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Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones)

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The diversity of reproductive strategies within the arachnids rivals all other arthropod groups. However, with the possible exception of spiders and scorpions, evolutionary biologists have overlooked these organisms. The order Opiliones is divided in three suborders (Cyphophthalmi, Palpatores and Laniatores) with considerable differences in morphology, habits and behaviour. In this review we focus on the life history, sexual behaviour and ecology of Opiliones, and discuss the possible causes of the diversity of forms of parental investment found in this order. In the Cyphophthalmi the forms of parental investment are restricted to the choice of oviposition sites. Among the Palpatores there is selection of microhabitats for oviposition, egg-hiding, and discharge of repugnant secretions on the eggs. The most common form of parental investment in Laniatores is probably egg-hiding by females but several species show subsocial behaviour, including both maternal and paternal care. The scarcity of paternal care among harvestmen and the differences when it does occur suggest that male care evolved independently in different laniatorean lineages from a plesiomorphic state of non-care rather than from female care. Both male and female care reduce egg mortality. Egg predation, rather than infection by fungi may be the most effective pressure favouring the evolution of subsocial behaviour in harvestmen. Subsocial behaviour appears to be restricted to members of the Laniatores since they show a conjunct of preadaptations that may favour prolonged associations between the parental and the offspring such as, restriction of the reproduction effort to specific periods and places, considerable adult longevity, and aggressive mechanisms of defence. On the other hand, many of these preadaptations mentioned are absent in the Palpatores. Reduced fecundity and increased egg size accompanied the evolution of subsocial behaviour in laniatorean harvestmen. Palpatores, which show very simple forms of parental investment, have significantly higher fecundity and a smaller egg size than Laniatores, which show subsocial behaviour.

KEY WORDS: Opiliones, subsocial behaviour, parental investment, maternal care, paternal care.

INTRODUCTION

Parental investment can be defined as any behaviour exhibited towards the progeny which increases its survival rate at the cost of the ability of the parent to invest in other progeny (TRIVERS 1972). This may include preparation of nests and territories, choice of appropriate oviposition site, the production of large and heavily yolked eggs, and also subsocial behaviour, that includes guarding, brooding or bearing eggs and young, provisioning offspring before and after birth, and supporting them after nutritional independence (WILSON 1975, CLUTTON-BROCK 1991).

Several factors and ecological conditions have been proposed to account for the evolution of parental care (WILSON 1975, CLUTTON-BROCK 1991). The order of gamete release (DAWKINS & CARLISLE 1976), the certainty of paternity (TRIVERS 1972, GROSS & SHINE 1981), and the association with the young (WILLIAMS 1975) have been used to explain which sex provides care (see review in RIDLEY 1978). Ecological and physiological constraints can also play an important role in the differentiation of certain modes of reproduction, affecting the costs and benefits of offspring guarding for both sexes (SCHALLER 1979, WITTENBERG 1981).

The diversity of reproductive strategies within arachnids rivals all other arthropod groups. However, with the possible exception of spiders and scorpions, evolutionary biologists have tended to overlook these organisms (THOMAS & ZEH 1984). Parental activities vary among arachnids, and maternal care is known in all orders, excluding the Palpigradi, whose reproductive behaviour is unknown (CLOUDSLEY-THOMPSON 1958; WEYGOLDT 1969, 1972; PITTARD & MITCHELL 1972; BRACH 1975; FOELIX 1982; POLIS 1990; GNASPINI 1995; PUNZO 1998). In contrast, paternal care is rare in Arachnida, and the few described cases are confined to the order Opiliones (RODRIGUEZ & GUERRERO 1976, MORA 1990, MARTENS 1993). Biparental care has not been reported for any species of the 11 arachnid orders.

The order Opiliones includes about 5000 species (SHEAR 1982) and belongs to the monophyletic clade Dromopoda that also includes Scorpiones, Pseudoscorpiones and Solifuga (SHULTZ 1990, WHEELER & HAYASHI 1998). The order is divided in three suborders, namely Cyphophthalmi, Palpatores, and Laniatores (review in SHULTZ 1998). The Cyphophthalmi is a basal group composed of small harvestmen, with short legs and superficially looking like mites, with about 50 species scattered throughout the world. Most Palpatores are small, round bodied animals, with usually unarmed pedipalps and long legs. Despite their widespread distribution they are mainly found in the Holarctic region. The Laniatores are often robust animals, with armed pedipalps as adults and variable leg length, distributed all over the world but mostly in the Neotropics (BERLAND 1949, CLOUDSLEY-THOMPSON 1958, MARTENS 1986).

Harvestmen lay eggs on a variety of substrates, such as soil, trunk crevices, under stones, mud, foliage, and other moist places (CLOUDSLEY-THOMPSON 1958). Most reproduce sexually, although parthenogenesis occurs in some species (PHILLIPSON 1959, TSURUSAKI 1986). Courtship in harvestmen is usually very simple and in most cases copulation is not preceded by behavioural displays (MARTENS 1969, MATTHIESEN 1983). Fertilisation is internal and females lay the eggs a few hours or days after mating (JUBERTHIE 1965). The forms of parental investment found among Opiliones range from heavily yolked eggs and microhabitat selection to oviposition, to subsocial behaviour. In this review we focus on the life history, sexual behaviour and ecology of harvestmen, and discuss the possible causes of the diversity of forms of parental investment found in Opiliones.

AN OVERVIEW OF REPRODUCTIVE PATTERNS IN OPILIONES

Suborder Cyphophthalmi

There are few records of the reproductive biology of Cyphophthalmi, probably because the species of this suborder are relatively rare. Copulation occurs with the male transferring a spermatophore-like structure into the female's genital operculum through the penis (JUBERTHIE 1964, 1965). Spermatophore genesis and its biological meaning are still unclear, and thus it is not possible to establish homologies with the spermatophores found in the other orders of arachnids. The form of parental investment in Cyphophthalmi is usually restricted to the choice of moist and protected oviposition sites. In some species such as *Siro rubens* (Sironidae) eggs are laid singly in small natural cavities on the ground, and covered with soil debris by the female (JUBERTHIE 1964).

Suborder Palpatores

Palpatores is the best known group of Opiliones probably because they are most diversified in the Holarctic region, where most biological studies have been conducted. The forms of parental investment described for this suborder are selection of a microhabitat for oviposition, egg-hiding, and the discharge of repugnant secretions on the eggs (Table 1). Subsocial behaviour has never been observed in Palpatores.

Most species have a long ovipositor and lay their eggs on substrates such as soil, trunk crevices, under stones, and other moist places (CLOUDSLEY-THOMPSON 1958). The female's ovipositor touches the substrate before egg-laying, providing information about dimensions of the oviposition site, and perhaps other characteristics such as moisture, temperature, and the presence of fungi (EDGAR 1971, MACÍAS-ORDÓÑEZ 1997). Females of several species carefully search for fissures in fallen trunks and the sites chosen are usually cylindrical and large enough for the ovipositor to enter (EDGAR 1971). The delicate eggs of the Trogulidae are laid in empty snail shells, which are sealed by a protective membrane secreted by the female's ovipositor (PABST 1953, CLOUDSLEY-THOMPSON 1958). In species with a short ovipositor, eggs are laid on substrates such as leaves, wood, and rock surfaces (JUBERTHIE 1964). Females of these species deposit eggs on moss branches or rock

Table 1.

Forms of parental investment within the suborder Palpatores. The type of oviposition was classified following Juberthie (1964), with modifications, in four categories: (1) females lay 1 or 2 eggs each time and during 1 year there are numerous ovipositions; (2) females lay less than 20 eggs each time and during 1 year there are from 5 to 20 ovipositions; (3) females lay a large number of eggs (usually more than 50) and during 1 year there are from 1 to 6 ovipositions; (4) females concentrate their reproductive effort in one or rarely two ovipositions during 1 year in which they can lay 20 to 200 eggs.

Species	Type of oviposition	Forms of parental investment	Source
Ischyropsalidae			
Ischyropsalis spp.	2	production of hygroscopic mucous that surrounds the egg-batch	Juberthie 1964
Nemastomatidae			
Mitostoma pyrenaeum	2	egg-hiding and mucous production	Juberthie 1964
Nemastoma bacciliferum	2	egg-hiding and mucous production	Juberthie 1964
N. quadripunctatum	2	egg-hiding	Kaestner 1968
Phalangiidae			
Oligolophinae			
Mitopus morio	2	egg-hiding	Kaestner 1968
Odiellus gallicus	3	egg-hiding and mucous production	Juberthie 1964
Oligolophus tridens	?	egg-hiding	Kaestner 1968
Phalangiinae			
Phalangium opilio	3	egg-hiding	Gueutal 1944, Edgar 1971
Sabaconidae			
Sabacon vizcayanum	2	production of hygroscopic mucous that surrounds the egg-batch	Juberthie 1964
S. paradoxum	2	production of hygroscopic mucous that surrounds the egg-batch	Juberthie 1964
Sclerosomatidae			
Leiobuninae			
Leiobunum calcar	3	egg-hiding	Edgar 1971
L. flavum	3	egg-hiding and covering with repugnant substances	Edgar 1971, Clawson 1988
L. aldrichi (= *longipes*)	3	egg-hiding	Edgar 1971
L. politum	3	egg-hiding	Edgar 1971
L. rotundum	3	egg-hiding	Juberthie 1964
L. vittatum	3	egg-hiding and covering with repugnant substances	Edgar 1971, Clawson 1988, Macías-Ordóñez 1997
Sclerosomatinae			
Homalenotus quadridentatus	3	egg-hiding	Juberthie 1964
Trogulidae			
Trogulus nepaeformis	2	egg-hiding inside empty snails' shells	Pabst 1953
T. tricarinatus	2	egg-hiding inside empty snails' shells	Pabst 1953
Anelasmocephalus cambrdgei	2	egg-hiding inside empty snails' shells	Pabst 1953

walls and the batch is covered by a highly hygroscopic mucous layer that maintains moisture around the eggs (JUBERTHIE 1964).

A long ovipositor allows the Palpatores to hide eggs from predators and parasites by inserting them into protective substrates (ZEH et al. 1989), without any additional care by the parents, as occurs in many insects (review in TALLAMY & BROWN 1999). The choice of appropriate oviposition sites can be crucial for offspring survival (CLUTTON-BROCK 1991). Among arthropods, sites that have low moisture and/or are subject to direct wind may negatively affect egg development and lead to dehydration (CHAPMAN 1982). On the other hand, eggs laid in very humid places may be more vulnerable to fungal attack (MACHADO & OLIVEIRA 1998). EDGAR (1971) recorded that eggs of *Phalangium opilio* develop and hatch at increased rates when incubated in an atmosphere of 94-98% relative humidity. Eggs in drier air lose too much moisture to develop completely, whereas those in higher humidity are destroyed by mould. Similar results were obtained for the laniatorean *Goniosoma longipes,* which reproduces within granitic caves in Southeast Brazil (MACHADO & OLIVEIRA 1998). For this species the intensity of fungal attack on egg batches was negatively correlated with the distance between the batch and the stream crossing the cave (MACHADO & OLIVEIRA 1998).

Perhaps the most elaborate form of parental investment among Palpatores has been observed in some Leiobuninae species in which females cover the egg batch with repugnant substances before burying the eggs (Table 1). This behaviour may prevent other females from ovipositing in the same place (CLAWSON 1988), and possibly may also deter predators and pathogens (see HOLMBERG 1983, COKENDOLPHER 1993 and citations therein).

Suborder Laniatores

Most descriptions of reproductive behaviour of harvestmen are anecdotal or conducted under laboratory conditions, with little information on reproductive seasonality or natural enemies of the brood. The most common form of parental investment among Laniatores is probably egg-hiding by females (Table 2). Eggs are laid in natural cavities on the ground or rock crevices, and covered by debris and soil particles, camouflaging them with the substrate and/or preventing egg dehydration. Even in *Pachylus quinamavidensis* and *Discocyrtus oliverioi,* whose females guard the eggs instead of hiding them, it is common that the parent covers the eggs with debris.

Oviposition in harvestmen may be linked with the avoidance of predation and parasitism of the brood. Both Palpatores and Laniatores lay eggs in one or several batches, with the females walking for some distance before laying successive batches of eggs. These types of oviposition may be shaped by the abilities of predators or parasites to find the eggs (EDMUNDS 1974). As the risk of predation on eggs is high (MORA 1990, MACHADO & OLIVEIRA 1998), it may be advantageous to lay eggs in several batches, or even scatter single or few eggs over a very wide area, so that detection by natural enemies is reduced (EDMUNDS 1974). Dispersing numerous small clutches through time and space is a very common mean of avoiding maternal care (TALLAMY & SCHAEFER 1997) and this behaviour is found in many asocial harvestmen species, including all palpatoreans and several groups of laniatoreans (Tables 1-2). On the other hand, some species lay eggs predominantly in a single cluster and, in these cases it is common to observe subsocial behaviour (Table 2).

Table 2.

Forms of parental investment within the suborder Laniatores (Opiliones). The types of oviposition are the same as in Table 1.

Species	Type of oviposition	Forms of parental investment	Source
Assamiidae			
Lepchana spinipalpes	?	egg/young guarding by male	Martens 1993
Cosmetidae			
Cynortoides cubanus	3	egg-hiding	Juberthie 1972
Erginulus clavotibialis	4	egg/young guarding by female	Goodnight & Goodnight 1976
Gryne orensis	2	egg-hiding	Canals 1936
Metalibitia paraguayensis	2	egg-hiding	Canals 1936
Vonones sayi	2	egg-hiding	Cokendolpher & Jones 1991
Gonyleptidae			
Bourguyiinae			
Bourguyia albiornata	4	egg/young guarding by female	Machado 1999
Goniosomatinae			
Acutisoma proximum	4	egg/young guarding by female	Ramires & Giaretta 1994
Goniosoma aff. *badium*	4	egg/young guarding by female	Pinto-da-Rocha 1993
G. geniculatum	4	egg/young guarding by female	G. Machado unpubl. data
G. longipes	4	egg/young guarding by female	Machado & Oliveira 1998
G. aff. *inermes*	4	egg/young guarding by female	Machado et al. 1999
G. spelaeum	4	egg/young guarding by female	Gnaspini 1995
Gonyleptinae			
Gonyleptes saprophilus	?	egg/young guarding by male	G. Machado & R.L.G. Raimundo unpubl. data
Geraecormobius orguensis	4	egg/young guarding by female	R. Pinto-da-Rocha unpubl. data
Ilhaia cuspidata	1	egg-hiding	L. Mestre & R. Pinto-da-Rocha in prep.
Ilhaia sp.	1	egg-hiding	Pereira et al. in prep.
Neosadocus aff. *variabilis*	4	egg/young guarding by female	Machado & Vidal in press
Hernandariinae			
Hernandaria scabricula	2	egg-hiding	Canals 1936
Mitobatinae			
Mitobates sp.	1 (?)	egg-hiding by females	G. Machado unpubl. data
Promitobates ornatus	1	egg-hiding by females	R.H. Willemart in prep.
Pachylinae			
Acanthopachylus aculeatus	4	egg/young guarding by female	Capocasale & Bruno-Trezza 1964
Discocyrtus dilatatus	2 (?)	egg-hiding by females	L.E. Acosta unpubl. data
Discocyrtus oliverioi	4	egg/young guarding by female	Elpino-Campos et al. 1999
D. pectinifemur	4	egg/young guarding by female	Mathiessen 1975, 1983
D. prospicuus	2	egg-hiding	Canals 1936
Pachyloidellus goliath	4	egg/young guarding by female	L.E. Acosta unpubl. data
Pachyloides thorelli	2	egg-hiding	Canals 1936
Pachylus quinamavidensis	4	egg guarding by female	Juberthie & Muñoz-Cuevas 1971
Parapachyloides fontanensis	3 (?)	egg-hiding	Canals 1936
Pygophalangodus canalsi	2	egg-hiding	Canals 1936

(*continued*)

Table 2. (*continued*)

Species	Type of oviposition	Forms of parental investment	Source
PROGONYLEPTOIDELINAE			
Iporangaia pustulosa	4	egg/young guarding by female	P. GNASPINI unpubl. data
MANAOSBIIDAE			
Zygopachylus albomarginis	?	egg/young guarding by male	RODRIGUEZ & GUERRERO 1976, MORA 1990
STIGNOPSIDAE			
Hoplobunus boneti	4	egg/young guarding by female	MITCHELL 1971
PHALANGODIDAE			
Scolotemon spp.	1	egg-hiding	JUBERTHIE 1964
Querilhacia querilhaci	1	egg-hiding	JUBERTHIE 1964
PODOCTIDAE			
Leytpodoctis oviger	?	egg transport by male	MARTENS 1993
TRAVUNIIDAE			
Peltonychia clavigera	1	egg-hiding	JUBERTHIE 1964
TRIAENONYCHIDAE			
SOERENSELLINAE			
Karamea spp.	4	egg/young guarding by female	FORSTER 1954
Sorensenella spp.	4	egg young guarding by female	FORSTER 1954
TRIAENONYCHINAE			
Hendea myersi	2	egg-hiding	FORSTER 1954

Subsocial behaviour has been reported for several species of Laniatores and appears as the most elaborate form of parental investment in Opiliones. Maternal care is widely distributed, at least within the Neotropical family Gonyleptidae (Table 2). Egg-guarding behaviour by females may present two variations: (a) the mother takes care of the eggs, and leaves the egg-batch just prior to hatching, as recorded for *Pachylus quinamavidensis* (JUBERTHIE & MUÑOZ-CUEVAS 1971), or (b) the mother takes care of eggs throughout their development and remains with the newly-hatched nymphs for 5 (*Erginulus clavotibialis*, see GOODNIGHT & GOODNIGHT 1976) to 14 days (*Goniosoma longipes*, see MACHADO & OLIVEIRA 1998). In some species the guarding female deserts before the nymphs disperse (e.g. *Erginulus clavotibialis*, GOODNIGHT & GOODNIGHT 1976), while in others the guarding female abandons the oviposition site only after the nymphs disperse (e.g. *Goniosoma* spp., see GNASPINI 1995, MACHADO & OLIVEIRA 1998).

Reproductive activities show wide seasonal variation across different taxa, and this may explain the different patterns of egg guarding by females. In species with a short reproductive season marked by a single annual peak, such as *P. quinamavidensis* (JUBERTHIE & MUÑOZ-CUEVAS 1971), the loss of new mating opportunities throughout the egg-guarding period may represent a high reproductive cost for the brood-caring female. A female that abandons an egg-batch before hatching, may increase her global reproductive success by laying another batch in the same season. Other species such as *Discocyrtus pectinifemur, E. clavotibialis, G. longipes* and *G. spelaeum* reproduce continuously throughout the year, or have two annual reproductive peaks. In these species, females may extend brood caring behaviour at a reduced cost to their global reproductive success, since they may lay eggs again in the same year. In *G. longipes,* few females were observed reproducing twice throughout their lives and the interval between ovipositions varied from 4 to 13 months, with females laying similar number of eggs during the two reproductive events (MACHADO & OLIVEIRA 1998).

Egg-guarding behaviour by males occurs in four laniatorean genera, and these are the only records of paternal care in the arachnids (Table 2). In *Zygopachylus albomarginis* (MORA 1990) and *Gonyleptes saprophilus* (G. MACHADO & R.L.G. RAIMUNDO unpubl. data) males care for eggs and juveniles, while in *Lepchana spinipalpis* and *Leytpodoctis oviger* (MARTENS 1993) only the eggs were guarded. In the later two species it is still unclear whether there is any association between the male and the nymphs. Paternal care in harvestmen takes two forms: (a) care of eggs laid directly on the substrate or in nests made by the male and (b) care of eggs attached externally to the male (Table 2).

WHY PATERNAL CARE IN HARVESTMEN?

The mode of fertilisation is considered the most important variable determining which parent is selected to care (RIDLEY 1978). In this sense paternal care usually correlates with external fertilisation, and the explanatory hypotheses are associated with three factors: the order of gamete release (DAWKINS & CARLISLE 1976), the certainty of paternity (TRIVERS 1972, ALEXANDER & BORGIA 1979), and the association with offspring (WILLIAMS 1975).

Low confidence of paternity reduces the benefits that males gain because it may cause a male to care for young that are not his offspring. This is particularly important in species with high levels of sperm competition such as some spiders (AUSTAD 1984, ELGAR 1998). However, the certainty of paternity cannot directly affect the evolution of paternal care since a male cannot increase his paternal confidence by adopting a caring role (WITTENBERGER 1981). Moreover, harvestmen males are unique among arachnids in that they have an extrusible penis and internal fertilisation, which excludes the order of gamete release hypothesis as an explanation for the evolution of paternal care in this group.

Internal fertilisation and delayed oviposition would predispose females towards parental care (WILLIAMS 1975), and could explain why maternal care is comparatively more common than paternal care among harvestmen. Under these conditions a male spends time and looses additional mates if he takes care of the offspring. The same occurs in the other arachnid orders in which indirect spermatophore transfer dissociates a male from his offspring (THOMAS & ZEH 1984). By contrast, the cost of male parental care is reduced when females spawn on the male's territory (RIDLEY 1978, ZEH & SMITH 1985). If one sex defends a territory before fertilisation, then that sex may be selected to care for the offspring as a consequence of territoriality. Again, the model is not universal, but has probably been important in the evolution of paternal care along several evolutionary lineages, such as some fish (RIDLEY 1978), amphibians (WELLS 1977), and probably harvestmen as well.

MORA (1990) suggested that paternal care in the harvestman *Zygopachylus albomarginis* probably evolved from no care rather than from female care. In her hypothetical scenario females would be attracted to suitable oviposition sites, which males would begin to defend against other males in order to acquire mates. Males defending a territory would increase their fitness because they also indirectly defend eggs against predation by conspecifics. A similar behaviour is observed in *Lepchana spinipalpes* (MARTENS 1993) and *Gonyleptes saprophilus* (G. MACHADO & R.L.G. RAIMUNDO unpubl. data) where males care for a "superbatch" (130 to 420 eggs) containing eggs in all developmental stages and even newly-hatch nymphs. In this case, possibly more than one female contributes to the batch at different times and differences in the number of eggs between batches may be related with the attractiveness of the oviposition sites (see WHITHAM 1986).

In *Goniosoma longipes* a male may defend a territory where females lay eggs and take care of the batches (MACHADO & OLIVEIRA 1998). When the females are experimentally removed from their egg-batches the male undertakes egg guarding for up to 2 weeks. These observations indicate that males of this species are able to care for the brood when the egg guarding females desert or die. Although egg guarding by males lasts only a few weeks, temporary paternal care may be crucial (especially just before hatching), since egg predators can consume entire batches in a single night (MACHADO & OLIVEIRA 1998). This behaviour is remarkably different from males caring for offspring during the entire developmental period, but it constitutes additional evidence that egg guarding by male harvestmen, even for short periods, can occur when the males defend a territory that is also an oviposition site. Therefore, we suggest that the association between the male and the offspring through the defence of an oviposition site may constitute the basis for the evolution of paternal assistance in most harvestmen species.

Leytpodoctis oviger (MARTENS 1993) presents the most bizarre form of paternal care known for laniatorean harvestmen, in which the male carries a few eggs attached to the fourth leg. This behaviour is similar to that found in sea spiders (Chelicerata Pycnogonida) (KING 1973) and some water bugs (Hemiptera Belostomatidae) (SMITH 1997). The main advantage to the male of this behaviour derives from increasing his mobility, and may result in: (a) higher defensive ability against egg predators since the male may flee carrying his offspring; (b) increased capacity to move to areas with suitable moisture and temperature conditions which are crucial for egg development (see MARTENS 1993), and (c) autonomy to forage while guarding the eggs, which is impossible for species that defend a nest. The main disadvantage of keeping the eggs attached to the body is probably a spatial limitation in the number of eggs that one male can carry. Moreover, in this species the eggs are laid on the femur of the fourth leg, where it is impossible for the male to groom the batch to remove pathogens such as fungi (MARTENS 1993). Unfortunately, there is not enough data on the reproductive behaviour of this species, as well as on the ecological pressures that it faces, to speculate on the evolution of this form of paternal care. The wide variety of forms of paternal care in harvestmen suggests that male care evolved independently in different laniatorean lineages (see MARTENS 1993).

EVOLUTION OF PARENTAL CARE IN OPILIONES

Parental care is a widespread behaviour among terrestrial arthropods and is confined to species in which eggs and young are clumped in time and space. Moreover, this behaviour is commonly associated with physically harsh or biologically dangerous habitats (CLUTTON-BROCK 1991, but see TALLAMY & SCHAEFER 1997). WILSON (1975) argues that predation on eggs by conspecifics and ants, and the high risk of fungal attack in tropical rain forests may have been the major forces favouring the evolution of parental care in arthropods. The typically small size of terrestrial arthropods limits their ability to defend themselves, or their broods, against an assortment of larger predators and therefore restricts the number of cases in which parental care confers net benefits (ZEH & SMITH 1985). On the other hand, in many cases parental care significantly reduces offspring mortality caused by parasites, which are generally smaller than their host species (WEST & ALEXANDER 1963, MORA 1990, SCOTT 1990, HOREL & GUNDERMANN 1992).

There are several sources of egg mortality among harvestmen but the most common are predation by conspecifics and other arthropods, and fungal attack (Table 3). MORA (1990) has shown, however, that egg-guarding by males in *Zygopachylus albomarginis* significantly reduces egg mortality due to predation and attack by fungi. Maternal care is crucial for egg survival in the harvestman *Goniosoma longipes*, as predators can consume entire batches in a 24 hr period. However, field experiments demonstrated that the guarding female is unable to protect her eggs against attack by fungi (MACHADO & OLIVEIRA 1998). In both cases the benefits of parental care in terms of fitness should be higher than the energy costs of egg-guarding and the loss of other reproductive opportunities.

Maternal care has been recorded in seven subfamilies of Gonyleptidae (Laniatores), including early lineages (KURY 1994) such as the Bourguyiinae (Table 2). The ancestral behavioural pattern within the family might be: (a) maternal care, and thus egg hiding behaviour would be a reversion of this character or (b) egg hiding behaviour and thus maternal care corresponds to autapomorphies of some species or even groups. In order to access the plesiomorphic state of this reproductive behaviour within the family Gonyleptidae we mapped forms of parental investment

Table 3.

Causes of brood mortality in harvestmen with parental care. Sources for cited species are the same as in Table 2.

Species	Causes of brood mortality				
	Dehydration	Fungi	Ants	Other arthropods	Cannibalism
Acanthopachylus aculeatus					x
Acutisoma proximum				x	x
Bourguyia albiornata		x	x	x	x
Discocyrtus oliverioi		x			x
Erginulus clavotibialis		x			x
Goniosoma longipes	x	x		x	x
Goniosoma spelaeum				x	
Gonyleptes saprophilus			x	x	
Pachylus quinamavidensis					x
Zygopachylus albomarginis		x	x		x
Percentage of occurrence	10	50	30	50	80

(Table 2) in a phylogenetic tree (A.B. KURY & R. PINTO-DA-ROCHA unpubl. data). The ancestral behaviour within the family was suggested through a method similar to parsimony (MADDISON 1994), assuming that the best character history is the one with the lower number of changes through the branches. Although there is no available data on reproductive biology for many subfamilies, including the early lineages Metasarcinae and Cobaniinae (KURY 1994), the result indicates that the ancestral form of parental investment within Gonyleptidae might be egg hiding behaviour, with multiple origins of maternal care within the family. Additional weak evidence is provided by the fact that in Cosmetidae, which are the sister family of Gonyleptidae (KURY 1994), egg hiding behaviour is widespread. Maternal care probably evolved independently in gonyleptid harvestmen in response to similar selective pressures, such as inter- and intra-specific predation (Tables 2-3). At least in one subfamily of Gonyleptidae (Goniosomatinae, about 40 species) and one of Triaenonychidae (Soerensenellinae, about 15 species), maternal care is present in all representative genera and species (Table 2), which indicates that in these groups subsocial behaviour has appeared in the respective ancestors and was retained throughout the evolution of the taxa. Moreover there are no harvestmen families in which the number of subsocial species is more than a small fraction of the total. It is likely that the extraordinary costs associated with parental care are closely related to its scarcity.

There remains an interesting question about the evolution of maternal care in Opiliones: why subsocial behaviour appears to be restricted to members of the Laniatores? It is assumed that a reproductive pattern evolves in response to many interacting factors including phylogenetic inertia, morphological and physiological characteristics of the taxon, and the presence or absence of critical behavioural preadaptations (STEARNS 1976). Even the most primitive interaction between parent and offspring cannot occur in the absence of certain preadaptations (sensu FUTUYMA 1986). Among arthropods the most important life history pattern determining the evolution of subsocial behaviour is to confine reproduction effort to specific periods and places, because it is physically impossible to defend a clutch that is dispersed through the time and space (TALLAMY & WOOD 1986). Parental assistance also requires considerable adult longevity, as parents must not only survive to oviposit, but also live long enough to care for one or more clutches. Finally, parental characteristics such as defensive posturing, aggression, and nest building are traits from which natural selection could shape parental behaviours that increase offspring survival. When life history features of the Laniatores and Palpatores are analysed comparatively it becomes evident that many of the preadaptations mentioned are absent in Palpatores but present in Laniatores.

In temperate regions the Palpatores show three basic life-cycle patterns: (a) individuals reproduce once a year, have fast development, and adults die after oviposition (see TODD 1949, PHILLIPSON 1959, JUBERTHIE 1964, EDGAR 1971, SCHAEFER 1983, HILLYARD & SANKEY 1989); (b) individuals live more than 1 year but reproduction takes place during a restricted period, usually in the autumn (TODD 1949, JUBERTHIE 1964, CANNATA 1988); (c) individuals live more than 1 year and reproduce continuously (TODD 1949, EDGAR 1971, CANNATA 1988). Pattern (a) is the most common in palpatoreans thus far studied, whereas pattern (c) is widespread among laniatorean harvestmen (JUBERTHIE 1964, MATTHIESEN 1975, GNASPINI 1995, MACHADO & OLIVEIRA 1998). The constraint imposed on many palpatoreans by their short life period, makes the prolonged association between parents and offspring unlikely, thus limiting the amount of parental assistance provided to offspring.

Unlike Palpatores, all the studied species of Laniatores live more than 2 years, and most of them reproduce throughout the year, thus they are not under the same life history constraints faced by Palpatores.

Besides reproducing during short periods of their lives, many palpatorean species scatter their eggs through time and space (Table 1). This oviposition pattern was probably maintained in laniatorean taxa where subsocial behaviour has not evolved (Table 2). Within the laniatorean families such as Cosmetidae, Phalangodidae and Travuniidae most species have egg hiding behaviour (Table 2), which we believe to be the plesiomorphic character in the group. These species spread their eggs throughout the reproductive season, laying several small batches. *Erginulus clavotibialis* is the only cosmetid known to show subsocial behaviour and as expected it lays eggs in a single large batch (Table 2). Thus, laying eggs aggregated in time and space is here proposed to be another preadaptation for the evolution of subsocial behaviour in several laniatorean species.

In order to test whether oviposition in clutches is a preadaptation to subsocial behaviour we compared this attribute with another group with species which have and lack this trait (WILSON 1987). The search for repeated, but independent, examples of support for the same adaptive hypothesis might serve as evidence of causation instead of a correlation between two traits (MARTINS 2000). We took the class Chilopoda, which is divided in five orders, as a phylogenetic replication. The orders Craterostigmomorpha, Geophilomorpha, and Scolopendromorpha present subsocial behaviour and, like laniatorean harvestmen, females lay eggs in compact masses. Both Lithobiomorpha and Scutigeromorpha orders, lay eggs in small batches in the soil after being covered with soil by the female that does not provide additional care to the offspring, as occurs in palpatorean harvestmen (CLOUDSLEY-THOMPSON 1958, KAESTNER 1968, LEWIS 1981, GIRIBET et al. 1999). In the case of Chilopoda, the comparative method leads to provisional support of the hypothesis that subsocial behaviour is commonly associated with oviposition in cluster and also that absence of care is associated with egg spreading. The same pattern emerges from some insect orders, such as hemipterans (reviewed by TALLAMY & SCHAEFER 1997).

Both Palpatores and Laniatores have repugnatorial glands that produce defensive secretions against various predators. However, palpatoreans are often smaller and more fragile than laniatoreans and their pedipalps are usually shorter and lack spines (BERLAND 1949). This is especially evident in the families Caddidae, Neopilionidae, Phalangiidae, and Sclerosomatidae which comprise about 70% of all Palpatores (MARTENS 1976, 1980; CRAWFORD 1992). Moreover, common defensive adaptations suggested as the most efficient among Palpatores are leg autotomy (BERLAND 1949, KAESTNER 1968, EDGAR 1971, GUFFEY 1998), the ability to flee rapidly (BRISTOWE 1925, EDGAR 1971), and bobbing (BERLAND 1949). None are likely to provide effective defence against potential egg predators. On the other hand, in large Laniatores, such as many gonyleptids, mechanical defence such as attacking with the pedipalps (GNASPINI & CAVALHEIRO 1998, MACHADO et al. 2000) and pinching the aggressor between the sharp projections of the femur and trochanter IV (BRISTOWE 1925, CAPOCASALE & BRUNO-TREZZA 1964, GNASPINI & CAVALHEIRO 1998, MACHADO et al. 2000) are common and could defend against egg predators. The distinct behavioural traits found in the harvestmen suborders may offer a satisfactory explanation of the causes of the evolution of maternal care in Laniatores but not in Palpatores.

Defence against fungi may be an exception since it does not depend on individual size or leg fragility and thus could be potentially accomplished by any harvestmen species. However there is only one species, *Zygopachylus albomarginis*, known to be able to control fungal attack on eggs (Mora 1990). The ability to control fungal infection may be very rare in Opiliones, and unlikely to have led to the evolution of subsocial behaviour in the whole order. In this sense it is possible that predation on eggs, instead of egg infection by fungi, is an effective pressure favouring the evolution of subsocial behaviour in harvestmen.

Once again a comparison with centipedes supports these ideas. Although all centipedes have poisonous glands, remarkable differences in morphological traits and defensive behaviours are found among the orders. First, at least Geophilomorpha and Scolopendromorpha (which have maternal care) are often larger than the Lithobiomorpha and Scutigeromorpha (which bury their eggs). Large animals are probably less likely to become prey, as predators may be unable to capture and handle them safely (Fernandez et al. 1993). Second, the venom of Geophilomorpha and Scolopendromorpha is relatively powerful, and can even cause serious damage to large mammals (Kaestner 1968). In addition, many species of these two latter orders also use their hind legs to pinch the aggressor and use repugnant fluids as in laniatorean harvestmen. Some species of Lithobiomorpha and Scutigeromorpha also have repugnant secretions but most commonly defend themselves by fleeing and by autotomy, as in Palpatores (Cloudsley-Thompson 1958, Kaestner 1968).

Finally we also compared the fecundity (expressed as the number of eggs laid per year) between palpatoreans and laniatoreans using a phylogenetic autocorrelation method (Gittleman & Kot 1990). Moran's I coefficient for the distinct taxonomic levels revealed a negative significant autocorrelation at the suborder level, indicating dissimilarity of fecundity at this taxonomic category. Despite the differences in the body size between species of each suborder, fecundity is higher in Palpatores (X ± SD = 160.4 ± 102.7 eggs, n = 23, range 41-500) than in Laniatores (X ± SD = 77.1 ± 28.8 eggs, n = 12, range 25-103) (Moran's I = – 0.20; $P < 0.01$). Furthermore, eggs also tend to be smaller in Palpatores (X ± SD = 0.93 ± 0.29 mm in diameter, n = 6, range 0.5-1.4 mm) than in Laniatores (X ± SD = 1.55 ± 0.45 mm in diameter, n = 8, range 1.0-2.2 mm). Due to the small sample size, however, it was not possible to perform a comparative analysis on egg dimension. Therefore it appears that reduced fecundity and increased egg size have accompanied the evolution of subsocial behaviour in laniatorean harvestmen.

CONCLUDING REMARKS

The notion that subsocial behaviour is rare among harvestmen (see Rodriguez & Guerrero 1976, Zeh et al. 1989, Edgar 1990) may now be dismissed. We present evidence that harvestmen join spiders (Foelix 1982), pseudoscorpions (Weygoldt 1969), camel spiders (Punzo 1998), millipedes (Cloudsley-Thompson 1968), coleopterans (Klemperer 1983, Scott 1990), orthopterans (West & Alexander 1963), hemipterans (Wilson 1971, Tallamy & Schaefer 1997) and hymenopterans (Wilson 1975), as highly labile arthropod taxa in forms of parental investment. There is considerable diversity among Opiliones in the forms of investment provided, including production of large and heavily yolked eggs, selection of microhabitats for oviposition, egg burying, egg-hiding and protection of egg and young by females or males against predators and pathogens.

During the past two decades a number of studies have provided new exciting and informative data about the reproductive biology of Opiliones from both tropical and temperate regions. However, additional studies on life history, sexual behaviour and ecology of harvestmen are critical, in order to determine how common are the diverse forms of parental investment, as well as to access the evolutionary transitions of subsocial behaviour within the order. In this sense, the family Gonyleptidae deserves special attention in future studies, as the available information about this taxon allows us to test evolutionary hypotheses and to establish the history of the character "parental care" among harvestmen.

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