DOI:10.55278/TNEF7155

Male parental care in insects

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Abstract

Parental care is traditionally defined as costly behaviour by parents that increase the fitness of offspring. It may be uniparental, biparental or alloparental. In uniparental care, paternity assurance is usually repeated for copulation just before oviposition. Biparental care is favoured when sexual selection is not intense and when the adult sex ratio of males to females is not strongly skewed. Alloparental care is a seemingly altruistic and reproductively costly behaviour observed in over 120 mammalians and 150 avian species. Male parental care evolved exclusively from no care. Supporting models like the "enhanced fecundity model" and "overlapping brood model" hypothesize that male care is favoured because females do avoid care of their offspring. Biparental care largely arose by males joining caring females and was more labile in Holometabola than in Hemimetabola. Paternal care can be maintained under sexual selection which helps caring males to attract more mates.

Introduction

A fundamental question in evolution is 'which sex should care for offspring'. The caring sex is thought to be determined by several non-exclusive factors, for example, mate competition, territoriality, physiology of gamete release, cuckoldry risk and sex-specific life history (Kokko and Jennions 2003). To date, though, comparative-phylogenetic studies of transitions in the caring sex have been restricted to vertebrates despite calls for similar studies of invertebrates (Mank *et al*. 2005). Insects constitute one invertebrate group where parental care is extremely diverse. Parental care is traditionally defined as costly behaviour by parents that increase the fitness of offspring. For the purpose of increasing offspring fitness, parental care was present, ranging from temporary egg-guarding to feeding of offspring by both parents up to adulthood. Care can be by females, males, or both (Beal and Tallamy 2006). Insects contain some of the best-characterized examples of exclusive male care, the rarest form of care in nature.

Why is parental care needed?

Behavioural process of increasing the offspring survival prospects by protecting them from predators, food shortages, desiccation, and a range of other

environmental hazards. Parental care represents only one among several alternative solutions to overcome problems associated with environmental hazards that reduce offspring survival.

Benefits of parental care

Parents increase offspring survival during the stage in which parent and offspring are associated. Parents improve some aspect of offspring quality, which leads to an increase in offspring survival and/or reproductive success in the future (*i.e.,* when parents and offspring are no longer associated) such as provisioning, protection from parasites, parasitoids and disease etc. Parents manipulate offspring development rate, which increases overall offspring survival or reproductive success across multiple life-history stages.

Types of parental care

Uniparental care: In uniparental care, the mechanism of paternity assurance is usually repeated copulation just prior to oviposition. A female may court a male to induce/carry more of her eggs, presumably because male care is a valuable resource that increases her lifetime fecundity.

Biparental care: Biparental care tends to be favoured when sexual selection is not intense, and when the adult sex ratio of males to females is not strongly skewed. For two parents to cooperate in caring for the young, the mates must be coordinated with each other as well as with the requirements of the developing young, and the demands of the environment (Remes *et al*. 2015).

Alloparental care: Alloparental care is a seemingly altruistic and reproductively costly behaviour that has been observed in over 120 mammalians and 150 avian species (Riedman, 1982). This parenting strategy involves individuals providing care to non-descendent offspring. There are both adaptive benefits and potential costs of alloparenting to the individuals involved.

Maternal versus paternal

Maternal care is the most exclusive form of parental care and the most rudimentary form and is provided by females who incorporate toxins into their eggs, oviposit them in protected places, or cover their eggs with a hard shell or wax-like compound before abandoning them. For example, many species of insects guard their young against predators by using chemicals or defensive behaviours and care may end when the young hatch, or it may extend until larvae or nymphs are mature. Paternal care is often evident in animal kingdom. For instance, in fish, about 30% of the 500 known families show some form of parental care, and most often (78%) care is provided by only one parent (usually the male). Male care (50%) is much more common than female care (30%) with biparental care accounting for about 20%, although a more recent comparative analysis suggests that male care may be more common (84%) (Farrell,

2011). In seahorses, males brood the eggs in a brood pouch until they are ready to hatch. In jawfish, the female lays the eggs and the male then takes them in his mouth. A male can have up to 400 eggs in his mouth at one time. The male can't feed while he hosts the young, but as the young get older, they spend more time out of the mouth. This is sometimes termed mouth brooding. Interestingly, the California mouse (*Peromyscus californicus*) is a monogamous rodent that exhibits extensive and essential paternal care, and hence has been studied as a model organism for this phenomenon.

Amphibians and in birds fathers contribute equally with mothers to the care of offspring in as many as 90%. In phylum Arthropoda, Giant water bugs, sea spiders, two genera of leaf-footed bugs, two genera of assassin bugs, three genera of Phlaeothripid thrips, three genera of harvestmen, and in millipedes of the family Andrognathidae (Fig. 1) display male parental care (Tallamy, 2011).

Indirect paternal contributions to offspring:

Males may invest in offspring with nutritional offerings to the female in the form of nuptial gifts of captured prey items or even their own bodies. They may transfer proteins or protective substances in a spermatophore: Male katydids, for example, provide a spermatophore during copulation that may be as much as 40% of their body mass; spermatophore nutrients have shown to be important to the reproductive success of females. Male arctiid moths, *Utetheisa ornatrix* provide a different sort of indirect paternal contribution when they transfer protective pyrrolizidine alkaloids to females during mating. These alkaloids are passed to the eggs, which are then unappealing to predators.

Rise of paternal care

The rise of paternal care can be explained by two hypotheses *viz*., the Mating Effort hypothesis and the Maternal Relief hypothesis given by Minge *et al*. 2016.

1) The Mating Effort hypothesis: It suggests that males may provide care for offspring in an attempt to increase their own mating opportunities and thus enhance their future reproductive success.
2) The Maternal Relief hypothesis: It proposes that males provide care to reduce the burdens associated with reproduction for the female, which ultimately generates shorter inter-birth intervals and produces more successful offspring.

Paternal certainty is relatively high in monogamous species (Rosenbaum *et al*. 2018). Males are less likely to be caring for unrelated offspring. In contrast, paternity certainty is reduced in polygamous species.

A few examples of paternal care in insects

Giant water bug: The male carries the clutch of eggs on his back. All the males of the subfamily Belostomatine carry their clutches

to the surface periodically. This allows the embryos developing inside eggs to breathe more efficiently. It is a lot easier to get oxygen from the air than from the water. Eggs that are abandoned or deposited anywhere other than on the backs of the male never hatch. In contrast, almost 100% of brooded eggs hatch. Brooding is thus an obligate behaviour, one that is necessary for the continued survival of these species. Exclusive paternal care of eggs or young is restricted to about 100 species of insects, almost all within the Hemiptera. For example, in a giant water bug, *Abedus herberti*, females adhere their eggs to the wing cover of a male, who stops feeding and instead spends his time until eggs hatch aerating and protecting them from predators. In the Giant water bug, *Diplonychus rusticus* (Heteroptera: Belostomatidae), it is seen that females prefer egg-caring males for a mate and as a result, more eggs are on the back of egg-caring males (Fig. 2).

Hemipteran Bugs: Especially among the Hemiptera, parental care is provided solely by the male. Without exception, the males involved go to great lengths to ensure their paternity. In several tropical assassin bugs (Reduviidae), males protect their paternity by riding their mates from copulation until oviposition, effectively preventing any additional mating (Odhiambo 1959). After oviposition, the male dismounts and straddles the eggs to guard them from parasites and predators. A well-documented example is the reduviid *Rhinocoris albopilosus* in which only males guard the broods (Odhiambo, 1959). Typically, in the brood guarding behaviour, the female lays multiple egg masses in a confined space and it seems that the number of egg masses corresponds to the amount a male will protect. Males guard as few as one, to as many as seven egg masses. The male usually assumes a guarding position directly over the egg masses or will stand not more than 3-4 cm from the nearest egg mass.

Pipe-organ mud-daubing wasp, *Trypoxylon politum*: In the pipe-organ mud-daubing wasp, *Trypoxylon politum* and a few other species, males guard females' nests during provisioning. They chase away parasites and ants and defend their position from conspecific males. Just before oviposition, males engage in an unusual sequence, repeatedly holding, pulling and copulating with the female. Male guards chase parasites and predators from the nest and its provisions. Cuckoo wasps and miltogrammine flies parasitize the nests during provisioning (Coville and Coville 1980) entering and ovipositing just after the host female has left. When a guard was present, these parasites never entered successfully, but when there was no guard, they did so readily. Also, the most obvious benefit of male guarding is that mating takes place at the nest and the male can defend his position from other males.

Conclusion

Parental care is an energy-expensive behaviour. In order to increase the survival of

offspring parental care is a must, it may be through the selection of a safe oviposition place to feeding of young ones. It also has negative effects on parents, it reduces the number of matings, some have to sacrifice themselves for their offspring and in many ways it affects the parents. In order to overcome the disadvantages, they have evolved like maternal and paternal care which improves offspring survival as well as their survival and other needs. Mostly parental care is studied in vertebrates but it has to be studied in insects as well. Among insects, maternal care is studied more while paternal care studies are less, which should be exploited more

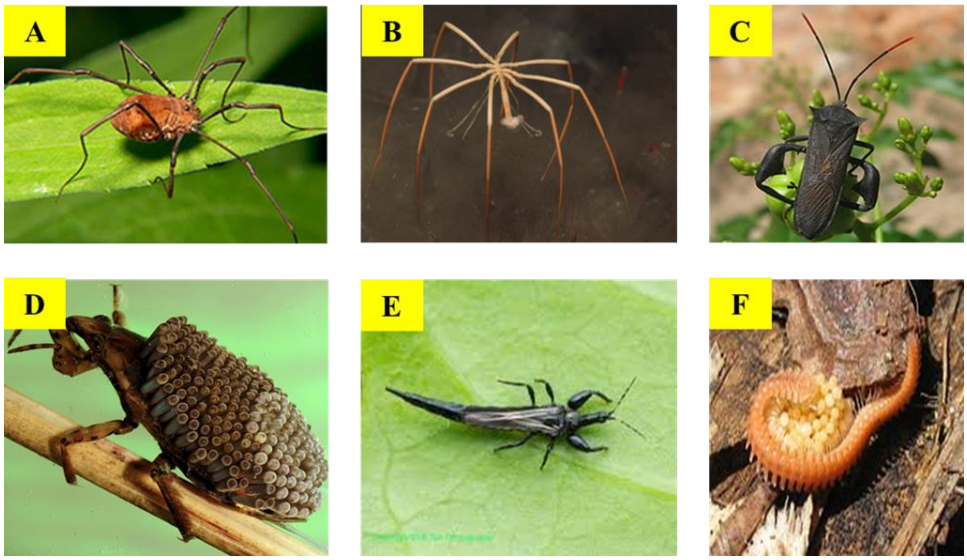

Fig. 1 Paternal care in phylum Arthropoda A) Harvestmen B) Sea spiders C) Leaf-footed bugs D) Giant water bug E) Phlaeothripid thrips F) Millipedes of Family Andrognathidae

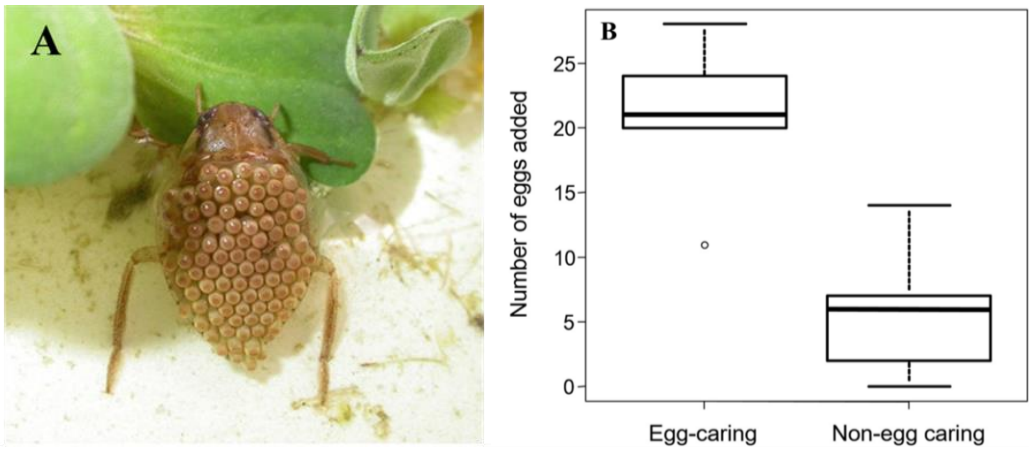

Fig. 2 A) Male of the giant water bug *Diplonychus rusticus* carrying clutch of eggs on his back B) Number of eggs added to the back of egg-caring and non-egg caring males of the water bug *Diplonychus rusticus* (Ohba *et al.* 2018)

Fig. 3 Male of reduviid bug, *Rhinocaris albopilosus*

Fig. 4 Male pipe-organ mud-daubing wasp, *Trypoxylon politum* guarding nest against a parasitic fly.

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MS Received on 05th October, 2023
MS Accepted on 20th November, 2023