develop and hatch without care from either parent.

In a substantial number of species, females have been selected to serve

their embryos in ways that could not have been accomplished by males (Eickwort 1980). All females provision their eggs with stored embryonic food in the form of yolk, and only the female can expend time and energy to locate appropriate microhabitat in which to deposit eggs; this assures optimal developmental conditions for embryos and abundant resources for emergent young. In many species, females have evolved special organs, ovipositors, to accomplish this task and to secrete eggs in protected locations less accessible to potential parasites and predators. Females of some species protect their embryos by thickening the chorion of individual eggs or by packaging the entire clutch in a protective covering, such as the dictyopteran ootheca. Another female egg protection strategy has been to distribute eggs over a wide area, decreasing their profitability to potential predators and parasites (Price 1976). Finally, ovoviviparous and viviparous species have simply declined to expose embryos to any potential external adversity. Most of these female-centered adaptations are irreversible, and have left little or no opportunity for a father to contribute.

Several services to eggs and young might be rendered with equal efficiency by either sex or cooperatively by both sexes (i.e. nest construction, guarding, external provisioning, and feeding), but in the overwhelming majority of species that provide such services, the tasks are performed by females exclusively (Wilson 1971, 1975; Melber and Schmidt 1977; Hinton 1977). There have been several recent attempts to explain why this is so.

Referring primarily to birds, Emlen and Oring (1977) proposed that exclusive male parental care is most likely to develop in groups having a phylogenetic history of shared parental investment. If this were the case for insects, the paucity of species with shared parental care might be proposed to explain the rarity of exclusive paternal care. This does not hold for insects, however, and the explanation would seem to beg the issue; most of the factors favoring shared parental investment would also promote exclusive male care.

Trivers (1972) has recognized that in species without parental care, female fitness is limited by individual egg production, and male fitness by the number of females the individual can inseminate. Nest building and egg and young tending may have begun as relatively inexpensive chores for female insects if feeding and egg production continued at a rate independent of modest maternal activities. Also, sperm stored in the spermathecae of most females assure fertility of subsequent clutches long after mating. Hence, maternal nurture in many species of insects may be rendered with little loss in future female fitness. Paternal care, on the other hand, is likely to interfere with a male's potential for future parentage in that any time spent caring is time lost courting and mating other females. This sexual inequity in cost for equal return has almost certainly offered considerable resistance to the evolution of paternal care.

Dawkins and Carlisle (1976) provide an elegant explanation for the rarity of paternal care in insects (and other animals having internal fertilization) independent of sexual cost-benefit asymmetries. In species with internal fertilization, there is time between mating and oviposition during which the male can (and usually does for the reasons just discussed) desert the eggs his sperm may eventually fertilize. This traps the female with her eggs and no opportunity to manipulate their father.

Finally, caring males must have high assurance of paternity (PA) for brooded eggs and young. This would be especially true if brooding initially conferred only a small net increase in fitness to recipient eggs and young. If added net fitness and PA are both low, any caring genes that arise in a population will diminish in frequency and eventually be lost. Surprisingly, a preliminary model, to be developed in detail elsewhere, has indicated that if added net fitness is very high, caring genes could initially increase in frequency in spite of a very large fault in PA. However, virtually perfect PA would be required to *fix* caring genes, because even a small fault would permit noncaring genes to program successful cheating strategies.

Paternity assurance is a special problem for insects because of the female's ability to store sperm (Parker 1970). Stored sperm threaten caring males with being cuckolded, i.e. brooding eggs fertilized by another male (Trivers 1972). Therefore, PA for insects may often involve competition between or among ejaculates within the female's reproductive tract. It should be clear that paternal care will most likely evolve in those species where the ejaculate of the current male preempts or displaces most or all previously stored spermathecal sperm. Conversely, paternal care is unlikely to evolve in species having a low rate of preemption or displacement. W. F. Walker (personal communication) has recently reviewed sperm utilization strategies in insects, and found that most species with high displacement have elongate or tubular spermathecae, whereas the spermathecae of those with low displacement are usually spherical or ovoid. Therefore, some candidate species may have failed to evolve paternal care because their females' spermathecae were maladapted to a high level of sperm displacement. In the membracids, for example, over 40 species have caring mothers, but no example of paternal care has been found in this group (T. K. Wood, personal communication). Perhaps some Hemiptera have spermathecae unusually well adapted for displacement, thus accounting for the occurrence of exclusive paternal care in this and no other order.

PATERNAL CARE IN GIANT WATER BUGS AND ASSASSIN BUGS

In the giant water bug subfamily Belostomatinae, males carry eggs deposited on their backs by conspecific females. Until the end of the 19th century, it was believed that egg-bearing belostomatids were females carrying their own eggs. Even as late as 1935, Bequaert declined to include members of this group in his review of presocial Hemiptera because: "It has been shown that in these insects the female forcibly seizes another individual of the same species (usually a male, more rarely a female) on whose back she lays the eggs." Dr. Bequaert had apparently overlooked Torre Bueno's (1906) revelation that copulation takes place in connection with oviposition for *Belostoma flumineum* Say, and Slater's (1899) observation that only males bear eggs.

More recently, Voelker (1968) demonstrated that *Limnogeton fieberi* Mayr always copulates with the female while receiving her eggs. I have studied the courtship and mating behavior of *Abedus herberti* Hidalgo and found that males of this species require the female to couple prior to accepting any of her eggs. Furthermore, oviposition is regularly interrupted by male demands for additional bouts of copulation after an average of each 2 eggs that are laid (Smith 1979a). Cyclical copulation and oviposition has

in fact been a characteristic of all of several speices of *Abedus* and *Belostoma* studied (Smith unpublished).

These observations led me to suspect that most of the eggs carried by a male contain his genes, and therefore whatever brooding services rendered them must represent a true paternal investment (Smith 1976a, 1976b, 1979a). I succeeded in validating this hypothesis by mating *A. herberti* females competitively with genetically marked males (Smith and Smith 1976, Smith 1979b). The result was virtually complete paternity assurance for all contestant males.

Torre Bueno (1906) and others have reported that male water bugs "dislike" having their backs used as oviposition substrates and that they attempt to get rid of the burden by kicking it off. This interpretation was apparently based on observations of a real male option: discarding eggs in the face of adverse brooding conditions. The option is frequently exercised in the laboratory when encumbered bugs are confined to a featureless aquarium, but rarely if the aquarium is provided with aquatic plants or other resting substrate at the surface (Smith 1976a, b).

Modern studies (Voelker 1968; Cullen 1969; Smith 1976a, 1976b) have demonstrated unequivocally that males provide essential services to eggs and emerging nymphs. *Limnogeton fieberi* males regularly expose their eggs to atmospheric air as do *Belostoma flumineum*, *B. malkini* Lauck, and *Abedus herberti*. In addition, some *Belostoma* species use the hind legs to stroke eggs while under water and *Abedus herberti* execute brood pumping (pushups) to move water over the eggs and aerate them while below the surface (Smith 1976a, b).

Detached belostomatine egg pads covered with static water apparently drown and eventually are attacked by fungi. Eggs exposed to open air desiccate rapidly and the embryos die. A very small percentage hatch can be achieved if a detached pad is placed in shallow water so that the unattached ends of the eggs are exposed to atmospheric air, but the young nymphs have great difficulty escaping the chorion. Most die and those that do escape are usually deformed (Smith 1976a, b). *Abedus herberti* males are apparently aware of eggs hatching on their backs and assist eclosing nymphs by going below the surface and brood pumping vigorously until the hatching bugs are freed from the chorion (Forey and Smith, in preparation). Brooding *A. herberti* males are also inhibited from feeding on teneral newly hatched nymphs that remain in the father's vicinity until their integuments have hardened and they are able to disperse (Smith 1976b). Nonbrooding males and females are in no way inhibited from cannibalism.

Brooding is an expensive occupation for male water bugs. The egg pad on the back of a brooding male may weigh twice as much as the bug alone, and its irregular wetted surface produces considerable drag as the bug swims. Males with eggs swim only half as fast as males without eggs (Smith 1976b). The dynamics of brooding (i.e. frequent exposure of eggs to the atmosphere, brood pumping, and egg stroking) betray the location of brooders. (Nonbrooding males and females are morphologically and behaviorally cryptic.) These factors surely reduce the brooder's access to prey, and may subject him to increased risk of being preyed upon. Furthermore, brooding behavior itself has a caloric expense. Nonbrooding males do nothing more than rest in a predatory stance and surface for air occasionally,

while in extreme cases, a brooding *A. herberti* pumped 716 times and a *B. flumineum* stroked its eggs 768 times in 1 hour. Also, a bug cannot spread its wings and fly when they are covered with an egg pad, so the brooder forfeits a dispersal option for the duration of his encumberment. By far the most significant cost for a brooding male is his loss of opportunity for polygynous mating; females reject encumbered males as mates (Smith 1979a).

Not all giant water bug males brood eggs. Females in the genus *Lethocerus* (subfamily Lethocerinae) deposit their eggs in tight clutches on emergent vegetation (e.g. *Typha*) at variable heights above the surface of the water (Hungerford 1925, Rankin 1935, Menke 1963, Cullen 1969, Tawfik 1969, Menke 1979). *Lethocerus* eggs are apparently hydrophobic. Cullen (1969) noticed a significant difference in the height above the water's surface at which eggs of *Lethocerus maximus* DeCarlo were laid during the wet and dry seasons in Trinidad. The average height during the wet season was approximately 7 times greater than during the dry season. Cullen speculates that this behavior pattern is an adaptation to prevent eggs from being submersed, and the large size of these ova (up to 7.4 mm) and their relatively very low surface to volume ratio indicate an unfavorable rate of gas exchange between the embryo and surrounding water. My future research will address this problem and attempt to explain why members of the genus are tied to emergent vegetation as an oviposition substrate.

The mating behavior of lethocerines has not been adequately studied, but preliminary observations (Tawfik 1969, Smith 1975) have revealed an aspect of great importance in the evolution of paternal brooding. Male lethocerines mate a single female repeatedly and may guard her until she lays her eggs. Male guarding of an appropriated mate is believed to be a sperm competition strategy evolved to prevent preemption of the guarding male's sperm by subsequent mating of the female with another male before laying her eggs (Parker 1970, 1974). After eggs are laid, guarding ends, and, male *Lethocerus* (unlike encumbered male Belostomatinae) are at liberty to court and mate other females.

Paternal brooding has also been reported for 2 species of reduviids, a group well known for maternal care of eggs and young (Hussey 1934, Bequaert 1935, Wilson 1971, Melber and Schmidt 1977). Bequaert (1912, 1913) first found that in an African assassin bug *Rhinocoris albopilosus* Signoret males guard the eggs; this observation was later confirmed by Odhiambo (1959, 1960) who observed that the male "rides" on the female for several hours after mating, then dismounts and remains with her for 2 or 3 days, during which time successive bouts of copulation may occur. Ultimately, the female lays her first clutch of eggs shortly after a mating bout. When the female completes her laying and moves away from the compact mass of ca. 100 eggs, the male approaches and stands over the clutch. Brooding males show extraordinary fidelity to the task through a variety of adverse conditions. While brooding males do not actively hunt for prey, they may impale any that come within range of the guarded eggs. Only eggs are brooded; males abandon young nymphs soon after they begin to hatch.

Odhiambo (1959, 1960) observed that the original female may return to the guarded egg mass to add eggs. Even more remarkable, other females also may add eggs to a common egg mass. Significantly (for reasons of paternity assurance) females that contribute to the guarded clutch first

mate with the brooding male. The function of male guarding for this species has not been established, but it is presumed that the brooding male must repel potential egg parasites and predators.

Zelus sp., another tropical reduviid, not only guards eggs but also remains with newly hatched nymphs for several days, and at least occasionally feeds them. Ralston (1977) empirically determined that male brooding reduces egg parasitism by *Telenomus* sp. (Scelionidae) from 55% for unguarded eggs to 21% for those guarded. Ralston also demonstrated that guarding males are significantly less likely to flee a simulated predator and more inclined to attack simulated parasites than non-guarding males. He noted that individual males of this species guarded as many as 7 egg masses. Although the author (Ralston) implied that multiple masses may have been deposited by a single female, it seems more likely that each mass was contributed by a different female. Apparently Ralston never directly observed mating and oviposition, but he inferred an association between the 2 activities in his prediction: ". . . that the guarding male is the genetic father of at least some of the eggs he guards."

EVOLUTION OF PATERNAL CARE IN
GIANT WATER BUGS AND ASSASSIN BUGS

Lauck and Menke (1961) proposed that the Belostomatinae (brooders) arose from the monotypic subfamily Lethocerinae (nonbrooders). Recall that members of the genus *Lethocerus* all lay their eggs on stout emergent vegetation in open air above the water. *Lethocerus* spp. are the largest aquatic bugs, having apparently specialized for great size (presumably to utilize large prey) in their divergence from the Nepinae of the Nepidae (see China 1955). An increase in egg size accompanied this specialization and the concomitant decrease in egg surface to volume ratio probably caused gas exchange problems, placing an upper size limit on members of the divergent line. A change in oviposition habits from subsurface endophytic or exophytic (characteristic of nepids) to above surface exophytic (characteristic of modern lethocerines) apparently lifted this upper size limit, permitting the evolution of huge bugs (up to 110 mm in length).

Modern lethocerines are extremely strong fliers capable of long dispersal flights which regularly expose adults to nonreproductive habitats, i.e. aquatic habitats lacking emergent vegetation for oviposition (Riley 1896, Menke 1963, Cullen 1969, Smith unpublished). It seems likely that transient ancestral lethocerines may have enjoyed an advantage by extending their stays in nonreproductive habitats, there exploiting food resources in a relatively less competitive environment. Females, however, ultimately would have been compelled to make dangerous dispersal flights to find habitats that contained suitable oviposition substrate (emergent vegetation). Females that could avoid searching for, and the intense competition in, traditional oviposition sites would have enjoyed a competitive advantage over those continuing in these activities. Not only would they conserve time and lessen risks to themselves, but their nymphs also would benefit from less competition for food and reduced predation if they hatched in a previously unexploited habitat.

This assumes that these females found some alternative to emergent vegetation as an oviposition substrate. One option would have been to lay

eggs on the back of the male. The diminished aggressivity, and prolonged interest in the female due to male guarding enhanced this possibility. Hungerford (1920) provided an anecdote demonstrating the ease with which this event may have occurred. He collected several *Lethocerus* sp. and placed them in an aquarium with no substrate that would normally be used for oviposition. He returned after several days to find that a female had deposited a few eggs on the back of a male.

The distribution of modern genera (3 Old World, 2 New World) in the subfamily Belostomatinae suggests that this special event must have occurred before the breakup of Pangaea. A female in a species with ancestry common to the 2 subfamilies mated a male, then laid some eggs on his back. Actually this occurrence was probably repeated sporadically over a relatively long period of time until the fortuitous pairing of some eggs (those architecturally and physiologically preadapted to tolerate prolonged wetting) with males predisposed to certain behavior patterns (those inclined to spend much time at the water's surface).

It is noteworthy that *Lethocerus* spp. have long retractile air straps (breathing tubes) that allow the bugs to breathe atmospheric air and secure air stores while completely submersed. In contrast, all modern members of the Belostomatinae have short spatulate air straps that force them to surface when obtaining air. It seems probable that males with shorter than average air straps may have been preadapted to brooding in that eggs attached to their backs would have been exposed to the atmosphere. Repeated exposure of eggs to the atmosphere would assure the hatching of some eggs from a male's back.

Natural selection would have begun to favor females programmed to lay eggs on their mates' backs if the value of these exceeded that of those laid on emergent vegetation. Value, of course, is measured in the number of resulting progeny that survive to reproduce. This value asymmetry could have been achieved through differential survival of either eggs or nymphs. For example, eggs on a male's back might have enjoyed differential survival due to reduced parasitism, predation, and cannibalism. Surprisingly, not a single datum exists on the parasites and predators of these huge eggs, but Cullen (1969) provided an anecdote on egg cannibalism. In the laboratory, he observed a female *Lethocerus maximus* ascend a sedge on which a clutch of eggs had previously been laid by another female. The second female ate the eggs of the first and replaced them with her own clutch.

Survival of eggs laid on males' backs in a new habitat need not necessarily have been higher than that of those laid in traditional habitats on emergent vegetation for the system to have progressed. The enormous advantage to nymphs of hatching into a previously unexploited habitat lacking specific predators might easily have offset an initial low egg survivorship during the transitional period. Corbet (1959) found that giant water bugs constituted ca. 75% of the stomach contents of immature crocodiles in Lake Victoria. Imagine the relief felt by the first nymphs that hatched from brooded eggs in a crocodile-free environment!

Male water bugs may have initially tolerated being encumbered with eggs if 1) they had equal or greater assurance of paternity for carried eggs over those laid on inanimate substrate, and 2) if carrying eggs did not interfere with their subsequent opportunities to mate. Both of these requisites are

likely to have been satisfied. A male that mates with a female and then allows her to lay eggs immediately on his back would surely be the biological father of most; males decorated with a few eggs were probably no less attractive to conventional females who mated them and continued to deposit their eggs on emergent vegetation.

As the frequency of females programmed to encumber males increased in the population, so also the number of males carrying eggs. This in turn began selecting a new female behavior—rejection of fully encumbered males. There would be no advantage for females to mate with males whose prior commitment precluded their investment in additional eggs.

Female choice for brooders and rejection of encumbered individuals would now begin to impose a system cost on males: a reduction in opportunity for polygamy, immune to any male manipulation. The males' only option would be to increase paternal investment, thereby appreciating the value of eggs received. This led to the evolutionary refinement of PA adaptations and the elaboration of male brooding skills. The resulting further increased survivorship of brooded eggs would eventually expand the female "conspiracy of choice" to fixation such that an encumbered male would have no opportunity to mate while brooding.

Is this the end point? It could be if paternity assurance adaptations have evolved to perfection. G. A. Parker (1970) reviewed the literature on sperm competition and found that in the majority of insects that had been studied, the last male to mate with a nonvirgin female succeeded in fertilizing from about 50% to 95% of the eggs she laid. Generally most of the eggs not fertilized by the last male were fertilized by stored sperm from the penultimate male. Parker has intensively studied the yellow dungfly *Scatophaga stercoraria*, and found its paternity assurance through sperm displacement relatively high, ca. 80%.

Let us examine what might happen if the water bugs had evolved paternity assurance only to an 80% level of efficiency. This would allow 20 of each 100 eggs brooded to have been fertilized by the female's previous mate, and the 20% fault would provide opportunities for cheating. It should be clear that a brooding male cannot disguise his commitment to eggs he wears on his back, so how to beat the system? There are 2 plausible methods. First, a male might mate repeatedly with a series of females, but decline to receive any of their eggs. Second, the cheater might mate with a female, receive her eggs, then kick the eggs off before meeting and courting additional females. In both cases, cheater males have removed the female criterion for rejection: carried eggs. What advantage would accrue to cheaters? Let us assume that 30 days are required for a male to brood a clutch of eggs, and that females lay an average of 100 eggs on a male's back. At the end of 30 days, an honest male will have brooded 100 eggs but fathered only 80. If a cheater can mate 5 females in 30 days by declining to receive eggs or by abandoning them after each mating, and the females each subsequently mate and encumber honest males, the cheater will eventually have fathered 100 eggs for a net gain of 20. The advantage of cheating probably oscillated with the number of cheaters eventually to some equilibrium with the level of opportunity provided by the average fault in paternity assurance. Perfection of PA by the belostomatids (Smith 1979b) has apparently blocked the opportunity for intrasexual cheating. This and

the loss of the ability for eggs of the Belostomatinae to develop and hatch unattended in open air apparently rendered the new system fixed and irreversible, an evolutionarily stable strategy (Maynard Smith and Price 1973, Maynard Smith 1976).

At least 2 species of assassin bugs have independently evolved paternal care in the form of egg guarding and I predict that others in this family will eventually be found to have caring fathers. This prediction is based on the apparent ease with which paternal care could evolve in species having territorial males and males that assure paternity by mate guarding. Furthermore, the eggs of many reduviids would seem to be vulnerable to parasitism and predation. These are laid in tight clutches on open plant parts and seem to lack special defensive adaptations (Cobben 1968). Consequently they could benefit from being guarded as attested to by the relatively large and growing list of species that have maternal guarding (Wilson 1971).

Mate "riding" found in *R. albopilosus* is thought to be a PA adaptation (Parker 1970, Sivinski 1977) similar to mate guarding by male *Lethocerus*. It has the same effect, placing fathers in the vicinity of their eggs when laid so that male caring could occur and be selected. Egg guarding by assassin bug males might have initially cost individuals opportunities for polygynous matings if searching were the historical mate acquisition method. Under this circumstance, caring genes would be selected only if the gain in survivorship of guarded eggs exceeded the potential gain from multiple clutches of unguarded eggs. Emlen and Oring (1977) have indicated that the degree to which an individual can take advantage of the potential for polygyny in its environment depends on the amount of paternal care required for rearing young. This concept might appropriately be reversed for male insects to indicate that the amount of care a father may be willing to render should depend on his opportunities for polygyny. If females are scarce or difficult to find, or if a male is not a good seducer, he might advantageously provide care even if it results in only a small increase in fitness to recipient progeny. Females should always have benefited from having their eggs guarded, and must have preferred nurturant males if they could be identified. Perhaps the only sure way for a female to have discriminated caring from noncaring males would have been to choose males already tending eggs. This would be an excellent female decision (if males effectively guard multiple clutches) because the brooding male has demonstrated not only his willingness and commitment to brood, but also his ability to seduce, both desirable characteristics from the female's standpoint. As noted earlier, *Zelus* and *Rhinocoris* males receive multiple clutches for brooding. This female preference and its potential for creating a high variance in male reproductive success surely placed a premium on the virgin male's ability to rapidly secure a clutch of eggs. This urgency may be reflected in the willingness of *Rhinocoris* males to compete for the privilege of guarding a clutch of eggs irrespective of their paternity (Odhiambo 1959). In this scheme, male territoriality would have been created by selection for paternal guarding and female choice restored polygyny for territorial males.

Another possible route circumvents the initial reduction in opportunity for polygyny by assuming that assassin bug paternal care arose in species initially having territorial males. If territoriality evolved as a mate acquisition strategy, males would have been selected to choose ideal feeding and/or

oviposition sites attractive to females. Attracted females could be mated by defending males in exchange for feeding or ovipositional privileges within the territority. These kinds of territoriality have been documented for species representing most insect orders (Price 1976). Intrasexual selection should operate to perfect PA by sperm displacement for males that invest in territory defense independent of paternal care. An outrageous sperm displacement adaptation has recently been discovered in the damselfly *Calopteryx maculata* (Beauvois) (Waage 1979). The territorial males of this species have genitalia equipped with sperm extractors which they use to remove any alien sperm present in the female's storage organ prior to ejaculation. Territorial males with perfected PA mechanisms would certainly have been excellent candidates for the evolution of paternal egg guarding.

Eggs laid in a defended territory may have enjoyed a small initial survival advantage over those laid on undefended substrate with little cost to the defending male. Some careless defenders (selected to repel conspecific males) may have occasionally mistakenly repelled heterospecifics including potential egg parasites and predators, thus incidentally protecting eggs and young containing genes for imperfect discrimination in territorial defense.

Competition among males probably operated to optimize the system by having eggs (or young nymphs) become the foci of heterospecific defense while the entire territory continued to be defended against conspecific males, some perhaps behaviorally disguised as females attempting to sneak copulations with attracted females. Transvestite behavior could succeed as a cheating strategy in spite of perfected PA through sperm displacement if a female impersonator were able to enter the territory, mate an attracted female, then distract the resident male long enough for the female to oviposit.

It is not known that transvestite cheating occurs for either of the 2 reduviid species, but it does occur in fishes. Ridley (1978) has indicated that in fishes with external fertilization, transvestite sneaking or cheating would undermine female choice; this may occur even in fishes with internal fertilization (e.g. Constantz 1975). Presumably territorial males of the 2 reduviid species have had sufficient control over the policing of their territories to prevent the diminution of female choice and reversal of the system.

SUMMARY

Factors that have resisted evolution of paternal care in the insect include: (1) A general inability of males to enhance the fitness of precocial eggs and young; (2) the deterrent of irreversible maternal care adaptations; (3) a sexual asymmetry of cost in future fitness (male loss of opportunity for polygyny) favoring maternal care; (4) the differentially greater opportunity for males to abandon eggs due to internal fertilization; (5) a problem with paternity assurance due to sperm storage by female insects. Species minimally restrained by these factors would be predisposed and preadapted to the evolution of paternal care, as seems to have been the case for the Belostomatinae and 2 species of Reduviidae.

The belostomatid system evolved because males had the opportunity to reduce parasitism and predation on eggs and to permit young to exploit new habitats. Males were available to brood eggs because female guarding (a PA strategy) kept them from abandoning their mates (and eggs) immediately after copulation. Female choice created selection for paternal brooding and

stabilized the system by selecting against male polygyny. Intrasexual selection favored increased male investment and perfected PA. Finally, the perfection of PA and physiological adaptations of eggs to being brooded under water fixed the system by blocking alternative male strategies. This general scheme may account for the evolution of paternal egg carrying in some gerrids and the coreid *Phyllomorpha laciniata* (Villers) (see Appendix).

Male guarding of eggs and young as found in the Reduviidae seems to have evolved via a slightly different pathway. Male bugs were capable of defending vulnerable clutches of eggs against potential parasites and predators. Mate guarding by males (a PA strategy) and/or male territoriality (a mate acquisition strategy) made males available at the time of oviposition. Territorial males defended eggs against heterospecific threats with little added effort while defending their territories against conspecific males. Female preference for brooding males increased opportunities for polygyny by brooders and resisted male cheating strategies. Intrasexual selection strengthened existing PA systems and optimized paternal defense of eggs and young. *Neuroctenus pseudonymus* Bergroth may have evolved paternal guarding in a similar way (see Appendix).

The foregoing narratives provide plausible event sequences leading to the evolution of paternal care for known and suspected insect examples. I am confident, at least, that the key elements: opportunity, paternal availability, female choice, male-male competition, and paternity assurance, have been identified. These may eventually be abstracted and incorporated into mathematical models as tests of the proposed and alternative scenarios.

APPENDIX

Representatives of the hemipteran families Gerridae, Coreidae, and the Aradidae are suspected of having paternal care, but have been inadequately studied to confirm its existence. I append this review of what is known of these species in the hope of stimulating further studies on them.

Paternal brooding may occur among the water skimmers (Gerridae). An undescribed species of *Rhagadotarsus* has been shown to court females while holding a floating or fixed object on the surface of the water (Wilcox 1972). Successful males mate with females which in turn use the guarded object as an oviposition site. A single male may accumulate eggs from several females, but it is not known how long a male may continue to guard his substrate or of what benefit this guarding may be to eggs or hatching nymphs.

Populations of pelagic species in the genus *Halobates* may be limited by the availability of floating oviposition substrate. Females of these species lay their eggs on a variety of floating objects including conspecifics (Walker 1893, Bequaert 1935). It seems unlikely that a female would be able to attach eggs to her own body so it would not be surprising if male *Halobates* were used in a manner similar to male' belostomatids. Anderson and Polhemus (1976) discount this possibility suggesting that specimens recovered with attached eggs were probably dead at the time eggs were attached to them.

The male of a coreid bug, *Phyllomorpha laciniata*, from Europe has been depicted carrying eggs attached to its back (Jeannel 1909). The drawing shows an individual with 15 large eggs placed loosely and at random on its concave back. The eggs appear to be held in place by a series of slanting spines adorning the pronotum and lateral margin of the abdomen. Signif-

icantly, the eggs appear to be sufficiently large that the 15 might represent the entire complement of a single female.

Bequaert (1935) excluded this species from consideration for the same reason that the belostomatids were ignored, and Miller (1971) states that both males and females have been observed with ova on their backs. He suggests that the presence of eggs on both sexes may have been fortuitous, the eggs having fallen from a nearby female; however, this seems highly unlikely. Miller cites no authority for these observations, but it is not clear that he was the observer. Apparently, early accounts of *Phyllomorpha* egg carrying Jeannel 1909, Oliver 1909, Reuter 1909) have accumulated some speculative embellishment while being carried forward in the literature.

This species needs to be intensively studied in order to validate or discredit the early accounts, and if validated, to determine the genetic relationship of egg-carrying adults to the eggs and discover the benefits of this system to eggs. This system, if facultative, would be an extremely important one to understand the evolution of paternal care.

Finally, paternal care is suspected in a species of flat bug (Aralidae). McClure (1932) observed that after the female *Neuroctenus pseudonymus* Bergroth laid her triangular masses of from 10 to 50 within channels cut in wood and bark by wood-boring insects, she departed, and another adult "probably the male" crawled astride the group and remained there until the eggs hatched. This guarding extended over a period of at least 2 weeks. Nothing is known of the genetic relationship of the guarding individual to the eggs, or how guarding may influence survivorship of the clutch.

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LITERATURE CITED

ANDERSON, N. M., AND J. T. POLHEMUS. 1976. Water-striders (Hemiptera: Gerridae, Veliidae, etc.). Pages 187-224 *In* L. Cheng, Ed. Marine Insects. American Elsevier Publ. Co., New York. 581 p.

BEQUAERT, J. 1912. L'instinct maternel de *Rhinocoris albopilosus* Sign. Rev. Zool. Afr. 2: 293-6.

―――. 1913. Note rectificative concernant l'ethologie de *Rhinocoris albopilosus* Sign. Rev. Zool. Afr. 2: 187-8.

―――. 1935. Presocial behavior among the Hemiptera. Bull. Brooklyn Ent. Soc. 30: 177-91.

CHINA, W. E. 1955. The evolution of the waterbugs. Nat. Inst. Sci. India Bull. 7: 91-103.

COBBEN, R. H. 1968. Evolutionary trends in Heteroptera. Part I: Eggs, architecture of the shell, gross embryology and eclosion. Center for Agricultural Publishing and Documentation, Wageningen, Netherlands. 475 p.

CONSTANTZ, G. D. 1975. Behavioral ecology of mating in the male Gila Topminnow, *Poeciliopsis occidentalis* (Cyprinodontiformes: Poeciliidae). Ecology 56: 966-73.

CORBET, P. S. 1959. Notes on the insect food of the Nile crocodiles in Uganda. Proc. Royal Ent. Soc. Lond. (A) 34: 17-22.

CULLEN, M. J. 1969. The biology of the giant water bugs (Hemiptera: Belostomatidae) in Trinidad. Proc. Royal. Ent. Soc. Lond. (A) 44: 123-37.

DAWKINS, R., AND T. R. CARLISLE. 1976. Parental investment, mate desertion and a fallacy. Nature 262: 131-3.

EICKWORT, G. C. 1980. Presocial insects. *In* H. R. Hermann, Ed. Social Insects. Academic Press. In press.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215-23.

HINTON, H. E. 1969. Respiratory systems of insect egg shells. Pages 343-68 *In* R. F. Smith and T. E. Mittler, Eds. Ann. Rev. Ent. 14: 343-68.

————. 1970. Insect eggshells. Sci. Amer. 223: 84-91.

————. 1977. Subsocial behavior and biology of some Mexican membracid bugs. Ecol. Ent. 2: 61-79.

HUNGERFORD, H. B. 1920. The biology and ecology of aquatic and semiaquatic Hemiptera. Kansas Univ. Sci. Bull. 11: 1-328.

————. 1925. Notes on the giant water bugs. Psyche 32: 88-91.

HUSSEY, R. F. 1934. Observations on *Pachycoris torridus* (Scop.) with remarks on parental care in other Hemiptera. Bull. Brooklyn Ent. Soc. 24: 133-45.

JEANNEL, R. 1909. Sur les moeurs et metamorphoses de *Phyllomorpha laciniata*. Bull. Soc. Ent. France (1909): 282-6.

LAUCK, D. R., AND A. S. MENKE. 1961. The higher classification of the Belostomatidae (Hemiptera). Ann. Ent. Soc. Amer. 54: 657-77.

MAYNARD SMITH, J. 1976. Evolution and the theory of games. Amer. Sci. 64: 41-5.

————. 1977. Paternal investment: A prospective analysis. Animal Behavior 25: 1-9.

————, AND G. R. PRICE. 1973. The logic of animal conflict. Nature 246: 15-8.

McCLURE, H. E. 1932. Incubation of bark bug eggs (Hemiptera: Aradidae). Ent. News 43: 188.

MENKE, A. S. 1963. A review of the genus *Lethocerus* in North and Central America, including the West Indies (Hemiptera: Belostomatidae). Ann. Ent. Soc. Amer. 56: 261-7.

————. 1979. Family Belostomatidae. Pages 1-166 *In* A. S. Menke, Ed. The Semiaquatic and Aquatic Hemiptera of California (Heteroptera: Hemiptera). Bull. of the California Insect Survey 21: 76-86.

MELBER, A., AND G. H. SCHMIDT. 1977. Sozial-phänomene bei Heteropteren. Zoologica (Stuttgart) 127: 19-53.

MILLER, N. C. E. 1971. The Biology of the Heteroptera. Second Edition. E. W. Classey Ltd., Hampton. 206 p.

ODHIAMBO, T. R. 1959. An account of parental care in *Rhinocoris albopilosus* Signoret (Hemiptera-Heteroptera:Reduviidae), with notes on its life history. Proc. Royal Ent. Soc. Lond (A)34: 175-85.

————. 1960. Parental care in bugs and nonsocial insects. New Scientist 8: 449-51.

OLIVER, R. 1909. Sur *Phyllomorpha laciniata* Vill. (Hem., Coreidae). Bull. Soc. Ent. France 1909: 350.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525-68.

————. 1974. Courtship persistence and female-guarding as male time investment strategies. Behaviour 48: 157-84.

PRICE, P. W. 1976. Insect Ecology. John Wiley & Sons, Inc., New York. 514 p.

RANKIN, K. P. 1935. Life history of *Lethocerus americanus* (Leidy) (Hemiptera, Belostomatidae). Kansas Univ. Sci. Bull. 15: 479-91.

RALSTON, J. S. 1977. Egg guarding by male assassin bugs of the genus *Zelus* (Hemiptera:Reduviidae). Psyche 87: 103-7.

REUTER, O. M. 1909. Quelques mots sur les Phyllomorphes (Hem., Coreidae). Bull. Soc. Ent. France 1909: 264-8.

RIDLEY, M. 1978. Paternal care. Animal Behaviour 26: 904-34.

RILEY, C. V. 1896. Notes upon *Belostoma* and *Benacus*. Proc. Ent. Soc. Wash. 3: 83-8.

SIVINSKI, J. 1977. Factors affecting mating duration in the stick insect *Diapheromera velii* Walsh (Phasmatodea, Heteronemiidae). M. S. Thesis, Univ. of New Mexico. 169 p.

SLATER, F. W. 1899. The egg-carrying habit of *Zaitha*. Amer. Nat. 33: 931-3.

SMITH, R. L. 1975. Bionomics and behavior of *Abedus herberti* with comparative observations on *Belostoma flumineum* and *Lethocerus medius* (Hemiptera:Belostomatidae). Ph.D. Thesis, Arizona State University. 171 p.

————. 1976a. Brooding behavior of a male water bug *Belostoma flumineum* (Hemiptera:Belostomatodae). J. Kansas Ent. Soc. 49: 333-43.

————. 1976b. Male brooding behavior of the water bug *Abedus herberti* (Hemiptera:Belostomatidae). Ann. Ent. Soc. Amer. 69: 740-7.

————. 1979a. Paternity assurance and altered roles in the mating behaviour of a giant water bug *Abedus herberti* (Heteroptera: Belostomatidae). Animal Behaviour 27: 716-25.

————. 1979b. Repeated copulation and sperm precedence: Paternity assurance for a male brooding water bug. Science 205: 1029-31.

————, AND J. B. SMITH. 1976. Inheritance of a naturally occurring mutation in the giant water bug *Abedus herberti* (Hemiptera: Belostomatidae). J. Heredity 67: 182-5.

TAWFIK, M. F. S. 1969. The life history of the giant water bug *Lethocerus niloticus* Stael (Hemiptera:Belostomatidae). Bull. Soc. Ent. Egypte 53: 299-310.

THORNHILL, R. 1976. Sexual selection and paternal investment in insects. Amer. Naturalist 110: 153-63.

THORPE, W. H. 1950. Plastron respiration in aquatic insects. Biol. Rev. Cambridge Phil. Soc. 25: 344-90.

TORRE BUENO, J. R. de la. 1906. Life histories of North American water bugs. I. Life history of *Belostoma flumineum* Say. Can. Ent. 38: 189-97.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-79 *In* B. Campbell, Ed. Sexual Selection and the Descent of Man, 1871-1977. Aldine, Chicago.

VOELKER, J. 1968. Untersuchungen zur Ernährung, Fortpflanzungsbiologie und Entwicklung von *Limnogeton fieberi* Mayr (Belostomatidae, Hemiptera) als Beitrag zur Kenntnis von natürlichen Feinden tropischen Süsswasserschencken. Ent. Mitt. 3: 1-24.

WAAGE, J. K. 1979. Dual function of the damselfly penis: Sperm removal and transfer. Science 203: 916-8.

WALKER, J. J. 1893. On the genus *Halobates*, and other marine Hemiptera. Ent. Mor. Mag. 29: 227-32.

WILCOX, R. S. 1972. Communication by surface waves: Mating behavior of a water strider (Gerridae). J. Comp. Physiol. 80: 255-66.

WILSON, E. O. 1971. The Insect Societies. Harvard University Press, Cambridge. 548 p.

————. 1975. Sociobiology: The New Synthesis. Harvard University Press, Cambridge. 697 p.