Universidade Estadual de Campinas
Instituto de Biologia
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História natural e ecologia comportamental de opiliões (Arachnida: Opiliones): defesa, socialidade e investimento parental

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"Uma chuva torrencial caía na mata enquanto na escuridão da caverna uma criatura suja e encharcada observava o demorado processo de oviposição de um opilião e pensava: 'o que é que eu estou fazendo aqui?!' Tenho certeza que essa pergunta já passou pela cabeça de muitos que estão lendo esta tese agora; seja no costão da praia quando aquela onda gelada estourava nas costas fazendo voscê se cortar inteiro nas cracas, ou às duas horas da madrugada no laboratório, com aquele maldito experimento que nunca dava certo. Mas, apesar de todas as adversidades da profissão, aqui estamos nós. Algo mais forte nos impele a continuar: uma inquietação por descobrir, solucionar problemas e brindar com uma resposta àquela pergunta que levantamos inicialmente. Isso me faz lembrar das crianças que dispensavam as brincadeiras com os colegas para ficarem observando os beija-flores no quintal, ou mesmo aquelas que já ensaiavam suas experiências misturando todos os produtos de limpeza da despensa buscando uma fórmula cabalística. Nessa época, já era essa coisa fantástica chamada Biologia que fazia cócegas nas caraminholas dessas crianças que todos nós fomos..."

GLAUCO MACHADO

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A história dessa tese começa, na verdade, no final de 1995 quando pela primeira vez eu entrei nas grutas de Atibaia e me deparei com umas criaturas pernudas que descansavam sobre as paredes internas. Nesse primeiro momento sou profundamente grato ao casal Ari e Katia que me deram toda a força e encorajamento para que eu pudesse iniciar minha pesquisa. Lembro claramente quando eles me disseram: "Faça tudo direito e isso dará uma tese". Na época eu não entendi completamente o que aquelas palavras significavam mas pude tangenciar de leve a importância do que eu tinha em mãos. Depois de alguns meses passei para a orientação formal do Prof. Dr. Paulo S. Oliveira. Aprendi e continuo a aprender muito com o meu amigo Paulinho.

Por incrível que pareça sou ligeiramente aracnofóbico e, apesar de não ter tido problemas com os opiliões, devo confessar que a presença incômoda de grandes aranhas nas grutas me deixou um pouco preocupado no início. Mas a companhia dos amigos no campo e as constantes descobertas sobre a biologia dos *Goniosoma* acabaram por tornar as viagens à Atibaia sempre uma grande diversão. Merecem especial destaque pela amizade, companheirismo e ajuda os amigos: Rafael L. G. Raimundo (o Simprão) que, além de acompanhar de perto o estudo de campo por mais de um ano, criou a tradição do leite condensado com granulado após o trabalho, e Vinícius Bonato (o mano Vini) que, apesar da dificuldade em se locomover pelos canais estreitos das grutas, acabou descobrindo nesse ambiente sua paixão pelos morcegos. Além desses gostaria de agradecer a ajuda de todos daqueles que, pelo menos uma vez, se aventuraram comigo pelas grutas. Não vou citá-los nominalmente pois tenho certeza que vou me esquecer de alguém...

Na "fase Cardoso" do trabalho o meu muito obrigado vai para a Lú que, além de me apresentar a ilha, me ajudou muito no campo. Agradecimentos especiais para a Cidinha e Adélia por sempre estarem dispostas a quebrarem os meus galhos. Mais uma vez nessa parte do trabalho de campo recebi ajuda de muitos amigos e, entre eles, gostaria de mencionar o meu mano Vini, Lú, Höll, Lígia, William e Miúdo.

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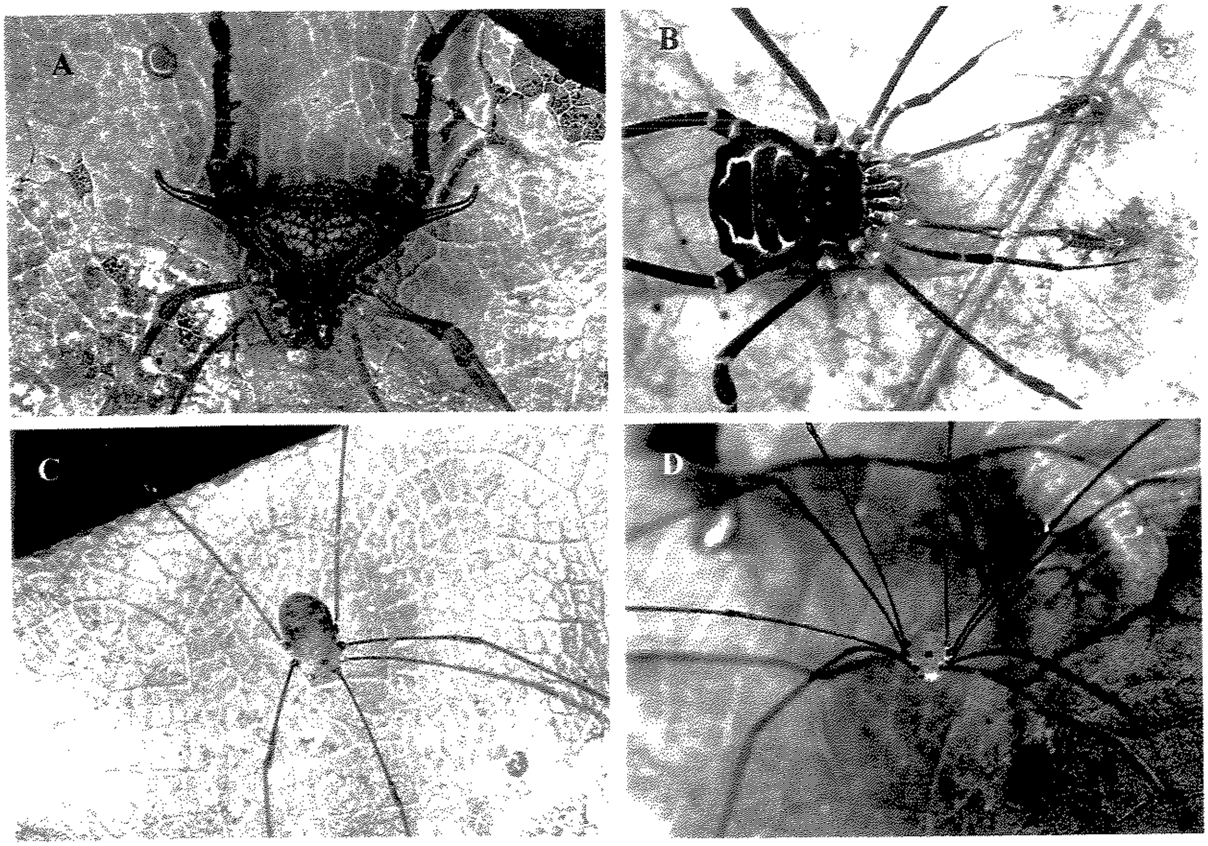
APRESENTAÇÃO



(A) Macho de *Discocyrtus* sp.; (B) Fêmea de *Sodreana sodreana*; (C) Fêmea de *Holcobunus* sp.1; (D) Macho de *Holcobunus* sp.2.

Caracterização geral da ordem Opiliones

A ordem Opiliones possui cerca de 7000 espécies (COKENDOLPHER & LEE, 1993) e pertence ao clado monofilético chamado Dromopoda, que também inclui as ordens Scorpiones, Pseudoscorpiones e Solifuga (SHULTZ, 1990; WHEELER & HAYASHI, 1998). A ordem é dividida em três subordens: Cyphophthalmi, Palpatores e Laniatores (revisão em SHULTZ, 1998). Os Cyphophthalmi são um grupo basal constituído por animais pequenos, com pernas curtas e distribuídos esparsamente por todo o mundo. A maioria dos Palpatores possui pernas longas, pedipalpos inermes e suas espécies, apesar de amplamente distribuídas, concentram-se na região Holártica, principalmente Paleártica. Os Laniatores, por sua vez, possuem corpo mais robusto, pernas de tamanho variável e pedipalpos armados com espinhos. As espécies desse grupo apresentam distribuição mundial mas são mais diversificadas nas regiões tropicais, principalmente na América do Sul (SHEAR, 1982; MARTENS, 1986).

Um pouco sobre história natural de opiliões

Defesa

De forma geral, os mecanismos de defesa em animais podem ser divididos em primários e secundários (EDMUNDS, 1974). As defesas primárias são aquelas que operam independentemente da presença de um predador e que diminuem a chance de um predador encontrar ou reconhecer a presa. Em artrópodes as principais formas de defesa primária incluem a camuflagem, a anacorese e o aposematismo (EDMUNDS, 1974; EVANS & SCHMIDT, 1994). As defesas secundárias são aquelas que operam somente diante do ataque de predador e que diminuem as chances de um ataque ser bem sucedido. Entre os artrópodes as formais mais comuns de defesa secundária incluem a fuga, a tanatose, o comportamento deimático, a autotomia de apêndices e a emissão de substâncias repugnatórias (EDMUNDS, 1974; EVANS & SCHMIDT, 1994).

Talvez um dos aspectos mais bem estudados da biologia de opiliões seja a defesa (HARA, 2001), em especial, os mecanismos de defesa secundários. Embora muitas espécies do grupo apresentem coloração críptica e outras, colorido intenso, nenhum estudo até hoje demonstrou experimentalmente funções defensivas como camuflagem ou aposematismo em opiliões.

Nos Palpatores o comportamento defensivo mais comum provavelmente seja a autotomia de apêndices locomotores (EDGAR, 1971; GUFFEY, 1998, 1999). A linha de fissão da perna se dá entre a coxa e o trocânter e a autotomia só ocorre quando o membro é agarrado pelo potencial predador (KAESTNER, 1968; G. MACHADO, *obs. pess.*). Em geral, a perna autotomizada permanece em movimento e o opilião foge do local de ataque (KAESTNER, 1968).

Em espécies de pernas longas, como a maioria dos Palpatores e alguns Laniatores, a fuga é um comportamento defensivo bastante difundido (EDGAR, 1971; HILLYARD & SANKEY, 1989; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000). Nos Palpatores, as espécies de pernas longas também exibem um comportamento de sacudir o corpo rapidamente para cima e para baixo através de contrações e distensões das pernas (HILLYARD & SANKEY, 1989). Isso provavelmente dificulta a identificação, localização e ataque ao corpo do animal por parte do predador.

Quando um opilião encontra-se acima do solo (sobre a vegetação ou sobre pedras) é comum que, diante do ataque de um potencial predador, o indivíduo solte-se do substrato, deixando-se cair no solo. As espécies de Laniatores e Palpatores que apresentam esse comportamento, em geral, possuem coloração críptica e, ao caírem no chão, permanecem imóveis por um certo tempo, o que dificulta sua localização por predadores visualmente orientados (EISNER *et al.*, 1971; HILLYARD & SANKEY, 1989; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000).

Quando manipulados pela perna IV, muitos Laniatores apresentam um comportamento de defesa mecânico que consiste em realizar um movimento brusco, trazendo o corpo de encontro ao fêmur IV e fazendo com que o agressor seja pinçado pelas projeções pontiagudas presentes na coxa, trocânter ou fêmur (BRISTOWE, 1925; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000). Outra defesa mecânica empregada por Laniatores durante a manipulação por seres humanos é o ataque com os pedipalpos (em geral, armados com espinhos) e com as quelíceras (GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000)

A forma mais comum e eficiente de defesa nos Laniatores (e talvez também nos Cyphophthalmi) é a emissão de substâncias repelentes sobre o agressor (EISNER *et al.*, 1978). A secreção defensiva é produzida por um par de glândulas exócrinas localizado na margem anterior do escudo dorsal cujas aberturas estão próximas às coxas I e II (JUBERTHIE, 1961). A natureza química da secreção repugnatória dos opiliões varia muito dentro e entre diferentes grupos taxonômicos e pode incluir fenóis, ésteres, cetonas e álcoois (revisão em HARA, 2001).

Socialidade

Muitos animais vivem em grupos durante uma parte de suas vidas (BERTRAM, 1978) e existem vários estudos teóricos e experimentais sobre os custos e benefícios do gregarismo (HAMILTON, 1971; TREISMAN, 1975; RASA, 1997). Historicamente, estudos sobre comportamento gregário têm enfocado principalmente espécies de vertebrados (DANCHIN & WAGNER, 1997) e insetos sociais (WILSON, 1971).

A idéia mais generalizada é a de que aracnídeos sejam animais solitários e intolerantes a co-específicos (CLOUDSLEY-THOMPSON, 1958). De fato, o comportamento gregário ou estágios mais elaborados de socialidade (como a eussocialidade) são muito raros em aranhas, escorpiões, pseudo-escorpiões, solífugos e amblipígios – ordens para as quais existem livros fornecendo um panorama mais detalhado da biologia de suas espécies (WEYGOLDT, 1969, 2000; FOELIX, 1982; POLIS, 1990; PUNZO, 1998). Nos poucos casos registrados, evidências apontam que os agrupamentos são compostos predominantemente por indivíduos aparentados (POLIS, 1990; EVANS, 1999).

Ao contrário das outras ordens de aracnídeos, entretanto, os opiliões apresentam muitas espécies com hábitos gregários (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). Em Palpatores as agregações podem conter centenas ou milhares de indivíduos, já tendo sido registrado um agregado com mais de 70.000 opiliões numa área desértica do México (WAGNER, 1954). Em geral, agregados de Palpatores formam massas compactas com várias camadas de corpos sobrepostos (WAGNER, 1954; HOLMBERG *et al.*, 1984; CODDINGTON *et al.*, 1990). Nos Laniatores, as agregações não são muito numerosas e os agrupamentos variam de 3 a 200 indivíduos (CAPOCASALE & BRUNO-TREZZA, 1964; PINTO-DA-ROCHA, 1993; MACHADO *et al.*, 2000; ELPINO-CAMPOS *et al.*, 2001). Nessa sub-ordem os agregados não formam massas compactas, mas os indivíduos apresentam estreito contato corporal e sobreposição de pernas. Para ambas as sub-ordens foram registradas agregações multi-específicas, ou seja, formadas por indivíduos de duas ou mais espécies (COCKERILL, 1988; MACHADO & VASCONCELOS, 1998; ELPINO-CAMPOS *et al.*, 2001).

Apesar de ser um comportamento comum, poucos estudos foram realizados no sentido de compreender o significado adaptativo do gregarismo na ordem Opiliones. Ao contrário do que ocorre com espécies de outras ordens de aracnídeos, não existe nenhuma evidência a favor de que as agregações de opiliões sejam compostas por indivíduos aparentados. Nesse sentido, algumas hipóteses eco-fisiológicas foram levantadas com base nos dados disponíveis na literatura (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000), mas nenhuma delas foi testada experimentalmente. A primeira sugestão relaciona-se à escolha de micro-habitats com condições adequadas de temperatura, umidade e incidência luminosa. A segunda hipótese propõe que o entrelaçamento das penas e a sobreposição de corpos possam reduzir a movimentação de ar, atenuando a perda d'água e conservando o calor dos indivíduos agregados. Finalmente, é possível que as agregações tenham uma função defensiva tanto através do efeito de diluição (*sensu* KREBS & DAVIES, 1978) como também pela ação combinada da secreção repugnatória dos indivíduos agregados.

Investimento parental

Investimento parental é definido como qualquer comportamento exibido por um indivíduo que aumente a chance de sobrevivência de sua ninhada em detrimento à habilidade desse indivíduo investir em outra prole (TRIVERS, 1972). Isto pode incluir uma grande variedade de comportamentos de cuidado à prole, sendo os mais simples a preparação de ninhos e a escolha de sítios apropriados para oviposição. O comportamento subsocial é uma forma elaborada de cuidado à prole que inclui uma associação prolongada entre um indivíduo parental e sua prole (WILSON, 1975). Em artrópodes as formas mais comuns de comportamento subsocial são a guarda de ovos e juvenis, provimento de alimentação à prole e, algumas vezes, assistência após a independência nutricional (CLUTTON-BROCK, 1991; FILIPPI *et al.*, 2001).

Muitos fatores e condições ecológicas têm sido propostos para explicar a evolução da subsocialidade (WILSON, 1975; CLUTTON-BROCK, 1991). A ordem de liberação dos gametas (DAWKINS & CARLISLE, 1976), a certeza da paternidade (TRIVERS, 1972), e a associação com a prole (WILLIAMS, 1975) são as teorias usadas para compreender qual sexo irá prover o cuidado parental (revisão em RIDLEY, 1978). Além desses fatores, limitações ecológicas e fisiológicas podem exercer um papel importante na diferenciação de certos modos de reprodução, influenciando os custos e benefícios da guarda da prole para ambos os sexos (WITTENBERG, 1981).

As formas de cuidado à prole são diversas entre os aracnídeos e a assistência maternal aos ovos é conhecida para todas as ordens, excluindo os Palpigradi, cujo comportamento reprodutivo é desconhecido (CLOUDSLEY-THOMPSON, 1958; KLINGEL, 1963; WEYGOLDT, 1969, 2000; PITTARD & MITCHELL, 1972; BRACH, 1975; FOELIX, 1982; POLIS, 1990; PUNZO, 1998; MACHADO & RAIMUNDO, 2001). Ao contrário, o cuidado paternal é um comportamento raro entre os aracnídeos e os poucos casos registrados estão restritos à ordem Opiliones (RODRIGUEZ & GUERRERO, 1976; MORA, 1990; MARTENS, 1993). Cuidado biparental ainda não foi descrito para nenhuma das onze ordens de Arachnida, entretanto, no opilião *Goniosoma longipes* machos podem assumir a guarda da prole por um período de até duas semanas caso a fêmea guardiã seja experimentalmente removida (MACHADO & OLIVEIRA, 1998).

A maior parte dos estudos sobre reprodução de opiliões é constituída por observações pontuais ou conduzidas em condições de cativeiro, o que fornece pouca informação sobre sazonalidade reprodutiva e predadores naturais de ovos. A forma mais comum de investimento parental em opiliões provavelmente é a ocultação de ovos pela fêmea (revisão em MACHADO & RAIMUNDO, 2001), que insere os ovos em cavidades naturais e, eventualmente, os cobre com partículas de solo ou outros detritos. Esse comportamento, além de oferecer um baixo custo para a fêmea em termos de tempo e energia, pode camuflar os ovos no substrato e também prevenir a sua desidratação (ver ELPINO-CAMPOS *et al.*, 2001; WILLERMART, 2001).

De forma geral, o comportamento de oviposição em opiliões parece ter evoluído em resposta à pressão de predadores e parasitas sobre a prole (MACHADO & RAIMUNDO, 2001). Muitos opiliões espalham seus ovos em várias desovas, com as fêmeas percorrendo uma certa distância entre os sucessivos eventos de oviposição. Como o risco de predação sobre ovos é alto (MORA, 1990; MACHADO & OLIVEIRA, 1998), deve ser vantajoso colocar ovos em várias desovas, ou mesmo espalhar um ou poucos ovos em uma área extensa, de modo a reduzir a probabilidade de detecção da prole por inimigos naturais (EDMUNDS, 1974). Dispersar muitas desovas pequenas no tempo e no espaço é uma alternativa comum à subsocialidade em artrópodes (TALLAMY & SCHAEFER, 1997) e este comportamento é encontrado em várias espécies de opiliões que apresentam formas incipientes de cuidado à prole, incluindo todos os Palpatores e muitos grupos de Laniatores (PHILLIPSON, 1959; JUBERTHIE, 1965; EDGAR, 1971). Por outro lado, algumas espécies colocam ovos predominantemente em uma única desova e, nesses casos, é comum encontrar comportamento subsocial (MACHADO & RAIMUNDO, 2001).

A subsocialidade já foi documentada para muitas espécies de Laniatores e parece ser a forma mais elaborada de investimento parental encontrada em opiliões. O cuidado maternal é amplamente distribuído na ordem, especialmente na família neotropical Gonyleptidae (GNASPINI, 1995 e referências incluídas). O comportamento de guarda de ovos pelo macho ocorre em quatro gêneros de Laniatores (RODRIGUEZ & GUERRERO, 1976; MORA, 1990; MARTENS, 1993), sendo um deles da família Gonyleptidae (G. MACHADO & R.L.G. RAIMUNDO, *dados não* *publicados*). A variedade de formas de cuidado paternal e sua distribuição taxonômica sugerem que o comportamento de assistência à prole por machos em opiliões evoluiu independentemente nas diferentes famílias de Laniatores (MARTENS, 1993).

Por que estudar opiliões?

Apesar de os opiliões constituírem a terceira maior ordem em número de espécies dentro da classe Arachnida, o conhecimento biológico sobre o grupo é ainda incipiente em muitos aspectos. O Brasil é o país com a maior riqueza de opiliões no mundo, com aproximadamente 950 espécies (PINTO-DA-ROCHA, 1999). A família Gonyleptidae, a maior entre os opiliões, concentra a maioria dos estudos ecológicos e comportamentais realizados com espécies da ordem até o momento em regiões neotropicais (veja referências em GNASPINI, 1995, 1996; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000; MACHADO & RAIMUNDO, 2001).

Os poucos trabalhos com opiliões não refletem necessariamente uma dificuldade de se trabalhar com as espécies deste grupo no campo. A provável explicação reside nos hábitos criptobióticos e noturnos da maioria das espécies, o que, em princípio, pode representar obstáculos a estudos comportamentais. Ao contrário de muitas aranhas e escorpiões, os opiliões são totalmente inofensivos aos humanos e algumas espécies apresentam populações numerosas, características que facilitam estudos comportamentais. Além disso, muitos opiliões, especialmente aqueles da família Gonyleptidae, são grandes (corpo entre 5 e 15 mm) e apresentam dimorfismo sexual acentuado com machos, em geral, maiores e mais armados do que as fêmeas (BERLAND, 1949). Essa última característica permite o fácil reconhecimento dos sexos no campo e a obtenção de dados comportamentais sem perturbação dos indivíduos.

Assim como as aranhas, provavelmente o grupo mais bem estudado de aracnídeos, opiliões têm se mostrado organismos especialmente adequados como modelos para trabalhos comportamentais. Muitas espécies prestam-se a manipulações experimentais diretamente no campo, permitindo testar hipóteses de maneira refinada (veja MORA, 1990; MACHADO & OLIVEIRA, 1998, CAPÍTULOS 3 e 5). Algumas espécies, principalmente os pequenos Laniatores, são facilmente mantidas em cativeiro, onde executam comportamentos similares aos observados no campo (veja CAPOCASALE & BRUNO-TREZZA, 1964; MATTHIESEN, 1983; ELPINO-CAMPOS *et al.*, 2001). Repertórios comportamentais na forma de etograma têm sido realizados em laboratório (ELPINO-CAMPOS *et al.*, 2001) e o incremento de informações nessa área permitirá comparações quantitativas e qualitativas entre espécies sobre a alocação de tempo e energia para diferentes atividades.

Aliado às facilidades operacionais, existe na literatura uma hipótese filogenética para as Gonyleptidae em nível de subfamílias (PINTO-DA-ROCHA, 2001). Existe informação filogenética também para algumas das subfamílias de Gonyleptidae como, por exemplo, Caelopyginae (PINTO-DA-ROCHA, 1997), Progonyleptoidellinae, Sodreaninae (PINTO-DA-ROCHA, *em preparação*) e Mitobatinae (KURY, 1991). Tendo em mãos as relações de parentesco entre espécies ou grupos, é possível fazer inferências sobre a história evolutiva de caracteres comportamentais e analisar dados quantitativos de forma comparativa, ponderando os efeitos filogenéticos (DINIZ-FILHO, 2000). Essa abordagem já foi usada preliminarmente por MACHADO & RAIMUNDO (2001) para traçar a possível história evolutiva das formas de investimento parental em Gonyleptidae e para testar as relações entre a fecundidade e a forma de investimento parental nas subordens Laniatores e Palpatores.

Objetivos gerais

Nesta tese estudei o comportamento de algumas espécies de opiliões da família Gonyleptidae, com ênfase nos mecanismos defensivos, socialidade e investimento parental. Meu objetivo principal por trás de todos os estudos de caso foi entender como diferentes formas de defesa (comportamental e química) podem influenciar outros aspectos da história natural de opiliões, tais como gregarismo e cuidado parental. De forma geral, estava interessado nas seguintes questões:

1. *A defesa química em opiliões, caracterizada pela liberação de substâncias repugnatórias, pode favorecer a evolução e/ou manutenção do comportamento gregário em opiliões?*

A liberação de substâncias químicas para defesa pode se relacionar com o comportamento gregário por duas vias distintas. A primeira possibilidade foi sugerida pela primeira vez por HOLMBERG *et al.* (1984), na qual a liberação coletiva da secreção repugnatória poderia intensificar o sinal de defesa. A segunda possibilidade é que as substâncias químicas, primariamente usadas em um contexto defensivo, podem funcionar também como feromônio de alarme, incitando uma resposta de fuga generalizada em indivíduos agregados. De acordo com essa hipótese, a secreção defensiva liberada por um indivíduo sob ataque em um agregado serviria também como sinal de alarme, disparando um comportamento de fuga generalizada (HOLMBERG, 1986). Em ambos os casos a defesa química estaria favorecendo o gregarismo entre indivíduos supostamente não aparentados.

2. *Como aspectos da morfologia geral do corpo, aliados aos mecanismos de defesa apresentados por uma espécie, podem influenciar sua forma de investimento parental?*

A guarda da prole em artrópodes só pode ocorrer quando o indivíduo parental possui características morfológicas e/ou comportamentais que o capacite repelir os principais predadores de ovos/ninfas de forma eficiente (ZEH & SMITH, 1986). Opiliões apresentam uma grande variação na morfologia externa (BERLAND, 1949) e nos mecanismos defensivos. Nesse sentido, espécies com corpo pequeno, pernas longas e frágeis, pedipalpos sem espinhos e que empregam principalmente mecanismos evasivos de defesa (como fuga e autotomia de apêndices) não devem ser capazes de guardar a prole de modo eficiente. Ao contrário, espécies com pernas e corpo robustos, pedipalpos com espinhos e que empregam mecanismos de defesa contundentes (como ataque com os pedipalpos e liberação de secreção repugnatória) devem ser capazes de guardar a prole eficientemente. Nesse último grupo, a subsocialidade pode vir a evoluir de acordo com pressões ecológicas específicas, tais como alto risco de predação sobre os ovos (TALLAMY & SCHAEFER, 1997).

Organização da tese

A tese está dividida em seis capítulos no formato de manuscritos para publicação. Por esta razão poderão ser encontradas repetições em alguns assuntos entre os capítulos, apesar de haver citações cruzadas entre eles. Foram usadas várias espécies para responder questões ligadas à defesa, socialidade e investimento parental pois, nem sempre, a mesma espécie era um bom modelo de estudo para todos esses três aspectos comportamentais. Os capítulos 1, 2, 3 e 5 tratam de estudos de caso, incluindo sete espécies de opiliões que ocorrem ao longo da Mata Atlântica. Os capítulos 4 e 6 foram inseridos na tese para dar coesão ao trabalho, pois fazem revisões sobre os principais tópicos tratados na tese e inserem os resultados obtidos dentro da teoria ecológica geral.

O Capítulo 1 descreve o comportamento reprodutivo do opilião *Goniosoma longipes,* cujas fêmeas ovipõem no interior de cavernas graníticas e apresentam cuidado à prole. Às observações naturalísticas são acrescidas manipulações experimentais conduzidas no campo para se avaliar o papel do cuidado maternal na sobrevivência dos ovos nessa espécie. O Capítulo 2 detalha outros aspectos da história natural de *G. longipes* tais como padrão diário de atividades, comportamento gregário, dieta, forrageamento e mecanismos de defesa. O Capítulo 3 aborda o comportamento gregário de *Goniosoma* aff. *proximum* e testa através de um experimento de campo se a secreção repugnatória, primariamente utilizada como defesa contra predadores, pode funcionar também como feromônio de alarme nessa espécie. O Capítulo 4 apresenta dados comportamentais sobre outras cinco espécies de *Goniosoma* e resume todas as informações biológicas disponíveis na literatura para espécies do gênero. Com base nesses dados são formuladas hipóteses sobre a vantagem do cuidado parental na colonização do ambiente cavernícola e sobre a evolução do comportamento gregário no gênero. O Capítulo 5 descreve a biologia reprodutiva de *Bourguyia albiornata,* um opilião que coloca os ovos na vegetação. Manipulações experimentais também foram conduzidas no campo para se avaliar a importância da fêmea na defesa dos ovos contra predadores. Esses dados foram comparados com aqueles obtidos para *G. longipes* no interior de cavernas a fim de se estabelecer quais são as pressões seletivas mais importantes favorecendo a manutenção do cuidado parental nos dois ambientes. No Capítulo 6 as informações sobre as formas de investimento parental obtidas na tese, aliadas aos dados disponíveis na literatura, são analisadas comparativamente a fim de se obter padrões comportamentais para cada uma das três subordens de Opiliones. Também são mapeadas as formas de investimento parental dentro da família Gonyleptidae e são feitas inferências sobre os processos que levaram à evolução das diferentes formas de investimento parental em opiliões como um todo.

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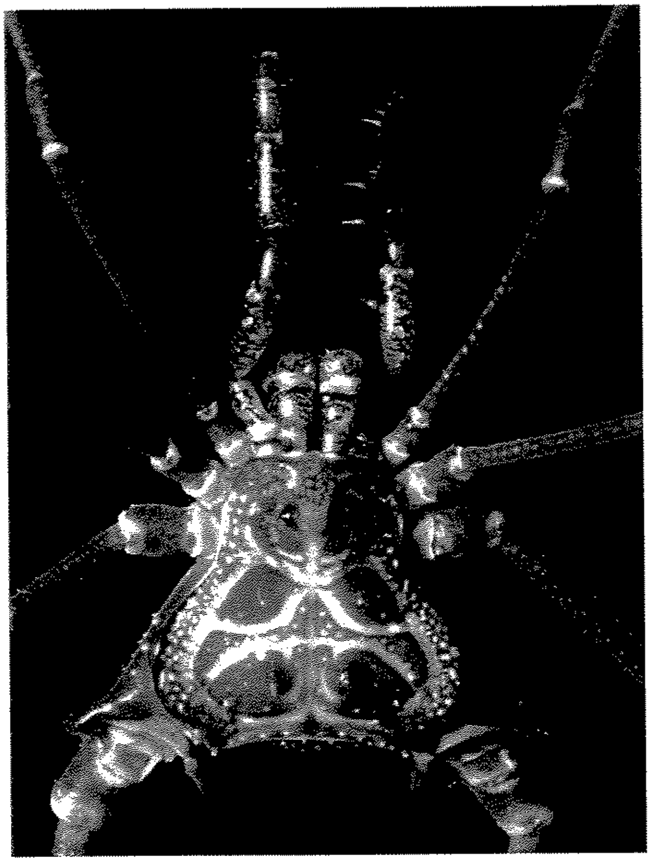
CAPÍTULO 1

Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida: Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care*



Macho de *Goniosoma longipes.*

*MACHADO, G. & P.S. OLIVEIRA. 1998. Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida: Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. *Journal of Zoology,* 246: 359-367.

1.1. Abstract

Goniosoma longipes is a Neotropical cavernicolous harvestman that exhibits parental care. Reproductive activity in *G. longipes* is more intense during the wet season. Mating lasts up to 3 min, and the whole oviposition process may take over 5 h. During oviposition the female may be reinseminated once or twice by the mating male. Females oviposit 60 - 210 eggs on the cave wall and guard egg batches for nearly two months, until the 1st-instar nymphs disperse. Four main factors can affect egg survival in *G. longipes*: dehydration, fungal attack, cannibalism, and interspecific predation. Frequency of fungal attack on egg batches was greater in the wet season and more intense near the river inside the study cave. Although egg-guarding by females failed to prevent fungal attack on eggs in *G. longipes*, the choice of a suitable oviposition site by the gravid female can reduce fungal attack within the cave habitat of this species. Guarding females successfully repel conspecific egg predators, but unguarded eggs are frequently consumed by adult and juvenile *G. longipes*, as well as *Strinatia* cave crickets. Field experiments in which females were removed from egg batches demonstrated that egg-guarding by the mother has an anti-predator role in *G. longipes*, with a significant positive effect on egg survival. Male *G. longipes* actively patrol their egg-guarding mates, and take over brood care for up to two weeks if the latter are experimentally removed. However, the degree to which male assistance can play a relevant role in parental care is still unclear for this species. Damage to brood is regarded as a major force favouring the evolution of parental care in harvestman species. This field study provides the first experimental demonstration that egg-guarding by females affords protection against egg predation in a harvestman species.

1.2. Introduction

Parental investment is defined by Trivers (1972: 139) as "any investment by the parent in individual offspring that increases the offspring's chance of surviving (and hence reproducti success) at the cost of the parent's ability to invest in other offspring". This may include investme by females in eggs, as well as incubation and egg-guarding, and the feeding of young by one or bo parents (Clutton-Brock, 1991). Parental care is present in all arachnid orders, but there a comparatively few well-documented cases for harvestmen (see Cloudsley-Thompson, 19 Klingel, 1963; Muma, 1966; Weygoldt, 1969, 1972; Pittard & Mitchell, 1972; Foelix, 1982; Pol 1990; Gnaspini, 1995). Maternal care in harvestmen has been reported for species from differe families around the world. In the neotropics, there are several records of maternal care for species the family Gonyleptidae (reviewed by Gnaspini, 1995). There is no record of biparental care harvestmen.

Harvestmen are generally nocturnal, vagile, photophobic and solitary omnivores (Savo 1938; Coddington *et al.*, 1990). The behavioural biology of harvestmen is poorly studie particularly for Neotropical species. Basic data about the natural history are scarce and scattered, a this hampers the formulation of testable hypotheses about their behavioural ecology. M harvestman species deposit a large number of eggs on a variety of substrates, such as soil, tru crevices, under stones, wood, foliage and other moist places (Cloudsley-Thompson, 1958). T most common reproductive mode in harvestmen involves copulation, although parthenogene may occur in some species (Phillipson, 1959; Tsurusaki, 1986). Mating in harvestmen is usually n preceded by courtship displays, but in some species the males may fight for access to femal (Berland, 1949) while in others the courtship is very simple (see Martens, 1969). The fertilization internal and females lay the eggs a few hours or days after mating (Juberthie, 1965).

The harvestman *Goniosoma longipes* (Gonyleptidae) commonly aggregates in sandstone a granitic caves in south-east Brazil (Gnaspini & Trajano, 1994). Foraging takes place outside t caves at night, and during the day many individuals are seen resting on the cave walls, which is al the preferred oviposition site. This paper provides a detailed field account of the behavioural biolo of *G. longipes* with special emphasis on reproductive seasonality, mating and oviposition behavio sources of brood mortality, and parental care. The study involves descriptions of harvestm behaviour, as well as field experiments designed to assess the relevance of parental care agai brood mortality caused by fungal attack, cannibalism, and interspecific predation.

1.3. Material & Methods

1.3.1. *Study area*

Field work was carried out in the Parque Florestal do Itapetinga (23°10'S, 46°25'W; altitude 1000 m), near Atibaia, State of São Paulo, south-east Brazil. The area is a microbasin formed by small perennial streams that flow on granitic and/or sandy beds. In some places the rivers are covered by large granitic rocks that form small caves. The climate has two well-defined seasons. The dry/cold season lasts from April to September, with mean monthly rainfall of 72 mm and temperature 17° C. Winter frosts are frequent, especially in June and July. The wet/warm season lasts from October to March, with mean monthly rainfall of 182 mm and temperature 21° C. The climatic data presented in this study was provided by the meteorological station of the Centro de Ensino e Pesquisa em Agricultura (Cepagri), located 11 km from the study site.

1.3.2. *Behavioural observations*

The reproductive biology of *Goniosoma longipes* was studied in a granitic cave (300 m long) crossed by a river (ca. 60 cm wide). Field observations were carried out weekly from August to November 1995, and at 7 - 14 day intervals from March 1996 to August 1997. Egg-guarding females of *G. longipes*, and the number of eggs per batch, were monitored during each census in the cave. Observations inside the cave were made with a flashlight covered by a red filter to avoid disturbing the organisms. Behavioural data on the harvestmen are based on more than 300 hours of field work.

Egg-guarding females of *G. longipes* (n = 69) were individually marked with coloured dots of enamel paint (Testors Co., Rockford, USA) on the dorsum of the cephalothorax and on the femur of one leg. The behaviour of females was apparently unaffected by this marking procedure (see also GNASPINI, 1995, 1996). The behaviour and mobility of marked females was evaluated by checking them, and their egg batches, at 1 hour intervals for periods of 3 - 8 hours. Continuous recording was made of all relevant behavioural events, such as a predator attack on eggs or agonistic interactions between individuals, as suggested by MARTIN & BATESON (1986).

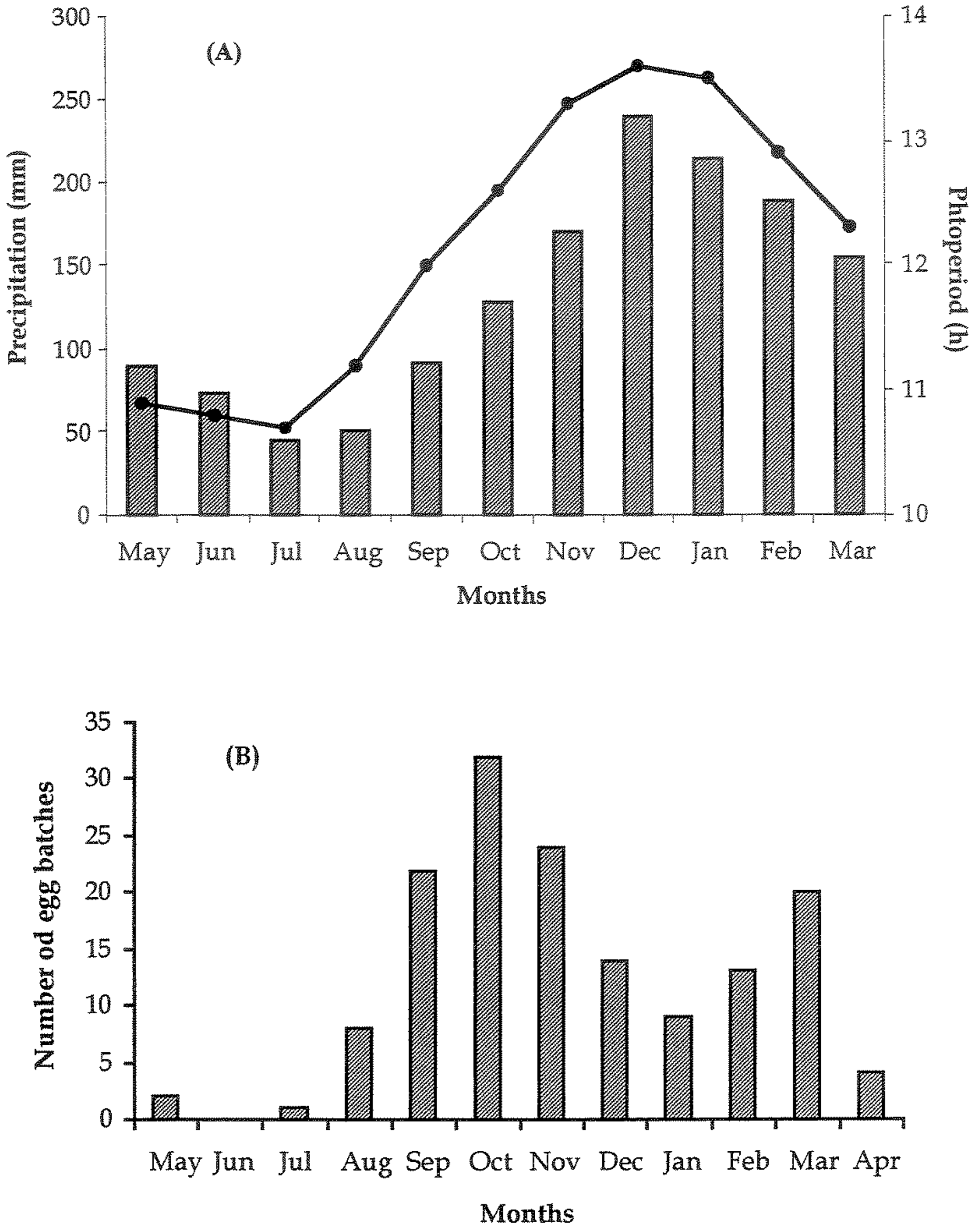


FIGURE 1. Climatic data (A) and reproductive activity (B) of *Goniosoma longipes* near Atibaia, sout east Brazil.

1.3.3. *Field experiments*

The effect of maternal care on egg survival was evaluated through field experiments in which the mother and/or eggs were kept isolated under 15 x 10 cm perforated plastic cages (3 cm high; 0.5 mm mesh), or the mother was removed from her uncaged brood. Four experimental groups were established (n = 10 egg batches per group): (a) guarding females and eggs caged (mean ± SD = 146.3 ± 9.1 eggs/batch); (b) guarding females removed, and eggs caged (142.5 ± 12.3 eggs/batch); (c) guarding females removed, and eggs left uncaged (154.4 ± 9.4 eggs/batch); (d) guarding females and eggs uncaged (139.7 ± 12.8 eggs/batch). There was no significant difference in initial egg numbers between treatments. Experimental egg batches were at initial developmental stages and undamaged, all under similar light and wind conditions within the cave. Experiments were carried out during the wet season, and lasted 14 days. Fungal attack on experimental batches of groups (a) and (b) was compared by performing Mann-Whitney *U*-tests on the percentages of fungus-infected eggs per batch on the 14th day (percent values were arcsin transformed). Groups (c) and (d) assessed the efficiency of maternal care against cannibalism by intruding *G. longipes*, and interspecific predation. After square-root transformations on the data, a repeated-measures ANOVA was performed on the number of eggs per batch before (day 1) and after (day 14) treatment.

1.4. Results

1.4.1. *Reproductive seasonality*

Sixty-nine egg batches of *Goniosoma longipes* were found in the cave from March 1996 to August 1997. Reproductive activity was much more intense during the wet/warm season (46 egg batches in 24 weeks) than during the dry/cold season (23 egg batches in 24 weeks) (FIGURE 1). The average number of eggs per batch also differed between the two seasons (wet/warm season: mean ± SD = 144.1 ± 33.9 eggs per batch; n = 42; dry/cold season: 113.2 ± 32.9 eggs per batch; n = 23; $t = -3.74$; DF = 63; $p < 0.001$). The number of egg batches per month is significantly correlated with mean monthly day length ($r_S = 0.706$; $p < 0.01$; $n = 12$) and rainfall ($r_S = 0.531$; $p < 0.05$; $n = 12$). During the wet/warm season, however, harvestman reproduction shows two distinct peaks: high in October and medium in March (FIGURE 1).

Females oviposit on the cave's granite walls, in chambers protected from external wind and light. Oviposition sites were 32 - 800 cm from the river crossing the cave (mean ± SD = 127.0 ± 95.5 cm; n = 88). Six females reproduced twice. The interval between ovipositions varied from 4 to 13 months, with the females laying similar numbers of eggs in the two reproductive events (fir oviposition 125.5 ± 25.1 eggs; n = 4; second oviposition 129.5 ± 46.3 eggs; n = 4).

1.4.2. *Mating and oviposition behaviour*

Oviposition in *G. longipes* occurs immediately after mating. Prior to copulation the ma approaches the female frontally and grasps her pedipalps with his pedipalps. Subsequently, bo raise the anterior portion of the body and mutually approach each other to place their ventral sid in contact. In this position the male everts his penis and penetrates into the female's genital orific The copulation process lasts 2 - 3 min (n = 2). The oviposition behaviour is stereotyped and ve similar to that described for other laniatorid harvestmen, and may last over 5 h (based on parti observations of 7 oviposition events). As the female lays the eggs, the male remains about 2 c behind her, waving his second pair of legs over her body and tapping her legs once in a while. T eggs are deposited on the substrate at regular intervals of about three min (3.2 ± 0.7 min; range = 1. 4.5 min; n = 13; see FIGURE 2). Occasionally the female interrupts the oviposition and touches t eggs with the second pair of legs. Even during the oviposition process the female may reinseminated once or twice by her mate. Many times (n = 20) mating males were observed to rema close to ovipositing females from 1 to more than 24 hours. One of such males copulated with h mate 5 hours after the termination of the oviposition process. On one occasion a satellite ma approached an ovipositing female, grasped her with his pedipalps and attempted to mate. T female responded by lowering the anterior portion of her body and directing her back towards t satellite male, who walked away as the female resumed oviposition. By end of the ovipositi process the resident male walked away, remaining 1.5 m from the female.

1.4.3. *Parental care*

All observed egg batches (n = 89) were guarded by one adult female, who may either sit on t eggs or remain next to the batch (FIGURE 3). Once in a while the guarding female touches the eg with the second pair of legs and also inspects the periphery of the egg batch. Although ma individuals of *G. longipes* leave the cave at night to forage, guarding females remain with their broo

Eggs of *G. longipes* change in colour and increase in size with maturation. Recently laid eggs a cream in colour and average 1.44 ± 0.09 mm in diameter (n = 20). The eggs darken with developme and become black just before hatching, when the average diameter is 1.91 ± 0.12 mm (n = 20). Eg are spaced out by 1 - 2 mm within the batch (FIGURE 3). Unfertilized eggs comprise up to 5.3% of t batch, and are easily recognizable by their creamish appearance amongst the darker fertilized eggs Unfertile eggs are not removed by the guarding female. Fertile eggs hatch in 45 - 64 d (53.1 ± 6.3; n = 32 batches), and 1st-instar nymphs remain aggregated with their mother for 7 - 14 d. During this period no egg or juvenile cannibalism has ever been observed within an egg batch. Maternal care towards eggs and nymphs may last 56 - 78 d (68.0 ± 7.8; n = 32 batches); the guarding female only leaves the oviposition site after all 1st-instar nymphs had dispersed.

After copulating with 2 - 5 females, males patrol for up to two months the area containing his mates and the egg batches (FIGURE 4A). On three occasions a male took over egg-guarding activities after the removal of the female from his reproductive area (FIGURE 4B, C). In these cases guarding males sit on the egg batch for up to two weeks, with no egg mortality being detected during this period. After male desertion, however, egg predators consume entirely the unguarded eggs (see below).

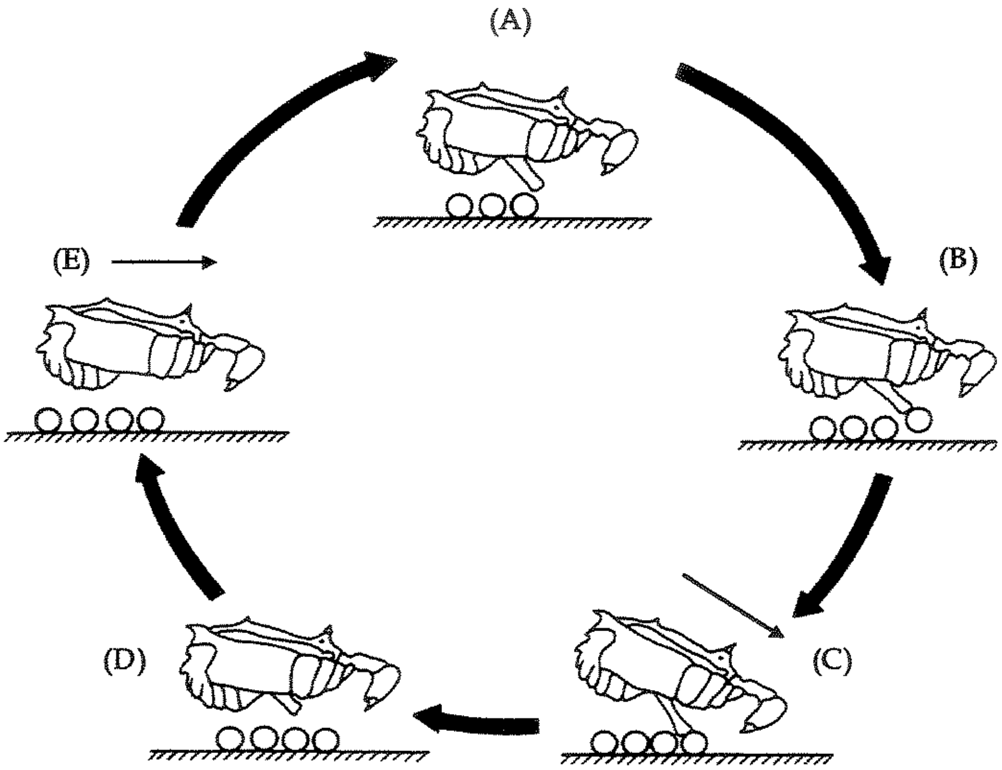


FIGURE 2. Schematic representation of the oviposition process of *Goniosoma longipes* (legs no drawn). (A) Female everts the ovipositor, (B) lays one egg, (C) lowers the anterior region of the body (D) retracts the ovipositor, (E) and moves forward to lay another egg.

1.4.4. *Sources of egg mortality*

Four main factors may affect egg survival in *G. longipes*: dehydration, fungal attac cannibalism, and interspecific predation. One dehydrated egg batch was found in April near th entrance of the cave, 8 m from the river. Although still guarded by the female, this batch had nearl 44% (47 of 107) of its eggs dried out.

Frequency of fungal attack on egg batches was greater in the wet (49.5%, n = 46) than in the dr season (16.6%; n = 23) ($\chi^2 = 22.8$; DF = 1; p < 0.001). The intensity of attack by fungi within batche ranged from 0.6% to 100% of the eggs, and did not differ between seasons (Mann-Whitney *U*-test, = 857.5; p = 0.314). On the other hand, the intensity of fungal attack on egg batches was negativel correlated with the distance between the batch and the river crossing the cave ($r_S = -0.231$; p < 0.02 n = 88). The average distance of the ovipositions from the river did not differ between the wet an dry season ($t = 0.74$; DF = 86; p = 0.46). Although fungus-infected eggs did not develop into juvenile guarding females of *G. longipes* did not eat or remove such eggs from their batches. Fungal attac within batches was apparently the same for fertilized and unfertilized eggs.

Conspecifics may attack eggs, even when these are guarded by females. Attack on eggs adult *G. longipes* was observed on six different occasions, and in every case the guarding fema successfully repelled the intruders. However, a reduction in the number of eggs of nine guarde batches suggests that the mother may occasionally fail to repel egg predators.

If the guarding female is experimentally removed (see below) the eggs can be cannibalized adult and juvenile *G. longipes*. Both male and female harvestmen may eat unguarded eggs, and single individual may consume 7 - 20 eggs of a batch (n = 9). Therefore, depending on the number attacks by conspecific harvestmen, entire egg batches can be destroyed by cannibalism in a sing night. On three occasions cave crickets (*Strinatia* sp., Phalangopsidae) were seen eating eggs fro unguarded batches (FIGURE 3; see below).

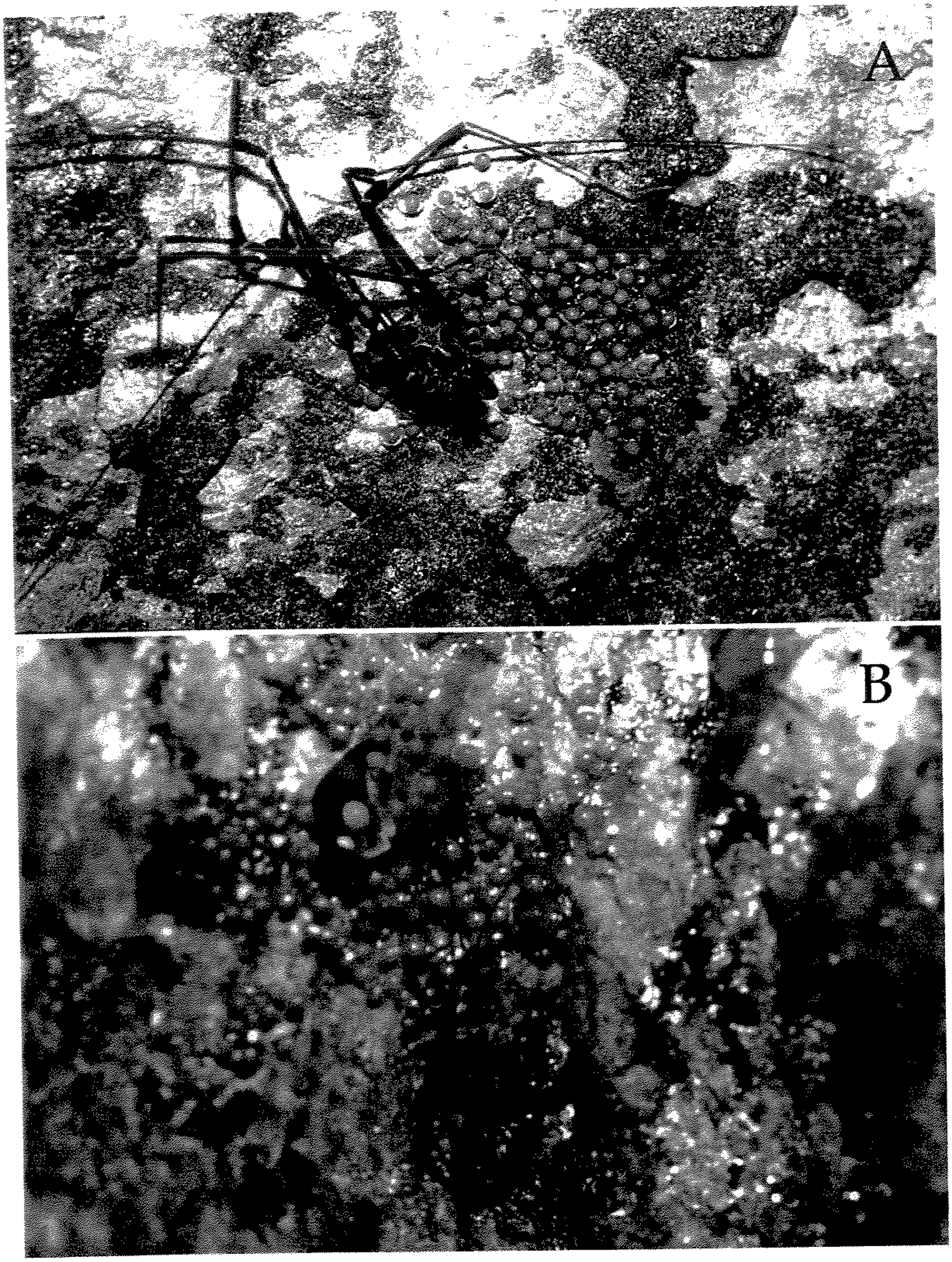


FIGURE 3. (A) Female of *Goniosoma longipes* (size ca. 1 cm) guarding her eggs on the wall of the study cave. (B) *Strinatia* cave cricket (size ca. 2 cm) feeding on unguarded eggs of *G. longipes*.

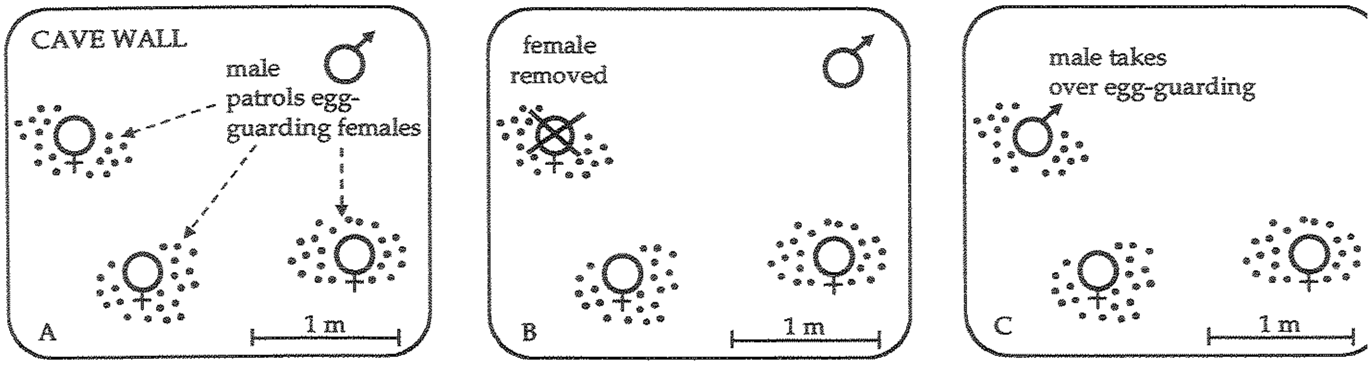


FIGURE 4. Schematic representation of male behavior toward females and eggs within its reproductive area on the cave wall. (A) Patrolling activity (dashed arrows) of a male of *Goniosom* *longipes* toward egg-guarding females. (B) Experimental removal of one female; eggs lef unguarded. (C) Male sits on the egg batch for up to two weeks. Organisms are not drawn to scale.

1.4.5. *Field experiments on parental care*

The results of the caging experiments revealed that egg-guarding by female *G. longipes* has n effect against fungal attack on the brood after two weeks (FIGURE 5). Similarly, guarding activity b the mother had no effect on fungal attack to uncaged egg batches (Mann-Whitney *U*-test, $U = 59.5$; p > 0.30). Although some eggs were attacked by fungi in caged batches with and without the mother no egg disappeared from batches in either experimental group. The experiments in which the mothe was removed from uncaged broods, however, revealed that guarding activity has a significan positive effect on egg survival. Less than 2% of the unguarded eggs survived the 2-week experimen (FIGURE 6). During this period, adult *G. longipes* (n = 2) and *Strinatia* cave crickets (n = 1; FIGURE 3 were seen preying on eggs at unguarded batches.

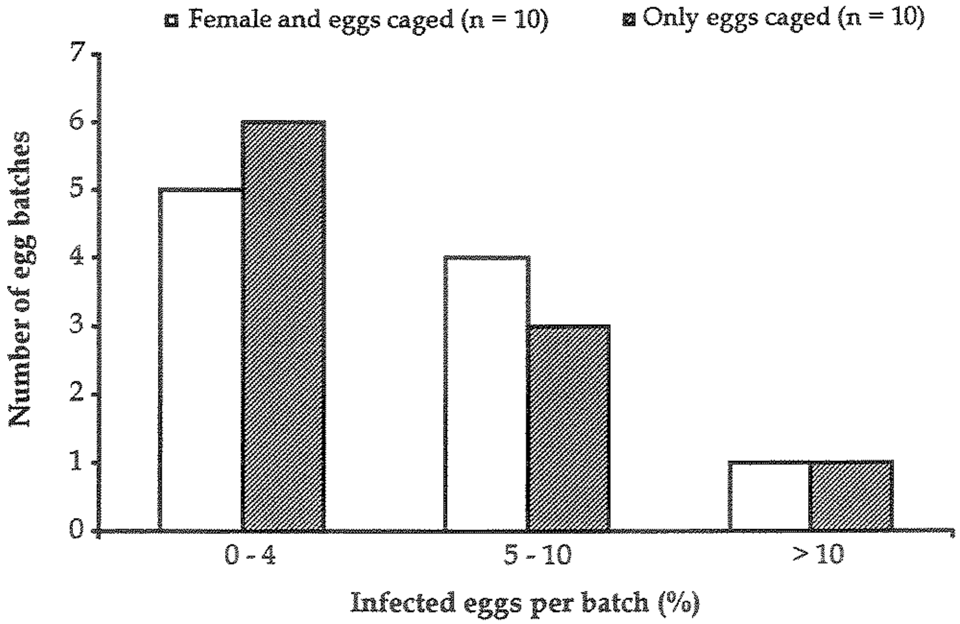


FIGURE 5. Intensity of fungal attack on caged egg batches of *Goniosoma longipes* after two weeks. Eg are equally attacked by fungi, irrespective of the presence of the mother (Mann-Whitney *U*-test, *U* 54; p = 0.757).

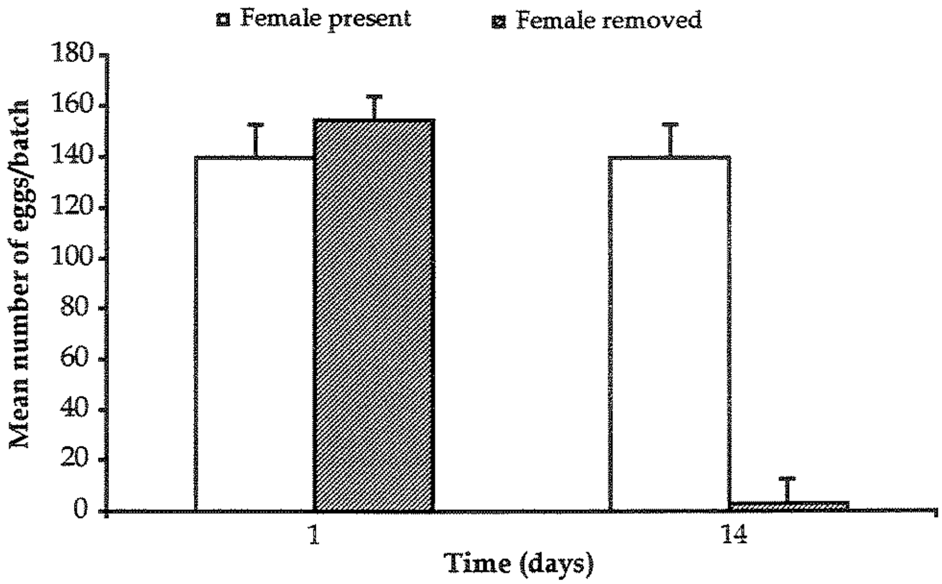


FIGURE 6. Effect of maternal care on egg survival in *Goniosoma longipes* after two weeks. E survivorship is significantly higher when batches are guarded by the female (Repeated measur ANOVA, $F_{1,18} = 455.27$; p = 0.0001).

1.5. Discussion

Life history patterns result from both evolutionary constraints and proximate responses of the organisms to specific environmental conditions (STEARNS, 1992). Therefore the biological activities of animal populations, including reproduction, can be closely linked to seasonal parameters such as temperature and rainfall, the latter being particularly important in tropical regions (OPLER *et al.*, 1976, WINEMILLER, 1989). Harvestman reproduction shows wide seasonal variation across different taxa Among neotropical laniatorids, some species have one (JUBERTHIE & MUÑOS-CUEVAS, 1971, COKENDOLPHER & JONES, 1991) or two annual reproductive peaks (GOODNIGHT & GOODNIGHT, 1976, GNASPINI, 1995), while others may reproduce steadily throughout the year (JUBERTHIE, 1972, MATTHIESEN, 1975). Reproductive activity in *Goniosoma longipes* is correlated with rainfall, showing two distinct peaks during the wet/warm season. Water absorption during egg maturation accounts for a 43% increase in egg volume. The importance of water for egg survival in *G. longipes* is further enhanced by the females' marked preference for moist oviposition sites within the study cave (see CHAPMAN, 1982), despite the increased risk of fungal attack at these locations.

The greater number of ovipositions in the beginning of the wet season (October) may represent a synchronization of the maternal investment in offspring with ideal conditions for hatching and juvenile growth during the peak of rainfall in January, when arthropod prey are more abundant (see WOLDA, 1978). The positive correlation between the number of egg batches and day length could suggest that reproductive activity in *G. longipes* is proximately adjusted by variations in the photoperiod, which is a good predictor of more favorable wet/warm conditions (CLOUDSLEY-THOMPSON, 1978, and citations within). Egg-guarding in *G. longipes* may last as long as 78 d, and during this period the female does not leave the brood to forage for food. However, as suggested by GNASPINI (1993) for *G. spelaeum*, an increased foraging activity by the ovigerous female prior to oviposition is possibly related with the storage of nutrients for the prolonged egg-guarding period, during which she will not feed.

Mating in most harvestmen species is usually fast (1 - 2 min) and without courtship, after which the mates leave the site and the female begins the oviposition (JUBERTHIE, 1965). However, in some laniatorid species such as *Zygopachylus albomarginis* (MORA, 1990), *Goniosoma spelaeum* (GNASPINI, 1995), and *G. longipes* (present study), the male remains close to the ovipositing female while waving his legs over the partner. GNASPINI (1995) speculated that this behaviour in *Goniosoma spelaeum* could have a protective role against predators, or function as a signal to promote egg laying. EDGAR (1971) has reported a similar behaviour for palpatorid *Leiobunum* spp. and suggest that leg-waving and tapping by the resident male could prevent the female from walking away a failing to oviposit. Although an ovipositing female would presumably be more vulnerable predation, we do not believe that male leg-waving per se would protect *Goniosoma* against predatc such as large arthropods, and marsupials (PINTO-DA-ROCHA, 1993; PELEGATTI-FRANCO & GNASPII 1996). Our observations with *G. longipes* indicate that a male may remain close to his mate for over h after insemination, and that during this period the female may be reinseminated once or twice the resident male. We also found no evidence that leg-waving by the resident male would de satellite males from inseminating the ovipositing female. In fact, our behavioral data on *G. longi* show that the resident male does not interact with approaching males, who are rejected by t ovipositing female herself (see also EDGAR, 1971). It is therefore possible that male leg-waving in *longipes* functions to prevent female desertion and/or stimulate oviposition, as suggested GNASPINI (1995) and EDGAR (1971). Alternatively, this behaviour in *G. longipes* could simp represent a relictual trait that had evolved in different ecological circumstances, with no adapti significance under the conditions currently faced by this species (see WANNTORP *et al.*, 1990).

The choice of appropriate oviposition sites can be crucial for offspring survival (CLUTTO BROCK, 1991). Among arthropod species, sites that have low moisture conditions and/or are subj to direct wind may negatively affect egg development and lead to dehydration (CHAPMAN, 198 Although cave habitats maintain relatively stable temperature and humidity conditions day a night (GAUTIER *et al.*, 1988), an increase of moisture levels during the wet/warm season make ca organisms considerably more vulnerable to fungal attack in this part of the year (CULVER, 198 Results with *Goniosoma longipes* in south-east Brazil support this view since a greater proportion egg batches was infected during the wet season.

Cannibalism is a common behaviour among many invertebrate taxa (ELGAR & CRESPI, 199 and among harvestmen there are some records of egg and juvenile cannibalism (CANALS, 19 CAPOCASALE & BRUNO-TREZZA, 1964; MORA, 1990; EDGAR, 1971). Because eggs are usually energ and nutrient-rich palatable food items (see ORIANS & JANZEN, 1974), they constitute a developmen stage particularly susceptible to interspecific predation and cannibalism when laid in unprotect sites and/or left unguarded by the parents (POLIS, 1981; CLUTTON-BROCK, 1991). Egg cannibalism *G. longipes* has two main advantages for foraging harvestmen. First, food can be obtained at a low energetic cost since there is no need to leave the cave for foraging. Second, it is probably a sa feeding strategy since outside the cave the foraging individual would be exposed to both an increased risk of predation and less favorable climatic conditions.

Our observations indicate that cave crickets and conspecific adults are the main egg predators of G. *longipes* in the study cave. Other predators known to prey on *Goniosoma* eggs also occur in the study site, and include the predatory reduviid bug *Zelurus travassosi* and the ctenid spider *Ctenus fasciatus* (GNASPINI, 1996). Ants are also reported to consume harvestmen eggs (MORA, 1990) and it is possible that *Odontomachus* ants (Ponerinae), which are commonly seen in the cave and usually have generalized feeding habits (BROWN, 1976), would occasionally feed on *Goniosoma* eggs.

Parental care, and more specifically egg-guarding, is known to reduce mortality of eggs in several arthropod taxa, including the Arachnida (TURNBULL, 1973; CLUTTON-BROCK, 1991; CASTANHO & OLIVEIRA, 1997). MORA (1990) has shown that egg-guarding by males in the harvestman *Zygopachylus albomarginis* significantly reduces egg mortality due to predation and attack by fungi. The current study with G. *longipes* demonstrated that maternal care is crucial for egg survival in this harvestman species. To our knowledge this is the first experimental demonstration of an anti-predator role of female egg-guarding in harvestmen. The caging experiments indicate that the mother does not consume her own eggs, and that egg-guarding prevents brood predation by conspecific harvestmen and *Strinatia* cave crickets. Although egg-guarding activity is known to prevent fungal attack on eggs in insects (SMITH, 1976a, b) and harvestmen (MORA, 1990), the field experiments with G. *longipes* demonstrate that the guarding female is unable to protect her eggs against attack by fungi (see also GOODNIGHT & GOODNIGHT, 1976).

Maternal care has already been reported for many harvestman species from different families (see GNASPINI, 1995). Paternal care is extremely rare among arachnids, and the only documented cases come from three harvestman species (RODRIGUEZ & GUERRERO, 1976; MORA, 1990; MARTENS, 1993). There is no record of biparental care in harvestmen. Although GNASPINI (1995) found pairs of *Goniosoma spelaeum* near the eggs, male egg-guarding has never been reported for this species. The current study shows that males of G. *longipes* actively patrol the area containing their mates and the egg batches. By removing one egg-guarding female from a male's reproductive area we also showed that the latter can take over egg-guarding activities (FIGURE 4), and prevent brood predation for up to two weeks (n = 3 males). This finding suggests that males can exert brood care in this species if the egg-guarding females deserts or dies. Although egg-guarding by the male lasts only a few days, temporal paternal care can be crucial for brood survival (especially just before hatching), since egg predators can consume entire batches in a single night.

Damage to brood caused by fungal infection and predation are regarded as major forc favouring the evolution of parental care (Wilson, 1975), especially in harvestmen (Goodnight Goodnight, 1976; Mora, 1990). Although egg-guarding failed to prevent fungal attack on eggs in *longipes*, the field experiments showed that the guarding mother effectively increases offspri survival by deterring potential egg predators. The degree to which male assistance with eg guarding can play a relevant role in parental care is still to be experimentally assessed for th species.

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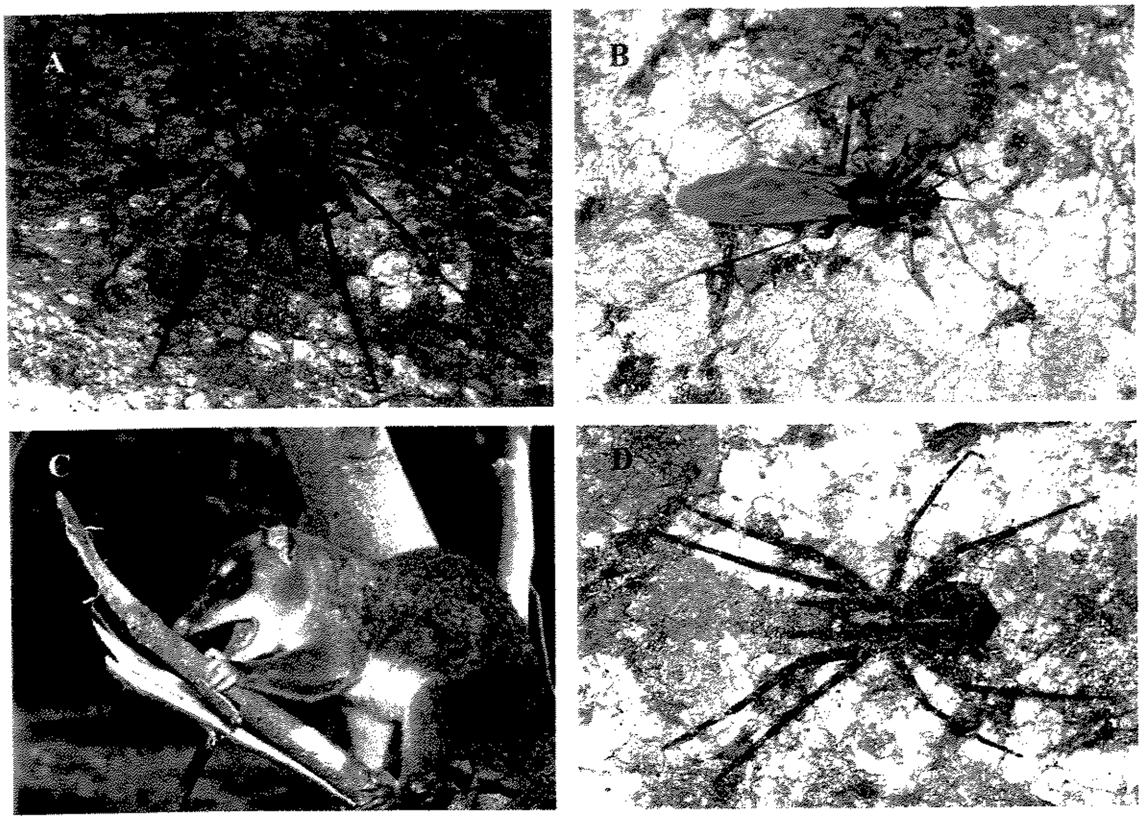
CAPÍTULO 2

Daily activity schedule, gregariousness, and defensive behaviour in the Neotropical harvestman *Goniosoma longipes* (Opiliones: Gonyleptidae)*



(A) Fêmea da aranha *Ctenus fasciatus*; (B) Adulto do hemíptero *Zelurus travassosi*; (C) Macho adulto da cuíca *Philander opossum*; (D) Fêmea da aranha *Enoploctenus cyclotorax*.

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2.1. Abstract

In this paper we provide a field account of some aspects of the behavioural biology of *Goniosoma longipes* (Roewer), a harvestman which commonly occurs in caves in Southeast Brazil. During daytime, solitary and aggregated individuals can be found resting on the cave walls. Just after sunset, however, many individuals leave the cave to forage for live and dead arthropods. Foraging individuals return to the cave before dawn. Aggregations of *G. longipes* contain on average 34 individuals (range 7 - 200), and the groups are usually found close to the water source and away from the cave entrance. The main predators of *G. longipes* are the spider *Ctenus fasciatus* Mello-Leitão (Ctenidae) and the opossum *Philander opossum* (L.) (Didelphidae). Upon disturbance solitary and aggregated individuals may either flee, or drop from the cave wall or vegetation. The harvestmen can also release a repugnatory liquid upon manipulation, and aggregated individuals collectively discharge this secretion toward the aggressor before fleeing. The activity schedule of *G. longipes* shows that individuals need to leave the cave periodically to forage, and therefore the population can be considered trogloxene. Data on the food items collected by *G. longipes* indicate that the harvestman is a generalist predator which also feeds on dead animal matter. Gregarious behaviour is considered relatively common among harvestmen and has been interpreted in several ways. We suggest that gregarious behaviour in *G. longipes* may be related with the choice of more suitable microconditions in the cave habitat and/or with group chemical defence.

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biology of G. *longipes* such as daily foraging schedule, gregarious behaviour, and defensive tactics.

2.3. Materials & Methods

2.3.1. *Study area*

Fieldwork was carried out in the Parque Florestal do Itapetinga (23° 10′ S; 46° 25′ W), near Atibaia, São Paulo State, Southeast Brazil. The area is a microbasin formed by small perennial streams (approximately 60 cm wide) that flow on granitic and/or sandy beds. In some places the rivers are covered by large granitic boulders that form small caves. The local climate has two well-defined seasons. The dry/cold season lasts from April to September, with mean monthly rainfall of 72 mm and temperature 17 ° C. Winter frosts are frequent in June and July. The wet/warm season lasts from October to March, with a mean monthly rainfall of 182 mm and temperature 21° C.

2.3.2. *Behavioural observations*

The biology of *Goniosoma longipes* was studied in two granitic caves (30 m and 300 m long) crossed by rivers. Preliminary field data were taken weakly from August to November 1995. Further data were regularly taken at 7 - 14 day intervals from March 1996 to June 1998, totalling over 500 hours of fieldwork. The observations inside the caves were made with a flashlight covered by a red filter to avoid disturbing the organisms. Rare events, such as the attack by predators, were recorded continuously, following the procedure suggested by MARTIN & BATESON (1986).

We considered an aggregation any group of at least three harvestmen whose legs were overlapping (FIGURE 2). All individuals found aggregated were measured for dorsal scutum length and sexed. We also measured the distance of the aggregates from the river and from the cave entrance. All harvestmen from five aggregations were individually marked with different colour codes on the dorsal scutum with enamel paint (Testors Co., Rockford, USA). Nocturnal observations were made outside the caves, where we searched for individuals with prey items. While manipulating or collecting the harvestmen, we recorded all the behavioural responses of the individuals, such as attempts to escape, and the discharge of odoriferous secretions.

The activity schedule of *G. longipes* was quantified at 2 h intervals during a 24 h period (01 - 02 May 1998). Sampling at each interval consisted of counting during 30 min the number of individuals leaving or entering the cave, as well as those stationary at the cave entrance. The routes taken by foraging harvestmen in the cave were also recorded.

Voucher specimens of *G. longipes* are deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

2.4. Results

2.4.1. *Foraging and activity schedule*

During daytime, individuals of *Goniosoma longipes* can be found resting in the caves either isolated or forming stationary aggregations. In the afternoon, approximately 1 hour before dusk, the aggregations disperse and the individuals move toward the entrance of the cave, where they remain stationary until complete darkness. Many individuals leave the cave in the first hour after sunset, although the harvestmen are also seen abandoning the cave up to four hours after dusk (FIGURE 1). Brood carrying females, however, never leave the cave to forage (see MACHADO & OLIVEIRA, 1998).

The vast majority (97%) of foraging harvestmen (n = 54) used two trails when leaving or returning to the cave. At night, most of the individuals were found motionless in the external environment, clinging on the vegetation and with the second pair of legs extended sideways. Some individuals were seen walking slowly, rubbing the substratum with the second pair of legs. Marked harvestmen were found up to 70 m from the cave. *Goniosoma longipes* feed mainly on live or dead arthropods and on other organisms with little sclerotized skin (TABLE 1). The food item is usually captured with a fast movement by the harvestman's pedipalps, and seized by the chelicerae. The prey can either be consumed on the spot (n = 3), or carried into the cave (n = 5). Some individuals (adults and juveniles) remaining in the cave can prey on conspecific eggs (see MACHADO & OLIVEIRA, 1998). The return of the foraging individuals to the cave peaked 1 hour before dawn (FIGURE 1). Two hours after dawn the harvestmen regrouped in the cave.

TABLE 1. Food items caught by individuals of *Goniosoma longipes* at Parque Florestal do Itapetinga, Southeast Brazil. Prey presenting clear signs of decay were categorised as dead items.

Food Item	Number of Items
	Dead/Alive
ANNELIDA	
Hirudinea	1 / 0
Oligochaeta	0 / 1
ARACHNIDA	
Opiliones (Gagrellinae)	1 / 0
INSECTA	
Diptera (Tipulidae)	0 / 1
Hymenoptera (Formicidae)	1 / 0
(Vespidae)	1 / 0
Lepidoptera (adult moth)	2 / 1
(larvae of moth)	0 / 1
Orthoptera (leg fragments)	1 / 0
Insect remains wrapped in silk	1 / 0
TOTAL	8 / 4

2.4.2. *Gregarious behaviour*

The aggregations of *G. longipes* consisted of groups of motionless individuals 0 - 5 cm apart from each other, and with legs widely overlapping (FIGURE 2). The groups contained on average 34.2 individuals (SD = 38.1; range = 7 - 200; n = 30), and were formed by adults and juveniles. The mean sex ratio in the aggregations was female-biased (1.8 ± 1.5; range = 0.3 – 5.3; n = 28). Harvestmen aggregated on the exposed cave wall (78%) or inside breaches (22%; n = 30). The groups were usually close to a water source such as the cave river or a dripping fissure (2.8 ± 2.1 m; range = 0.9 - 8.0 m; n = 28), and away from the cave entrance (6.2 ± 2.5 m; range = 1.5 - 9.0 m; n = 28). Although harvestman aggregations can remain in the same site for up to four months (n = 2), on one occasion a group moved closer to the cave river during the peak of the 1996 dry season (June to September). Aggregations were never found on the cave ceiling or on the floor.

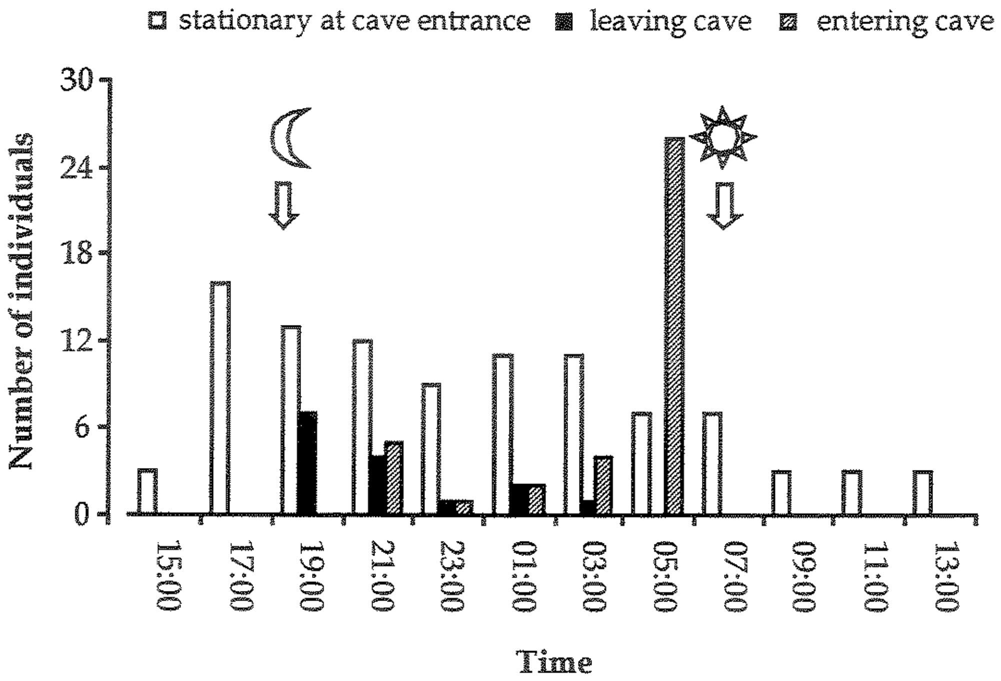

FIGURE 1. Activity schedule of *Goniosoma longipes* at Parque Florestal do Itapetinga, Southeast Brazil. The moon and the sun indicate dusk and dawn, respectively.

2.4.3. *Predators and parasites of* **Goniosoma longipes**

The spider *Ctenus fasciatus* MELLO-LEITÃO (Ctenidae) was twice seen feeding on juvenile *G. longipes* (3rd and 5th instars). Foraging activity by the opossum *Philander opossum* (L.) (Mammalia: Didelphidae) inside the caves was usually nocturnal. *Goniosoma* fragments were found both in the stomach contents of one opossum collected in the study area, as well as in two faeces found inside the caves.

Individuals of *G. longipes* were frequently infected by fungi on the dorsal scutum. Fungal attack was mostly directed toward the eye mound (n = 13) and the region between coxae I and III (n = 6). A detailed inspection of two preserved harvestmen revealed that the fungus is saprophytic since it does not penetrate the cuticle. In the laboratory we also recorded the death of one adult female parasitised by four dipteran larvae.

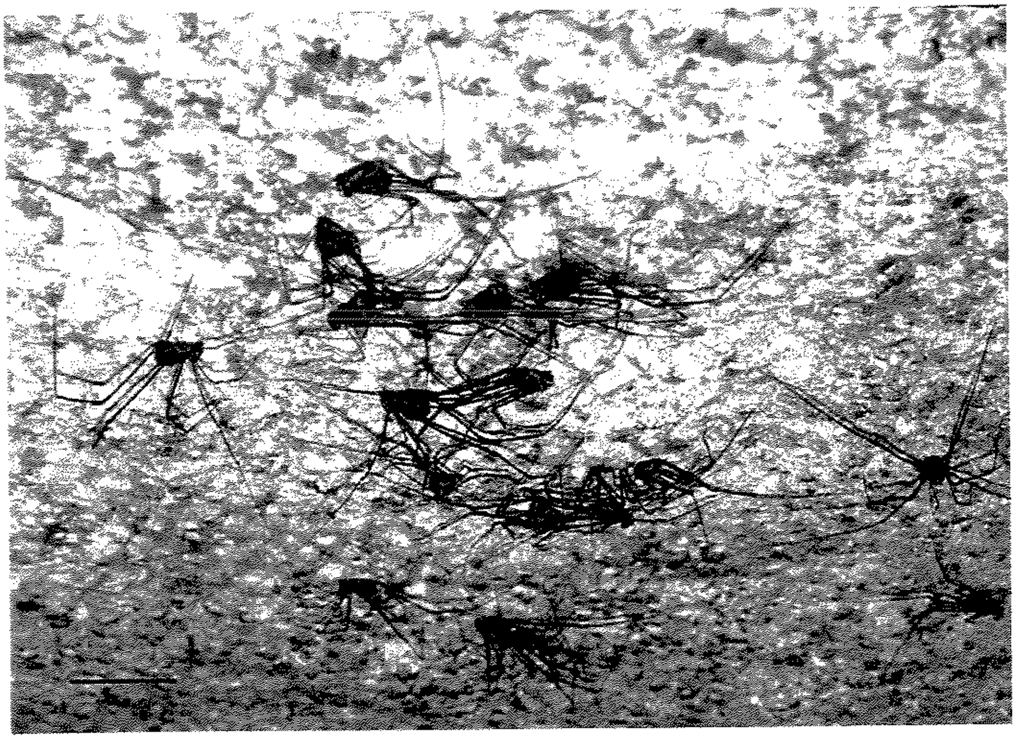

FIGURE 2. Small aggregation of *Goniosoma longipes* on a cave wall at Parque Florestal do Itapetinga, Southeast Brazil. Note the overlapping of legs. Scale bar = 2 cm.

2.4.4. *Defensive behaviour*

The most common defensive behaviour of solitary and aggregated individuals of *G. longipes* was to flee when disturbed. For instance, two females of the spider *Enoploctenus cyclothorax* (BERTKAU) (Ctenidae) were seen attacking adult males of *G. longipes*. On both occasions the harvestmen escaped by fleeing. BRISTOWE (1925) also described a defensive behaviour in *G. longipes* in which the harvestman, when handled by the 4th pair of legs, moves vigorously femur IV so as to promote a pinch between the sharp projections of the femur and trochanter IV. Attacking with the pedipalps before seizing or pinching the aggressor was very common. These two types of mechanical defensive behaviours were observed more frequently in adult males. Another common behaviour upon disturbance was to fall from the wall or vegetation to the ground. In this case the harvestman quickly hides under stones and/or stays motionless (feigning dead) during some time, as also recorded for *G. spelaeum* (MELLO-LEITÃO) (GNASPINI & CAVALHEIRO, 1998), and many Cosmetids (EISNER *et al.*, 1978; KAESTNER, 1980). Brood-guarding females frequently exhibit this behaviour.

Finally, individuals of *G. longipes* can release a repugnatory liquid upon manipulation. Aggregated harvestmen collectively discharge this secretion before fleeing (n = 28 aggregations). The repellent liquid is released in drops, or sprayed directly toward the aggressor. In the first case a large transparent drop slips along the lateral area of the scutum, runs by capillarity in tegumentary grooves, and accumulates in the posterior portion of the body (enteric fluid). If persistently disturbed, a second fluid can also be secreted by the repugnatorial glands which adds to the previously colourless fluid a yellowish coloration and a characteristic sour smell. The mixture of these secretions promotes red stains on human skin. Overall, the delivery of the defensive secretions in *G. longipes* occurs much in the same way as described by ACOSTA *et al.* (1993) for the other gonyleptid *Pachyloidellus goliath* ACOSTA.

2.5. Discussion

Harvestmen generally hide in wet and dark sites during daytime (CAPOCASALE & BRUNO-TREZZA, 1964; ANURADHA & PARTHASARATHY, 1976) and many species are photophobic (SAVORY, 1938). The conditions of moisture and temperature tend to be highly constant in cave habitats (GAUTIER *et al.*, 1988). At night, humidity at ground and vegetation level increases and allows harvestmen to leave their shelters and extend their foraging range (PHILLIPSON, 1960). The activity rhythm displayed by *G. longipes* shows that the individuals use the cave as shelter and reproductive site (see MACHADO & OLIVEIRA, 1998) but need to leave the cave periodically to forage at night. Therefore the studied population can be considered trogloxene and not an occasional user of the cave habitat.

The traffic from and toward the cave by *G. longipes* seems to be influenced by the photoperiod since the harvestmen leave the cave just after dusk and return before dawn. Such a daily activity pattern is also reported for many cavernicolous bat species (KUNZ, 1982). Foraging individuals of *G. longipes* use the same route within the cave, both when entering or leaving the shelter. A similar behaviour was also reported for G. *spelaeum* (GNASPINI, 1996) and field experiments are needed to test if route fidelity in *Goniosoma* is mediated by chemical cues or if the harvestmen have a spatial memory of the trail, or both.

Harvestmen apparently do not have specialised predators but can be eaten by spiders, heteropterans and several vertebrates such as toads, lizards and mammals (BRISTOWE, 1949; EDGAR, 1971; GNASPINI, 1996). However, PELLEGATI-FRANCO & GNASPINI (1996) showed that the cavernicolous harvestman G. *spelaeum* is an important item in the diet of the opossum *P. opossum* throughout the dry/cold season in south-eastern Brazil. In the same region, *Goniosoma* aff. *badium* (PINTO-DA-ROCHA, 1993) and G. *spelaeum* (GNASPINI, 1996) were often seen being eaten by the assassin bug *Zelurus travassosi* (COSTA-LIMA) and the spider *Ctenus fasciatus*. Although these three predators were also seen in the caves of our study area, we only observed one entire event of predation. A possible explanation for this fact is the low density of invertebrate predators in the caves. Moreover the hunting activity of the opossum in the caves occurs mainly at night and in this period the observations were focused on the behaviour of *G. longipes* in the external environment. Another possible predator of *G. longipes* present in the study area is the large spider *Enoploctenus cyclothorax*, which was seen attacking the harvestman.

Harvestmen are usually considered as predators or scavengers (BERLAND, 1949; BRISTOWE, 1949; CLOUDSLEY-THOMPSON, 1958; see review in GNASPINI, 1996). According to our field observations, *G. longipes* is a generalist predator, which can also feed on dead animal matter. The insect remains wrapped in silk (see TABLE 1) may suggest food robbing from spiders. Food robbing has already been described for a *G. longipes* female, which was seen stealing a moth prey from the large spider *Enoploctenus cyclothorax* (SABINO & GNASPINI, 1999). Contrary to *G. spelaeum* which feeds outside the cave (GNASPINI, 1993), *G. longipes* may consume its prey on the spot or carry it into the cave prior to ingestion. CAPOCASALE & BRUNO-TREZZA (1964) described a similar behaviour for the harvestman *Acanthopachylus aculeatus* (KIRBY) (Laniatores: Gonyleptidae), which also transports prey into the shelter before consumption. This strategy possibly protects foraging harvestmen from predation and kleptoparasitism.

Harvestmen may exhibit a number of defensive and evasive traits when disturbed (DUFFIELD *et al.*, 1981; ACOSTA *et al.*, 1993). For members of the suborder Palpatores leg autotomy is considered the most frequent and efficient defensive behaviour (ROTH & ROTH, 1984). Fleeing is also relatively common in species of long-legged harvestmen, such as the Palpatores and several Laniatores (BRISTOWE, 1925; EDGAR, 1971). Although autotomy has not been recorded for *G. longipes*, fleeing and falling from the cave wall were very frequently exhibited by isolated and aggregated individuals when disturbed by light. On the other hand, physical disturbance usually provokes the discharge of repellent secretions by *G. longipes*. Field and captivity observations suggest that the repugnatory secretion can deter predators such as ants (CAPOCASALE & BRUNO-TREZZA, 1964; DUFFIELD *et al.*, 1981), and in some Laniatores the fluid is also a powerful antibiotic against bacteria, protozoa and fungi (ESTABLE *et al.*, 1955; see also

COKENDOLPHER, 1993). The defensive role of these secretions in *G. longipes* is still to be experimentally assessed.

The role of harvestmen secretion for intraspecific communication is unclear. WAGNER (1954) suggests that the secretion acts as an aggregation pheromone, but there is no evidence supporting this hypothesis. HOLMBERG (1983), suggests that the secretion produced by the harvestmen serves as an alarm pheromone. Field observations with *G. longipes* apparently support this hypothesis, since the collective fleeing is preceded by the discharge of the fluid.

Gregariousness has already been described for many species of Palpatores (ANURADHA & PARTHASARATHY, 1976; CODDINGTON *et al.*, 1990; COCKERILL, 1988 and included references), but there are few records of gregarious behaviour among Laniatores. In Brazil there are reports of gregariousness in *Goniosoma* aff. *badium* (9 - 34 individuals; PINTO-DA-ROCHA, 1993), *G. spelaeum* (P. GNASPINI, *pers. comm.*), and in *Despirus montanus* MELLO-LEITÃO, *Holoversia nigra* MELLO-LEITÃO and *Eugyndes* sp. which form multi-species aggregations (5 - 35 individuals; MACHADO & VASCONCELOS, 1998). Although gregarious behaviour is considered relatively common among harvestmen (CODDINGTON *et al.*, 1990), little is known about its ecological meaning. According to HOLMBERG *et al.* (1984) this behaviour has been interpreted in several ways. The first interpretation is that harvestmen groups result from many individuals choosing places with decreased risk of dehydration and low exposure to light. The aggregations of *G. longipes* were found close to a water source, in complete darkness, and protected from wind - which seems to support this suggestion. Therefore the common choice of a suitable site within the cave probably favours gregariousness in *G. longipes*. Females of *G. longipes* also prefer similar sites for oviposition (MACHADO & OLIVEIRA, 1998).

A second hypothesis states that the overlapping legs of compactly aggregated individuals reduce air movement and consequently decreases evaporation and dehydration. Aggregations of *Leiobunum paessleri* (ROEWER) (Palpatores: Leiobunidae) form a compact mass (2.5 individuals/cm^2) which probably reduces the air flow between individuals in the group (HOLMBERG *et al.*, 1984). Since aggregations of *G. longipes* have a low density of individuals (0.013 ind./cm^2), and do not form a compact mass as in *L. paessleri*, it is very unlikely that the aggregate can block air flow or retain humidity between the harvestmen.

Another hypothesis suggests that gregariousness increases the defensive ability against predators by the collective action of the repulsive fluid secreted by the group (HOLMBERG *et al.*, 1984). The behavioural data on *G. longipes* support this suggestion since the aggregated individuals immediately discharge the repugnatorial fluid upon physical disturbance. The gregarious harvestman *Pachyloidellus goliath* (Laniatores: Gonyleptidae) also discharges a repugnatorial liquid when the group is disturbed (ACOSTA *et al.*, 1993). A fourth hypothesis states that harvestman aggregation would have a mating function (HOLMBERG *et al.*, 1984), but this is unlikely for *G. longipes* since the mating pairs in this species are formed in isolation (MACHADO & OLIVEIRA, 1998).

Finally, it is also possible that gregariousness may decrease the individual risk of predation through a dilution effect (*sensu* KREBS & DAVIES, 1987; see also MACHADO & VASCONCELOS, 1998). Our results suggest that gregarious behaviour in *G. longipes* may be related to the choice of more suitable microconditions in the cave habitat and/or with group chemical defence. Further experiments are needed to assess the ecological meaning of gregariousness across different harvestman species.

2.6. Acknowledgements

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CAPÍTULO 3

Alarm communication: a new function for the scent gland secretion in harvestmen (Arachnida: Opiliones)*

Vista de um riacho de interior de mata na Ilha do Cardoso onde são encontrados muitos indivíduos de *Goniosoma* aff. *proximum*.

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*MACHADO, G.; V. BONATO & P. S. OLIVEIRA. Alarm communication: a new function for the scent gland secretion in harvestmen (Arachnida: Opiliones). *Naturwissenschaften*, submetido.

3.1. Abstract

Most harvestmen are nocturnal, nonacoustical, and nonvisual arthropods. They have a pair of exocrine glands on the cephalothorax that produce defensive volatile secretions. We investigated in the field the possible alarm effect of these secretions in the gregarious harvestman *Goniosoma* aff. *proximum*. One cotton swab soaked with the species' own exudate (treatment), or with water (control), was held 1-2 cm from the center of harvestmen aggregations. Experimental results show that the gland secretion elicits an alarm response in *Goniosoma*: while 73.3% of the aggregations dispersed after being stimulated with the gland exudate, only 3.3% responded to the water control. Respondent groups are larger than non-respondent ones, and the time of reaction to the secretion was inversely related with group size. This is the first demonstration of a chemically-mediated alarm effect in harvestmen. The alarm response in gregarious harvestmen has possibly evolved as a by-product of a primarily defensive reaction under the context of predator avoidance.

3.2. Introduction

Over half of all terrestrial arthropod orders contain species that use chemical deterrents for defense. Most of these products are secreted by exocrine glands and are often complex mixtures that serve multiple roles (BLUM, 1981). In fact, for many arthropods, compounds that were once believed to be primarily defensive have been subsequently found to function parsimoniously as chemical signals associated with intraspecific communication (WHITMAN *et al.*, 1994). Such signals are known as pheromones (*sensu* KARSON & LÜSCHER, 1959)., and may be used in a variety of contexts, including sexual, gregarious, alarm, or territorial behavior (BLUM, 1985).

The species of the order Opiliones are characterized by a pair of exocrine glands located at the anterior margins of the cephalothorax near the base of the second pair of legs (SHULTZ, 1990). These glands produce a variety of volatile secretions that are released under the threat of predation (EISNER *et al.*, 1971; ACOSTA *et al.*, 1993; MACHADO *et al.*, 2000). Most harvestmen are nocturnally active, nonacoustical and nonvisual, and have a long slender second pair of antenniform legs. The combination of these features suggests that chemical signals could be important for intraspecific communication in those animals.

BISHOP (1950) was the first to suggest that the scent-gland secretions in harvestmen could be used for intraspecific communication and proposed that individuals could deposit chemical signals on the ground as trail markers. It has also been suggested that such secretions could be used for sexual recognition or attraction pheromone (HOLMBERG, 1986). However this hypothesis is unlikely since other glandular structures (on the chelicerae and legs) have been found that serve these functions (MARTENS & SCHAWALLER, 1977; MARTENS, 1979). Moreover there is no chemical difference between the secretions from males and females (MEINWALD *et al.*, 1971), as would be expected if the substances had a sexual role (BLUM, 1985).

Many harvestmen species show gregarious habits and form dense diurnal aggregations consisting of nymphs and adults of both sexes (COCKERILL, 1988; MACHADO *et al.*, 2000 and included references). There is evidence suggesting that gregariousness may be related with the choice of suitable microconditions and/or with group defense (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). WAGNER (1954) postulated that harvestmen are attracted to aggregation sites by the scent of odoriferous glands. However, it is also possible that the secretion could be used in the opposite way, eliciting an alarm response upon disturbance of the group. Indeed group living is a prerequisite for the evolution of alarm signals, and these substances have been identified in many gregarious species of treehoppers, aphids, true bugs, water striders, and social insects, such as termites, wasps, bees, and ants (BLUM, 1969; HÖLLDOBLER, 1977). In these groups, chemical alarm signals are generally perceived by multiporous sensilla located on the antennae and may result in attack or dispersion (BLUM, 1985). Moreover, the propensity to respond to the alarm signal increases with group size (VULINEC, 1990). With the exception of the Acari (NOGUCHI *et al.*, 1998), chemically-mediated alarm signals have not been discovered in any other major group in the Arachnida.

Species of harvestmen in the Neotropical genus *Goniosoma* are highly gregarious, and normally take shelter inside caves, rock crevices, and tree trunks (PINTO-DA-ROCHA, 1993; GNASPINI, 1996; MACHADO & OLIVEIRA, 1998; MACHADO *et al.*, 2000). Chemical studies have shown that the secretions produced by *Goniosoma* are mainly quinones (GNASPINI & CAVALHEIRO, 1998), widespread predator deterrents among arthropods (BLUM, 1981). In *G.* aff. *proximum*, the chemical composition of the repugnatorial secretion consists of two pairs of isomers of alkyl-1,4-benzoquinones (MW 136 and 150; G. MACHADO & J.R. TRIGO, unpublished data). In this study we address three questions: (1) does the defensive secretion produced by *G.* aff. *proximum* elicit an alarm response in aggregated individuals? (2) are respondent groups larger than non respondent ones? (3) is there a direct relation between aggregation size and time of response?

3.3. Material and Methods

Fieldwork was carried out in the rainforest of Cardoso Island (25° 18′ S; 48° 05′ W), South coast of São Paulo state, SE Brazil, from January to July 2000. Field observations and experiments were conducted during daylight in a 2-km transect along a 6-m wide stream. Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP), Brazil.

We considered as an aggregation any group of at least three harvestmen whose legs were overlapping (MACHADO *et al.*, 2000). The role of the defensive secretion in alarm communication was evaluated through a field experiment in which aggregations of *G.* aff. *proximum* were exposed to the species' own gland exudate (treatment), or to water (control). Aggregations were randomly designated by the flip of a coin as treatment or control. Immediately before each trial two previously collected individuals of *G.* aff. *proximum* were milked of secretion by seizing them by hand. The fluid that oozed from the harvestmen' glands was then deposited on a cotton swab (20 cm long). The tip of the cotton swab, the point of emission of the evaporating secretion, was held 1-2 cm from the center of an aggregation of harvestmen resting on the rock surface (n = 30 aggregations; FIGURE 1). The same procedure was repeated using a cotton swab wetted in distilled water as control (n = 30 aggregations). A new cotton swab was used in each trial of either experimental group, and no harvestmen aggregation was tested more than once. Since repeated milking of the same 'source individuals' could reduce the concentration of the chemical compound secreted, two new unmilked harvestmen were used for each trial.

The behavior of the individuals was recorded within 60 s after the presentation of the swab. Aggregations were categorized in two behavioral groups: (i) individuals in the 'respondent' group abandoned the resting location, and ran away at least 50 cm from the periphery of the aggregation; (ii) individuals in the 'non-respondent' group remained motionless during and after the trial. The number of individuals of all tested aggregations were counted both before and after each trial. Since it is not easy to distinguish or define alarm in a bioassay (BILLEN & MORGAN, 1998), we adopted the concept of "panic alarm" proposed by WILSON & REGNIER (1971) in which respondent animals present excited bursts of nondirectional running.

3.4. Results and Discussion

The mean number of *Goniosoma* individuals per aggregation was 19.45 ± 18.40 (range = 3 – 79 individuals; n = 82 aggregations) and the mean sex ratio was nearly 1:1 (*X* ± S.D. = 1.07 ± 1.39, range = 0.25 – 7). Harvestmen usually aggregated close to the water (range = 0.02 – 2.0 m, n = 82 aggregations) on exposed rocks or, more frequently, inside breaches. When disturbed by intensive exposure to light or touching, aggregated individuals fled away or occasionally fell from the rock to the river. Individuals also collectively discharged scent gland secretions upon manipulation.

The results of the experiment revealed that the scent gland secretion unequivocally elicits an alarm response in G. aff. *proximum*. In 22 out of 30 aggregations (73.3%) the individuals in the center of the group dispersed rapidly after being stimulated with the gland exudate. On the other hand, just one of 30 aggregations (3.3%) responded to the water-soaked cotton swab (Yates corrected χ^2= 31.09, $p < 0.0001$). The respondent individuals were fast at running away from their resting location (*X* ± S.D. = 19.68 ± 11.49 s, range = 2 – 53 s). Since the alarmed harvestmen bump other individuals, the alarm reaction is also probably mechanically spread through the aggregation, resulting in a general erratic scattering of the group. A similar "Trafalgar effect" (*sensu* THEHERNE & FOSTER, 1981) occurs in tight aggregations of thysanurans, aphids, and water striders in which the disturbance promoted by body contacts is used as a cue for approaching danger (reviewed by VULINEC, 1990).

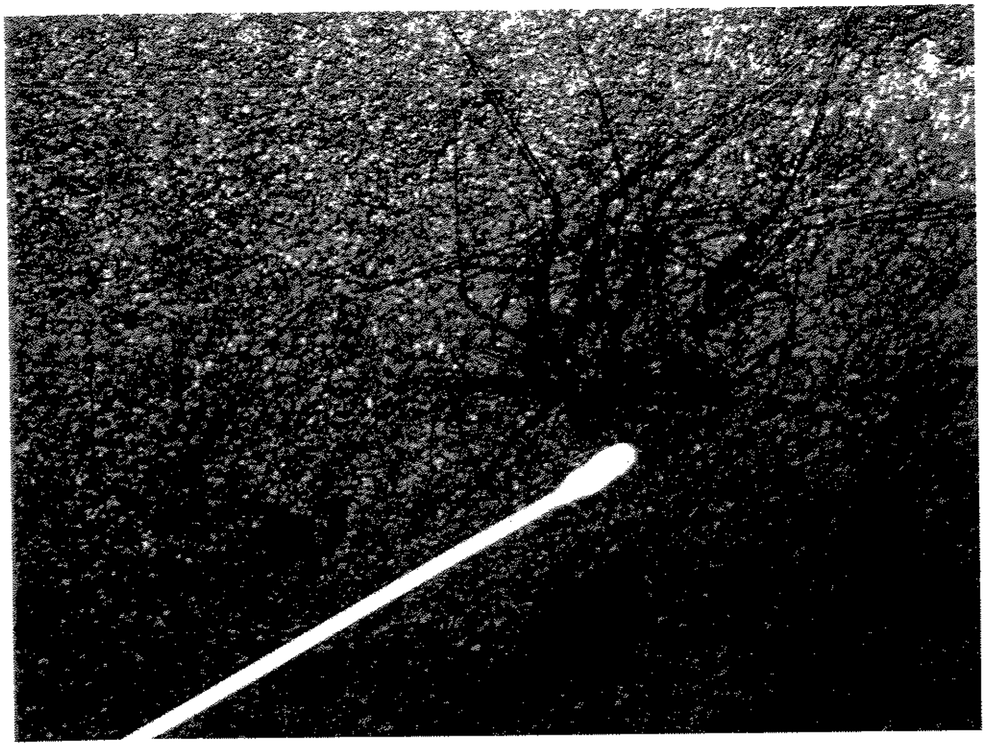

FIGURE 1. Experimental method for testing the alarm effect of the scent gland secretion of the harvestman *Goniosoma* aff. *proximum*. Aggregated individuals in the treatment group (n = 30 aggregations) were stimulated with a cotton swab (20 cm long) soaked with the species' own secretion, while individuals in the control group (n = 30 aggregations) were exposed to a water-soaked cotton swab.

Our experiments with *Goniosoma* also showed that respondent aggregations (X ± S.D. = 20.55 ± 11.10, range = 6 - 42 individuals) had significantly more individuals than non-respondent ones (X ± S.D. = 10.50 ± 8.55, range = 4 - 30 individuals) (Mann-Whitney test: U = 142.0, $n_1 = 22$, $n_2 = 8$, $p < 0.02$). Moreover, among respondent groups, the time to react to the scent gland secretion was inversely related with group size (FIGURE 2).

Harvestmen scent gland secretions can provide an effective defense against ants and other invertebrate and vertebrate predators (references in HOLMBERG, 1986). Several studies have shown that scent-gland secretions by harvestmen are only discharged after physical contact with a potential predator (EISNER *et al.*, 1971; DUFFIELD *et al.*, 1981). In this study we demonstrated that the defensive secretion can also elicit alarm behavior among aggregated individuals, causing them to disperse from a chemically marked, and presumably risky, area. Signals that are released upon mechanical damage to the sender are known as damage-release alarm signals, and act as reliable indicators of predation risk since they indicate that a nearby conspecific was recently attacked (CHIVERS *et al.*, 1996). This is the first demonstration of such a chemically-mediated signal in harvestmen.

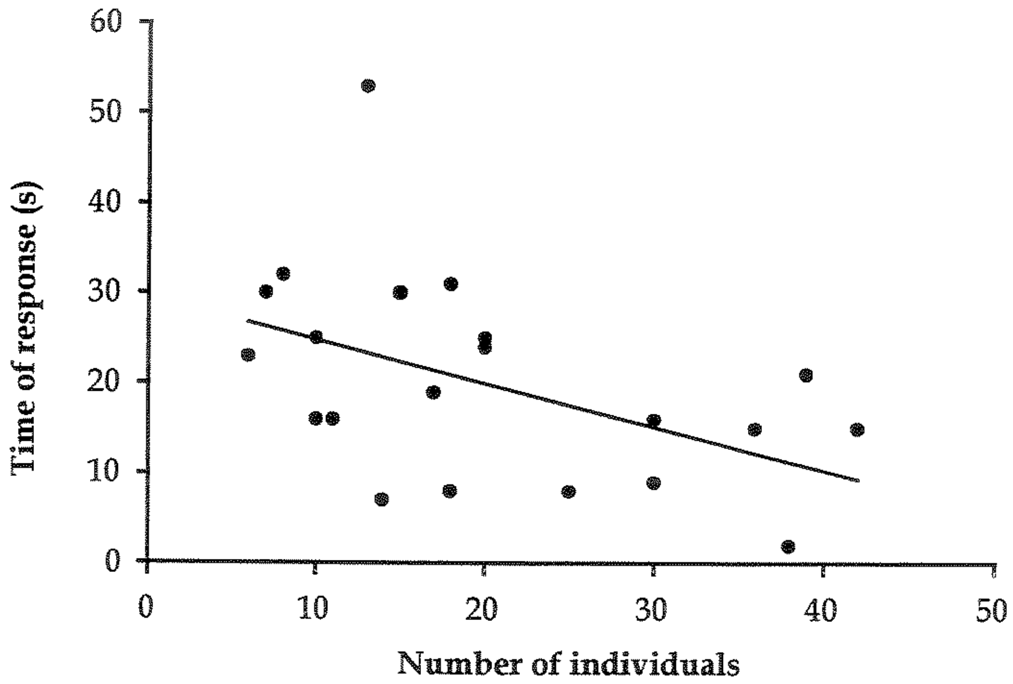

FIGURE 2. Relationship between group size and time of response by aggregated individuals of the harvestman *Goniosoma* aff. *proximum*, upon stimulation with a cotton swab imbibed with the species' own scent gland secretion (Pearson correlation: r_s= -0.467; n = 22; p < 0.03).

We also demonstrated for the first time among arachnids that the reaction response to the alarm signal varies with the size of the group. Larger groups apparently react faster to the chemical signal as a consequence of the increased number of sensorial legs used for surveillance. An analogous behavior is observed in other arthropods such as water-striders, in which large groups respond faster than small groups to an approaching predator due to an increased visual surveillance (Vulinec, 1990). Such a positive relationship between number of individuals and promptness of reaction is also well documented among visually-oriented vertebrates (Kenward, 1978; Hoogland, 1981).

Apart from the deterring function of such secretions, one might still ponder about an individual harvestman's advantage of chemically signaling to neighboring conspecifics upon a predator attack. Is there any additional benefit for the sender? As stressed by Blum (1985) for many insects, our results suggest that scent gland secretion in *Goniosoma* still functions as a defensive allomone, its pheromonal role being probably secondarily derived. Therefore it is reasonable to infer that the alarm effect in gregarious harvestmen has evolved as a by-product of a primarily defensive reaction under the context of predator avoidance. In case there is an individual advantage of signaling, it would probably depend on a confusion effect on the predator generated by the general fleeing, and/or on the genetic relatedness among aggregated individuals.

3.5. Acknowledgements

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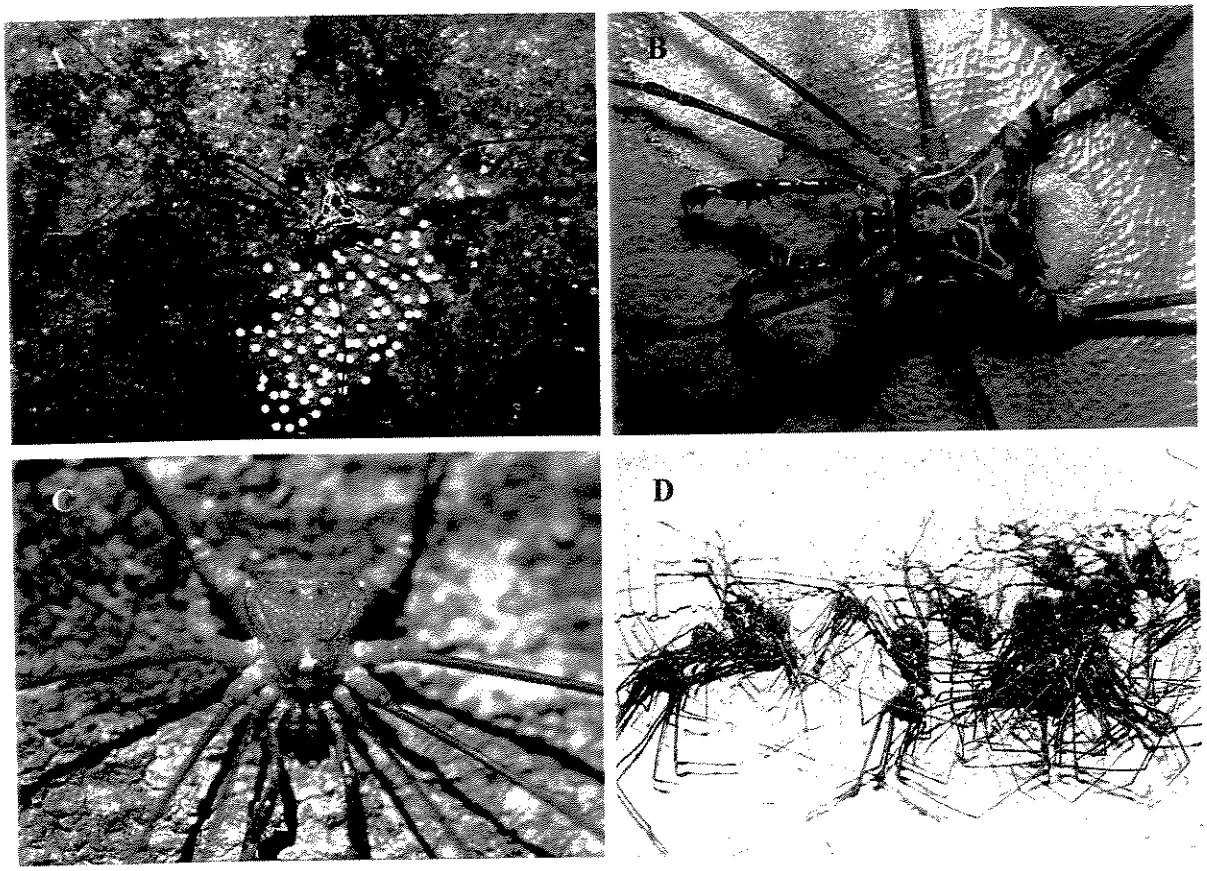
CAPÍTULO 4

Maternal care, defensive behavior, and sociality in Neotropical *Goniosoma* harvestmen (Arachnida: Opiliones)*



(A) Fêmea de *Goniosoma proximum* cuidando dos ovos; (B) Fêmea de *Goniosoma inscriptum*; (C) Macho de *Goniosoma* sp.1.; (D) Agregação de *Goniosoma catarina*.

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*MACHADO, G. Maternal care, defensive behavior, and sociality in Neotropical *Goniosoma* harvestmen (Arachnida: Opiliones). *Insectes Sociaux*, submetido.

4.1. Abstract

Biological information on Neotropical harvestmen is generally scarce, except for the genus *Goniosoma,* as several species have already been studied from an ecological and behavioral viewpoint. This study reports on maternal care, defensive behavior, and gregariousness of five species of *Goniosoma* (*G. geniculatum, G. inscriptum, G.* aff. *proximum, Goniosoma* sp.1, and *Goniosoma* sp.2), and analyses all published biological information for the genus. The study also discusses some behavioral patterns within the genus, and elaborates a hypothesis for the emergence of gregariousness in the group. Representatives of *Goniosoma* are found mainly inside caves or in rock fissures. Although species of the genus comprise only 5% of the harvestmen fauna in Brazil, they account for 20.6% of all harvestmen species recorded in Brazilian caves. Maternal care of eggs and first-instar nymphs is present in all species studied so far. Maternal care probably confers a special advantage in the cave habitat since intra- and inter-specific predation are supposed to be very strong. All studied species rely on similar defensive mechanisms: fleeing, dropping from the substrate to the ground, and when manipulated individuals try to pinch the aggressor with the sharp projections of the femur and coxae IV, and also release scent gland secretions. Several species of *Goniosoma* form dense diurnal aggregations that range from three to about 200 individuals. In a hypothetical scenario for the evolution of the sociality in *Goniosoma,* physiological constraints acting on individual harvestmen would promote a behavioral response for the selection of sites with appropriate microclimatic conditions. The lack of cannibalism among individuals may favor the tolerance to conspecifics, which is proposed as a pre-aptation to gregariousness. The derived functions of the gregarious behavior may include the strengthening of the defensive signal due to collective releasing of the repugnant secretion, the dilution effect, and promptness to flee upon a predator attack as a consequence of the additional alarm role of scent gland secretions. These defensive functions may overcome the costs of group living and be responsible for the maintenance of the gregariousness in the group.

4.2. Introduction

Biological information on Neotropical harvestmen is generally scarce, except for the genus *Goniosoma* PERTY (Arachnida: Opiliones: Gonyleptidae), as several species have already been studied from an ecological and behavioral standpoint (BRISTOWE, 1925; PINTO-DA-ROCHA, 1993; RAMIRES & GIARETTA, 1994; GNASPINI, 1995, 1996; GNASPINI & CAVALHEIRO, 1998; MACHADO & OLIVEIRA, 1998; SABINO & GNASPINI, 1999, MACHADO *et al.*, 2000, *in press*; OLIVEIRA *et al.*, 2001; SANTOS & GNASPINI, *in press*). The genus includes large and conspicuous harvestmen species that occur exclusively along the Brazilian Atlantic Forest. Despite the importance of the genus as a model for ecological and behavioral studies, its systematics is still confusing. About 50 species are currently recognized, but more species will be added as systematic studies of the group advance (M.B. SILVA, *pers. comm.*).

Maternal care has been recorded for all species of *Goniosoma* studied so far (PINTO-DA-ROCHA, 1993; RAMIRES & GIARETTA, 1994; GNASPINI, 1995; MACHADO & OLIVEIRA, 1998; MACHADO *et al.*, *in press*). Females lay their eggs mainly on a rocky substrate and take care of the eggs for 45 - 64 days. After hatching, first-instar nymphs remain aggregated under the guarding female for up to two weeks and then they disperse (GNASPINI, 1995; MACHADO & OLIVEIRA, 1998).

Several species of *Goniosoma* form dense diurnal aggregations consisting mainly of subadults and adults of both sexes. Among these species are *G.* aff. *badium* (PINTO-DA-ROCHA, 1993), *G. longipes* (MACHADO *et al.*, 2000), *G. catarina* (MACHADO *et al.*, in press), *G.* aff. *proximum* (OLIVEIRA *et al.*, 2001), and *G. spelaeum* (P. GNASPINI, *pers. comm.*). In general, individuals aggregate in protected sites, such as rock fissures, and close to a water source (MACHADO *et al.*, 2000; OLIVEIRA *et al.*, 2001). The number of aggregated individuals ranges from three to about 200, and upon manipulation they collectively discharge scent gland secretions (MACHADO *et al.*, 2000; OLIVEIRA *et al.*, 2001).

Defensive behaviors in animals may be divided into primary responses, which operate regardless of the presence of a predator, and secondary responses, which operate when a prey finds its potential predator (EDMUNDS, 1974). Among harvestmen, especially the large Gonyleptidae such as *Goniosoma*, secondary defensive mechanisms seem to be the best studied (CAPOCASALE & BRUNO-TREZZA, 1964; ACOSTA *et al.*, 1993; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000). These defenses include both mechanical (attack with the pedipalps and pinching with spines) and chemical responses (releasing of repugnant secretions). Evasive responses such as fleeing are also commonly employed by *Goniosoma* (GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000), as well as by other long-legged harvestmen species (HILLYARD & SANKEY, 1989).

This paper reports on behavioral observations of parental activities, defensive behavior, and gregariousness of five species of *Goniosoma* occurring in different regions of Brazil, and summarizes all published biological information for the genus. The study also discusses some behavioral patterns within the genus, and elaborates a hypothesis for the emergence of gregariousness in the group.

4.3. Material & Methods

The observations presented herein were made during fieldwork from 1998 to 2001, and include visits to several localities of the Brazilian Atlantic Forest. TABLE 1 presents the studied species and localities where they were found. It was regarded as an aggregation any group of at least three harvestmen whose legs were overlapping (cf. MACHADO *et al.*, 2000). Whenever possible the aggregations were collected and the individuals were counted and had their sexes determined. Females taking care of the offspring were measured for dorsal scute length and a sample of eggs was taken from the batches and preserved in 70% ethanol. In the laboratory, the egg diameter was measured with calipers (near 0.02 mm). Continuous recording (*sensu* MARTIN & BATESON, 1986) was made of relevant behavioral events, such as interactions between individuals and defensive responses. Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, Brazil.

TABLE 1. Studied species of *Goniosoma* and the localities in the Atlantic Forest where they were found. *Goniosoma* sp.1 and sp.2 are undoubtedly undescribed species (R. PINTO-DA-ROCHA, *pers. comm.*).

Species	Locality	State	Habitat	Elevation (m)
G. geniculatum	Nova Friburgo	Rio de Janeiro	granitic cave	900
G. inscriptum	Ubatuba	São Paulo	forest stream	100
G. aff. *proximum*	Ilha do Cardoso	São Paulo	forest stream	100
Goniosoma sp.1	Alto Caparaó	Minas Gerais	granitic cave	700
Goniosoma sp.2	Itororó	Bahia	hematite boulders	1100

4.4. Results

4.4.1. *Maternal care*

Eggs of all *Goniosoma* species studied so far are laid in a single layer, spaced out by 1-5 mm within the batch and generally are covered by a thick mucous layer. Recently laid eggs are cream and have a mean diameter ranging from 1.44 to 1.58 mm (TABLE 2). Eggs darken with development and just before hatching the average diameter may reach 2.3 mm (TABLE 2).The increase in egg volume probably occurs due to water intake during the embryonic development (MACHADO & OLIVEIRA, 1998). The number of eggs laid shows a wide variation both within and among species, and ranges from 26 to 204 (TABLE 2).

The egg-batches were mainly located at low-illuminated and wet places (1 – 2 m from a water source), such as between gaps of rocks in river margins (*e.g. G. catarina, G. inscriptum, G. proximum,* and *G.* aff. *proximum*) and caves (*G.* aff. *badium, G. geniculatum, G. longipes, G. spelaeum,* and *Goniosoma* sp.1). Females take care of the eggs and the first instar nymphs before they disperse. For *G.* aff. *proximum* (this study), *G. longipes* (MACHADO & OLIVEIRA, 1998), and *G. spelaeum* (GNASPINI, 1995) ovipositions were found throughout the year, which indicate that there is not a seasonal break in the reproductive activities of these species.

4.4.2. *Potential egg-predators and fungal attack*

Cave crickets of the genus *Strinatia* (Ensifera: Phalangopsidae), previously recorded as egg predators for *G. longipes* (MACHADO & OLIVEIRA, 1998), were commonly found near (10 – 50 cm) the batches of *G. geniculatum* and *Goniosoma* sp.1. For the non-cavernicolous species (*Goniosoma* sp.2, *G.* aff. *proximum*, and *G. inscriptum*) the potential egg predators found near the batches were predacious tiger beetles (Coleoptera: Cicindellidae), and ants. TABLE 3 summarizes the available information on potential predators of *Goniosoma* eggs. One batch of *Goniosoma* sp.1 and five batches of *G.* aff. *proximum* were attacked by fungi and the number of infected eggs ranged from 1 (1.3% of the total) to 38 (100% of the eggs).

4.4.3. *Defensive behavior*

All species of *Goniosoma* studied so far seem to rely on similar defensive mechanisms (BRISTOWE, 1925; GNASPINI, 1996; GNASPINI & CAVALHEIRO, 1998; MACHADO *et al.*, 2000). Fleeing is the most common defensive response upon disturbance by touch or by illumination with artificial light. Sometimes individuals also try to escape by dropping from the substrate to the ground, and this behavior seems to be more common among guarding females. On the ground, the fallen individuals remain motionless for a while, probably to avoid detection by the potential predator. Attacking the aggressor with the pedipalps and trying to bite it with the chelicerae is a frequent behavior upon manipulation. When handled by the forth pair of legs, males move vigorously the femur IV promoting a pinch between the sharp projections of the femur and coxae IV.

The manipulation of the individuals may also cause the release of scent gland secretions. First, a transparent and inodorous droplet (enteric fluid) is released through the mouthparts and oozes throughout the lateral margins of the dorsal scute. After that, a yellowish secretion with a sour smell is released by the exocrine glands located over the second pair of legs. This secretion also oozes throughout the margins of the body and mixes with the transparent liquid. The scent secretion may also be released while the enteric fluid is passing near the opening of the scent glands or even may be sprayed directly toward the aggressor without previous release of the oral liquid. Under contact with the human skin the repugnant secretions of all observed species promoted reddish spots, which indicate that the chemical nature of these substances is probably a quinone (GNASPINI & CAVALHEIRO, 1998). The chemical nature of the scent gland secretion was determined for three *Goniosoma* species, being composed by a blend of two alkyl-1,4-

benzoquinones in G. *spelaeum* (GNASPINI & CAVALHEIRO, 1998) and G. *longipes* (G. MACHADO & J.R. TRIGO, unpublished data), and of four different alkyl-1,4-benzoquinones in G. aff. *proximum* (MACHADO *et al., submited*).

4.4.4. *Gregariousness*

Aggregations of *Goniosoma* consist of motionless individuals (bodies 0 - 5 cm apart from each other), with their legs widely overlapped. They are found during daytime, generally in a wet and light protected place (see also MACHADO *et al.*, 2000). Just before dusk, the aggregations disperse and the individuals leave the diurnal shelter to forage. The mean number of individuals per aggregation may range from 3 to about 200 (TABLE 2). The mean sex ratio in aggregations of G. aff. *proximum* was nearly 1:1 (mean ± SD = 1.07 ± 1.39; range = 0.25 - 7; n= 82 aggregations), different from G. *longipes* in which the sex ratio was female biased (mean ± SD = 1.8 ± 1.5; range = 0.3 - 5.3; n= 28 aggregations) (MACHADO *et al.*, 2000).

4.5. Discussion

The cave habitat is characterized by darkness, high moisture, little variation of temperature throughout the year, and low food availability (BARR, 1968), characteristics that may impose constraints for the colonization of caves by epigean animals (GNASPINI & HOENEN, 1999). The lack of light restricts the cave colonization for visually oriented animals and makes impossible cave occupation by photosynthetic organisms. Generally, animal groups with cavernicolous representatives show nocturnal habits in the external environment and this feature may be regarded as a pre-aptation for the occupation of caves. In fact, cave-dwelling arthropods rely mostly on non-visual structures, such as antennae or antenniform legs (GNASPINI & HOENEN, 1999 and references therein). Many cavernicolous species also present special adaptations to the scarcity of food, with high resistance to starvation and/or an omnivorous and opportunistic diet (BARR & HOLSINGER, 1985). Harvestmen are an arachnid order with many cavernicolous species (GOODNIGHT & GOODNIGHT, 1981; PINTO-DA-ROCHA, 1995) and the presence of several of the morphological and physiological pre-aptations cited above may explain their success in the colonization of this particular environment.

Several representatives within the genus *Goniosoma* live inside caves, mainly as trogloxenes (GNASPINI, 1996; MACHADO *et al.*, 2000). It means that they use the caves as shelter and reproductive site, but they need to leave this habit to forage outside. Although species of the genus comprise only 5% of the harvestmen fauna in Brazil, they account for 20.6% of all harvestmen species recorded in Brazilian caves (PINTO-DA-ROCHA, 1995 - it does not include the undescribed species studied here). Allied to several morphological and physiological features that probably favor the occupation of caves, species of *Goniosoma* present another pre-aptation that may confer a special advantage in this particular environment: the subsocial behavior. Subsociality includes guarding, brooding eggs and young, provisioning offspring before and after birth, and supporting them after nutritional independence (CLUTTON-BROCK, 1991). Maternal assistance to eggs and nymphs has been reported for several harvestmen species of the suborder Laniatores and appears as the most elaborate form of parental investment in Opiliones (MACHADO & RAIMUNDO, 2001).

TRIVERS (1972) proposed that maternal care will evolve when the individuals' benefit (in terms of offspring survival) overrides the costs of the parental behavior. Constant exposure to heavy predation may be an important selective pressure favoring the evolution of parental care if unprotect eggs have a high chance of being consumed (TALLAMY & DENNO, 1981). Inside caves the scarcity of food and the strong predation pressure (cave fauna is constituted mainly by predators and detritivores), may provide the scenario in which the maternal care confers overall benefits for females. Despite the physiological costs of such behavior, unprotected eggs may have low chance of survival. Indeed, for the harvestman *G. longipes*, whose females reproduce mainly inside caves, maternal care is crucial for egg survival since predators (mainly conspecifics and cave crickets) may consume entire batches in a single night (MACHADO & OLIVEIRA, 1998). The results presented here showed that most *Goniosoma* species seem to be exposed to these sources of egg mortality, since similar egg predators were found in the same microhabitat of the guarding females (TABLE 3).

TABLE 2. Life history traits related to habitat occupation, reproduction, and gregariousness of several *Goniosoma* species. When the sample size (n) for the quantitative categories was smaller than 10 only the range is presented; otherwise the numbers correspond to the mean ± SD, with the range between brackets.

Species	Cave dweller	Female size (mm)	Number of eggs	Egg diameter (mm)		Increase in egg volume	Oviposition substrate	Gregarious habits	Number of individuals
				Recently laid	Prior hatching				
G. aff. *badium*[1]	yes	?	72 - 105 (n = ?)	-	-	-	calcareous rocks	yes	9 - 34 (n = ?)
G. aff. *proximum*[2, 4]	no	7.80 ± 0.22 (n = 14)	95.1 ± 31.9 (38 - 165; n = 18)	1.46 ±0.08 (n = 10)	1.89 ± 0.10 (n = 10)	29.5%	granitic rocks	yes	19.5 ± 18.4 (3-79; n = 82)
G. *catarina*[3]	no	8.1 (n = 1)	ca. 100	-	-	-	granitic rocks	yes	16 - 37 (n = 3)
G. *geniculatum*[4]	yes	7.96 ± 0.25 (n = 18)	47 - 156 (n = 2)	1.58 ± 0.04 (n = 10)	2.11 ± 0.06 (n = 10)	33.5%	granitic rocks	yes	30 - 50 (n = 3)
G. *inscriptum*[4]	no	6.90 ± 0.28 (n = 10)	26 - 93 (n = 9)	1.44 ± 0.12 (n = 10)	1.85 ± 0.07 (n = 10)	28.5%	granitic rocks	no	-
G. *longipes*[5]	yes	7.83 ± 0.24 (n = 33)	131.05 ± 38.62 (27 - 209; n = 33)	1.44 ± 0.09 (n = 20)	1.91 ± 0.12 (n = 20)	43%	granitic rocks	yes	34.2 ± 38.1 (7-200; n=30)

TABLE 2. Continued.

Species	Cave dweller	Female size (mm)	Number of eggs	Egg diameter (mm)		Increase in egg volume	Oviposition substrate	Gregarious habits	Number of individuals
				Recently laid	Prior hatching				
G. proximum[6]	no	7.4 – 7.8 (n = 2)	49 - 77 (n = 3)	-	2.01 ± 0.18 (n = 15)	-	granitic rocks	no	-
G. spelaeum[7]	yes	~ 8.0	30 - 120	-	2.1 - 2.3 (n = ?)	-	calcareous rocks	yes	?
Goniosoma sp.1[4]	no	7.56 ± 0.20 (n = 11)	85 - 173 (n = 4)	1.51 ± 0.08 (n = 10)	1.91 ± 0.19 (n = 10)	24.8%	hematite rocks	no	-
Goniosoma sp.2[4]	yes	7.0 (n = 1)	97 (n = 1)	-	1.86 ± 0.10 (n = 10)	-	granitic rocks	no	-

SOURCES: 1 = PINTO-DA-ROCHA (1993); 2 = OLIVEIRA *et al.* (2001); 3 = MACHADO *et al.* (in press); 4 = This study; 5 = MACHADO & OLIVEIRA (1998) and MACHADO *et al.* (2000); 6 = RAMIRES & GIARETTA (1994); 7 = GNASPINI (1995) and *personal communication*.

TABLE 3. List of potential predators of *Goniosoma* eggs based on literature data. The symbol * indicates species that were found preying on eggs in the field. Sources for cited species are the same as in TABLE 2.

Species	Potential egg-predators
G. aff. *badium*	*Zelurus travassosi* (Heteroptera: Reduviidae), *Strinatia* sp. (Ensifera: Phalangopsidae), and conspecifics
G. aff. *proximum*	*Pachycondyla* sp. and *Camponotus* sp. (Hymenoptera: Formicidae), *Oxychila* sp. (Coleoptera: Cicindelidae), and conspecifics
G. catarina	Conspecifics
G. geniculatum	*Strinatia* sp. (Ensifera: Phalangopsidae) and conspecifics
G. inscriptum	Conspecifics
G. longipes	*Odontomachus chelifer* (Hymenoptera: Formicidae), *Zelurus travassosi** (Heteroptera: Reduviidae), *Strinatia* sp.* (Ensifera: Phalangopsidae), and conspecifics*
G. proximum	Conspecifics
G. spelaeum	*Zelurus travassosi** (Heteroptera: Reduviidae), *Sepedophilus* sp.* (Coleoptera: Staphylinidae), *Strinatia brevipenis* (Ensifera: Phalangopsidae), and conspecifics
Goniosoma sp.1	Ants (Hymenoptera: Formicidae) and conspecifics
Goniosoma sp.2	*Strinatia* sp. (Ensifera: Phalangopsidae) and conspecifics

Several hypotheses have been proposed to explain the adaptative meaning of harvestmen aggregations, including mating, defense, hydro- and thermoregulation (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). Contrary to pseudoscorpions (WEYGOLDT, 1969), spiders (EVANS, 1999), and some species of scorpions (POLIS, 1990), there is no evidence that individuals in a harvestmen aggregation are genetically related (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). This lack of evidence discards the possibility of kinship selection as a selective pressure leading to gregariousness in harvestmen, and also has an heuristic relevance for the comprehension of the evolution of the sociality among non-related individuals. Perhaps the most important behavioral feature that differentiates harvestmen from the other arachnid orders cited above is the lack of cannibalism among adults. All records of cannibalism in harvestmen were of adults eating eggs or early instar nymphs (EDGAR, 1971; GOODNIGHT & GOODNIGHT, 1976; MORA, 1990; MACHADO & OLIVEIRA, 1998). Despite their carnivorous habits, harvestmen are generalist feeders with tendency to necrophagy (GNASPINI, 1996; MACHADO & PIZO, 2000; MACHADO *et al.*, 2000). The non-cannibalistic habits among adults may have favored the conspecific tolerance and the evolution of gregarious behavior in harvestmen (FIGURE 1).

Gregariousness has been recorded for several species of *Goniosoma* and it seems to be another common behavioral feature shared by most species of the genus (TABLE 2). Group living in *Goniosoma* may confer advantages for an individual harvestman in three different ways (FIGURE 1). First, aggregations may strengthen the repulsive signal of the scent gland secretions to predators (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). Chemical studies have shown that the secretions produced by *Goniosoma* are mainly benzoquinones (GNASPINI & CAVALHEIRO, 1998; MACHADO *et al., submited*), widespread predator deterrents among arthropods (BLUM, 1981). Second, resting in a group may decrease the risks of being singled out by a predator according to the selfish herd hypothesis (HAMILTON, 1971). Third, it was demonstrated that the scent gland secretion also works as an alarm pheromone in *G.* aff. *proximum*, and that larger groups respond faster to the chemical stimulus as a consequence of the increased number of sensorial legs used for surveillance (OLIVEIRA *et al.*, 2001). Gregarious behavior may be, however, primarily induced by microclimatic factors, such as relative humidity, temperature, and light conditions (HOLMBERG *et al.*, 1984; MACHADO *et al.*, 2000). Therefore it seems reasonable to suppose that the defensive functions of gregariousness in *Goniosoma* harvestmen have evolved as a by-product of a primarily behavioral response to environmental stress (FIGURE 1).

The importance of behavioral studies on a wide set of related species lies mainly on the basic information that can be used to test evolutionary hypotheses about the origin and maintenance of several life history traits (BROOKS *et al.*, 1995). Recently, several researchers have been using behavioral characters to construct phylogenies (review in DE QUEIROZ & WIMBERGER, 1993). Therefore, information on the behavior of organisms can be useful both for ecological and systematic studies (see ALEXANDER, 1962). The genus *Goniosoma* is certainly the most studied among Neotropical harvestmen. The amount of published information on *Goniosoma*, coupled with a phylogeny for the genus, would allow researchers to test hypotheses about the evolution of some characters such as colonization of the cavernicolous environment, gregariousness, chemical nature of the repugnatorial secretions, and life history traits associated with subsociality.

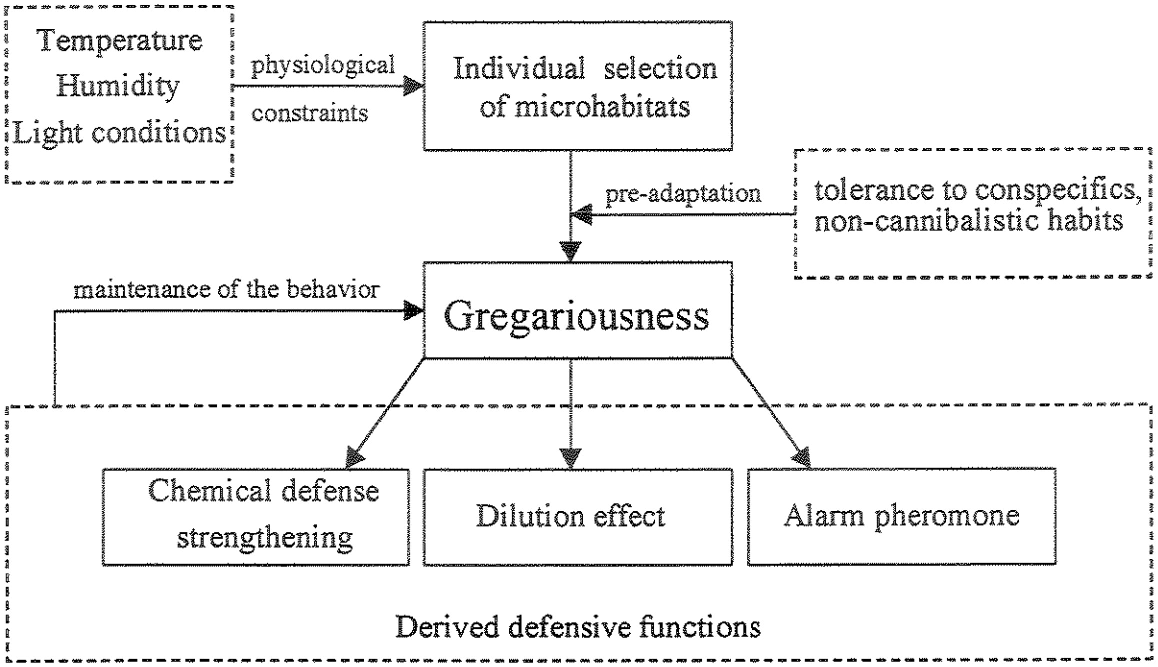

FIGURE 1. Hypothetical scenario for the evolution of gregariousness in harvestmen of the genus *Goniosoma*. Physiological constraints acting on individual harvestmen would promote a behavioral response for the selection of sites with appropriate conditions of light, temperature and humidity. The lack of cannibalism among individuals may favor the tolerance to conspecifics, which is proposed as a pre-aptation to gregariousness. The derived functions of the gregarious behavior in *Goniosoma* harvestmen may include the strengthening of the defensive signal due to collective releasing of the scent gland secretion, the dilution effect (*sensu* VULINEC, 1990), and promptness to flee upon a predator attack as a consequence of the additional alarm role of defensive secretions. These defensive functions may overcome the costs of living in group and be responsible for the maintenance of the gregariousness in the group.

4.6. Acknowledgements

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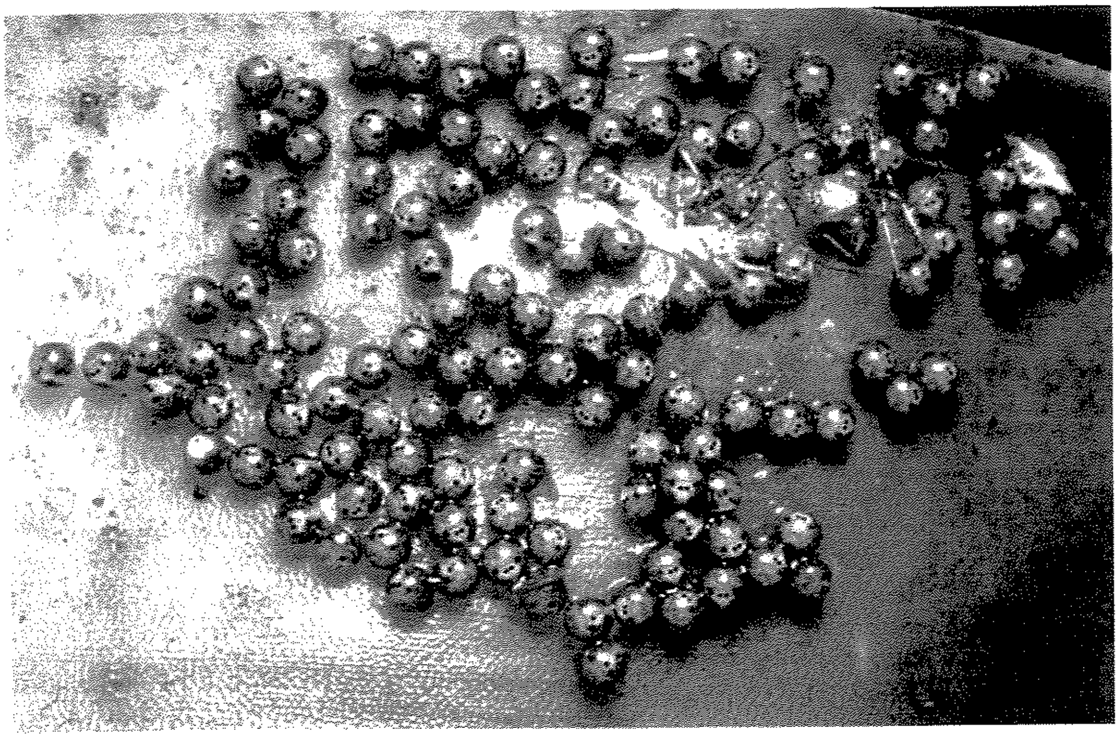
CAPÍTULO 5

Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida: Opiliones)*



Desova de *Bourguyia albiornata* no momento da eclosão das primeiras larvas.

*MACHADO, G. & P.S. OLIVEIRA. Maternal in the Neotropical harvestman *Bourguyia albiornata* (Arachnida: Opiliones). *Journal of Ethology,* submetido.

5.1. Abstract

This study provides a field account of the reproductive biology of the Neotropical harvestman *Bourguyia albiornata,* and experimentally assesses the effects of the mother on offspring survival. Fieldwork was carried out in a sandy plain forest at Cardoso Island, southeast Brazil. Females of *B. albiornata* oviposit almost exclusively inside the bromeliad *Aechmea nudicaulis,* which accounts for only 10% of all epiphitic bromeliads at study site. This bromeliad accumulates water inside the tube formed by the curled of leaves and may provide protection for the offspring from streessful climatic factors and moisture fluctuations. Reproductive activity occurs from February to October and the number of egg-batches per month is not correlated with rainfall. There is, however, a negative correlation between the number of flowering individuals of *A. nudicaulis* and the monthly number of egg-batches. During the flowering season, the the interior of the tubes of leaves of the bromeliads are occupied with the inflorescence stalk and thus are not available for oviposition. The synchronization of the maternal investment in offspring with the phenology of nest bromeliad suggests that the reproductive activities of *B. albiornata* are more closely related with the availability of appropriate oviposition sites than with the climatic factors, such as moisture. During one year 83.6% of the females produced one egg-batch, 14.3% produced two, and only 2.1% oviposited three times. The mean number of eggs per batch along successive reproductive events decreased significantly, suggesting physiological costs of reproduction and a trade-off between egg production and maternal care. A field experiment in which females were removed from the nest bromeliad showed that the mother plays a crucial protective role: less than 7% of the unprotected eggs survived beyond two weeks. On the other hand, in the control group (females maintained over the eggs) only one egg-batch was attacked by predators. The main source of egg mortality was ants, but cannibalism was also recorded. In the study area at least 20 ant species nest and/or forage on the same bromeliad used by *B. albiornata* as oviposition site, and the most abundant ones are also the most important egg predators. Severe predation pressure on *B. albiornata* eggs could have favored the evolution and maintenance of parental care in this species.

5.2. Introduction

Subsociality is the most primitive presocial condition and occurs when adults care for their own offspring for some period of time (WILSON, 1971). This behaviour is known to have evolved in all arachnid orders except for the Palpigradi whose reproductive behaviour is unknown (WEYGOLDT, 1969, 2000; PITTARD & MITCHELL, 1972; BRACH, 1975; FOELIX, 1982; POLIS, 1990; PUNZO, 1998; MACHADO & RAIMUNDO 2001). Particularly among the order Opiliones, there is a wide diversity of forms of parental activities, varying in complexity and duration, and ranging from the choice of microhabitats for oviposition to subsocial behaviour (see review in MACHADO & RAIMUNDO, 2001).

Harvestmen constitute a highly diversified order in terms of morphology and habits, including approximately 7000 species widespread throughout the world (COKENDOLPHER & LEE, 1993). Subsocial behaviour has been recorded for more than 30 harvestmen species in at least seven not closely related families. All subsocial harvestmen belong to the suborder Laniatores, and most occur in tropical regions (MACHADO & RAIMUNDO, 2001). The great majority of reports about subsociality in harvestmen is anecdotal or based on studies conducted under laboratory conditions, lacking data on reproductive seasonality and on natural enemies of the brood. Therefore such studies provide little information on the environmental conditions in which the subsocial behaviour may be adaptive.

The relevance of subsocial behaviour was experimentally assessed only for two harvestmen species: *Zygopachylus albomarginis*, the first arachnid known to exhibit paternal care (MORA, 1990), and *Goniosoma longipes*, whose females reproduce inside caves (MACHADO & OLIVEIRA, 1998). In both cases the parental individual has a crucial protective role, and actively defends the offspring against egg-predators such as ants and/or conspecifics. Additionally, males of *Z. albomarginis* are able to prevent fungal attack on the eggs, a fact not observed in *G. longipes*. Despite the importance of these examples, more studies on the role of parental care in harvestmen are needed to understand their adaptive meaning in different environments, and to construct hypotheses on the evolution of parental behaviour in the Opiliones.

The Gonyleptidae is the richest harvestman family and possesses a strictly Neotropical distribution (SHEAR, 1982). Species in the subfamily Bourguyiinae, a basal group within the family Gonyleptidae, are endemic to the Brazilian Atlantic rainforest (KURY, 1994). *Bourguyia albiornata* is a large-bodied harvestman (7 mm) frequently found on vegetation. Females of *B.*

albiornata lay eggs within bromeliad leaf tubes and take care of eggs and nymphs. In this paper we describe some aspects of the reproductive biology of this harvestman species and address the following questions: (a) where and when do females lay their eggs?; (b) what are the main sources of egg mortality?, and (c) what is the effect of the mother on offspring survival? We also discuss the implications of our results for understanding the evolution of maternal care in harvestmen.

5.3. Material & Methods

5.3.1. *Study area*

The study was carried out at Cardoso Island (25°18′ S; 48°05′ W; sea level), South coast of São Paulo State, Southeast Brazil. The climate is generally warm and wet throughout the year but may be divided in two seasons. The cold season lasts from June to September and is characterized by less frequent rainfall (ca. 500 mm) and mean temperature of 17.4° C. From October to May there is a warm season when rainfall is abundant (1800 mm) and the mean temperature is 25.5° C (FUNARI *et al.*, 1987). The vegetation in the study site is mainly a plain forest, consisting of small trees (6 m high) growing in sandy soil; the understory is dominated by terrestrial bromeliads, herbs, and a few shrubs (BARROS *et al.*, 1991).

5.3.2. *Naturalistic observations*

Field observations were conducted at 15 - 25 day intervals from January to December 2000. All epiphytic bromeliads present along an 1-km transect (1 m wide) inside the forest were censused, looking ovipositions of *Bourguyia albiornata*. The censuses were generally conducted between 08:00 and 15:00 h. Behavioural data on harvestmen are based on 53 days of fieldwork and more than 300 h of naturalistic observations, of which nearly 40 h comprised nocturnal observations from 18:00 to 01:00 h. All egg-guarding females were marked on the dorsum with colored dots of enamel paint (Testors, Rockford Co., USA), and the number of eggs was counted. This procedure apparently did not affect females' behavior (see also MACHADO & OLIVEIRA, 1998). The nest bromeliad was also marked with the corresponding colour dot of the guarding female. The number of eggs per batch along successive reproductive events, as well as the interval between these events, were tested through a Mann-Whitney rank sum test. Continuous recording (up to 30 min) was made of all relevant behavioral events (see MARTIN & BATESON, 1986), such as interactions between guarding females and other animals and attacks of egg-predators. Voucher specimens were deposited in the arachnological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP), Brazil.

5.3.3. *Field experiment*

The protective role of maternal care against egg predation was evaluated through a field experiment in March 2001. Two experimental groups of 10 egg-batches each were randomly designated by the flip of a coin as treatment or control. In the treatment group guarding females were removed from the nest bromeliads and the eggs were left unattended (mean ± SD= 131.4 ± 25.8 eggs/batch). In the control group guarding females were removed from the nest bromeliads and placed again in the same location after 5 min (123.5 ± 20.2 eggs/batch). There was no significant difference in the initial number of eggs per batch between the two groups. All experimental egg-batches were on bromeliads of similar size and height (1 - 1.5 m above the ground), at least 5 m apart, and at initial developmental stage (determined by egg size and coloration, see Results). During 14 days, the batches of both experimental groups were checked at least twice a day in order to identify egg predators. A repeated-measures ANOVA was performed on the number of eggs per batch before (day 1) and after (day 14) treatment. Additional data on egg predators were also gathered from six egg-batches whose females were experimentally removed during a 24h-period in a preliminary phase of this study, and from 11 egg-batches whose females had deserted.

5.3.4. *Abundance of egg predators*

Ants were the most important egg predators (see below) and to assess their abundance and the composition of species that nest and/or forage on vegetation, 100 tuna baits were distributed on the vegetation (at least 5 m apart) along the 1 km-transect. Baits were placed on leaves of the bromeliad *Aechmea nudicaulis* (the preferred oviposition site) and were checked twice within a 3h-interval. Ant workers attending the baits were counted and collected for identification.

5.4. Results

5.4.1. *Oviposition site*

Females of *Bourguyia albiornata* used almost exclusively the bromeliad *Aechmea nudicaulis* (FIGURE 1A, B) as oviposition site (n = 281). Only once another bromeliad species, *Aechmea* sp., was found being used by *B. albiornata*. There are more than 15 epiphytic species of bromeliads in the study site, but only these two *Aechmea* species have curled leaves forming a tube (up to 50 cm long) that accumulates water and also confers protection from the sunlight (FIGURE 1A).

The great majority of the nest bromeliads contained only one egg-batch (n = 275), but in a few cases the same leaf tube hosted two ovipositions (n = 7). In these cases, no agonistic interactions were observed between the egg-guarding females. Copulation occurs on the same bromeliad used as oviposition site (n = 3 observations) and the male remains close (2 - 5 cm) to the mating female, inside the nest bromeliad, for up to 4 days (n = 25).

5.4.2. *Reproductive seasonality*

A total of 189 egg batches of *B. albiornata* were found during 2000. Reproductive activity occured between February and October, being more intense from March to May (FIGURE 1A). The number of egg-batches per month was not correlated with rainfall ($r_s = -0.159$; n = 12; NS). However, the percentage of individuals of *A. nudicaulis* used as brood site by females of *B. albiornata* was negatively correlated with the percentage of flowering individuals of this bromeliad (FIGURE 2B). The mean number of eggs per batch differed between the two seasons, with females laying more eggs in the warm months (X ± SD= 104.5 ± 35.0; range= 14 - 169; n = 82) than in the cold months (57.9 ± 24.0; range = 11 - 108; n = 76) (t = 9.674; df = 156; $p < 0.001$).

During one year of monthly records, 83.6% of the females produced only one egg-batch, 14.3% produced two, and only 2.1% oviposited three times. The mean number of eggs per batch along successive reproductive events was significantly different (Mann-Whitney U test = 16.52, $p < 0.001$). Females laid more eggs in the first oviposition (median = 83.5; range = 11 - 169 eggs; n= 130) than in the second (median = 54.5; range = 11 - 124 eggs; n = 24) and third (median = 52; range = 18 - 66 eggs; n = 4) reproductive events. The median interval between the first and second ovipositions was 85 days (range = 28 - 171 days; n = 27), and between the second and third was 63.5 days (SD = 47.5 days; range = 33 - 129 days; n = 4). These intervals were not significantly different (Mann-Whitney U test = 62.0; p = 0.635).

5.4.3. *Parental care*

All observed egg-batches (n = 282) were guarded by one adult female, either siting on the eggs or remaining next to the batch (FIGURE 1C). The guarding female was frequently observed touching the eggs with the first and second pairs of legs and also inspecting the periphery of the egg-batch. This activity sometimes lasted up to 30 min. As opposed to non-reproductive individuals, guarding females of *B. albiornata* were never observed leaving the nest bromeliad to forage at night.

Eggs are spaced out by 1 - 2 mm within the batch, laid in a single layer, and are covered by a thin mucus (FIGURE 1C). As in other laniatorean harvestmen (GNASPINI, 1995; MACHADO & OLIVEIRA, 1998), eggs of *B. albiornata* become darker and increase in volume during the embryonic development. At the moment the eggs are laid, they have a cream coloration and average 1.19 ± 0.10 mm in diameter (n = 20 eggs). Just before hatching the mean egg diameter is 1.34 ± 0.07 mm (n = 20 eggs).

The hatching of all nymphs within a clutch was asynchronous and lasted up to eight days between the emergence of the first and the last nymphs (range 1 - 8 days; n = 15). The mean time of embryonic development was 35.2 days (SD = 2.1 days; range = 30 - 39 days; n = 19). After hatching, the nymphs were observed to remain aggregated under the guarding female for up to six days before dispersal. The total period of maternal care towards eggs and nymphs may last 35 - 43 days. The guarding females were only observed to leave the oviposition site after all 1st-instar nymphs had dispersed.

Females of *B. albiornata* actively defended their offspring against other organisms that enter the bromeliads. On one occasion a female was seen repelling from the nest bromeliad a katydid (Ensifera: Tettigoniidae) twice her size. Two other females were each observed fighting with conspecifics (one juvenile and one adult male), and in both cases they expelled the intruder from the bromeliad. When not brooding eggs, however, females are very tolerant to conspecifics and may be found in small aggregations (up to 12 individuals), including adults (males and females) and juveniles, inside the tube of leaves of *A. nudicaulis*. Large spiders (*Phoneutria nigriventer, Ctenus* sp., and another unidentified species) were seen preying on egg-guarding females on three occasions.

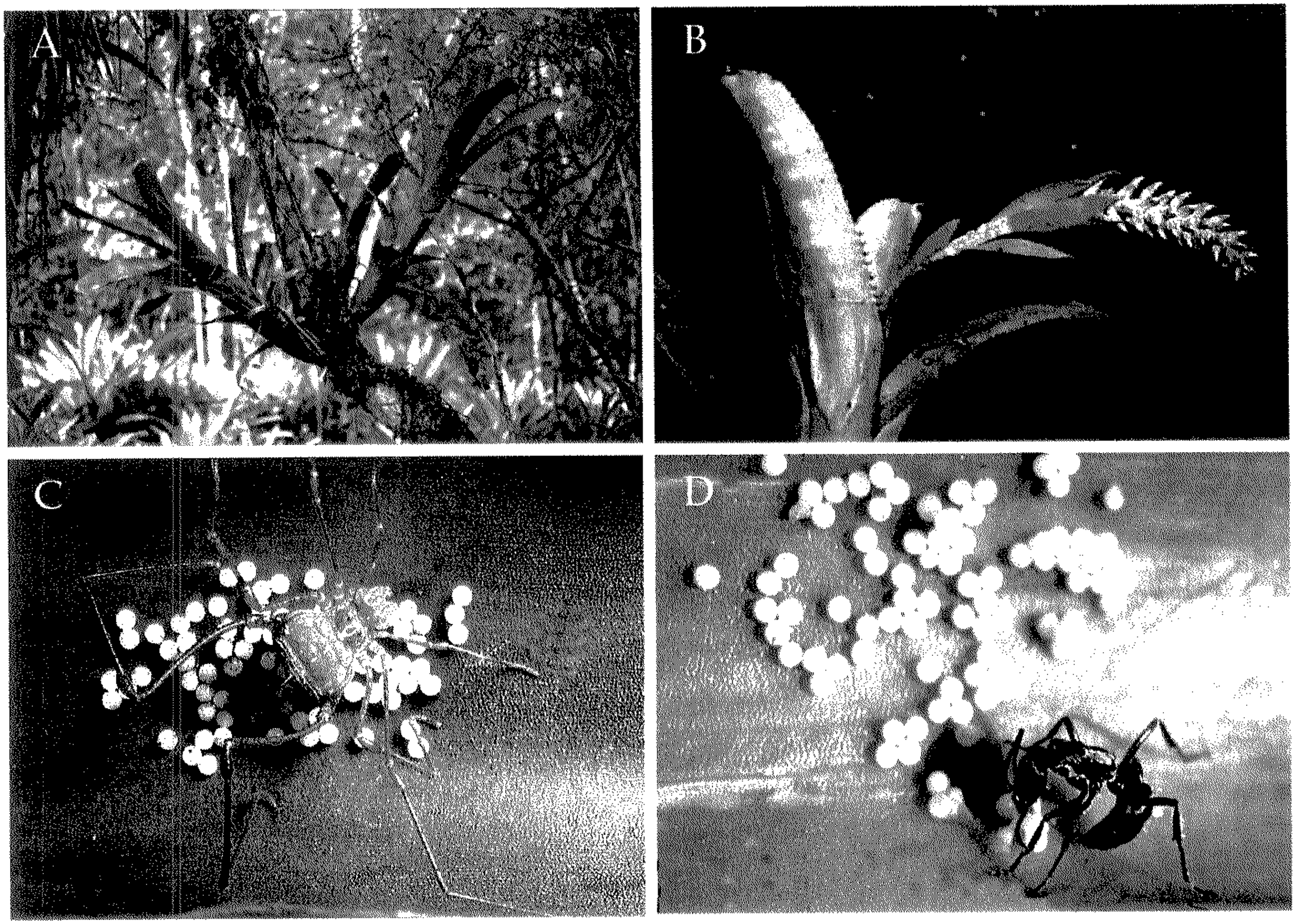


FIGURE 1. (A) A small clump of the epiphytic bromeliad *Aechmea nudicaulis* at Cardoso Island, SE Brazil. The curled leaves form a tube that accumulates water, and are used as oviposition site by the harvestman *Bourguyia albiornata*. (B) Flowering individual of *A. nudicaulis*: note that the inflorescence stalk occupies the tube of leaves. (C) Female of the harvestman *B. albiornata* (body size = 7 mm) guarding her eggs inside the tube of leaves of the bromeliad *A. nudicaulis*. (D) A worker of the ponerine ant *Pachycondyla villosa* preying on unprotected eggs of *B. albiornata*.

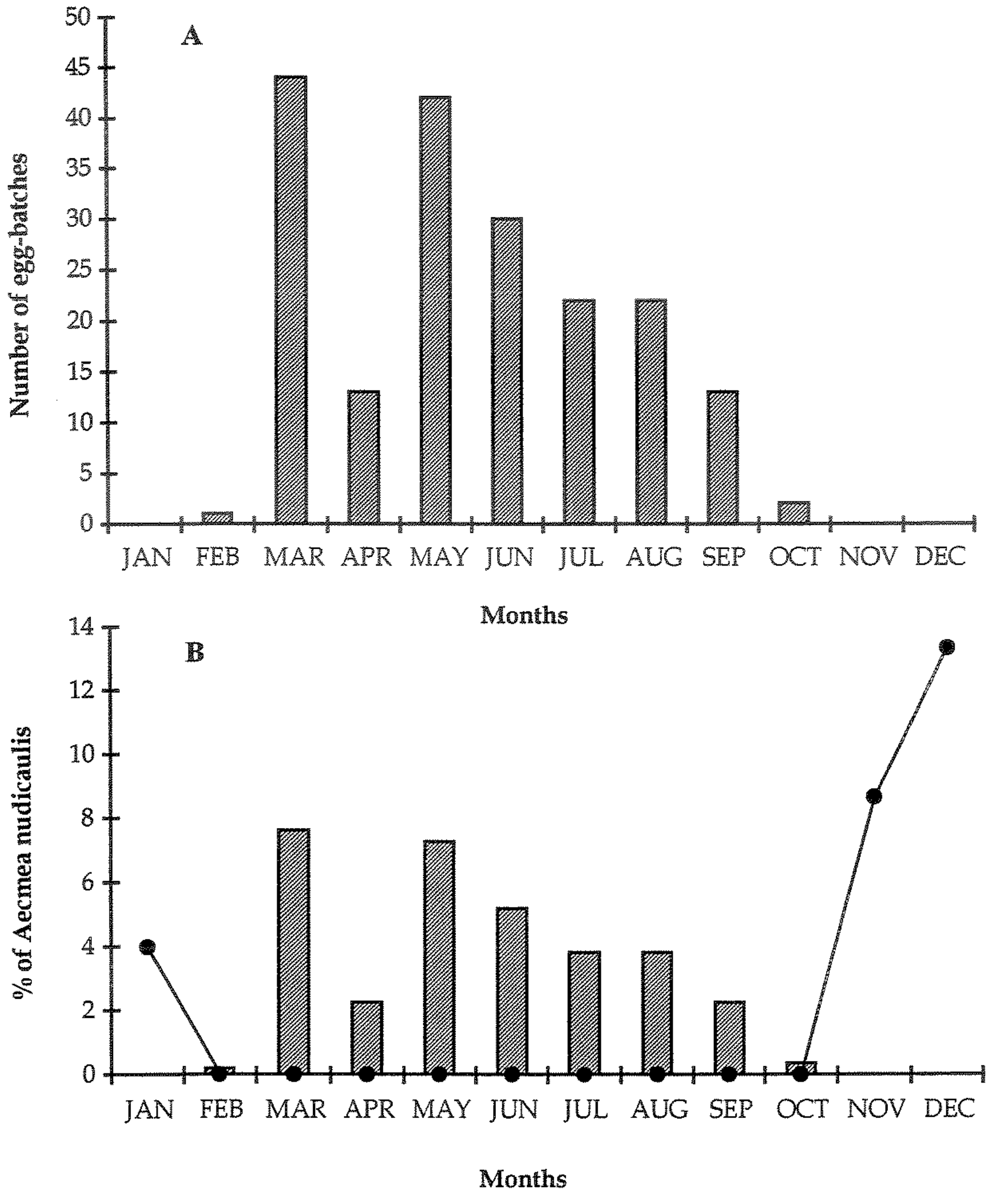


FIGURE 2. (A) Number of egg-batches of the harvestmen *Bourguyia albiornata* observed monthy from January to December 2000 at Cardoso Island, SE Brazil. (B) Relationship between the percentage of individuals of the bromeliad *Aechmea nudicaulis* used as oviposition site by the harvestman *B. albiornata* (bars) and percentage of flowereing individuals (line) ($r_s = -0.751$; $p < 0.01$; $n = 12$).

5.4.4. *Effects of maternal care on egg survival*

The results of the field experiment unequivocally showed that guarding females have a protective role and a positive effect on egg survival (repeated measures ANOVA, $F_{1,18}$= 26.18, p < 0.001). All egg-batches were attacked by predators in the treatment group, and less than 7% of the unguarded eggs survived the 2-week experiment (FIGURE 3). In the control group, however, only one egg-batch was attacked and entirely consumed. In this case, the leaf tube previously containing the female and her eggs was taken over by a colony of *Crematogaster* ants (Myrmicinae). It was not possible to know if the guarding female was expelled from the nest bromeliad by the ants or if she was preyed on before ant invasion.

The main source of mortality for unprotected egg-batches was ants (FIGURE 1D), but cannibalism was also recorded. Five ant species were seen eating eggs of *B. albiornata* in the field: *Gnamptogenys moelleri* (n = 4), *Pachycondyla villosa* (n = 2), *Crematogaster* sp. (*N* = 1), *Pheidole* sp. (*N* = 2), and *Dolichoderus attelaboides* (n = 1). Predation of entire egg-batches by recruited ants usually began about 5 h after female removal. The sampling with tuna baits revealed that 73% of the individuals of *A. nudicaulis* (n = 100) are occupied by ants and/or within the foraging range of ant colonies. Twenty ant species were found attending tuna baits on the bromeliads, and the most common species were *Crematogaster* sp. (17.5%), *G. moelleri* (14.4%), *Pheidole* sp. (13.4%), and *D. attelaboides* (12.4%). Another potential predator that is very abundant at the study site is the army ant *Eciton burchelli*. This ant species forages both on ground and on vegetation and was seen entering the leaf tube of *A. nudicaulis* several times.

Both males (n = 2) and females (n = 1) of *B. albiornata* were observed consuming conspecific eggs. Cannibalistic harvestmen may eat 2 – 18 eggs and were not observed consuming entire egg-batches. On two occasions one cockroach species (Dictyoptera: Blattidae) was found over unprotected egg-batches in which a small fraction of the eggs had disappeared. It is not possible, however, to be sure that the reduction in the number of eggs was caused by the cockroaches.

Finally, an additional source of egg mortality was fungal attack. Two egg-batches out of 282 were infected by fungi; the number of affected eggs was 2 and 10. Guarding females did not remove or eat the infected eggs.

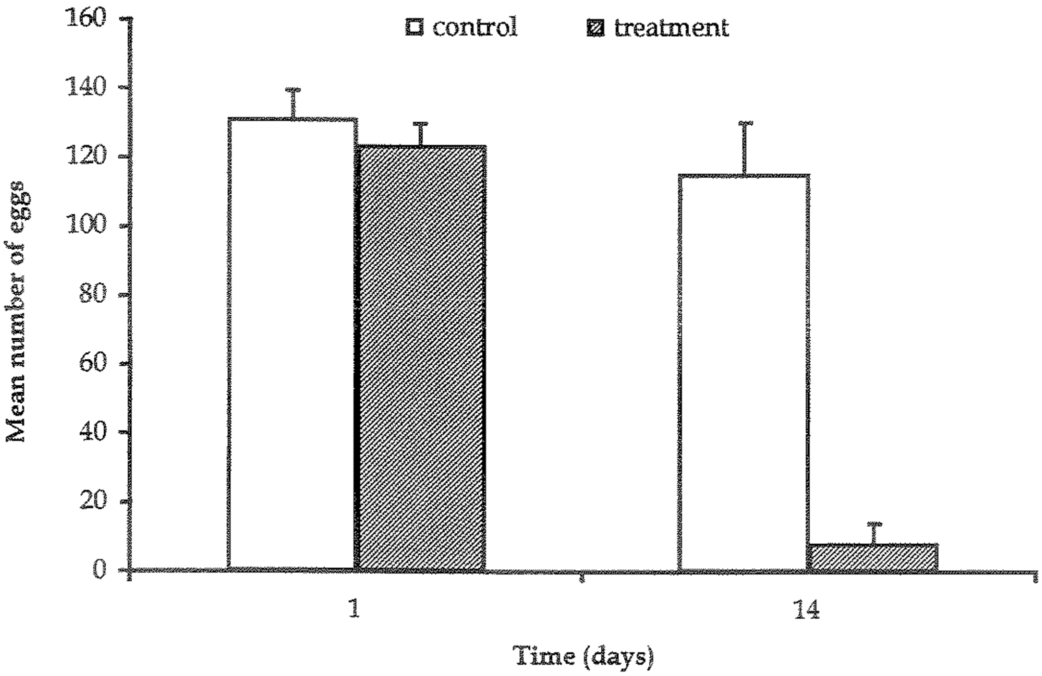


FIGURE 3. Effect of maternal care on egg survival in the harvestman *Bourguyia albiornata* after two weeks (bars = SE). Egg survival is significantly higher when the egg batch is guarded by the female.

5.5. Discussion

5.5.1. *Choice of nest-site*

Nest-site selection is one of the most important decisions made by animals that lay eggs. For brood-guarding species, the selected site must present appropriate physical conditions for the development of the eggs as well as for the parental individuals (MORSE, 1985; RESETARITS, 1996). An inadequate place may subject both the offspring and the parents to a wide range of unfavorable factors such as dehydration, predation, and parasitism (WILSON, 1975; CLUTTON-BROCK, 1991). Many spiders exhibit precise nest-site selection for oviposition (see MORSE, 1985), and this behaviour also seems to be important among harvestmen (MACHADO & RAIMUNDO, 2001).

In the population studied, females of *Bourguyia albiornata* oviposit almost exclusively inside the bromeliad *Aechmea nudicaulis*. To talk in nest site preference, however, it is necessary to assess the relative abundance of bromeliads available in the population. In a census conducted at the study site, CAMARGO (2002) showed that *A. nudicaulis* accounts for only 10% of all epiphitic bromeliads. This species, as well as *Aechmea* sp., accumulate water inside the tube of leaves and provide a suitable microenvironment for the offspring, such as protection from streessful climatic factors and moisture fluctuations (MACHADO & OLIVEIRA, *in preparation*). Harvestmen eggs develop and hatch with greatest success when brooded in humid atmosphere; while eggs laid in dry sites dissecate and do not develop completely (EDGAR, 1971; MACHADO & OLIVEIRA, 1998).

The most common epiphitic bromeliad at the study site, *Vrisea procera* (relative abundance of 80%), also accumulates some water in the leaves axil but do not form a tube of leaves, as in *A. nudicaulis* and *Aechmea* sp. (WANDERLEY & MOLLO, 1992). The same occurs with *A. cylindrata* Lindman that despite to belong to the same genus of preferred nest bromeliad, has a leaf architeture similar to *V. procera* (WANDERLEY & MOLLO, 1992). Therefore, this species probably is not an appropriate nest site for the reproduction of *Bourguyia albiornata*.

As opposed to what was found for the cave-dwelling harvestman *Goniosoma longipes* (MACHADO & OLIVEIRA, 1998), the reproductive activity of *B. albiornata* is not correlated with rainfall. Females of *B. albiornata* may be less dependent of rainfall since the leaf tube of *A. nudicaulis* accumulates water throughout the year, and the wet microhabitat maintained inside the nest bromeliad probably favours egg development. The reproductive activity of *B. albiornata* peaked just after the flowering period of *A. nudicaulis*. During the flowering season, the interior of the tubes of leaves of the bromeliads are occupied with the inflorescence stalk and thus are not available for oviposition (FIGURE 1B). The synchronization of the maternal investment in offspring with the phenology of *A. nudicaulis* suggests that the reproductive activity of *B. albiornata* is more closely related with the availability of appropriate oviposition sites than with climatic factors.

5.5.2. *Costs of maternal care*

The costs of reproduction for parental individuals can be analyzed at two levels (see BELL, 1976): first the ecological cost associated with an increased exposure to predation while searching for an appropriate oviposition site, laying eggs, or guarding the offspring; and second the physiological cost associated with the allocation of energy to egg production and other parental activities rather than individual growth or maintenance. The results obtained in this study illustrate these two kinds of costs imposed to a harvestman female. Guarding females of *B. albiornata* remain over an egg-batch for up to 43 days and during this period they may become more vulnerable to predators. Although the nest bromeliad provides an effective refuge against large predators (mainly birds and mammals) it also represents a dead end tube if a female is attacked by a predator that is able to enter the bromeliad, such as spiders. In fact, the only three predation events on adults observed in the field were directed toward guarding females (see section Parental Care).

From the physiological standpoint, females first invest a great amount of energy to produce large and nutritionally-rich eggs. Moreover, they may spend time and energy searching for a bromeliad to be used as oviposition site. Although *A. nudicaulis* is an abundant species in the study site , females of *B. albiornata* select a sort of morphological features of the bromeliads such as length of the leaf tube, amount of debris inside the leaf tube, and inclination of the bromeliad (MACHADO & OLIVEIRA, *in preparation*). Therefore, it is reasonable to suppose that females invest some time and energy looking for an appropriate nest bromeliad. Finally, besides being deprived from food during the brooding period, females of *B. albiornata* have additional energetic costs associated with the protection of the eggs against predators. The possible physiological costs of reproduction in this harvestman species is further supported by the significant decrease in female fecundity in subsequent reproductive events, which suggests a trade-off between egg production and maternal care (TALLAMY & DENNO, 1982).

5.5.3. *Evolution of maternal care*

Despite the ecological and physiological constraints, parental investment theory predicts that maternal care will evolve when the individuals' benefit (in terms of offspring survival) overrides the costs of the parental behavior (TRIVERS, 1972). There are four main environmental situations that may account for the evolution of subsocial behaviour in arthropods: (a) a physically harsh environment (WILSON, 1971); (b) a stable and structured environment that favours philopatry, large body size, iteroparity, and reduced brood size (WILSON, 1975); (c) food specialisation leading to feeding facilitation or protection of resources from competitors (WOOD, 1976); and (d) constant exposure to heavy predation (ODHIAMBO, 1960). There is no evidence that harvestmen females enhance the feeding efficiency of their nymphs nor that parents are able to actively protect the offspring against physical stress of the environment, such as dehydration (review in MACHADO & RAIMUNDO, 2001). The available information, however, suggests that severe predation pressure on eggs could be the most important selective pressure leading to the evolution and maintenance of maternal care in harvestmen species (MORA, 1990; MACHADO & OLIVEIRA, 1998; this study). Our field experiment corroborated this idea and showed that predation on eggs is the main mortality factor in *B. albiornata,* and that egg-guarding by the female is crucial for brood survival. Unprotected eggs are promptly attacked by ants, which may consume an entire batch in a few hours.

The effectiveness of the maternal care in harvestmen was previously demonstrated for *Goniosoma longipes,* whose females reproduce inside caves (MACHADO & OLIVEIRA, 1998). In the cavernicolous environment, however, the most important predators are conspecific individuals that are capable of cannibalizing entire batches (MACHADO & OLIVEIRA, 1998). This difference in the nature of predation pressures between *Goniosoma* and *Bourguyia* is probably related with the low frequency of ants inside caves, and the high density of *Goniosoma* in this type of habitat (see also MACHADO *et al.*, 2000). In the external environment ants are by far the most important predator group (WILSON, 1975; HÖLLDOBLER & WILSON, 1990), and at our study site at least 20 species nest and/or forage in the same bromeliad used by females of *B. albiornata* as oviposition site.

Maternal care evolved independently several times within the suborder Laniatores (MACHADO & RAIMUNDO, 2001). In the family Gonyleptidae, however, it is not clear if maternal care is primitive or if this behaviour has risen repeatedly in different species. Although there is no information on reproductive biology for some subfamilies of Gonyleptidae, it seems that the ancestral form of parental care within the family is egg-hiding behaviour, with multiple origins of maternal care within the different subfamilies (MACHADO & RAIMUNDO, 2001).

Working on hemipterans, TALLAMY & SCHAEFER (1997) proposed that offspring assistance would be an extremely costy behaviour and species that developed alternative mechanisms to avoid maternal care would be positively selected. In hemipterans, however, the evolution of a piercing ovipositor allowed many lineages to hide eggs from predators and parasites by inserting them into protective plant tissues or soil (ZEH *et al.*, 1989; TALLAMY & BROWN, 1999). Additionally, there is evidence that maternal care is no more effective in protecting offspring than hiding eggs or spreading them through time and space (TALLAMY & SCHAFFER, 1997).

Laniatorean harvestmen (such as the Gonyleptidae), however, have a short ovipositor and therefore are unable to insert their eggs in sheltered places (BERLAND, 1949; MACHADO & RAIMUNDO, 2001). Most asocial laniatorean species deposit eggs on exposed surfaces (rocks or vegetation) and, sometimes, cover them with debris (CANALS, 1934; JUBERTHIE, 1964; COKENDOLPHER & JONES, 1993; WILLEMART, 2001). Thus, if this behaviour is less effective than parental care in egg protection, natural selection would favour the evolution of prolonged association between parents and offspring, despite the costs in terms of fecundity. Contrary to the Laniatores, harvestmen of the suborder Palpatores have a long ovipositor and are able to hide their eggs in sheltered places (BERLAND, 1949; EDGAR, 1971; MACÍAS-ORDÓÑEZ, 1997). This structure, analogous to the hemipterans piercing ovipositor (TALLAMY & SCHAEFFER, 1997), enable the species of this group to confer protection to the eggs and avoid the costs maternal care. Indeed, no palpatorean harvestman is known to present subsocial behaviour, and their fecundity is significantly higher when compared with laneatoreans (MACHADO & RAIMUNDO, 2001).

5.6. Acknowledgements

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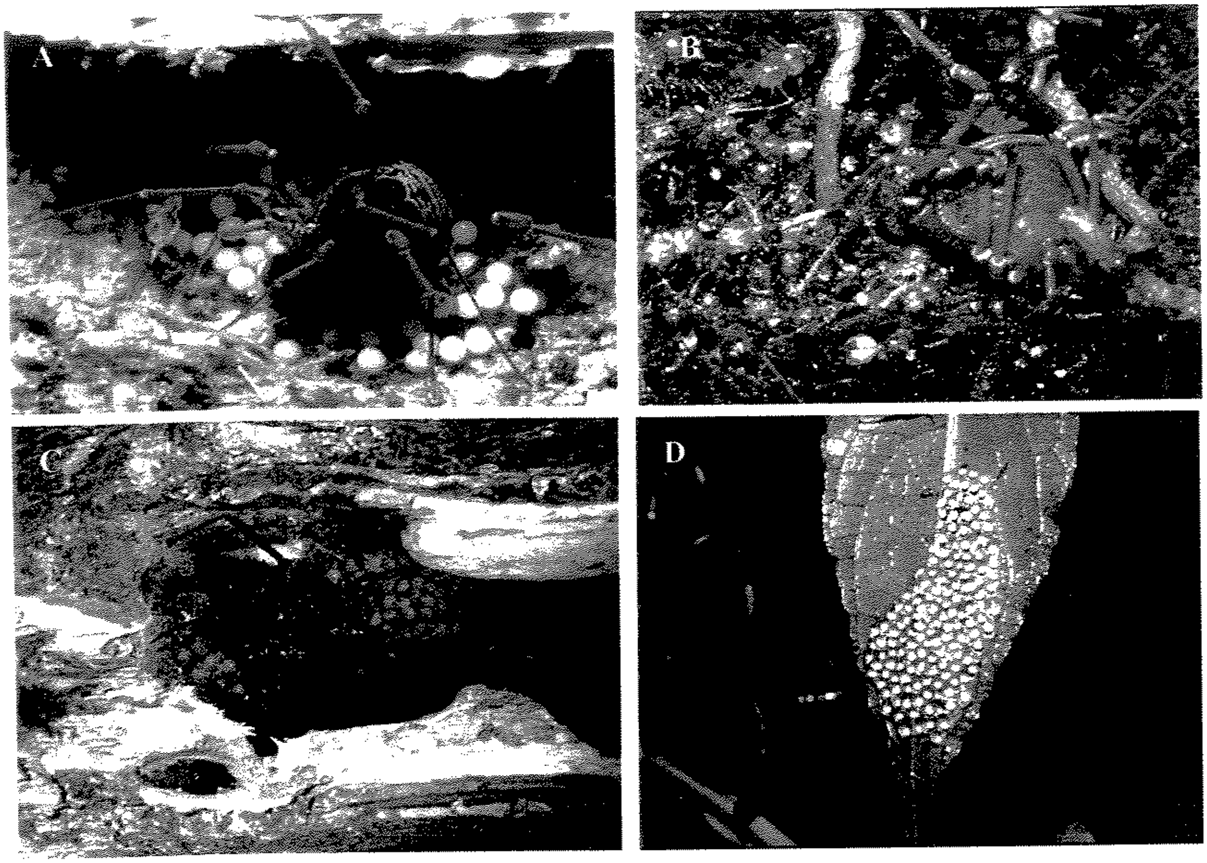
CAPÍTULO 6

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



(A) Fêmea de *Erginulus clavotibialis* e (B) *Discocyrtus oliverioi* cuidando dos ovos; (C) Macho de *Gonyleptes saprophilus* cuidando dos ovos; (D) Desova de opilião sobre a vegetação.

*MACHADO, G. & R.L.G. RAIMUNDO. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones). *Ethology, Ecology & Evolution*, 13: 133-150.

6.1. Abstract

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 repugnatory secretions on 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 decrease 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 fecundity significantly higher than in Laniatores which show subsocial behaviour and the egg size is smaller than in Laniatores.

6.2. Introduction

Parental investment can be defined as any behaviour exhibited towards the progeny which increases its survival rate at the cost of the aptitude 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 by small harvestmen, with short legs and superficially look like mites, including 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, mood, 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 such a diversity of forms of parental investment found in Opiliones.

6.3. An overview of reproductive patterns in Opiliones

6.3.1. *Suborder Cyphophthalmi*

There are few records on 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 a 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).

6.3.2. *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 discharge of repugnatory secretions on eggs (TABLE 1). Subsocial behaviour has never been observed in Palpatores.

Most species have a long ovipositor and lay their eggs in 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 on 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 rocks surfaces (JUBERTHIE, 1964). Females of these species deposit eggs on moss branches or rock 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 under 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 repugnatorial 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).

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 in each time and during 1 year there are numerous ovipositions; (2) females lay less than 20 eggs in 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 mucus that surrounds the egg-batch	JUBERTHIE, 1964
NEMASTOMATIDAE			
Mitostoma pyrenaeum	2	egg-hiding and mucus production	JUBERTHIE, 1964
Nemastoma bacciliferum	2	egg-hiding and mucus 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 mucus 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 mucus that surrounds the egg-batch	JUBERTHIE, 1964
S. paradoxum	2	production of hygroscopic mucus that surrounds the egg-batch	JUBERTHIE, 1964

Table 1. Continued.

Species	Type of oviposition	Forms of parental investment	Source
Sclerosomatidae			
Leiobuninae			
Leiobunum calcar	3	egg-hiding	Edgar, 1971
L. flavum	3	egg-hiding and covering with repugnatorial substances	Edgar, 1971; Clawson, 19
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 repugnatorial substances	Edgar, 1971; Clawson, 19 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 cambridgei	2	egg-hiding inside empty snails' shells	Pabst, 1953

6.3.3. *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 behaviour of 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 conjunct of eggs. These types of oviposition may be shaped by the abilities of predators or parasites at finding 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 the 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).

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).

Table 2. Forms of parental investment within the suborder Laniatores (Opiliones). The types of oviposition 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, 1
Gryne orensis	2	egg-hiding	Canals, 1936
Metalibitia paraguayensis	2	egg-hiding	Canals, 1936
Vonones sayi	2	egg-hiding	Cokendolpher & Jones, 199
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. catarina	4	egg/young guarding by female	Machado *et al., in press*
G. spelaeum	4	egg/young guarding by female	Gnaspini, 1995

TABLE 2. Continued.

Species	Type of oviposition	Forms of parental investment	Source
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 preparation*
Ilhaia sp.	1	*egg-hiding*	PEREIRA *et al., in preparation*
Neosadocus 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	WILLEMART, 2001
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.*, 2001
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

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

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 through 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 in 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 1). 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 eggs were guarded. In the later two species it is still unclear whether there is any association between the male and 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 1).

6.4. 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 hypotheses to explain this 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, which 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 adopting a caring role (WITTENBERGER, 1981). Moreover, harvestmen males are unique among arachnids by having an extrusible penis and internal fertilisation, which excludes the order of gamete release hypothesis as an explanation for the evolution of paternal care in harvestmen.

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 the 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 fishes (RIDLEY, 1978), amphibians (WELLS, 1977), and probably harvestmen as well.

MORA (1990) suggested that the 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 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-hatched 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 oviposition sites (see WHITHAM, 1986).

In *Goniosoma longipes* a male may defend an 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 takes egg guarding for up to two 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 the male caring for the offspring during the entire developmental period, but it constitutes an 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 fourth leg femur, 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).

6.5. 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 the 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 h 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 1). 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 1) in a phylogenetic tree (A.B. KURY & 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 points out that the ancestral form of parental investment within Gonyleptidae is egg hiding behaviour, with multiple origins of maternal care within the family. An additional weak evidence is provided by the fact that in Cosmetidae, which are the sister family of Gonyleptidae (KURY, 1994), the 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 is closely related to its scarcity.

TABLE 3. Causes of brood mortality in harvestmen with parental care. Sources for cited species same as in TABLE 2.

Causes of brood mortality Species	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

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 one year but reproduction takes place during a restricted period, usually in the autumn (TODD, 1949; JUBERTHIE, 1964; CANNATA, 1988); (c) individuals live more than one 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 studied species of Laniatores live more than 2 years, and most of them reproduce throughout the year, thus being 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 the 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 an 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). In the case of Chilopoda, the comparative method leads to a 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 repugnatory 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 on the causes of the evolution of maternal care in Laniatores in detriment to Palpatores.

Defence against fungi may be an exception since it does not depend on the 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, Craterostigmomorpha, 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 repugnatorial fluids as in laniatorean harvestmen. Some species of Lithobiomorpha and Scutigeromorpha also have repugnatorial 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 (mean ± SD = 160.4 ± 102.7 eggs; n = 23; range = 41 - 500) than in Laniatores (mean ± SD = 77.1 ± 28.8 eggs; n = 12; range = 25 – 103) (Moran's I = -

0.20; $p < 0.01$). Furthermore, egg also tends 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 (mean ± 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.

6.6. 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 hypothesis and to establish the history of the character "parental care" among harvestmen.

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CONCLUSÕES

Fêmea ovígera de *Gonyleptes guttatus*.

Principais conclusões dos capítulos

No primeiro capítulo desta tese ficou demonstrado experimentalmente que fêmeas do opilião *Goniosoma longipes*, que se reproduzem preferencialmente no interior de grutas na região de Atibaia (SP), são capazes de defender ativamente a prole contra predadores. Desovas sem a proteção materna podem ser consumidas rapidamente e, no experimento realizado no campo, menos de 5% dos ovos desprotegidos sobreviveram após duas semanas. Os principais predadores de ovos são co-específicos e grilos cavernícolas. Fêmeas de *G. longipes*, entretanto, não conseguem deter o ataque de fungos sobre os ovos, o que, em alguns casos, pode afetar uma desova inteira. Neste capítulo também foi demonstrado que machos de *G. longipes* patrulham ativamente uma área contendo suas parceiras e suas respectivas desovas. Removendo experimentalmente uma fêmea de sua desova o macho pode assumir temporariamente a guarda dos ovos, prevenindo a predação da prole. Isto sugere que o macho pode cuidar da prole caso a fêmea deserte ou morra.

No segundo capítulo, uma complementação ao estudo da história natural de *G. longipes*, foram descritos o padrão de atividades, dieta, gregarismo e comportamentos defensivos. Durante o dia, os indivíduos foram encontrados no interior das grutas (isolados ou em agregações), prostrados sobre as paredes internas. Cerca de uma hora antes do anoitecer os indivíduos moveram-se para a entrada da gruta onde se concentraram até a escuridão completa. Em seguida, abandonaram a gruta para forragearem no chão e, principalmente, sobre a vegetação. Pouco antes do amanhecer todo os indivíduos retornaram para a gruta e recompuseram os agregados. As agregações de *G. longipes* consistiram principalmente de adultos (machos e fêmeas), variaram de sete a cerca de 200 indivíduos e foram encontradas preferencialmente perto da água e longe da entrada da gruta. Os principais comportamentos defensivos foram a liberação de secreção repugnatória, a fuga e o desprendimento do substrato.

No terceiro capítulo foi testada a possível função de feromônio de alarme atribuída à secreção defensiva de opiliões (HOLMBERG, 1986). O experimento foi realizado em condições de campo com a espécie *Goniosoma* aff. *proximum*, que forma agregações sobre rochas graníticas nas margens de riachos de interior de mata na Ilha do Cardoso (SP). Os resultados apontaram que a secreção repugnatória dessa espécie de opilião é indubitavelmente capaz de mediar uma resposta de alarme, incitando uma fuga generalizada dos indivíduos agregados. Além disso, foi demonstrado que, quanto mais indivíduos houver em uma agregação, mais rápida se dá a resposta de alarme. Provavelmente o sinal químico é percebido através das pernas sensoriais e agregados maiores possuem mais pernas capazes de detectar a liberação da secreção.

No quarto capítulo foram estudadas cinco espécies de *Goniosoma* que ocorrem nas regiões sudeste e nordeste do Brasil. Analisando os dados obtidos nesse estudo, juntamente com as informações disponíveis na literatura sobre outras espécies de *Goniosoma,* foi possível caracterizar o gênero como um grupo onde o cuidado à prole é onipresente, em que muitas espécies ocuparam o ambiente cavernícola e no qual o comportamento gregário é amplamente difundido.

No quinto capítulo ficou demonstrado que fêmeas do opilião *Bourguyia albiornata,* que ovipõem exclusivamente em bromélias, são capazes de defender ativamente a prole. Da mesma forma que em *G. longipes,* desovas desprotegidas são inteiramente predadas em pouco tempo. No caso de *B. albiornata,* entretanto, os principais predadores de ovos são formigas, animais extremamente abundantes na vegetação de mata de restinga na Ilha do Cardoso (SP). O estudo mostrou também que as fêmeas ovipõem preferencialmente no interior do tudo de folhas formado pela bromélia *Aechmea nudicaulis,* sugerindo que, além da guarda de ovos, a seleção de micro-habitats para oviposição também possa ser uma forma importante de investimento parental em *B. albiornata.* Durante um ano de estudo as fêmeas da população se reproduziram até três vezes e o número de ovos por desova decresceu significativamente ao longo dos eventos reprodutivos. Este decréscimo sugere um alto custo do cuidado parental em termos de fecundidade para as fêmeas.

No sexto capítulo são revisadas as formas de investimento parental apresentadas por opiliões e uma das principais conclusões é que existe uma grande diversidade de comportamentos de cuidado à prole no grupo. Esses comportamentos variam em complexidade e podem abranger desde a seleção de micro-habitats para oviposição até interações prolongadas entre um indivíduo parental e sua prole. Ao contrário do que se imaginava inicialmente, o cuidado maternal é amplamente difundido dentro da sub-ordem Laniatores. O cuidado paternal ocorre em pelo menos quatro espécies da ordem e estes são os únicos casos de guarda da prole pelo macho em aracnídeos. A melhor teoria para explicar a evolução da assistência paternal é associação com a prole (WILLIAMS, 1975). Segundo essa teoria, machos que defendem um território reprodutivo no qual as fêmeas vão ovipor estariam mais propensos a cuidar da prole, pois o custo adicional de defesa dos ovos seria reduzido. A guarda da prole tanto pelo macho quanto pela fêmea previne a predação e, aparentemente, é crucial para a sobrevivência dos ovos.

Através de análises comparativas ficou demonstrado que a evolução da subsocialidade nos Laniatores foi acompanhada por um decréscimo significativo na fecundidade em relação aos Palpatores, cujas espécies apresentam somente formas simples de cuidado à prole.

Interconectando defesa, gregarismo e investimento parental

A primeira grande questão desta tese buscou entender se a defesa química em opiliões, caracterizada pela liberação de substâncias repugnatórias, poderia favorecer a evolução e/ou manutenção do comportamento gregário em opiliões. Os dados obtidos na tese, assim como informações disponíveis na literatura, permitem elaborar um cenário hipotético para a evolução da socialidade no gênero *Goniosoma*, o mais bem estudado até o momento em regiões neotropicais (ver CAPÍTULOS 1, 2, 3 e 4). Primariamente, limitações fisiológicas agindo em opiliões individuais promoveriam uma resposta comportamental para a seleção de micro-ambientes com condições adequadas de umidade, temperatura e incidência luminosa. A ausência de canibalismo entre os indivíduos pode ter favorecido a tolerância entre coespecíficos, que é proposta aqui como uma pré-aptação ao gregarismo em opiliões.

As funções derivadas do comportamento gregário podem incluir:

(a) Redução na probabilidade individual de ser predado (efeito de diluição);
(b) Reforço na defesa química pela liberação coletiva de secreções repugnatórias;
(c) Aumento na eficiência de fuga como conseqüência do sinal de alarme.

Em conjunto, estas funções defensivas podem superar os custos da vida em grupo (como aumento na conspicuidade e na chance de propagação de patógenos) e podem ser responsáveis pela manutenção da socialidade em indivíduos não geneticamente relacionados (FIGURA 1).

A segunda grande questão desta tese buscou entender como aspectos da morfologia geral do corpo, aliados aos mecanismos de defesa apresentados por uma espécie, podem influenciar sua forma de investimento parental. Segundo ZEH & SMITH (1986), a guarda da prole em artrópodes só pode ocorrer quando o indivíduo parental possuir características morfológicas e/ou comportamentais que o capacite repelir de forma eficiente os principais predadores de ovos/ninfas (FIGURA 1).

Nos Palpatores, cujas espécies possuem corpo pequeno, pernas longas e frágeis, pedipalpos sem espinhos e empregam mecanismos evasivos de defesa, não existem casos de subsocialidade, provavelmente porque os indivíduos não são capazes de guardar a prole de modo eficiente (CAPÍTULO 6). Entretanto, ao contrário dos Laniatores, os Palpatores possuem um ovipositor longo, o que lhes permite inserir os ovos em locais inacessíveis a muitos predadores, conferindo proteção à prole sem a necessidade de defendê-los ativamente (CAPÍTULOS 5 E 6). Nos Laniatores, cujas espécies possuem pernas e corpo robustos, pedipalpos com espinhos e que empregam mecanismos de defesa contundentes, os indivíduos são capazes de guardar a prole eficientemente (CAPÍTULOS 1, 5 E 6). Nesse grupo a subsocialidade é um comportamento amplamente difundido e deve ter evoluído em resposta a pressões ecológicas como o alto risco de predação dos ovos (CAPÍTULOS 1, 5 E 6).

A principal conclusão desta tese é que características morfológicas e comportamentais relacionadas à defesa parecem influenciar direta ou indiretamente a evolução e/ou manutenção da subsocialidade a da socialidade em opiliões (FIGURA 1). Ainda existem muitos aspectos da história natural de opiliões que precisam ser estudados ou testados experimentalmente. Da mesma forma que para aranhas e escorpiões, o aumento no conhecimento biológico sobre os opiliões pode trazer importantes contribuições teóricas para a ecologia comportamental como um todo. Entre estas, merecem destaque questões relacionadas aos custos e benefícios do cuidado parental, competição espermática e cortejo copulatório, inversão dos papéis reprodutivos e pressões ecológicas e evolutivas levando ao gregarismo em indivíduos não geneticamente aparentados.

Espero, por fim, que os trabalhos apresentados nesta tese sirvam de estímulo para que novos pesquisadores iniciem sua carreira científica adotando os opiliões como grupo de estudo. Nas últimas duas décadas houve um aumento expressivo no número de trabalhos publicados sobre ecologia e comportamento de opiliões. Trabalhos com espécies neotropicais correspondem atualmente a 50% do total publicado no mundo. O estudo dos opiliões está, no entanto, em seu princípio e informações básicas sobre a história natural das espécies ainda são cruciais para a formulação de hipóteses testáveis sobre o significado adaptativo de diferentes comportamentos.

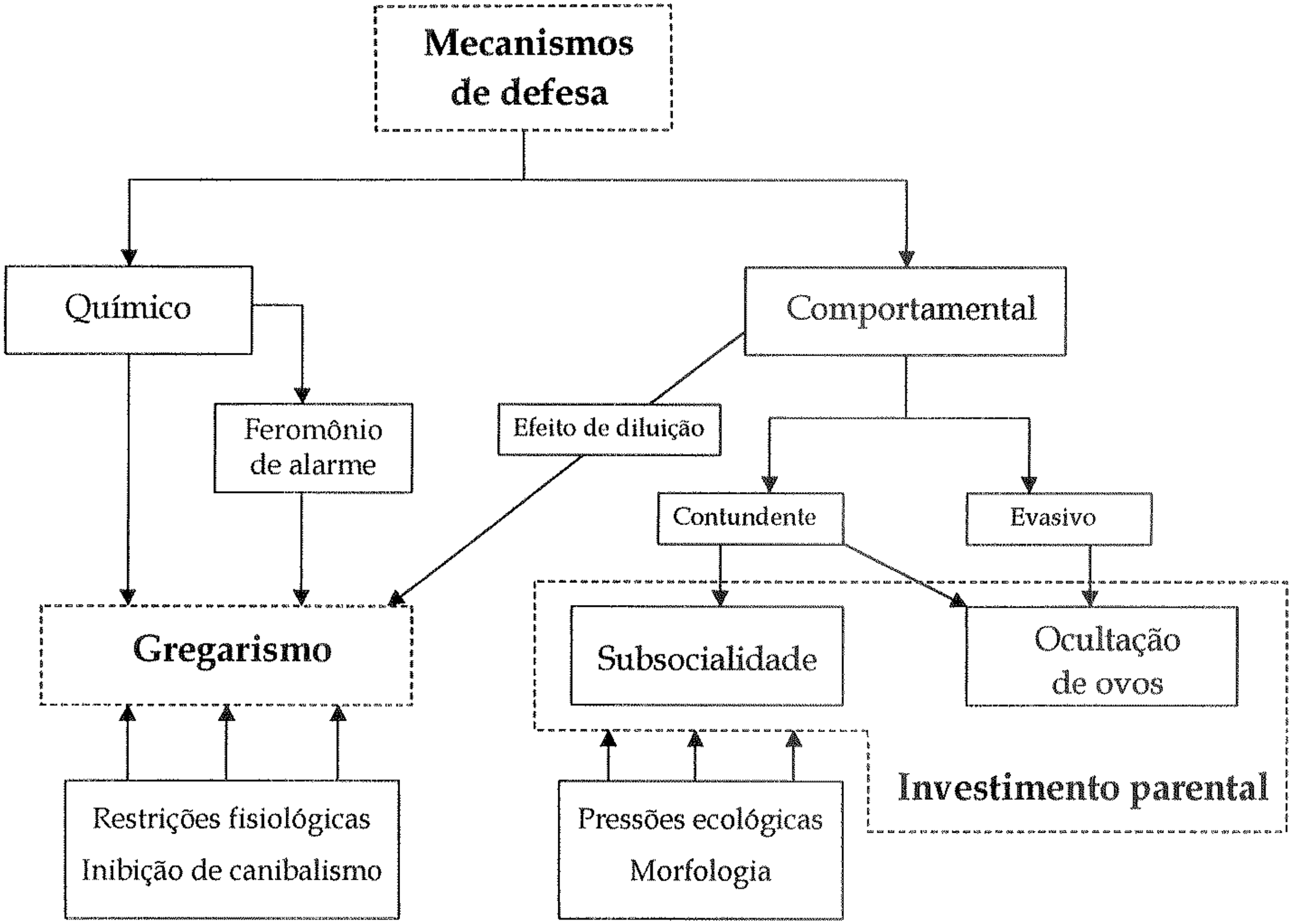

FIGURA 1. Diagrama representando como os mecanismos de defesa podem influenciar a evolução e/ou manutenção do gregarismo e as formas de investimento parental em opiliões. Veja texto para detalhes.

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