The evolution of parental care in insects

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For my wonderful family.

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Uganda

Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. No part of this thesis has been submitted for another qualification at Cambridge or at any other university. The text of this thesis does not exceed 80,000 words.

Signed . . . .

Date . . . .

Abstract

This thesis concentrates on evolutionary costs and benefits of insect parental care. I use phylogenetic methods to test large-scale hypotheses, and field studies to test proximate hypotheses. Initially I look at the evolution of variation in the sex performing care, reconstructing transitions across insect evolutionary history. Consistent with theory, early insects had no care, and their descendants evolved either male care, or female care followed sometimes by biparental care. Secondly, I investigate parental care trade-offs. I find that in insects, care is associated positively with offspring survival but negatively with fecundity, suggesting a general trade-off between current and future reproduction. In the second part of the thesis, I use the assassin bug genus *Rhinocoris* to investigate proximate costs and benefits influencing male care, the rarest form of care. High density is predicted to favour male care; I investigate why male-caring *Rhinocoris* live at high density on the plant *Stylosanthes*. Plant preference is rare in predators and I show that the plant protects eggs from predators as well as harbouring favourable prey, factors not usually linked to parental care. Lastly I investigate an unstudied sexual conflict in male-carers. If females prefer caring males, males should be selected to display their eggs conspicuously. Conspicuousness may carry costs to eggs, so females should prefer inconspicuous locations. In the field this conflict exists for one *Rhinocoris* species but is absent in a sister species, showing that parental care can have complex effects. My results show that while broad patterns of costs and benefits largely follow theory, finer patterns depend on subtle ecological factors.

Contents

Chapter 1

Introduction

1.1   Parental care behaviour

Parental care, where animals guard, incubate or feed developing zygotes after fertilization, is a major theme in behavioural ecology (Clutton-Brock, 1991). Behavioural ecology focuses on proximate costs and benefits of behaviour to individuals and the ways in which these are predicted to affect evolutionary patterns (Krebs & Davies, 1993, 1997), and so authors studying parental care have traditionally taken two approaches: (1) field tests of the immediate costs and benefits of parental care to the individual, and (2) theoretical hypotheses about how those costs and benefits have affected the evolution of parental care. In this thesis, I use comparative studies of insects to look on a large scale at the evolutionary costs and benefits of parental care. Then I focus on one group of insects, the assassin bugs, to look on a small scale at some of the evolutionary costs and benefits of the rarest form of parental care in nature: care performed by the male alone. Lastly, I investigate a case where male care in assassin bugs

can create a situation in which costs and benefits for males and females come into conflict.

A major question for those attempting to understand factors influencing parental care evolution is "why is there so much variation in the sex that provides care?". Across the animal kingdom, parental care can be done by either or by both sexes, and patterns differ depending on the taxonomic group in question (Gross & Shine, 1981; Kokko & Jennions, 2003; Queller, 1997; Smith, 1977; Trivers, 1972). The costs and benefits behind the evolution of such diversity in parental care are complex: costs and benefits are predicted to be different for each sex, and so the factors driving each sex to care should correspondingly be different. Testing these hypotheses involves reconstructing the most likely parental care states in ancestral species, and calculating which states have been historically most likely to evolve into which others (e.g. Beck, 1998; Burley & Johnson, 2002; Gittleman, 1981; Goodwin *et al.*, 1998; Mank *et al.*, 2005; Reynolds *et al.*, 2002).

In field studies, parental care is usually shown to be costly to the parent that has to perform it (Balshine-Earn, 1995; Beissinger, 1990; Shine, 1980; Székely & Cuthill, 2000; Vandenberghe, 1992). Parental care is an energetic investment in the survival of the current brood of offspring, which is assumed to take up part of a finite resource budget that an animal can allocate to reproduction. It is therefore predicted to trade off against future reproduction (e.g. Clutton-Brock, 1991; Smith, 1977; Trivers, 1972; Winkler, 1987). As predicted, looking at single species, many authors have found that investment in parental care is indeed traded off against future reproduction (e.g. Badyaev & Ghalambor, 2001; Clutton-Brock *et al.*, 1983; Heideman *et al.*, 2005; Lummaa, 2001; Tallamy

& Denno, 1982, reviewed in Clutton-Brock, 1991). What is less commonly or thoroughly addressed is whether or not we are justified in drawing the general conclusion that this trade-off applies to all species (Clutton-Brock, 1991).

The biggest puzzle for students of parental care evolution is the existence of male-only care. According to theory, males of sexually reproducing animals are highly unlikely to evolve to care for offspring since their small, cheap gametes allow them effectively unlimited potential offspring, whilst females are limited to the numbers of gametes that each can physically produce (Trivers, 1972). This means that a male caring for offspring would forego more potential offspring than would a female. This is compounded in species where fertilization is internal: here, following intromission the male is able to desert his mate before eggs are fertilized, leaving the female in the 'cruel bind' of having dependent offspring. Despite this, small numbers of species have evolved male-only parental care, and the costs and benefits surrounding care in these species have attracted much attention (Manica & Johnstone, 2004; Smith, 1997; Tallamy, 2000; Zeh & Smith, 1985).

Male-only parental care also may have a specific potential consequence which is, to my knowledge, unstudied: it creates a potential conflict of interest between males and females. If males care for eggs, it is often beneficial for a female to prefer to add eggs to the brood of an already-caring male rather than to initiate a brood herself (Forsgren *et al.*, 1996; Lindstrøm, 2000; Marconato & Bisazza, 1986; Thomas & Manica, 2005). This means that males gain mating benefits by caring, so we would predict that caring males should want to maximize the conspicuousness of the eggs, to attract females. However, females have no interest in a male's potential to attract other mates, and they should

want to *minimize* their own eggs' conspicuousness, to reduce predation and parasitism.

1.1.1 Parental care in insects

To date, most work on the evolutionary diversity and life-history consequences of parental care has been on vertebrate taxa. However, invertebrates, particularly insects, provide an excellent group in which to explore these questions further. Insect parental care has many evolutionary origins, having arisen at least once in each of at least thirteen orders (Tallamy & Wood, 1986), can be performed by either sex, or by both sexes, and ranges from simple guarding of eggs by one individual to the extended social systems we call 'eusocial', with care and provisioning by specialized non-reproductive castes of workers (Crespi & Choe, 1997; Eickwort, 1981; Hinton, 1981; Trumbo, 1996; Wilson, 1971, table 1.1). Insect parental care is costly to the parent, in terms of loss of energy (Agrawal *et al.*, 2005; Tallamy & Denno, 1982; Thomas, 1994), increased predation risk (Reguera & Gomendio, 1999) and lost mating opportunities (Thomas, 1994). As predicted, parental care has often been found to trade off against future reproduction (Agrawal *et al.*, 2005; Kaitala & Mappes, 1997; Tallamy & Denno, 1982; Zink, 2003), although it is not yet known whether insects generally incur this trade-off. Furthermore, it is relatively easy to measure life-history variables in insects which in vertebrate taxa would be considered the 'holy grail': measures of survival in the field, or measures of total reproduction such as lifetime fecundity or lifetime reproductive success. Given this ease of study, a gigantic wealth of life-history data exists in the lit-

erature (see summaries in e.g. Cornell & Hawkins, 1995; Garcia-Barros, 2000; Hinton, 1981).

However, comparative work on insects is relatively scarce. To answer comparative questions between species we need a phylogeny, or an evolutionary tree. We cannot take existing species simply as independent data points, since related species might be similar simply because they are related, not for reasons related to our hypothesis (Harvey & Pagel, 1991; Martins, 1996). The paucity of comparative work for insects may stem from a lack of confidence in insect phylogeny (e.g. Addo-Bediako *et al.*, 2002): owing to insects' extreme diversity, the student of insect systematics faces an immense challenge. With the advent of quick and inexpensive molecular sequencing methods, the number of published phylogenies has hugely increased over the last decade (Caterino *et al.*, 2000), making it possible at last to consider compiling a preliminary phylogeny of insects. Comparative tests that require a phylogeny are therefore increasingly feasible. They have been done for subsets of the insect tree (e.g. Fagan *et al.*, 2002), but never explicitly for taxa covering the whole class Insecta.

1.1.2   Parental care in assassin bugs

Assassin bugs (Hemiptera-Heteroptera: Reduviidae) are a very large ($\sim$3000 spp.) family of generalist predatory bugs (Ambrose, 1999; Capriles, 1990) distributed worldwide. There are several records of parental care in this group, most notably male-only and female-only care in sympatric species within one genus, *Rhinocoris*, in the subfamily Harpactorinae (table 1.2). Male-only care occurs in *R. tristis* (Thomas, 1994), *R. albopilosus* (Odhiambo, 1959) and *R. al-*

Group	Review reference	Care	Predominant care
Isoptera	Wilson (1971)	E	E
Hymenoptera	Wilson (1971)	N, F, B, E	F,E
Thysanoptera	Morris *et al.* (2002)	N,M,F,B,E	N
Coleoptera	Hinton (1981)	N, F, B,E	N
Dermaptera	Eickwort (1981)	F	F
Hemiptera	Tallamy & Schaefer (1997)	N, M, F, E	N
Embioptera	Nalepa (1988)	B	B
Dictyoptera	Hinton (1981)	N, F, B	N
Orthoptera	Eickwort (1981)	N, F	N
Psocoptera	New (1985)	N, F	N
Lepidoptera	Nafus & Schreiner (1988)	N, F	N

Table 1.1: Records of parental care for different orders of insect. Key: N = No care, F = Female-only care, M = Male-only care, B = Biparental care, E=Eusocial care.

bopunctatus (Nyiira, 1970), all native to central and east Africa. In these species males are simultaneously polygynous, caring for asynchronously-laid batches of eggs from multiple females. Parental care in *R. tristis* lasts for 11–43d depending on the number of batches a male accumulates (Thomas, 1994; Thomas & Manica, 2005).

R. tristis and *R. albopilosus* are sympatric in Uganda. They are medium-sized (10–15mm), generalist predators of arthropods up to their own size, and are multivoltine, aseasonal breeders. They are reported to live at high population density on plants of the genus *Stylosanthes* (Fabaceae), which are leguminous pasture crops grown for their high protein content and ability to withstand variability in soil nutrients. I found *S. guianensis* growing at the Namulonge Agriculture and Agronomy Research Institute (NAARI) near Gayaza, approximately 40km north of Kampala, Uganda (figure 1.1). NAARI is one

Reference	Species	Care	Distribution
Thomas (1994)	*Rhinocoris tristis*	Male-only*	Cent. & E. Africa
Nyiira (1970)	*R. albopunctatus*	Male-only	East Africa
Bequaert (1935)	*R. albopilosus*	Male-only*	East Africa
Edwards (1962)	*R. carmelita*	Female-only	Cent. & W. Africa
Dispons (1965)	*R. erythropus*	Female-only	Africa
Parker (1965)	*Pisilus tipuliformis*	Female-only	Cent. & S. Africa
Louis (1974)	*Endochus* sp.	Female-only	West Africa
Bequaert (1935)	*Ghilianella* spp.	Female-only	Asia
Ralston (1977)	*Zelus* spp.	Female-only†	Cent. & S. America
Tallamy *et al.* (2004)	*Atopozelus pallens*	Female-only	Cent. & S. America

Table 1.2: Records of parental care in assassin bugs. *Female care has also been observed in the laboratory in *R. tristis* (Beal & Tallamy, 2006, and pers. obs.) and *R. albopilosus* (pers. obs.); however, females have never been recorded caring in the field (Thomas, 1994, and pers. obs.). †Originally claimed to be male-only care, this unnamed species is now thought to be synonymous with *A. pallens* and to be a female-carer (Tallamy *et al.*, 2004).

of several agricultural field stations maintained by Uganda's National Agriculture Research Organization (NARO) that maintain cultures of *Stylosanthes* since populations were devstated by an outbreak of the anthracnose fungus (Irwin *et al.*, 1984). Consistent with reports in the literature, I found *R. tristis* and *R. albopilosus* living sympatrically on the *Stylosanthes* at NAARI. Apart from *Stylosanthes*, vegetation around NAARI is mixed, with various agricultural crops grown in monoculture (cassava, *Manihot esculenta*; sweet potato, *Ipomoea batatas*; cotton, *Gossypium* spp.; banana and 'matooke', *Musa* spp.) as well as pasture land and patches of wild tropical forest. I conducted field studies between October 2003 and June 2005 with permission from NARO and the Uganda National Council of Science and Technology.

Figure 1.1: Location of the Namulonge Agriculture and Agronomy Reseach Institute (NAARI).

1.2 Chapters of this thesis

I am interested in how different patterns of insect behaviour and life-history can influence the costs and benefits leading to the evolution of parental care, and how the evolution of parental care can in turn influence patterns of insect behaviour. I restrict my analysis to parental care provided only by the parent or parents and not by helpers or workers, since the evolution of sociality in insects is a gigantic literature in itself and would warrant a separate study. There are many hypotheses about why different modes of insect parental care

should evolve. The first two chapters of this thesis present some of the first comparative analyses of factors influencing the evolution of different forms of parental care in insects. Chapter 1 asks 'what are the major transitions in insect parental care evolution?' and looks at parental care transitions across all insects, testing the predictions of hypotheses about the selective pressures driving the evolution of different parental care strategies. Chapter 2 looks at the costs and benefits of parental care in extant insect species, asking 'do insects incur a trade-off between parental care and subsequent reproduction?'. Single-species studies typically find trade-offs between parental care and fecundity; in this chapter I test how generally the trade-off applies, the first test of a general trade-off across all insects. Since comparative studies require a phylogeny, for these chapters I compile a large tree from published phylogenies. This phylogeny comprises most insect orders, and is the first of its kind.

Within assassin bugs, the factors contributing to the evolution of care have been discussed by several authors (Tallamy, 1999; Tallamy & Wood, 1986; Zeh & Smith, 1985), and explicitly modelled once (Manica & Johnstone, 2004), while the potential evolutionary consequences of parental care remain unstudied. In the second two chapters of my thesis, I use field studies on *Rhinocoris* assassin bugs in Uganda to look in more detail at the costs and benefits of the rarest form of parental care in insects and in nature as a whole: male-only care. First, I ask in chapter 3: 'what factors lead *Rhinocoris tristis* to aggregate on one species of plant, bringing about conditions for the evolution of male parental care?', exploring some of the factors contributing to high population density through specialization on the legume *Stylosanthes*, which is predicted to favour the evolution of male care (Manica & Johnstone, 2004). Lastly, in chapter 4 I

look at a specific consequence of male care, asking 'is there a sexual conflict over egg placement in male-caring *Rhinocoris*?'. This is the first investigation of the sexual conflict over conspicuousness of eggs as outlined above, which can arise in a system where males care for eggs and where females prefer to lay eggs with already-caring males.

Chapter 2

Parental care transitions in the insects

2.1 Abstract

Insects provide an excellent opportunity to test theories of parental care evolution owing to the diversity of insect parental care behaviour. Here, I look at variation in the sex of the parent providing care, a traditional focus for behavioural ecology. Using a composite phylogeny based on published studies spanning the whole class Insecta, I reconstruct ancestral care states and estimate the most likely directions of transitions in parental care. The earliest insects lost the female care that is widespread in their ancestors, and during their diversification either (1) re-evolved female care, which in some groups evolved further into biparental care, or (2) evolved male care. These data are consistent with most of the transitions predicted by current theory. In the Hemiptera, where the ancestral state is debated, I estimated that the ancestor probably had female care, consistent with the

idea that female care in this order is costly and has often reverted to no care. Of the other orders containing care, I estimated that most had ancestors with no care, suggesting that parental care arose repeatedly in these groups. However, the Dictyoptera was estimated to have had a male-caring ancestor, despite there being no extant male-carers in this group. These results show that the historical pattern of parental care evolution in insects is largely consistent with existing theories. The broad patterns I present here should form a framework within which to conduct similar, more detailed analyses for each insect order.

2.2 Introduction

Which sex should care for offspring? One way to address this problem is to analyse the evolutionary costs and benefits to each parent, test hypotheses in extant species, and thus infer the most probable direction of parental care evolution for different taxa (e.g. Dawkins & Carlisle, 1976; Gross & Shine, 1981; Manica & Johnstone, 2004; Trivers, 1972; Williams, 1975, reviewed in Clutton-Brock, 1991, Krebs & Davies 1993). A complementary approach is to reconstruct the most likely historical pattern of parental care evolution across the evolutionary tree based on extant patterns, and estimate the likelihood of evolution from one mode of care into another. This has been done successfully for many vertebrate groups (Beck, 1998; Burley & Johnson, 2002; Goodwin *et al.*, 1998; Mank *et al.*, 2005; Reynolds *et al.*, 2002; Székely & Reynolds, 1995) and a small number of invertebrate taxa (e.g. Lin *et al.*, 2004). Here I look for the first time at parental care transitions across the whole insect phylogeny.

While homeotherms have largely female care (mammals) or biparental care (birds), in poikilothermic animals, mode of fertilization has been the best predictor of which sex cares. In internal fertilizers the sex predisposed to care is the female, while in external fertilizers it is the male (Gross & Shine, 1981, reviewed in Clutton-Brock, 1991). Mode of fertilization determines which sex is able to desert the brood first, and hence which sex is left 'holding the baby' (Dawkins & Carlisle, 1976); internal fertilization also makes males less certain of their paternity, and hence potentially more likely to desert (Trivers, 1972); lastly, in external fertilization, oviposition and fertilization happen at the same time, so males are commonly 'associated' with eggs, especially since males often defend territories on which females can oviposit (Williams, 1975). The predictions of these hypotheses have largely been borne out by studies estimating historical transitions in the caring sex (table 2.1).

Insects are poikilothermic, with internal fertilization, and therefore transitions in care are predicted to be largely between no care and female care. The distribution of care among extant insects mostly agrees with this: of at least thirteen orders of insect whose members have independently evolved parental care (Tallamy & Wood, 1986), twelve contain examples of uniparental female care (the exception being the Embioptera, whose known members are all biparental), while only one contains uniparental male care (the Hemiptera-Heteroptera; a tiny number of examples also exist in the Thysanoptera). However, insect parental care is extraordinarily diverse and can be by either sex or both, sometimes with multiple strategies within families and genera (Eickwort, 1981; Hinton, 1981; Tallamy & Wood, 1986).

The selection pressures driving the evolution of parental care within in-

Ref	Taxon	Parental care	Ancestral state	Major transitions
Homeothermic (Internal fertilization)				
Reynolds *et al.* (2002)	Mammals	91% FC 9% BC	FC	FC⇌BC
Reynolds *et al.* (2002) Burley & Johnson (2002)	Birds	90–95% BC 5–10% FC <1% MC	BC (or MC)	FC→BC BC→MC
Székely & Reynolds (1995)	Shorebirds	44% BC 44% MC 13% FC	BC	MC→BC BC→FC
Reynolds *et al.* (2002)	Shorebirds (re-analysis)	–	–	BC→MC BC→FC
Poikilothermic (External fertilization)				
Mank *et al.* (2005) Gross & Shine (1981)	Teleosts (external)	21% MC 3% BC 3% FC	NC	NC→MC MC→BC
Reynolds *et al.* (2002) Beck (1998)	Anurans (mostly external)	9% MC 9% FC 1% BC	NC	NC→MC NC→FC
Poikilothermic (Internal fertilization)				
Mank *et al.* (2005) Gross & Shine (1981)	Teleosts (internal)	90% FC <1% MC	Many origins	NC→FC
Reynolds *et al.* (2002)	Squamate reptiles	97% NC 3% FC	NC	NC→FC
Kutschera & Wirtz (2001)	Leeches	Mostly NC Two families FC	NC	NC→FC

Table 2.1: Previous studies on parental care transitions in various taxa. Key to symbols: NC, no care; FC, female care; MC, male care; BC, biparental care.

sects are still under debate. The earliest insects probably lost the female care that is predominant in their arthropod ancestors when they evolved tough, desiccation-resistant eggs, and ovipositors with which to hide them (Zeh *et al.*, 1989). From there, insects that re-evolved parental care are those with unusually harsh and unusually rich environments, stable, structured environments, and high levels of predation (Wilson, 1971); or those that lost their ovipositor or reduced investment in the protective egg wall (Smith, 1997; Zeh *et al.*, 1989).

Female care could evolve from no care through internal fertilization (Gross & Shine, 1981), semelparity (Tallamy & Brown, 1999), or low population density and high costs of gamete production (Manica & Johnstone, 2004). By contrast, male care could evolve out of no care by 'association' with eggs through territoriality or mate guarding (Zeh & Smith, 1985); or by guarding overlapping broods from multiple females, high population density and short female gamete replenishment time (Manica & Johnstone, 2004). Alternatively, male care could evolve from female care or biparental care, since care is highly costly in the Hemiptera that show it (they are mostly hunters of live prey, and caring is incompatible with hunting; Tallamy & Wood, 1986), and females could enhance their fecundity by transferring care to males (Tallamy, 2000, 2001). Biparental care is proposed to evolve by males joining females when they have few alternative breeding opportunities, and they can effectively help the female defend a nest from competitors (Trumbo, 1994; Zeh & Smith, 1985). The Hemiptera in particular have been a source of debate: Tallamy & Schaefer (1997) argue that female care in this group is ancestral and that the patterns we observe today are a result of multiple losses rather than multiple gains, since care is costly to the caring female; however, a recent test of transitions among a particularly diverse group, the Membracine treehoppers (Lin *et al.*, 2004) found no evidence for this. Which state is ancestral to the entire Hemiptera remains to be formally tested.

Here I present the first attempt to reconstruct systematically ancestral states and transitions in the caring sex across the entire insect phylogeny, and hence to test the predictions arising from these theories. I am not explicitly testing the mechanisms behind the existing hypotheses of insect parental care evolution,

but testing the direction in which they predict parental care will evolve. Hence I predict (1) that the ancestor to insects was a female-carer, but that insects lost that care early in their evolution; (2) that there were subsequent transitions between no care and female care; and (3) that biparental care evolved from female care, not from male or no care. For the evolution of uniparental male care there are two alternative hypotheses: (1) male care arose from no care, and (2) male care arose from female or from biparental care. I also reconstruct the ancestral parental care state for each order that contains parental care, specifically testing the hypothesis of Tallamy & Schaefer (1997) that female care is ancestral in the Hemiptera, and discussing the biological significance of my results.

2.3 Methods

2.3.1 Parental care type

I gathered data on insect parental care (the sex of the care-giver), from literature searches using ISI Web of Knowledge (`http://wok.mimas.ac.uk`) and Google Scholar (`http://scholar.google.com`) plus various university libraries. Source references can be supplied on request. I defined parental care as post-ovipositional guarding of offspring, whether or not accompanied by pre- or post-ovipositional provisioning. I coded parental care as a factor with four discrete, unordered levels ('character states'): 'No care', 'female care', 'male care' and 'biparental care'. Care by the male was only included when it was not clearly related to mating effort (I did not include, for example, nuptial gifts, or male nest-building if this was a prerequisite for securing mates and the male left immediately after copulation).

All species used and raw data can be found in table B1 (appendix B).

2.3.2 The phylogeny

Insect phylogenies are becoming increasingly common in the literature owing to relatively recent advances in molecular sequencing techniques (Caterino *et al.*, 2000), although some claim that this may have led to a decline in the rigour of such studies (Ogden *et al.*, 2005). To reconstruct insect phylogeny I chose a subset of published phylogenies according to the following criteria: where there was a choice, I preferred total evidence over molecular phylogenies, which in turn I favoured over morphological phylogenies; I also preferred phylogenies constructed using maximum likelihood or Bayesian methods over those constructed using maximum parsimony techniques (Yang, 1996). Above these, I favoured the synthetic findings of current reviews of the state of systematics for individual taxa which summarized recent phylogenetic work. The principal sources of such reviews were the Tree of Life (`http://tolweb.org/`), which contains many phylogenetic syntheses based on recent work; and Gullan & Cranston (2005), a recent textbook. The source trees are given in table 2.2, indicating where a review was used.

Where source phylogenies conflict, they can be combined using a 'supertree' approach (Bininda-Emonds, 2003; Bininda-Emonds *et al.*, 2003, see e.g. Mank *et al.*, 2005). I did not do this for two reasons: firstly, the suitable published trees I found had a low degree of overlap, and hence a low degree of conflict, so combining them statistically is not currently worthwhile. Secondly, different supertree algorithms for combining phylogenies can provide very different solutions to the same problem depending on properties of the topology of the source trees (Wilkinson *et al.*, 2005), so the supertree approach is currently best treated with caution, especially where there is a large amount of uncertainty in the tree (M. Wilkinson, pers. comm.). In addition, since

none of the source phylogenies was based upon reproductive characters, any error in these phylogenies can be assumed to be random with respect to the transitions in the caring sex across the tree (Goodwin *et al.*, 1998).

Due to the vast diversity of insects, a great many taxa for which data exist have not been formally placed on a phylogeny. Where this occurred, I added the group at the node corresponding to the appropriate taxonomic level, creating a polytomy (multiple node). The resulting tree had 1128 species, spanning 24 out of an estimated 30 insect orders. In addition to insect orders, I also included outgroups from the Myriapoda, Isopoda, Arachnida and Crustacea. 22% of nodes were polytomous, i.e. with three or more daughter nodes.

The full tree can be found on the attached CD in NEXUS format ("Phylogeny_Full.nex") plus an image in PDF format. In addition, the CD contains the phylogeny of the Hemiptera alone ("Phylogeny_Hemiptera.nex").

2.3.3   Analysis: ancestral states and transitions

I used the program Discrete, implemented through the recent `Bayestraits` program (Pagel & Meade, 2006, available from authors on request). For discrete characters, this program uses a maximum likelihood approach to find the set of ancestral character states and transition probabilities between different states ('transition rates') that maximises the likelihood of the observed data on the tree.

To test hypotheses about the relative probabilities of each transition rate, I treated each rate essentially as a parameter in a model, and compared the likelihoods of 'nested models'. For example, to test whether the probability of male care evolving from no care was different from zero, I compared the likelihood of the full model (i.e. with no restrictions and all rates free to differ) with that of a model where the transition rate 'no care to male care' was restricted to be zero (i.e. constraining the model

Taxon	Reference
Hexapoda	Kjer (2004)
Paraneoptera	Gullan & Cranston (2005)
Holometabola	Gullan & Cranston (2005)
Neuropteroidea†	Aspöck (2002); Wheeler *et al.* (2001)
Embioptera†	Szumik (1996, 1997)
Dictyoptera†	Kambhampati (1995)
Blattodea	Maekawa & Matsumoto (2000)
Coleoptera†	Beutel & Haas (2000)
Polyphaga†	Kukalová-Peck & Lawrence (1993); Wheeler *et al.* (2001)
Scarabaeoidea	Browne & Scholtz (1999)
Elateroidea†	Lawrence (1987); Maddison (1995)
Scarabaeinae	Philips *et al.* (2004)
Chrysomelidae	Reid (2000)
Scolytidae	Normark *et al.* (1999)
Passalidae	Boucher (2005)
Bolboceratidae	Verdú *et al.* (2004)
Geotrupinae	Verdú *et al.* (2004)
Diptera†	Oosterbroek & Courtney (1995); Yeates *et al.* (2003)
Trichoptera†	Holzenthal *et al.* (1997)
Lepidoptera†	Kristensen & Skalski (1999); Wiegmann *et al.* (2002)
Ditrysia†	Kristensen & Skalski (1999)
Papilionoidea†	Kristensen & Skalski (1999); Wahlberg *et al.* (2005)
Bombycoidea†	Lemaire & Minet (1999)
Noctuoidea†	Kitching & Rawlins (1999); Mitchell *et al.* (2000)
Hymenoptera†	Ronquist (1999); Schulmeister (2003); Sharkey & Roy (2002); Vilhelmsen (1997, 2000)
Apocrita†	Dowton & Austin (2001); Ronquist (1999); Sharkey & Roy (2002); Whitfield (1998)
Aculeata†	Brothers (1999)
Apoidea†	Brothers (1999)
Cynipoidea	Ronquist (1999)
Grylloblattidae†	Jarvis & Whiting (2006)
Ephemeroptera	Kjer (2004)
Dermaptera	Jarvis *et al.* (2005)
Orthoptera	Jost & Shaw (2006)
Hemiptera	Bourgoin & Campbell (2002); Yoshizawa & Saigusa (2001)
Cicadomorpha	Cryan *et al.* (2004)
Membracoidea†	Dietrich & Deitz (1993); Maddison (1995)
Nepomorpha	Hebsgaard *et al.* (2004)
Gerromorpha	Andersen (1998)
Pentatomomorpha†	Li *et al.* (2005)
Cimicomorpha†	Schuh & Stys (1991)
Psocodea	Gullan & Cranston (2005)
Phlaeothripidae (Thysanoptera)	Morris *et al.* (2002)

Table 2.2: Selected references for source trees in phylogeny. Orders and higher levels are given in bold; families and lower levels are given in italics. I do not cite phylogenies where (1) tree topology is irrelevant (e.g. if my species fell into a perfectly dichotomous hierarchy, if, for example, I had two species in each of two genera in each of two subfamilies); (2) The phylogeny for a higher group encompasses lower taxa, or (3) where I could find no phylogeny for the taxon. †Phylogenies taken from recent reviews from the Tree of Life (http://tolweb.org)

such that male care never evolves out of no care). If the likelihood ratio of the two models was above the threshold for significance at 5% (for χ^2 with 1 degree of freedom, this is 3.81) then I concluded that this rate was significantly different from zero, or that there was a non-zero probability that male care will evolve from no care. Similarly I tested whether two rates were *equal* by comparing the unrestricted model with a model where these two rates are constrained to be equal.

Using this method, I built up a 'minimal model' of which transition rates explained most of the variance in the observed data. To do this I used a systematic approach. I first examined the magnitudes of the rates in the unrestricted model. Then, beginning with the smallest rate (the lowest probability of transition), I tested each successive rate for departure from zero. Following this, I looked at the rates that did differ significantly from zero, and tested each combination of non-zero rates to see whether they were equal.

To reduce the effect of uncertainty in the phylogeny where I had added taxa according to their taxonomy, I ran multiple tests. Based upon the original phylogeny, I created 200 'subtrees' with random resolutions of all polytomies in the phylogeny, and ran the program on each subtree. Essentially, I took a sample of 200 random, possible phylogenetic scenarios given the uncertainty due to the polytomies. If we test a hypothesis 200 times, under the null hypothesis we would expect 5% of the results to be significant by chance. Hence, when testing transition rates for departures from zero or for equality of rates, I rejected the null hypothesis if more than $200 \times 5\% = 10$ of the likelihood ratio statistics exceeded the threshold for significance.

In my analysis I assumed that that only one sex could change care state at once, since for both sexes to change their behaviour would require the unlikely scenario of two simultaneous behavioural mutations (this is a standard assumption in the literature; see Burley & Johnson, 2002; Mank *et al.*, 2005; Reynolds *et al.*, 2002). However,

the prediction that male care should evolve out of female care involves both males and females simultaneously gaining and losing parental care respectively. Hence, I used the 'Multistate' program (again implemented in `Bayestraits`), which allows for two sexes to change care state at once, to test the magnitude of direct transitions between male and female care.

Data were analysed using the `Bayestraits` program as described above, and R versions 2.2.0 through 2.4.1 (R Development Core Team, 2005) using the package 'ape' (Paradis *et al.*, 2006). Phylogenies were compiled using the CAIC-phylogeny program (Purvis & Rambaut, 1995) and manipulated in R and in Mesquite (Maddison & Maddison, 2003).

2.4 Results

2.4.1 Ancestral care states

The basal phylogeny (that of Kjer, 2004) is shown in figure 2.1 along with extant and estimated ancestral parental care states for each insect order. Female care was the most likely care state in the ancestor of the whole tree including outgroups to insects (myriapods, crustaceans, arachnids and isopods; figure 2.2a). However, the basal insect most likely had no care (figure 2.2b). The ancestral Hemipteran was most likely to have been a female-carer (figure 2.2c). Of other orders containing parental care, female care was also the likely ancestral state in the Dermaptera (figure 2.2d); no care was ancestral in the Coleoptera (figure 2.2e), Lepidoptera (figure 2.2f), Hymenoptera (figure 2.2g), Psocoptera (figure 2.2h), Orthoptera (figure 2.2i) and Thysanoptera (figure 2.2j); biparental

care was the most likely ancestral state for the Embioptera (figure 2.2k); while for the Dictyoptera, unexpectedly, male care was estimated to be ancestral (figure 2.2l; all probabilities given in table 2.3).

Order	Probability in ancestor			
	No care	Male care	Female care	Biparental care
Outgroup	**0.038** (0.007–0.128)	**0.007** (0.001–0.026)	**0.952** (0.843–0.991)	**0.000** (0.000–0.001)
Insecta	**0.667** (0.385–0.897)	**0.084** (0.038–0.345)	**0.245** (0.007–0.555)	**0.000** (0.000–0.001)
Hemiptera	0.138 (0.003–0.649)	0.014 (0.000–0.089)	0.842 (0.261–0.993)	0.000 (0.000–0.000)
Dermaptera*	0.002 (0.000–0.250)	0.000 (0.000–0.250)	0.998 (0.250–0.998)	0.000 (0.000–0.250)
Coleoptera	0.777 (0.070–0.941)	0.147 (0.012–0.910)	0.028 (0.003–0.831)	0.000 (0.000–0.101)
Lepidoptera	0.871 (0.250–0.972)	0.116 (0.011–0.474)	0.011 (0.006–0.250)	0.000 (0.000–0.250)
Hymenoptera	0.828 (0.250–0.886)	0.113 (0.011–0.449)	0.057 (0.018–0.250)	0.000 (0.000–0.250)
Psocoptera	0.716 (0.250–0.789)	0.085 (0.011–0.409)	0.198 (0.124–0.294)	0.000 (0.000–0.250)
Orthoptera	0.865 (0.250–0.968)	0.118 (0.011–0.473)	0.015 (0.007–0.250)	0.000 (0.000–0.250)
Thysanoptera	0.889 (0.250–0.924)	0.081 (0.035–0.499)	0.002 (0.000–0.250)	0.017 (0.000–0.330)
Embioptera*	0.002 (0.000–0.250)	0.000 (0.000–0.250)	0.000 (0.000–0.250)	0.998 (0.250–0.999)
Dictyoptera	0.033 (0.021–0.250)	0.778 (0.250–0.841)	0.048 (0.011–0.250)	0.143 (0.078–0.462)

Table 2.3: Median and range of the estimated probability of each ancestral parental care state over 200 subtrees, for orders of insects with parental care. Orders where all known representatives invest in parental care are marked with an asterisk.

2.4.2 Parental care transitions

The most likely parental care transitions were transitions away from female care: female to no care and female to biparental care, with low rates of transition from both of those states back to female care (figure 2.3). No care and male care also interchanged at low rates. Transitions between male care and biparental care were not significantly different from zero. Transitions between female care and male care under the 'Multistate' analysis were also not significantly different from zero. All non-zero rates in the analysis were statistically different from each other (statistics for all comparisons are given in table 2.4).
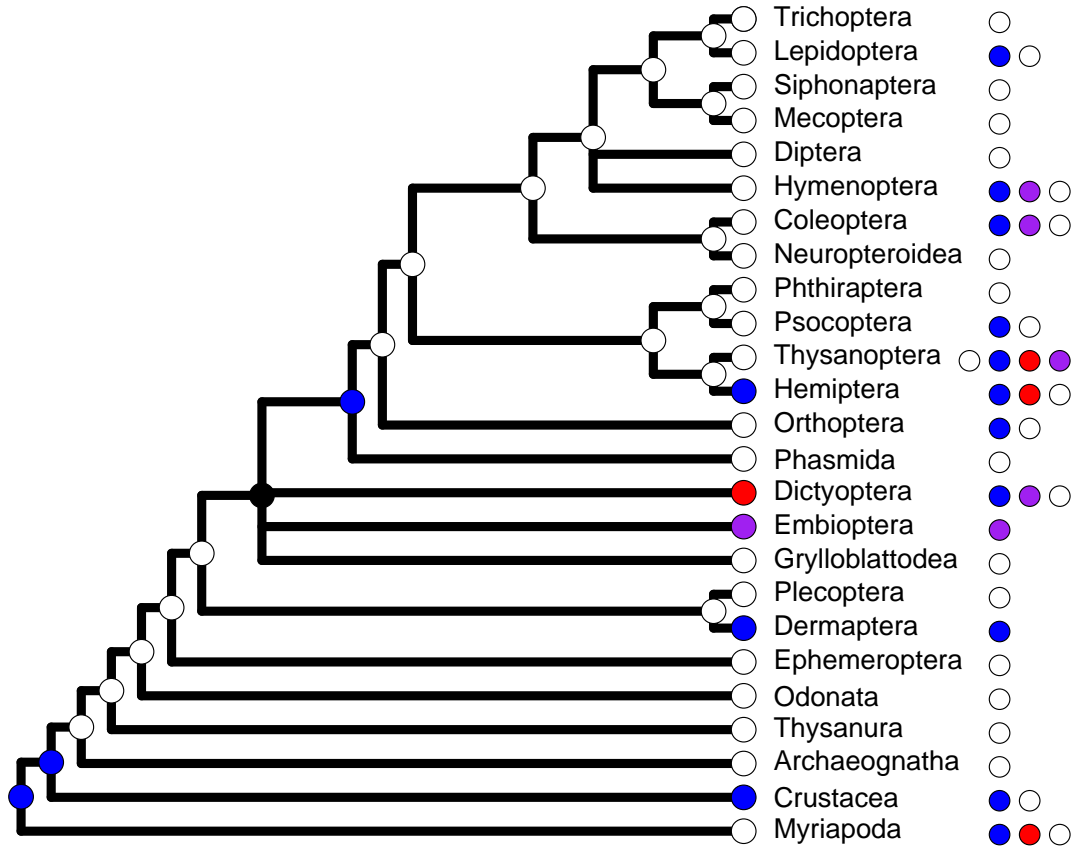
Figure 2.1: Basal phylogeny showing extant and estimated ancestral parental care states in each group. Circles on tree show estimated ancestors; circles to right of tree show extant parental care states in each order. Key: white circles, no care; blue circles, female care; red circles, male care; purple circles, biparental care; black circles, equivocal.

2.5   Discussion

These results support the prevailing view in the literature: insects began by losing the female parental care of their ancestors (Zeh *et al.*, 1989), and their descendant lineages evolved down at least two separate routes: (1) no care to female care and in some cases further to biparental care (e.g. Zeh & Smith,
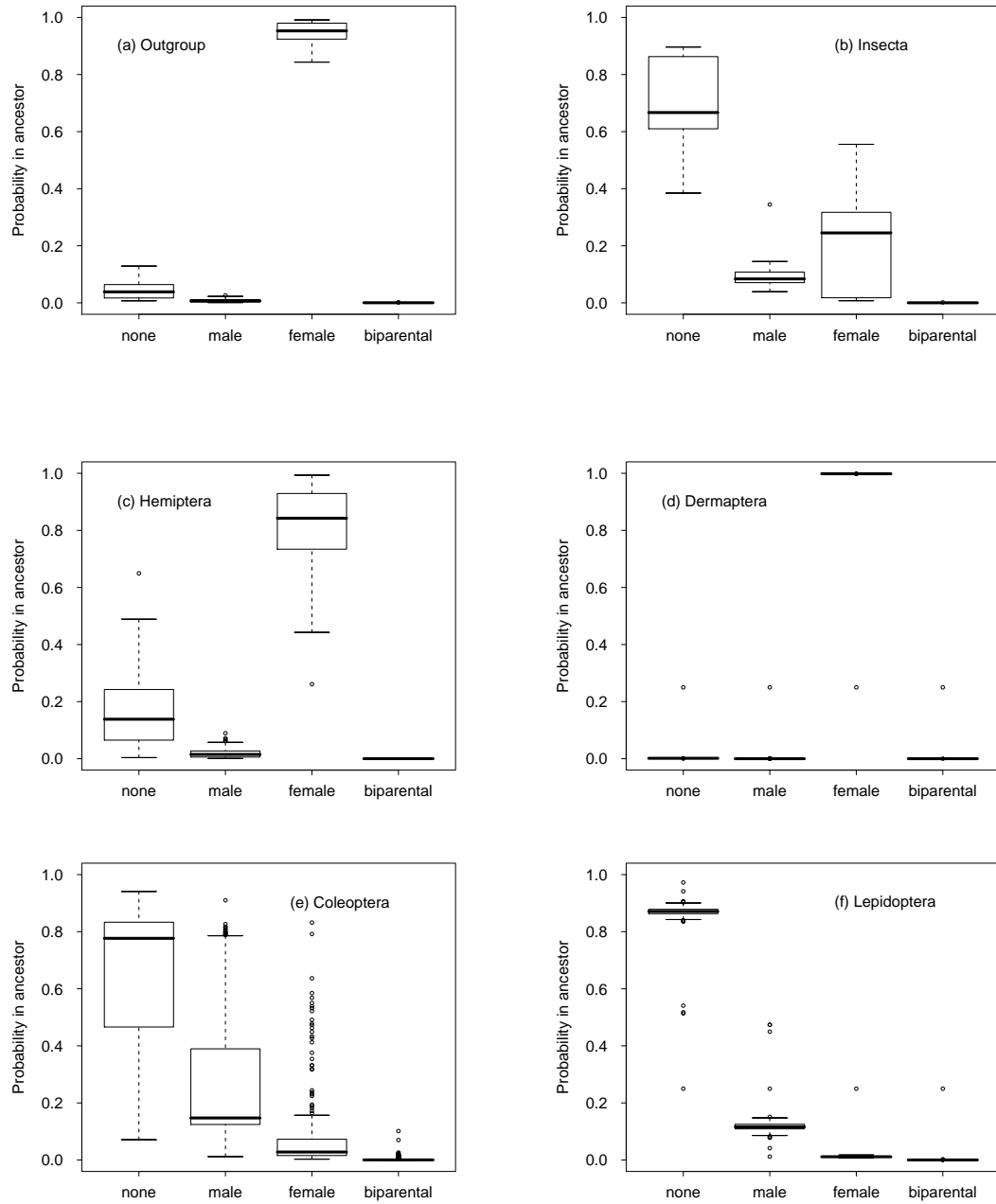
Figure 2.2: Median estimated probabilities of each care state over 200 subtrees for different insect taxa. Boxes show inter-quartile range; whiskers show range of data. Continued overleaf.
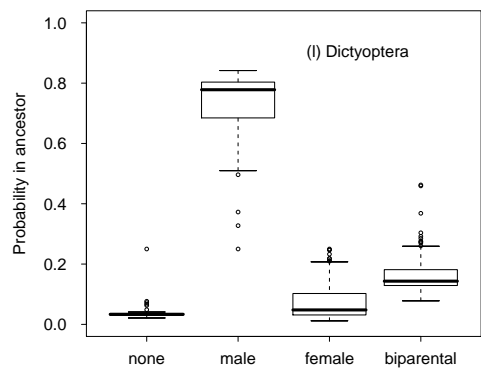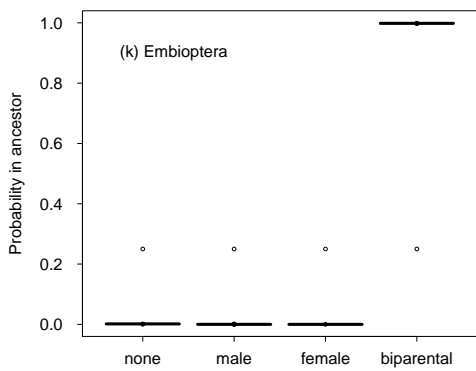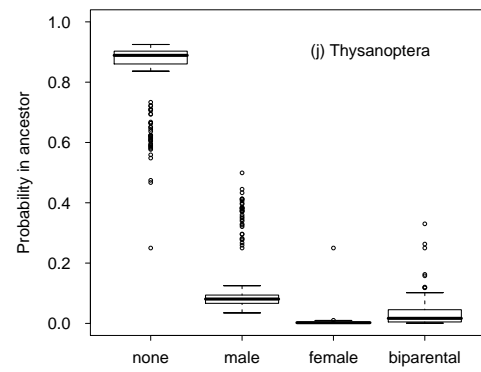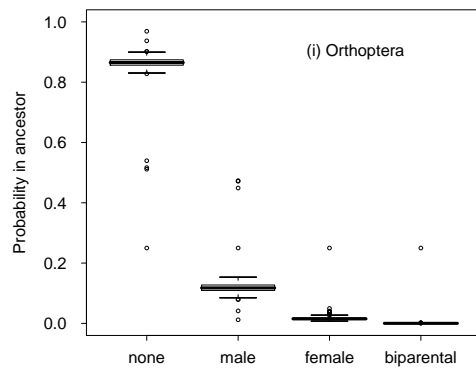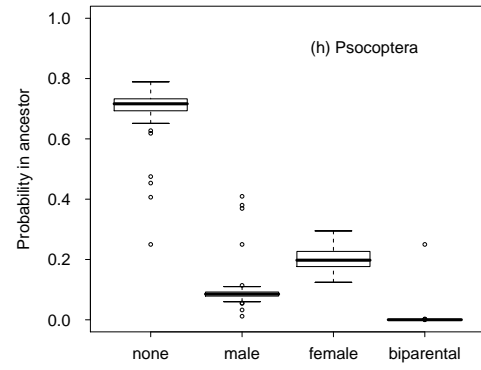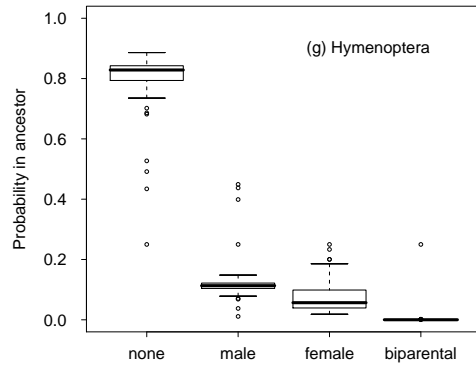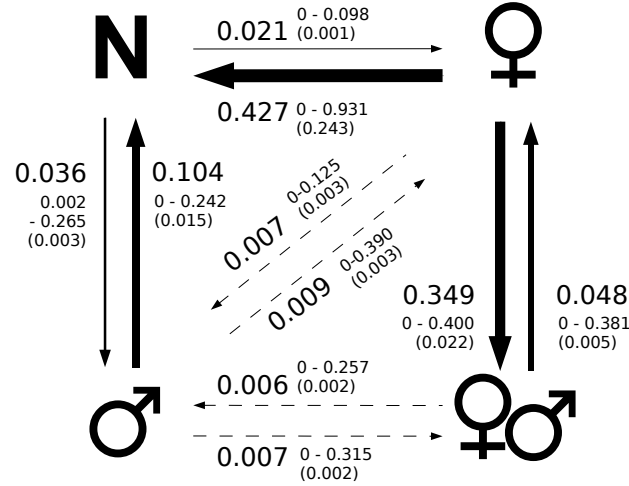
Figure 2.3: Parental care transitions. Numbers show the median and range of transition rates (IQR in parentheses), relative to the largest rate for each subtree (n=200). Line thickness represents relative magnitude (not to scale). Dashed lines, transitions not significantly different from zero.

	Rate against which tested					
Rate	**Zero**	**N→M**	**F→N**	**F→B**	**M→N**	**B→F**
Proportion of 200 tests significantly different						
N→F	1.000	**0.923**	**1.000**	**1.000**	**0.942**	**0.878**
N→M	1.000	–	**1.000**	**1.000**	**0.985**	**0.746**
F→N	1.000	–	–	**0.719**	**1.000**	**1.000**
F→B	0.995	–	–	–	**1.000**	**1.000**
M→N	1.000	–	–	–	–	**0.780**
B→F	0.996	–	–	–	–	–
Rates not significantly different from zero						
B→M	0.028	–	–	–	–	–
M→B	0.015	–	–	–	–	–
Rates tested using 'Multistate' program						
F→M	0.046	–	–	–	–	–
M→F	0.047	–	–	–	–	–

Table 2.4: Results of likelihood-ratio tests between transition rates. Numbers show proportions of χ^2 values above the threshold for significance (one test for each of 200 subtrees). Two rates are significantly different where proportions of tests attaining significance exceed 5% (in bold). Key to symbols: N, No care; F, Female care, M, Male care, B, biparental care.

1985), and (2) no care to male care (Manica & Johnstone, 2004; Zeh & Smith, 1985). There is little support for the hypothesis that male care evolves out of female or biparental care (Tallamy, 2000). The Hemiptera probably had a female-caring ancestor, which supports the hypothesis of Tallamy & Schaefer (1997) that patterns of parental care in this group arose largely as a result of the loss rather than the gain of female care. Of the other orders containing parental care, most were likely to have had non-caring ancestors. Surprisingly, the Dictyoptera most likely had a male-caring ancestor, despite the absence of male care in this group.

2.5.1 Ancestral care states

In the outgroups ancestral to insects, female care was estimated as the likely ancestor. By contrast, as predicted, the basal insect was estimated to have had no care. Zeh *et al.* (1989) argued that this transition probably happened when insects evolved tough, desiccation-resistant eggs and ovipositors, generating the hypothesis that that care should subsequently re-evolve in groups that have secondarily lost ovipositors, like the Dermaptera and Embioptera (and also the Isoptera, termites, which are eusocial and were not included in this analysis). Although I did not explicitly test for an association between parental care and ovipositor loss, these are the only insect orders whose members *all* perform parental care, providing strong circumstantial support for this hypothesis.

In most orders, the most likely ancestral care strategy generally reflected the type of care prevalent in that order: female care in the Dermaptera, bi-

parental care in the Embioptera, and no care in the Coleoptera, Lepidoptera, Psocoptera, Orthoptera and Thysanoptera, suggesting independent origins of parental care within these groups. In the Hymenoptera, no care was the most likely ancestral state even though very many Hymenopterans are eusocial or have female care. However, the most basal group of Hymenoptera, the sawflies, are generally phytophagous with independent larvae and no parental care, so it is not surprising that the ancestor to the Hymenoptera was estimated to be a non-carer.

The ancestor to the Hemiptera was estimated to have been a female carer, suggesting that the diversity of parental care in this group is due to multiple losses of parental care rather than multiple gains. As predicted by Tallamy & Schaefer (1997), parental care may be a uniquely costly behaviour in the Hemiptera. Although Lin *et al.* (2004) reconstructed parental care states within the Membracine treehoppers, finding that no care was ancestral in that subfamily and that reversals from female care to no care were relatively uncommon, this finding is not necessarily contrary to my results; the pattern within the Membracinae may not reflect the Hemiptera in general. In particular, treehoppers very often form complex mutualisms with ants (e.g. Bristow, 1982; Zink, 2003), which may reduce the costs of parental care behaviour and make it more evolutionarily stable. A more fine-grained analysis of the Hemiptera should now be pursued to confirm this finding, especially since it is the Hemiptera that contains almost all examples of male care (see below).

One group where the esimated ancestral state did not reflect the extant pattern of parental care was the Dictyoptera (the cockroaches, mantids, and termites). That male care should be estimated as basal to the Dictyoptera is

28

surprising, and warrants further investigation, firstly since uniparental male care does not currently exist in this group and secondly since this group contains a major origin of eusociality, that of termites. Dictyopteran relationships are not fully resolved owing to uncertainty of the placement of the enigmatic genus *Cryptocercus*, the woodroach (Nalepa, 1988), which lies in its own family, and whose members are all biparental (e.g. Park *et al.*, 2002). The phylogeny I present here uses the hypothesis of Kambhampati (1995) and Wheeler *et al.* (2001), that *Cryptocercus* are basal to cockroaches which are monophyletic. However, it would be interesting to incorporate alternative hypotheses into a similar analysis, for example that *Cryptocercus* are really basal to termites which in turn arise from within the cockroaches (e.g. Hennig, 1981; Lo *et al.*, 2000). A more detailed analysis is highly recommended before any strong conclusion is drawn regarding the ancestors of this group.

2.5.2 Parental care transitions

Evolution of female care

Transitions from no care to female care were strongly expected based on the traditional arguments of anisogamy (Trivers, 1972) and internal fertilization (Gross & Shine, 1981) and since female care is the most common form of insect parental care. Unsurprisingly, my data support these hypotheses: transitions from no care to female care were significantly more probable than zero. However, they were of relatively low probability and were less likely than the evolution of male care, despite female care being many times more frequent in nature. It may be that, rather than being more likely to evolve, female care may instead

promote diversification of lineages. This could be tested using existing phylogenetic methods for comparing diversification of different clades (see Harvey & Pagel, 1991; Martins, 1996).

Evolution of male care

The evolution of exclusive male care is more debated: authors argue male care could arise out of no care (Manica & Johnstone, 2004; Zeh & Smith, 1985) or out of female care, perhaps through a biparental intermediate (Tallamy, 2000, 2001). However, my results were unequivocal. Male care evolved consistently out of no care, never out of female care or biparental care. Considering extant taxa with male care, (within the Hemiptera, *Rhinocoris* assassin bugs, *Phyllomorpha* Coreid bugs, and the entire family Belostomatidae), all lie in clades containing mostly no care (Reduviidae, Coreidae and Nepomorpha respectively). This offers support for Manica & Johnstone's (2004) and Zeh & Smith's (1985) theory that males will evolve to care alone when the costs of caring are mitigated by high mating opportunities; however, it offers less support for Tallamy's (2000) hypothesis that males should assume the burden of care from the female, thus increasing her fecundity. Again, a more fine-grained formal analysis of parental care within the Hemiptera should now address these hypotheses further, incorporating directional, comparative predictions from both.

It is interesting that the only known instances of male parental care *outside* the Hemiptera (excluding the reconstructed ancestor to the Dictyoptera) should be in their sister order, the Thysanoptera. The two orders are collectively known as the 'Condylognatha' or 'jointed jaws', and their sister-group status is based almost totally on shared features of the mouthparts (Yoshizawa

& Saigusa, 2001), which are of the piercing-sucking type. It has been suggested that feeding habits could affect the costs and benefits leading to the evolution of male parental care (Tallamy, 1994; Tallamy & Wood, 1986, also see chapter 4 of this study); that these groups share features of their mouthparts may not be coincidental, although male-caring thrips are mostly fungus-feeders (Crespi, 1988) while male-caring Hemiptera are predatory (Tallamy, 2001).

Interestingly, reversals of both female and male care were more likely than gains, but rates of gains and losses were more similar for male care than for female care. This supports the theory of Tallamy & Schaefer (1997) that female care is evolutionarily unstable due to high costs for the caring female. Male care, by contrast, may be less labile than female care when it arises, leading to fewer observed reversals. This could be because once males care for eggs, females could evolve to exploit them by laying more eggs to take advantage of having increased offspring survival without the associated trade-off with investment in parental care. Once this investment is made, a reversal to no care would be difficult since the eggs would be highly dependent upon the male's care (a 'parental care trap' initially proposed in female-caring pentatomid bugs by Eberhard, 1975). Alternatively, once males start caring for eggs it often becomes a good idea for females to prefer to lay eggs in the nest of already-caring males (see chapter 5), which gives caring males a large benefit over non-caring males. This factor could stabilize and maintain male care in a population, relative to populations of female carers where this factor would be absent.

Evolution of biparental care

Pathways to biparental care can be readily identified in insect taxa. With few exceptions those non-eusocial female-caring insects that further evolved biparental care are restricted to a few lineages: beetles (Coleoptera), cockroaches (Dictyoptera) and webspinners (Embioptera; all webspinners exhibit biparental care). In addition, a small number of solitary wasps show a degree of division of labour, with the male defending one or more females and incidentally protecting against predators and parasitoids; also a tiny number of thrips (Thysanoptera) which are ancestral to eusocial lineages. In most (but not all) cases, biparental carers lie in clades containing female care (e.g. many Scarabaeine beetles, *Salganea* cockroaches, *Trypoxylon* wasps), so it is unsurprising that I found biparental care evolved out of female care and not male care. This direction of parental care evolution supports Zeh & Smith (1985)'s and Trumbo (1994)'s scenario, that males join females in caring when their breeding opportunities are otherwise low, and they can help by defending nests against competitors.

In support of Zeh & Smith (1985)'s and Trumbo (1994)'s hypotheses, in most cases biparental insect species exploit ephemeral, 'bonanza' resources that are difficult to exploit and highly in demand by conspecifics, and where roles have been studied, the male is usually involved more in nest defence than the female (e.g. Monteith & Storey, 1981; Sato, 1998; Scott, 1998), although defence is more shared in some others, like passalid beetles (Schuster & Schuster, 1985) and the tenebrionid *Parastizopus* (Rasa *et al.*, 1998). By contrast those species with uniparental female care that are *not* ancestral to biparental species (for example, female-caring bugs, flower beetles, praying mantids, etc) do not

exploit bonanza resources or guard resources from competitors, but rather usually forego feeding themselves in order to guard clutches from predators and/or parasitoids, and either lay the clutch on the future food substrate, or provision their offspring from dispersed resources. A comparative analysis among female-only caring species could easily test this formally: species descended from lineages ancestral to biparental care species would be predicted mainly to exploit patchy, ephemeral and highly competed-over resources, whereas species in lineages not ancestral to biparental care would be predicted to exploit dispersed, long lasting resources but to have comparatively higher predation or parasite pressure.

Further work on evolutionary transitions in insects should now aim to increase confidence in the insect phylogeny. As well as incorporating uncertainty due to polytomies as I have done here, further work should also incorporate different published phylogenetic hypotheses. One approach is to use a phylogenetic supertree (Bininda-Emonds, 2003; Bininda-Emonds *et al.*, 2003). As more and more phylogenies are published, a supertree of insects becomes increasingly feasible, and will open up exciting new avenues of research for students of comparative entomology. However, where published phylogenies directly conflict, as in the case of the Dictyoptera mentioned above, a compromise resolution incorporating elements of both hypotheses is not necessarily closer to the true phylogeny (Wilkinson *et al.*, 2005, and M. Wilkinson, pers. comm.). Another approach is to perform tests using multiple hypotheses, accepting conclusions that hold across all hypotheses, and discussing biological reasons for any differences (e.g. Goodwin *et al.*, 1998). In the case of the insects there is plenty of conflict over phylogenetic hypotheses for some groups; see,

for example, exchanges between Wheeler *et al.* (2001), Kjer (2004) and Ogden *et al.* (2005), or between Kambhampati (1995) and Grandcolas (1999). One way to incorporate alternative phylogenetic scenarios while also modelling multiple parameters at once is to use Bayesian methods (see Gelman *et al.*, 2004). In addition to maximum likelihood methods, the `Bayestraits` program implemented in this chapter also allows for estimation of rate parameters using Markov Chain-Monte Carlo methods to sample from multiple phylogenetic trees and multiple models of relationships between transition rate parameters (Pagel & Meade, 2006), which could be used to model trait evolution over many alternative phylogenies at once.

To my knowledge this is the first formal analysis of parental care transitions across the insects. My results show largely that the most likely directions of parental care evolution closely mirror existing theories based on separate taxa, and can be pieced together into a wider picture of the evolution of insect parental care. Similar but more fine-grained studies should now be possible to reconstruct patterns of evolution within each order, to confirm the findings presented here. In particular, the Hemiptera should be scrutinized most closely, since this contains most of the examples of male care in the insects. Secondly, the Dictyoptera should be addressed in the light of alternative phylogenetic reconstructions.

Chapter 3

Parental care trade-offs and life-history relationships in insects

3.1 Abstract

Investment in offspring survival is predicted to trade off against offspring number. Experimental manipulations have often been used to identify parental care trade-offs within insect species. Here, I use the complementary approach of comparative-phylogenetic analysis to investigate evolutionary trade-offs *among* species across a wide range of insects. Firstly, insects with parental care had higher offspring survival, but also lower lifetime fecundity, than related species without care. Secondly, insects with increased levels of care (i.e. care with provisioning as opposed to care without provisioning) had correspondingly lower fecundity. Analysis of the results of published carer-removal experiments revealed that insects with care and provisioning also had a greater beneficial impact on offspring survival than insects with care alone. We are thus more justi-

fied in making the generalization that insects incur a trade-off between parental care and lifetime reproduction.

3.2 Introduction

Parental care is often an effective way of increasing the survival of offspring (e.g. Balshine-Earn, 1997; Diesel, 1989; Székely & Cuthill, 1998). However, it is also often costly, in terms of energy (Balshine-Earn, 1995; Thomas, 1994; Vandenberghe, 1992), exposure to predation (Shine, 1980) and lost mating opportunities (Balshine-Earn, 1995; Beissinger, 1990; Székely & Cuthill, 2000, but see Grüter & Taborsky, 2005), and in many cases individuals must trade off parental care behaviour against future reproduction (e.g. Clutton-Brock *et al.*, 1983, 1982; Heideman *et al.*, 2005; Lummaa, 2001, reviewed in Clutton-Brock, 1991). Hence, we would expect under a tightly constrained energy budget that parental care, an investment in offspring quality, would generally trade off against the number of offspring produced in a lifetime (Clutton-Brock, 1991; Lack, 1954; Roff, 1992; Sibley & Calow, 1986; Smith & Fretwell, 1974; Stearns, 1992; Williams, 1966).

In this chapter, I use comparative-phylogenetic methods to investigate the trade-off between parental care and lifetime reproduction in insects. In comparative studies, the effect of trade-offs within individuals is removed because variation within and among individuals is averaged out. However, we can use among-species patterns to investigate how species with different ecologies resolve the same trade-offs. In previous comparative studies of life-history, parental care has been found to have mixed effects. Annual fecundity is nega-

tively related to parental care effort along elevation gradients in birds (Badyaev & Ghalambor, 2001), but Martin *et al.* (2006) found that clutch mass in passerines is not negatively related to parental effort. Similarly, Simpson (1995) found that spiders with parental care do not have smaller clutch sizes than non-caring relatives, while cursorial spiders that carry their eggs even have bigger clutches. However, in these cases 'annual fecundity' and 'clutch size' referred to only part of the total lifetime fecundity, and may therefore be poor indicators of the individuals' total reproduction. Lifetime fecundity is the best measure of an animal's allocation of resources to offspring number, since it is not affected by age-specific decisions about how many eggs to lay at one time. However, in most taxa it is rarely measured extensively enough for comparative studies to be possible.

In insects, by contrast, the complete reproductive history for individuals is often recorded, in the laboratory (e.g. Kudo & Nakahira, 2004; Peres & Corrêa-Ferreira, 2001, see meta-analysis in Honek, 1993) and less frequently in the field (e.g. Stegmann & Linsenmair, 2002; Zink, 2003, see collated data in Cornell & Hawkins, 1995), and lifetime fecundity has been measured for many species (e.g. del Claro & Oliveira, 2000; Hirschberger, 1999; Stegmann & Linsenmair, 2002, see collated data in Hinton, 1981). This makes insects an excellent target group for comparative life-history studies.

Supporting findings in other taxa, parental care in insects has been generally found to be beneficial in terms of offspring survival (Stegmann & Linsenmair, 2002; Thomas, 1994; Zink, 2003, but see Eberhard, 1975) and costly in terms of energy (Agrawal *et al.*, 2005; Tallamy & Denno, 1982; Thomas, 1994), predation risk (Reguera & Gomendio, 1999) and lost mating oppor-

tunity (Thomas, 1994). As predicted, within species, parental care has been found to trade off against future reproduction (Agrawal *et al.*, 2005; Kaitala & Mappes, 1997; Tallamy & Denno, 1982; Zink, 2003) as well as other behavioural traits (e.g. hunting success: Strohm & Marliani, 2002).

However, there has to my knowledge been no comparative assessment of the life-history correlates of parental care in insects. Comparative work on insect life-history is relatively scarce and generally confined to single insect orders, especially the Lepidoptera (Garcia-Barros, 2000; Jervis *et al.*, 2005; Wiklund *et al.*, 1987) and Hymenoptera (Blackburn, 1991; Jervis *et al.*, 2001, 2003, but see also Carrière *et al.*, 2004, on crickets). This scarcity may be due to a perceived lack of a phylogeny; it is increasingly accepted that comparative tests need statistical correction for non-independence among species due to shared ancestry (Harvey & Pagel, 1991; Martins, 1996; Martins & Hansen, 1997). Papers as recent as Addo-Bediako *et al.* (2002) have talked about the 'absence of a hexapod phylogeny'. However, insect phylogenies are being published at an unprecedented and increasing rate (Caterino *et al.*, 2000); methods for combining phylogenies into 'supertrees' are progressing rapidly (see Bininda-Emonds, 2003; Bininda-Emonds *et al.*, 2003; Wilkinson *et al.*, 2005, for discussion); and advances are being made in techniques for accounting for phylogenetic uncertainty in comparative analysis (Huelsenbeck & Rannala, 2003; Huelsenbeck *et al.*, 2000; Martins, 1996).

Here I use literature data to investigate the effect of parental care on insect life-history. In a preliminary analysis, I look at the way lifetime fecundity scales with body size in insects, since comparative life-history studies usually assume that this relationship is positive. Then I use a comparative-

phylogenetic method, with a phylogeny of more than 250 species, to test the hypothesis that parental care affects both fecundity and offspring survival, correcting for body size. I predict that there will be a trade-off between parental care and fecundity, i.e. that parental care will be associated with increased offspring survival to adulthood but with decreased lifetime fecundity. I also predict that increased parental effort (care with provisioning as opposed to care without provisioning) will be associated with a stronger trade-off against fecundity. Insects that invest more in parental care should therefore have higher survival but lower fecundity. Lastly, I conduct a small analysis of experimental manipulations from the literature, specifically carer-removal experiments that test the benefits of parental care. I predict that increased parental effort will be associated with increased benefits of parental care, measured by the improvement in survival when the caring parent is present as opposed to when it is experimentally removed.

3.3   Methods

3.3.1   The dataset

I gathered data from a literature search using ISI Web of Knowledge (`http://wok.mimas.ac.uk`) and Google Scholar (`http://scholar.google.com`) and various university libraries. I recorded parental care strategy, lifetime fecundity and offspring survival in the field. For fecundity the main source was Hinton (1981) and references therein. Other sources are available on request. I deliberately excluded eusocial species, species living in social groups with any degree of reproductive skew, or with helpers at the nest. In these species, trade-offs incurred by the female parent may be obscured by help from

nonparental individuals. I also excluded uniparental male care since there were few life-history data for these species.

Parental care

Insect parental care behaviour is arguably the most diverse in the whole animal kingdom, and is the subject of many detailed reviews (Clutton-Brock, 1991; Eickwort, 1981; Hinton, 1981; Tallamy, 1999; Tallamy & Wood, 1986; Wilson, 1971). Where it occurs, it can be by either sex or both, and ranges from the simple guarding of small clutches of eggs for a few hours after oviposition to elaborate patterns of biparental care with division of labour between parents, the precise construction of climate-controlled nests and the feeding of offspring up to and into adulthood. This makes it a daunting task to classify, and authors have chosen to do this in several ways (e.g. with and without nests: Eickwort, 1981, Gullan & Cranston, 2005; according to degree and type of sociality: Crespi & Yanega, 1995; or according to the costs and benefits arising from the parents' lifestyle and diet: Tallamy & Wood, 1986). I chose a three-tier classification that represents a clear increasing scale of investment: I classified insects into 'non-carers', 'carer-guarders', i.e. with post-ovipositional parental guarding of eggs or young without supplying food; or 'carer-provisioners', i.e. with post-ovipositional parental guarding of eggs or young plus supplying of food. Supplying of food could be through pre- or post-oviposition mass provisioning (e.g. most dung beetles), or progressive provisioning (e.g. all earwigs).

Offspring survival

I collected field data for offspring survival to adulthood. I only accepted offspring survival as the percentage of offspring surviving *in the field* from the egg to the adult stage including hatch rate, i.e. the percentage of laid eggs that successfully reach the

imago stage. The majority of studies were from life tables (e.g. Cornell & Hawkins, 1995), but survival of 'control' groups from field experiments were also accepted (e.g. Zink, 2003). Survival values over experimental periods shorter than the egg-adult period were excluded.

Lifetime fecundity

I gathered data on lifetime fecundity from any study that recorded the mean number of eggs that one female produces in her lifetime, preferably in the field, but I also accepted values from the laboratory under non-extreme conditions. A range of values was often recorded under different conditions, e.g. different temperatures or humidities. In this case, I determined (usually from the study in question) which of the conditions best represented the field values for the relevant species, and accepted this value. I preferred cases where a mean $\pm$ standard error were reported; where the value was a range, I took the mid-point. Where there was more than one study reporting data for the same species, I accepted the value from the study with the largest sample size, and conducted closest to field conditions. Where no other figure was available, I also accepted statements such as 'females of species x lay 500 eggs,' where backed up by a citation from a peer-reviewed journal. Unreferenced estimates of fecundity were not recorded. Physiological fecundity estimates, based on counts of ovarioles or embryos, were only accepted when they were discussed and adjusted with reference to how they would translate into fecundity in the field, otherwise they were treated as incompatible with field measures of lifetime fecundity (Leather, 1988).

For this study, error in data collected from the literature was not taken into account owing to time constraints. Although standardization of error is possible for data obtained by diverse methods (see, for example, Honek, 1993), in this case such procedures would have been extremely laborious, considering the diversity of data

sources, collection methods and kinds of error reporting that I found in the literature.

3.3.2 Life history and parental care

To test for relationships between parental care and life-history variables, I constructed models with and without incorporating phylogenetic information. For models without the phylogeny, I used ordinary least squares models (OLS; Crawley, 2002). For models with the phylogeny, I used a modification of the Generalized Least Squares method (GLS; Martins & Hansen, 1997), which uses matrices to incorporate nonindependence in data that are structured, in this case due to phylogeny. GLS methods work as follows.

If data points are independently distributed, we can analyse them using OLS regression models for which statistical independence is a key assumption. An OLS model takes the form

$d_{observed} = d_{expected} + \varepsilon(0, \sigma^2)$

Where $d_{observed}$ is the observed trait value, $d_{expected}$ is the expected trait value represented by a model formula consisting of the explanatory terms, and $\varepsilon(0, \sigma^2)$ is a normally distributed error term with mean 0 and constant variance. If we were to express this error term as a matrix , we would do so as follows:

$\sigma^2 \mathbf{I}$

Where $\mathbf{I}$ is the "identity matrix" i.e. with ones along the diagonal and zeroes on the off-diagonals. The resultant "variance-covariance matrix" carries constant variance in the diagonal elements and values of zero (representing zero covariance or independence) on the off-diagonal elements.

However, if species data are related to each other via a phylogeny, residuals (i.e. ε) for randomly chosen species will not be independent of each other, but will systematically covary according to the phylogenetic distance separating them.

GLS methods are a way of analysing nonindependent data whose residuals covary systematically, in this case with increasing phylogenetic separation. In this case, the off-diagonal elements in the variance-covariance matrix (**V**) represent the expected or estimated covariance in the trait between all pairs of species. Given that species are related by their phylogenetic history, this matrix will be a function of both (1) variance within species (along the diagonal of the matrix) and (2) correlations between species due to shared evolutionary history (off-diagonal elements).

This matrix **V** is incorporated into the error structure of a linear mixed model, i.e. treated as a random term describing the expected variance for each species. Hence, the statistical model takes the form

$$d_{observed} = d_{expected} + \varepsilon(0, \mathbf{V})$$

where the error term ε is now drawn from a *multivariate normal* distribution with a variance-covariance matrix **V** describing the variances in trait values for each species and the covariances in trait values between each species-pair. Hence, the error term is still a vector of values for each species; because the errors are correlated, they cannot be described separately for each species but are jointly estimated based on the expected relationship for covariances between species (a function of phylogenetic distance) and on the variance in the data. The use of the variance-covariance matrix in a GLS framework to deal with correlations among observations is analogous to the univariate procedure of adjusting the data to unit variance by dividing each observation by the standard deviation (Butler *et al.*, 2000).

The mathematical relationship that best describes the off-diagonal elements of the matrix **V** (i.e. how covariance between species changes with phylogenetic distance) can be subject to a number of assumptions about the model of evolution along branches of the phylogeny. If traits are evolving via random genetic drift, or by fluctuating directional selection, for example, we would expect a linear decay of correlation

with phylogenetic distance (this is the model of evolution assumed in the more commonly used method of "Independent Contrasts", henceforth IC; Felsenstein, 1985). However, the adaptationist paradigm holds that most traits are adaptations to their environment, so we would expect most measured traits to be under stabilizing selection. In this case, the most appropriate assumption is one of exponential decay in covariance between species with increasing distance (Hansen & Martins, 1996; Martins & Hansen, 1997)

$$cov_{ij} = \sigma_i \sigma_j \times e^{-\alpha d_{ij}}$$

Where cov_{ij} is the covariance between two species i and j, d_{ij} is a measure of phylogenetic distance between species i and j, and α (estimated from the statistical model) describes how rapidly the correlation between pairs of species decays to zero. If α is large, there is very rapid decay in correlation and data are essentially independent; smaller values of α indicate increasing degrees of phylogenetic 'inertia' in the data.

In addition to its ability to incorporate more flexible assumptions about the model of evolution along branches of a phylogeny, the GLS approach has several other advantages over IC. GLS methods allow for multiple categorical and continuous explanatory variables in one analysis, which is central to this study, since I want to construct models with 'parental care' (categorical) and 'dry weight' (continuous) as explanatory variables. GLS methods can also formally compare models with and without phylogenetic structure, which I use in tests for 'phylogenetic signal' (see below).

To determine the minimal model for both OLS and GLS methods, I used a backwards stepwise approach, beginning by fitting all explanatory terms and all possible interactions between them, and testing successively the effects of dropping each term. Terms and interactions were dropped if doing so did not result in a 'significant' decrease in the explanatory power of the model. To test for significance, under OLS the difference between two models follows an F distribution and so I used an F-statistic. In

the GLS, I used the likelihood ratio (the difference in log-likelihood) between the two models (which therefore were fitted using Maximum Likelihood and not Restricted Maximum Likelihood; Crawley, 2002; Pinheiro & Bates, 2000), testing this ratio against a chi-squared distribution and checking my result using Akaike's Information Criterion (AIC; Sakamoto *et al.*, 1986, cited in Crawley, 2002). This procedure was followed until the model only included terms and interactions whose elimination resulted in a significant reduction in the explanatory power of the model.

Where factors had more than two levels, the levels were tested against each other using Helmert contrasts (Crawley, 2002), which correct for non-orthogonality by putting the factor levels in order of increasing difference from each other, and testing each factor level against the pooled mean of previously tested levels. Since this results in unintelligible estimates for effect sizes and standard errors, effect sizes and standard errors were calculated using conventional treatment contrasts.

Appropriateness of using phylogenetic information

Firstly, I tested whether my data were truly non-independent due to phylogeny, and whether a phylogenetic-comparative analysis was therefore justified. If much of the variance in a trait can be explained simply by the taxon to which an insect belongs, this suggests that the data show a strong phylogenetic correlation and that methods that incorporate phylogenetic information are appropriate. I first allocated different proportions of the variance in each trait to each taxonomic level (order, family, genus, and species) by fitting a linear mixed model with no fixed factors and an error structure of the form order/family/genus, and used the `varcomp()` function under the *ape* package to perform a variance component analysis.

For each trait, I also constructed a GLS model with no fixed explanatory terms, and compared its fit with that of a similar model where the data points had been ran-

domly permuted across the tree tips, destroying any association due to the phylogeny. This is a good estimator of 'phylogenetic signal' *sensu* Blomberg *et al.* (2003). Here, the models being compared are not 'nested' one within the other, so they are not formally comparable using log-likelihood ratios, and so I used a difference of two in AIC values as a criterion for a significant difference (Crawley, 2002). In addition, I also compared the GLS with no predictor variables to the equivalent OLS model, which has no phylogenetic structure (as opposed to a randomized phylogenetic structure). Here, the models are formally comparable using log-likelihood ratio tests against a χ^2-distribution (K. Isvaran, pers. comm.).

Body size

Any meaningful study involving life-history relationships must incorporate the effect of body size (Peters, 1983; Reiss, 1989; Schmidt-Nielsen, 1984). Since there is no standardized measure of body size in insects, I developed a relatively quick and easy method of measuring insects' dry weight from museum specimens and investigated its performance relative to previous studies. The procedure and its results are detailed in appendix A. Weights were obtained from 891 museum specimens from 263 species, 110 families and 14 orders. These weights were used to estimate the weights of a further 451 specimens, from 121 species and 9 orders, for which the weight was unobtainable (due to e.g. being mounted on a card rather than on a pin), from their body length or, better, body length×pronotum width. I then added estimates of dry body weight from literature records of body length and, where available, pronotum width. Where appropriate I have indicated how many weights were directly recorded and how many were estimated for each analysis.

Allometric scaling of lifetime fecundity

Several authors have considered the effect of body size upon lifetime fecundity independently of parental care. To compare my results for the allometric scaling of lifetime fecundity with theirs, I first looked at the effect of dry weight upon fecundity for different orders independently of parental care, using models with and without phylogenetic information, with 'fecundity' as the response term and 'dry weight' and 'taxonomic order' as predictor variables. This also allowed me initially to spot any trends that might potentially confound the next analysis, which incorporates parental care.

Costs and benefits of parental care

I then investigated the effects of parental care upon the life-histories of the insects in the analysis, looking at the cost in terms of lifetime fecundity and the benefit in terms of offspring survival to adulthood.

Firstly, to look at how parental care affects lifetime fecundity in different species, I fitted models with and without phylogenetic information, with 'fecundity' as the response term and 'parental care', 'dry weight' and 'taxonomic order' as predictor variables. To fit an interaction between 'parental care' and 'order', I could only use those orders that contain all three levels of parental care, which is a restricted dataset. I checked for this interaction using the restricted data, and if it had a non-significant effect, dropped the term and fitted the model with all the data. I checked by eye that the estimates and effect sizes did not change appreciably between the models.

Secondly, I looked at the benefits of parental care in terms of offspring survival, by fitting models with 'offspring survival' as the response term, and 'parental care' and 'dry weight' as predictors. I also included 'fecundity' as a covariate since it is strongly predicted to be negatively related to measures of survival in any set of stable

populations (Gustafsson & Sutherland, 1988; Sutherland *et al.*, 1986). In this case there were not enough data to include 'order' as a factor.

I predicted that parental care would have a positive effect on offspring survival but that it would be associated with a decrease in fecundity. Additionally, since caring with provisioning is a bigger investment than caring alone, if insects generally incur a trade-off between parental care and fecundity, carer-provisioners should have higher survival and lower fecundity than carer-guarders.

The phylogeny

To describe the relationship between species I used the subset of the phylogeny described in chapter 2 for which life-history data were available, a tree of 272 tips. Subsets of this tree were used for subsequent analyses. Subsets of this tree were used for subsequent analyses. Polytomies were left unresolved. Phylogenetic distance was measured in arbitrary units; since branch lengths were unknown, I applied a range of transformations, comprising (1) setting all lengths to an arbitrary length of one, and (2) scaling branches according to their relative depth in the phylogeny using Grafen's 1989 rho method under a range of scaling parameters (using the `compute.brlen()` function under the *ape* package in R). I used the transformation that resulted in the lowest AIC values when comparative models were constructed. In all cases, AIC values were lowest when all branch lengths in the phylogeny were set to 1 (data not shown).

3.3.3   Experiments measuring the benefits of parental care

To compare experiments measuring the benefits of care in carer-guarders and carer-provisioners, I gathered instances from the literature where the author had removed caring parents in the field. For each, I recorded the mean offspring survival to adult-

hood, in the same way as described above, both with and without the carer present. The difference between the two I took as a measure of the mean benefit of care for the species. Differences in hatch rate alone for insects that care without provisioning were treated as incompatible and were not accepted. I predicted that carer-provisioners would have a bigger impact upon the survival of their offspring than carer-guarders.

Data were analysed using R versions 2.2.0 through 2.4.1 (R Development Core Team, 2005) using the package 'ape' (Paradis *et al.*, 2006). Phylogenies were compiled using the CAIC-phylogeny program (Purvis & Rambaut, 1995) and manipulated in R and in Mesquite (Maddison & Maddison, 2003).

3.4 Results

3.4.1 Life-history and parental care

Parental care strategy was determined for each species in the analysis ($n = 272$), a subset of the data used in chapter 2. In total, I analysed data for 219 non-carers, 22 carer-guarders and 31 carer-provisioners.

Lifetime fecundity was obtained for 483 species from 20 orders of insects. Values ranged from 2 (Coleoptera: *Kheper*) to 12,500 (Hymenoptera: *Kapala*). Data were log-transformed before analysis. Insect orders differed significantly in lifetime fecundity ($F_{19,463} = 5.25, p < 0.0001$), ranging from a mean of 128 ± 77.9 (Dermaptera, n=5, excluding orders with fewer than 5 data points) to $1,665 \pm 290$ (Ephemeroptera, n=16).

Offspring survival in the field was obtained for 51 species and ranged from 1% (Lepidoptera: *Epiphyas*) to 98% (Coleoptera: *Canthon*). The data were nor-

mally distributed after arcsin-square root transformation, as is recommended for proportion data (Sokal & Rohlf, 1995).

All species used and raw data, including dry body weights, can be found in table B2 (appendix B).

Appropriateness of phylogenetic-comparative method

For each trait I recorded, I tested whether the phylogenetic-comparative method was justified by calculating the variance allocated to different taxonomic levels. I also estimated the 'phylogenetic signal', assessed by comparing a GLS model with phylogenetic structure against (1) a GLS model with *randomized* phylogenetic structure, and (2) an OLS model with no phylogenetic structure. For dry weight, taxonomic order and family explained a large percentage of the variance ($> 80\%$), suggesting a strong correlation with the phylogeny (table 3.1). By contrast, for lifetime fecundity the variance components for the order and family levels summed to 48%, with 52% at the generic and specific levels. In no case did one taxonomic level account for a disproportionately large component of the variance, although for offspring survival the genus level accounted for a very small component. 'Phylogenetic signal' was very strong in fecundity, since the GLS with the phylogeny explained much more variance than both the shuffled GLS ($\triangle$AIC=136.98) and the OLS model (Lik. Ratio=1978.47, p<0.0001). By contrast, 'phylogenetic signal' was very weak in offspring survival, since the GLS with phylogenetic structure did not explain significantly more variance in the data than a GLS with the tips randomly shuffled ($\triangle$AIC=0.19) or a conventional OLS model without phylogenetic structure (Lik. Ratio<0.01, p=0.96).

| Trait | Percent variance components | | | |
	Order	Family	Genus	Species
Log(Dry weight)	42.3	38.0 (80.3)	12.2 (92.5)	0.07
Log(Fecundity)	17.6	30.4 (48.0)	22.7 (70.6)	29.4
Arcsin(sqrt(Offspring survival))	20.9	41.2 (62.1)	<0.1 (62.1)	37.9

| Trait | GLS test for 'phylogenetic signal' | | | |
| | Randomized GLS | GLS vs. OLS | | |
	ΔAIC	Lik. Ratio	p	ΔAIC
Log(Dry weight)	25.92	581.72	<0.0001	583.72
Log(Fecundity)	136.98	1978.47	<0.0001	1980.47
Arcsin(sqrt(Offspring survival))	0.19	<0.01	0.96	1.99

Table 3.1: Breakdown of variance component analyses and tests for 'phylogenetic signal'. Levels of the taxonomy were treated as nested random factors in a mixed-effects model with no fixed terms. Values in brackets show cumulative variance components: high values at deep taxonomic levels suggest that phylogenetic correction is required (Smith & Cheverud, 2002). Tests for phylogenetic signal compare models with no fixed factors and the trait in question as the response variable. Where a model with phylogenetic structure explains significantly more variance than one without, phylogenetic correction is required.

Allometric scaling of lifetime fecundity

I investigated the effect of body size upon fecundity independently of parental care, for comparison with previous authors and to identify any trends that might potentially affect the analysis with parental care included. For this analysis 222 species weights were directly measured and 50 were estimated. Without the phylogeny, log(lifetime fecundity) scaled differently with log(body weight) for different orders (OLS model, $F_{12,266} = 2.35, p = 0.007$). This interaction was also evident when incorporating the effects of phylogeny using GLS (dropping the weight:order interaction, log-likelihood ratio $= 21.43, \Delta$df $= -11, p = 0.029, n = 272$ [ΔAIC $= 0.58$]; table 3.2). Separate regression parameters for each order are given in table 3.3, for comparison with previous

Scaling of fecundity with dry weight (n=289)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
Weight×order	2.35	-12	0.007	21.43	-11	0.029	0.58
Table of coefficients	Estimate±s.e.	Slope±s.e.		Estimate±s.e.	Slope±s.e.		
I'cept (Coleoptera)	4.59 ±0.276	0.02 ±0.086		4.45 ±1.415	-0.08±0.067		
Dermaptera	-2.79 ±2.044	0.82 ±0.654		-4.07±1.884	1.51±0.597		
Dictyoptera	-2.06 ±1.344	0.45 ±0.238		-2.88±1.197	0.64±0.208		
Diptera	0.33 ±0.434	0.46 ±0.191		0.15 ±0.366	0.69±0.162		
Ephemeroptera	2.15 ±0.636	0.44 ±0.416		1.96 ±0.580	0.22±0.381		
Hemiptera	0.19 ±0.375	0.02 ±0.128		0.40 ±0.338	0.16±0.069		
Hymenoptera	-0.37 ±0.345	-0.17 ±0.112		-0.42±0.299	-0.02±0.096		
Lepidoptera	-0.03 ±0.430	0.33 ±0.134		0.02 ±0.404	0.34±0.126		
Neuroptera	0.16 ±1.039	-0.30 ±0.834		0.32 ±0.913	-0.12±0.864		
Orthoptera	-1.32 ±2.120	0.33 ±0.370		-0.68±1.756	0.32±0.302		
Trichoptera	0.74 ±1.250	0.15 ±0.594		-1.72±1.163	1.08±0.628		

Table 3.2: Factors affecting lifetime fecundity in insects. Coefficients other than that for Coleoptera are given as the estimated difference from the Coleoptera. For main effects that are involved in significant interactions, estimates are shown but not p-values. 'Estimate' refers to the main effect of the factor 'order'; 'slope' refers to the effect size for the weight-order interaction, i.e. the slope of the weight-fecundity relationship for each level of 'order'.

authors. Lifetime fecundity scaled positively with body weight in the Diptera, Dictyoptera, Ephemeroptera and Lepidoptera, and also in the Dermaptera although the relationship was not significant. The steepest significant relationship was in the Diptera, where the slope was estimated at 0.581. In the Hymenoptera, Hemiptera and Orthoptera there was no relationship, with very little variation in fecundity explained by variation in dry weight.

The Coleoptera were problematic, in that initially there was no weight-fecundity relationship and negligible variation in fecundity was explained by dry weight (figure 3.1). However, on examination of figure 3.1, beetles of the family Scarabaeidae (shown by the open circles) appeared to skew a generally positive relationship, a family whose members are known sometimes to reduce the number of functioning ovaries to one instead of two (Lopez-Guerrero,

1996). Excluding scarabs from the analysis, fecundity scaled positively with weight in the Coleoptera (table 3.3). Scarab beetles therefore had unusually low fecundity for their body size. Within scarabs themselves, there was no weight-fecundity relationship (OLS model, $F_{1,18} = 1.709, p = 0.208$). To avoid this influencing later results, I performed subsequent analyses twice: with and without the scarabs.
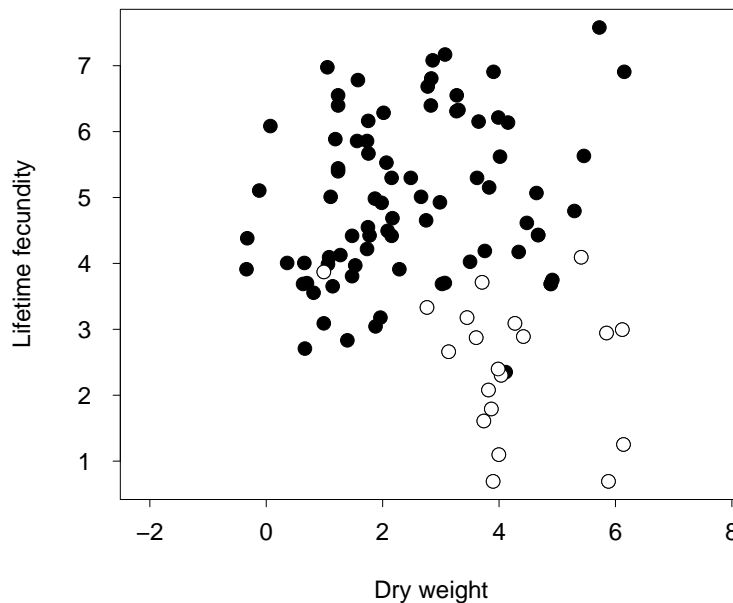
Figure 3.1: Log(lifetime fecundity) against log(dry weight) for the Coleoptera (closed circles). Open circles denote beetles of the family Scarabaeidae.

Costs of parental care

I then looked at the effect of parental care, dry weight and taxonomic order upon lifetime fecundity, without the phylogeny using OLS models, and incorporating the phylogeny using GLS models. Here, as in the previous analysis, 222 species weights were directly measured and 50 estimated. All models are

Taxon	Mean	±s.e.	n	Intercept	Slope	r^2	p
Dermaptera	128.5	77.9	5	1.803	0.843	0.45	0.130
Diptera	621.8	122.3	26	4.911	0.581	0.38	<0.001
Dictyoptera	313.7	67.7	13	2.537	0.471	0.27	0.040
Ephemeroptera	665.2	290.9	15	6.752	0.461	0.30	0.021
Lepidoptera	333.2	48.0	38	4.517	0.321	0.35	<0.001
Orthoptera	397.1	170.2	14	3.275	0.345	-0.02	0.413
Hemiptera	443.0	190.8	39	4.760	0.073	<0.01	0.323
Hymenoptera	381.5	156.2	38	3.921	0.007	-0.03	0.923
Coleoptera	234.9	29.1	92	4.877	-0.098	<0.01	0.316
(−Scarabaeidae			77	4.503	0.203	0.05	0.033)

Table 3.3: OLS regression parameters of log(lifetime fecundity) on log(dry weight) for different insect orders, excluding orders with fewer than five data points, and sorted by slope in decreasing order. Coleoptera are shown with and without Scarabaeidae (see text for discussion)

shown in table 3.4.

To be able to model differences in the effect of parental care between taxonomic orders, I could use only orders with all types of care: Coleoptera, Hemiptera and Dictyoptera. Even with the restricted dataset, parental care had a significant interaction with dry weight, showing that parental care had a negative effect on the *slope* of the relationship between dry weight and fecundity, both without the phylogeny (OLS model, $F_{2,128} = 3.62, p = 0.029$) and with the phylogeny (GLS, log-likelihood ratio $= 13.04, \Delta\text{df} = -2, p = 0.002, n = 136$ [$\Delta\text{AIC} = -9.04$]; figure 3.2a). The weight-fecundity slope was positive in insects with no parental care and in carer-guarders, but negative in carer-provisioners (Helmert contrasts: weight-fecundity slope under CP against pooled mean of weight-fecundity slopes under NC and CG, t=-2.461, p=0.015).

However, using these restricted data, there was no order×parental care in-

teraction, both without (OLS model, $F_{4,126} = 0.92, p = 0.455$), or with the phylogeny (GLS, log-likelihood ratio $= 3.11, \Delta df = -4, p = 0.539, n = 136$ [ΔAIC $= -4.89$]), so I dropped this term. There was therefore no need for a restricted subset of orders.

When I re-ran the analysis for all orders, the estimates and standard errors of the effects did not appreciably change. Parental care still had a significant negative effect upon the slope of the weight-fecundity relationship, both without the phylogeny (Parental care×dry weight, OLS model: $F_{2,251} = 3.74, p = 0.026$) and with the phylogeny (GLS, log-likelihood ratio $= 55.47, \Delta df = -2, p < 0.0001, n = 272$ [ΔAIC $= 31.47$]; figure 3.2b). With more orders included, lifetime fecundity now scaled differently with weight between orders both without (dry weight×order interaction, OLS model, $F_{10,239} = 2.04, p = 0.021$) and with the phylogeny (GLS, log-likelihood ratio $= 42.44, \Delta df = -10, p < 0.0001, n = 272$ [ΔAIC $= 22.44$]).

When I excluded scarab beetles from the analysis, parental care had only a marginal negative effect on the slope of the relationship between weight and fecundity, both without (OLS model, $F_{2,214} = 2.35, p = 0.097$) and with the phylogeny (GLS, log-likelihood ratio $= 5.93, \Delta df = -2, p = 0.051, n = 240$ [ΔAIC $= +1.93$]) and so the parental care× weight interaction was dropped from the model, but parental care had a significant and strongly negative main effect upon fecundity itself, both without (OLS model, $F_{2,216} = 8.84, p < 0.0001$) and with the phylogeny (GLS, log-likelihood ratio $= 24.11, \Delta df = -2, p < 0.0001, n = 240$ [ΔAIC $= +20.12$]). Caring-provisioning also had a stronger negative effect on fecundity than caring-guarding (Helmert contrast: CG against NC, t=-4.05, p<0.0001; CP against pooled mean of NC and CG; t=-2.01, p=0.045).
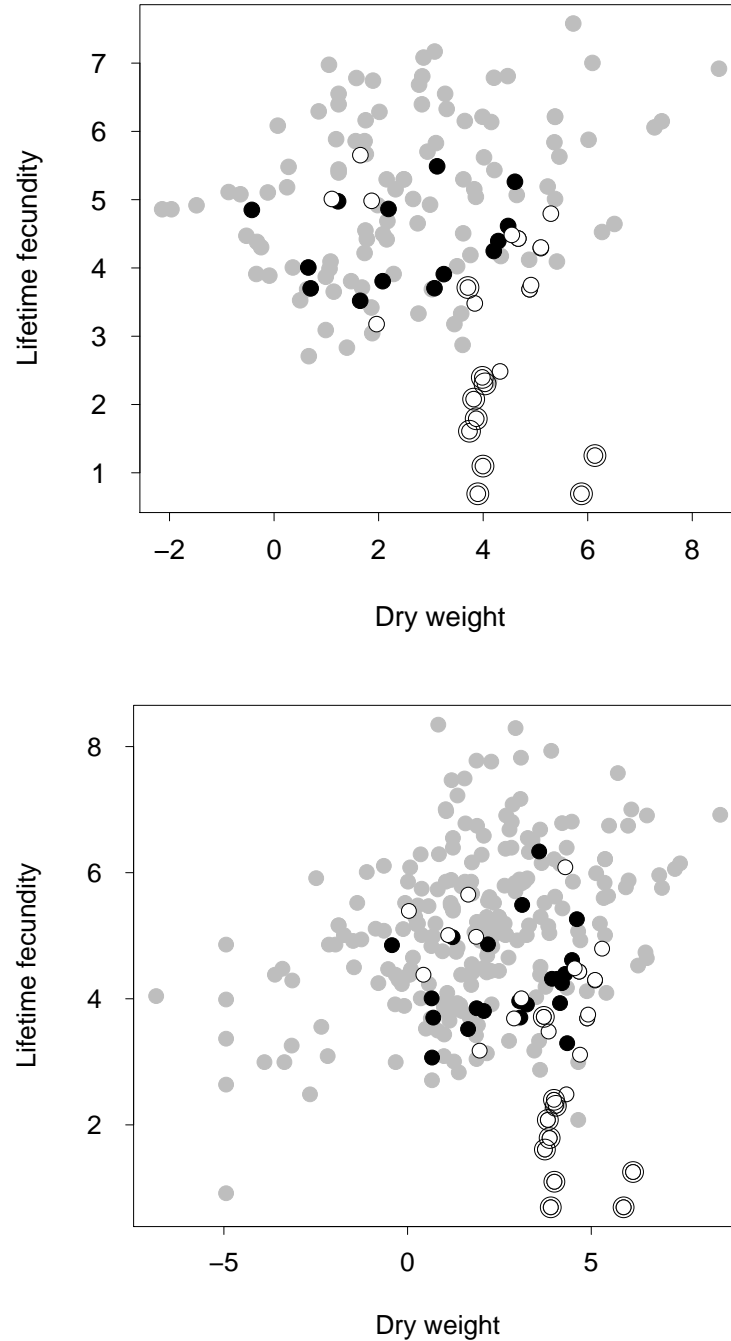
Figure 3.2: Mean fecundity, log-transformed, for species with different parental care strategies, (a) excluding and (b) including orders without representatives from all types of parental care. Key to symbols: Grey circles, non-carers; closed circles, carer-guarders; open circles, carer-provisioners. Double open circles show beetles of the family Scarabaeidae.

(a) Coleoptera, Hemiptera and Dictyoptera (n=142)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
DW$\times$PC	3.62	-2	0.029	10.54	-2	0.052	6.537
O	1.58	-2	0.210	7.22	-2	0.027	3.222
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (NC)	4.75	0.377		4.89	0.391		
DW	-0.08	0.092		-0.07	0.102		
PC (CG)	-0.30	0.311		-0.40	0.343		
PC (CP)	0.14	0.285		0.35	0.277		
DW$\times$PC (CG)	-0.04	0.104		0.01	0.111		
DW$\times$PC (CP)	-0.16	0.072		-0.21	0.071		

(b) All orders (n=272)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
DW$\times$PC	3.70	-2	0.026	55.47	-2	<0.0001	31.47
DW$\times$O	2.04	-12	0.021	42.44	-12	<0.0001	22.44
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (NC)	4.69	1.217		4.31	1.366		
DW	0.02	0.563		0.09	0.038		
PC (CG)	-0.38	0.267		-0.79	0.557		
PC (CP)	0.18	0.265		0.64	0.751		
DW$\times$PC (CG)	-0.04	0.086		0.03	0.137		
DW$\times$PC (CP)	-0.18	0.067		-0.65	0.188		
DW$\times$O	(Coefficients not shown)						

(c) All orders minus Scarabaeidae (n=240)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
PC	8.84	-2	<0.001	24.11	-2	<0.0001	7.84
DW$\times$O	2.45	-10	0.008	36.08	-10	<0.0001	16.07
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (NC)	4.61	0.237		4.45	1.361		
DW	0.19	0.085		0.08	0.081		
PC (CG)	-0.53	0.281		-0.56	0.226		
PC (CP)	-1.17	0.299		-0.83	0.330		
DW$\times$O	(Coefficients not shown)						

Table 3.4: Factors affecting lifetime fecundity, for (a) only those orders including all types of parental care; (b) all orders; and (c) all orders minus scarab beetles. Key to model terms: DW = dry weight; PC = parental care; CG = carer-guarder; CP = carer-provisioner; O = taxonomic order. For main effects that are involved in significant interactions, estimates are shown but not p-values. Coefficients for factor levels other than NC are given as the difference from the estimate for NC. Coefficients for the order:dry weight interaction are not shown since they are discussed elsewhere (see table 3.3).

Benefits of parental care

Parental care was not associated with increased offspring survival to adulthood without the phylogeny (OLS model, $F_{2,18} = 2.32, p = 0.112$), but when I incorporated phylogenetic information using GLS, parental care had a positive effect on survival (GLS, log-likelihood ratio $= 7.23, \Delta df = -2, p = 0.027, n = 34$ [$\Delta AIC = +3.23$]; figure 3.4; all models shown in table 3.5). There was no difference in offspring survival between the two types of parental care (Helmert contrasts; CP against pooled mean of NC and CG, t=-1.13, p=0.269). Offspring survival was also negatively associated with lifetime fecundity, both without the phylogeny (OLS model, $F_{1,18} = 7.23, p = 0.012$) and with the phylogeny (GLS, log-likelihood ratio $= 7.55, \Delta df = -1, p = 0.006, n = 34$ [$\Delta AIC = +6.78$]; figure 3.3a), and was positively correlated with dry weight, both without (OLS model, $F_{1,18} = 4.63, p = 0.04$) and with the phylogeny (GLS, log-likelihood ratio $= 8.78, \Delta df = -1, p = 0.003, n = 34$ [$\Delta AIC = +5.55$]; figure 3.3b). For the data in this analysis, dry weight and fecundity were not correlated with each other (OLS model; $F_{1,31} = 2.57, p = 0.118$). There were no significant interactions between any model terms. For this analysis, 30 species weights were directly measured and 4 estimated. When Scarab beetles were removed from the analysis, the results were not affected.

3.4.2 Experiments measuring the benefits of parental care

I found ten studies involving experimental removal of the carer, in the field, that recorded the consequent survival of nymphs to adulthood (table 3.6). With the carer removed there was no difference in offspring survival between carer-

(a) All data (n=34)

Model	Ordinary Least Squares			Generalized Least Squares			
	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
DW	4.63	-1	0.040	8.78	-1	0.003	5.55
LF	7.23	-1	0.012	7.55	-1	0.006	6.78
PC	2.32	-2	0.112	7.23	-2	0.027	3.23
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (NC)	0.75	0.377		0.65	0.214		
DW	0.05	0.025		0.10	0.034		
LF	-0.09	0.035		-0.09	0.034		
PC (CG)	0.07	0.137		0.06	0.135		
PC (CP)	0.32	0.151		0.46	0.176		

(b) All data minus Scarabaeidae (n=23)

Model	Ordinary Least Squares			Generalized Least Squares			
	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
DW	7.28	-1	0.015	7.81	-1	0.005	5.81
LF	3.47	-1	0.078	4.05	-1	0.044	2.05
PC	2.93	-2	0.079	6.49	-2	0.039	2.49
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (NC)	0.59	0.262		0.59	0.262		
DW	0.10	0.039		0.10	0.038		
LF	-0.08	0.045		-0.08	0.045		
PC (CG)	-0.01	0.159		-0.01	0.159		
PC (CP)	0.46	0.191		0.46	0.191		

Table 3.5: Factors affecting offspring survival to adulthood, for (a) all data; and (b) all data minus scarab beetles. Key to model terms: DW = dry weight; PC = parental care; CG = carer-guarder; CP = carer-provisioner. Coefficients for factor levels other than NC are given as the difference from the estimate for NC. For main effects that are involved in significant interactions, estimates are shown but not p-values.

guarders and carer-provisioners ($F_{1,8} = 0.96, p = 0.355$; figure 3.5a). However, even with this small sample size, as predicted the benefit of care in carer-provisioners was significantly greater than in carer-guarders ($F_{1,8} = 9.68, p = 0.014$; figure 3.5b). These two findings persisted after I incorporated the effects of phylogenetic non-independence using GLS (survival when carer removed: dropping 'parental care', log-likelihood ratio $= 0.390, \Delta$df $= -1, p =$
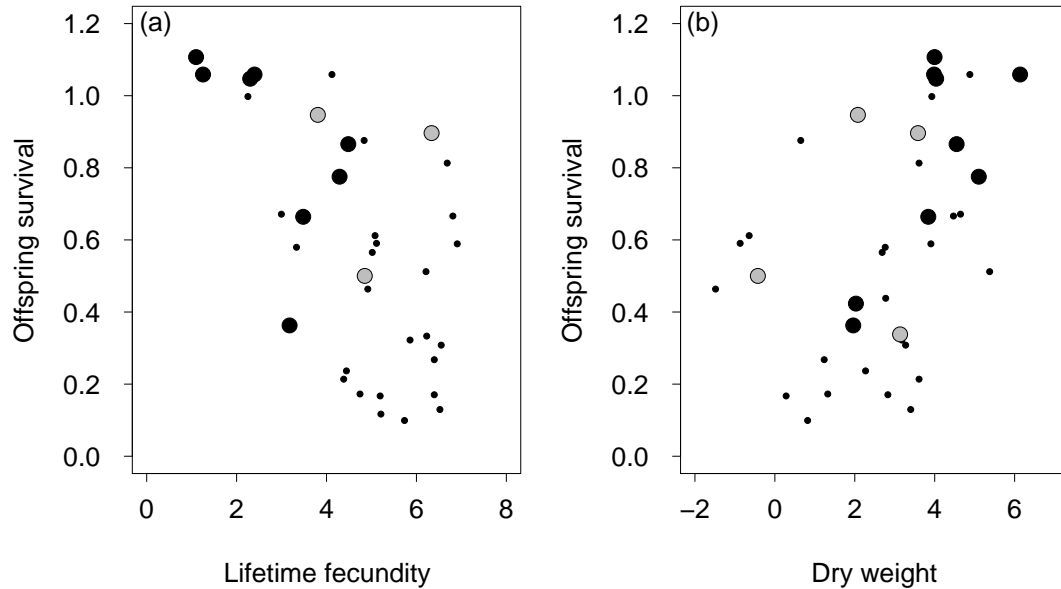
Figure 3.3: Offspring survival (arcsin-square root transformed) against (a) lifetime fecundity (log transformed) and (b) dry weight (log transformed). Key to symbols: Points, non-caring species; open circles, carer-guarders; closed circles, carer-provisioners.

			% Offspring survival	
Reference	Species	Care	carer removed	carer present
Wood (1976)	*Umbonia crassicornis*	CG	2	38
Tallamy & Denno (1981)	*Gargaphia solani*	CG	3	23
Faeth (1989)	*Corythucha hewitti*	CG	11.7	45.3
Nafus & Schreiner (1988)	*Hypolimnas anomala*	CG	36	61
Nalepa (1988)	*Cryptocercus punctulatus*	CP	0	49
Halffter *et al.* (1996)	*Copris incertus*	CP	22	76
Halffter & Matthews (1966)	*Copris fricator*	CP	59	93
Favila (1993)	*Canthon cyanellus*	CP	68	98
Tyndale-Biscoe (1984)	*Copris diversus*	CP	32	76
Windsor (1987)	*Acromis sparsa*	CP	0	11

Table 3.6: Studies investigating benefits of parental care in insects. CP stands for carer-provisioners, CG for carer-guarders.

$0.532, n = 10$ [ΔAIC $= +1.60$]; Improvement when carer present: dropping 'parental care', log-likelihood ratio $= 6.83, \Delta$df $= -1, p < 0.01, n = 10$ [ΔAIC $= -4.82$]; table 3.7).
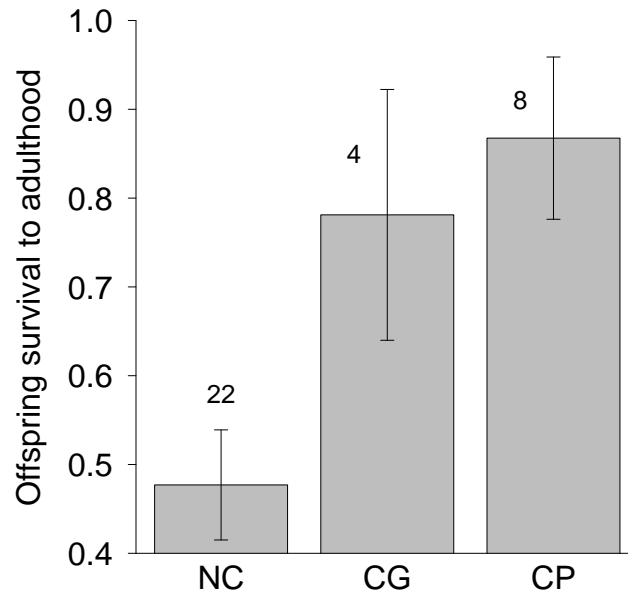
Figure 3.4: Mean±s.e. survival to adulthood, arcsin-square root transformed, for species with different parental care strategies. Key to symbols: NC, non-carers, CG, carer-guarders, CP, carer-provisioners.

3.5 Discussion

In this chapter I found that species with parental care laid fewer eggs in their lifetime than species without parental care, despite the finding that lifetime fecundity is not always related to body size. Further, as predicted, carer-provisioners laid fewer eggs than carer-guarders. Species with parental care also had a higher proportion of offspring survive to adulthood than species without care, although here carer-provisioners did not have higher survival than carer-guarders. Additionally, caring-provisioning negatively affected the *association* between body size and lifetime fecundity: carer-provisioners laid fewer eggs as they got bigger, not more (as in non-carers and carer-guarders).

(a) Survival with carer removed (n=10)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
PC	0.34	-1	0.579	0.43	-1	0.510	1.566
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (CG)	0.32	0.283		0.32	0.282		
CP	0.19	0.326		0.19	0.326		

(b) Increase in survival when carer present (n=10)

	Ordinary Least Squares			Generalized Least Squares			
Model	F	Δdf	p	Lik. Ratio	Δdf	p	ΔAIC
PC	10.02	-1	0.019	6.83	-1	0.009	4.82
Table of coefficients	Estimate	s.e.		Estimate	s.e.		
Intercept (CG)	0.43	0.072		0.59	0.262		
CP	0.26	0.084		0.10	0.038		

Table 3.7: Factors affecting (a) offspring survival in the absence of a carer, and (b) the concomitant increase in survival when the carer is present, from manipulation studies. Key to model terms: PC = parental care; CG = carer-guarder; CP = carer-provisioner. Coefficients for CG are given as the difference from the estimate for CP. For main effects that are involved in significant interactions, estimates are shown but not p-values.

At the same time, using an analysis of experimental manipulations in the literature and incorporating the effect of phylogeny, I found that carer-provisioners were more effective carers than carer-guarders. A similar analysis of the *costs* of care to both groups is currently impossible because of the lack of standardized data. However, both types of care in insects have been shown to be costly (table 3.8).

Body size had mixed associations with insect lifetime fecundity depending on taxonomic order. Between species, this has hardly ever been demonstrated, since existing studies focus on single orders. In an extensive review of the field twenty years ago, Peters (1983) found not one study investigating the
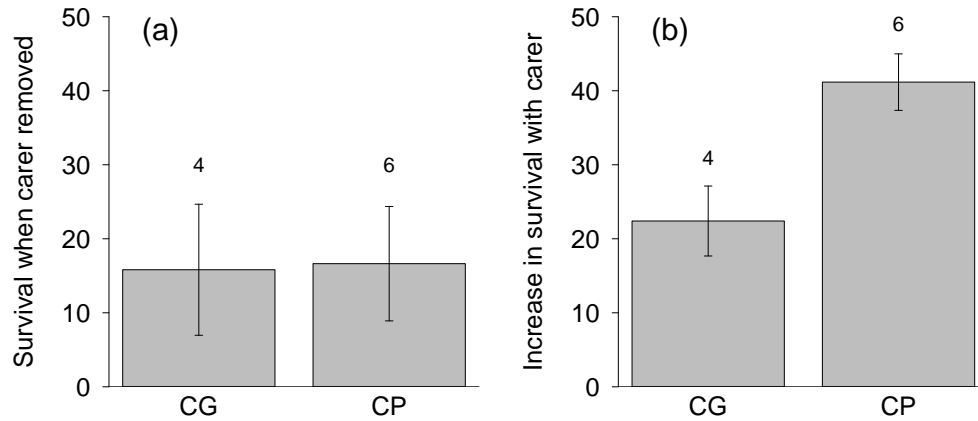
Figure 3.5: Survival of offspring to adulthood in literature experiments (a) when the caring parent is experimentally removed; (b) increase when caring parent is present. For carer-provisioners, the benefit of care is greater than for carer-guarders. Key to symbols: CG, carer-guarders; CP, carer-provisioners.

Reference	Species	Care	Cost investigated	Costly?
Agrawal *et al.* (2005)	*Sehirus cinctus*	CP	Fecundity	N
			Interclutch interval	Y
Hunt *et al.* (2002)	*Onthophagus taurus*	CP	Longevity	Y
Kaitala & Mappes (1997)	*Elasmucha* spp.	CG	Pr. of 2nd clutch	Y
Rankin *et al.* (1996)	*Euborellia annulipes*	CP	Interclutch interval	Y
Thomas (1994)	*Rhinocoris carmelita*	CG	Weight loss	Y
Nalepa (1988)	*Cryptocercus punctulatus*	CP	Interclutch interval	Y
Tallamy & Denno (1982)	*Gargaphia solani*	CP	Fecundity	Y
			Interclutch interval	Y
			Longevity	Y

Table 3.8: Studies investigating costs of parental care in insects. CP stands for carer-provisioners, CG for carer-guarders.

interspecific allometry of fecundity in insects. Subsequently to this the only study encompassing multiple orders has been that of Berrigan (1991), who found similarly mixed effects of size on fecundity. In agreement with previous findings, my results show a strongly positive correlation between body weight and fecundity in Lepidoptera (Garcia-Barros, 2000; Jervis *et al.*, 2005; Wiklund *et al.*, 1987) and Diptera (Berrigan, 1991), and no relationship in the Hymenoptera (Berrigan, 1991; Blackburn, 1991). In the Coleoptera, the lack of allometric relationship agreed with Berrigan (1991) when I included Scarabs in the analysis; however, excluding the Scarabs I found a positive scaling of lifetime fecundity. To these I can add novel results for the Dictyoptera and Ephemeroptera (with positive scaling of fecundity), and the Hemiptera and Orthoptera (with no fecundity-weight relationship).

Hence, in three cases shown here (the Hymenoptera, Hemiptera and Orthoptera), there was no interspecific scaling of fecundity with weight. Now, *intraspecifically*, in insects as in most poikilotherms, fecundity almost universally scales positively with size (reviewed by Clutton-Brock, 1991; Honek, 1993, but see Ohgushi, 1996). The interspecific results I report here clearly do not mirror this pattern. This further highlights the importance of the scale at which life-history relationships are studied: trade-offs and patterns at the within-species level do not have to mirror intraspecific patterns, and frequently they do not. Blackburn (1991) argues that the fecundity of parasitic wasps (Hymenoptera) is largely constrained by the size of the parasite's host rather than the size of the female. For my analysis, 'Hymenoptera' was not confined to parasitic wasps but also included the sawflies, Symphyta, but this pattern may still hold. In the Hemiptera and Orthoptera, both orders that contain a diver-

sity of reproductive strategies, this explanation is not applicable. Some other ecological variable in these orders may impose a stronger constraint on fecundity than body size. Within species there may be taxon-specific, compensatory strategies for small body size: for example, compensatory feeding is known to obscure fecundity trade-offs in some Orthopterans (Mole & Zera, 1994). Alternatively if energy budgets are not tightly constrained, the trade-off may not be evident.

However, parental care was always associated negatively with fecundity, despite fecundity not scaling uniformly with body size. While comparative studies can demonstrate associations between life-history variables, it is impossible to ascertain the direction of causality without manipulation studies, which would require evolutionary time to conduct. However, the prior knowledge that many previous studies on single species have demonstrated parental care trade-offs in insects, combined with the results of the small analysis of experimental findings I present here, lend weight to an interpretation of my results in terms of a trade-off. The pattern we see between species could be an emergent property of trade-offs between investment in offspring survival and number at the individual level, and hence supports the idea of a trade-off between parental care and fecundity. This inference is often made, but usually only implicitly. Trade-offs at the individual level will partly define the individual's 'option set' of possible values of the two traits, will place a limit on variation between individuals, and constrain possible evolution (Partridge & Sibly, 1991). In the absence of confounding variables, the combined option sets of many different species should be a curve that describes the form of this constraint. Alternatively, species with parental care may *not* be constrained by

a trade-off to have fewer offspring, but other selection pressures may make this solution adaptive. For example, offspring in environments that select for parental care may also incur higher costs of competition, reducing the optimal number (Borgerhoff Mulder, 2000).

Interestingly, in carer-provisioners, the trade-off affected not only the absolute number of eggs laid, but also the weight-fecundity relationship. Carer-provisioner species laid *fewer* eggs as they got bigger in contrast to non-carers and carer-guarders. In carer-provisioners, unlike in the other types of care, offspring requirements for growth must be satisfied by parental effort, usually in the form of feeding. Parental care has been shown to have negative effects on foraging rate (Paez *et al.*, 2004; Strohm & Marliani, 2002; Thomas, 1994; Townsend, 1986, but see Reed Hainsworth, 1977), so may well negatively affect a parent's ability to feed a brood (although see Agrawal *et al.*, 2005, who did not find a cost of provisioning as opposed to guarding). Larger parents will have larger offspring, which will have accordingly larger requirements (e.g. Smith, 1997), and the ability of a larger parent to satisfy these requirements will not necessarily scale at the same rate. The relationship between a parent's size and how many offspring she can successfully provision (in addition to feeding herself) will depend on factors that influence foraging efficiency, which are complex (Mittelbach, 1981). By contrast, I would argue the ability of carer-guarder mothers simply to defend larger broods of offspring is more likely to be directly related to the mother's size (see, for example, Cocroft, 2002; Eberhard, 1975).

One finding also worthy of note is that offspring survival was positively associated with dry weight, even though dry weight and fecundity were mostly

positively related in the wider analysis, and for the subset where survival data were available, weight and fecundity were not related. This directly contradicts Peters (1983, p. 133), who, in his review of the subject, is explicit in stating that 'larger poikilotherms have higher birth rates and higher death rates than do smaller species', contrasting this against homeotherms for which the reverse is the case. If larger insects have higher offspring survival, this may reflect a evolutionary advantage of large adult size to offspring in general, manifest at the between-species level (remembering that all species are considered to be at local adaptive peaks, and it is meaningless to compare 'fitness' between species). However, while the advantage of being large is well-recognized, it is usually attributed to adult payoffs that are not relevant at the offspring stage: fecundity advantage, or sexual selection – one exception being the avoidance of predation (Blanckenhorn, 2000). This positive relationship goes against published reports, estimates and theory (e.g. Banse & Mosher, 1980; Blanckenhorn, 2000; Peters, 1983). In most cases, survival is predicted to be *lower* in larger poikilotherms, since this balances the almost universally-observed increase in fecundity with size. The mechanisms by which this might operate are diverse: viability cost of long development, or of fast growth (predation, parasitism, or starvation), reduced agility, increased detectability, or heat stress (Blanckenhorn, 2000). Hence, that I found a positive relationship between insect size and survival to adulthood certainly warrants further investigation.

To my knowledge this is the first phylogenetic-comparative study of insect life-history that spans multiple orders of insects. My results show that insect species lay variable numbers of eggs according to a pattern that sug-

gests they incur a trade-off between parental care and lifetime fecundity. This is consistent with previous experimental findings that individuals from various species actually do incur such trade-offs. Furthermore, increasing investment in parental care is associated with a stronger trade-off with fecundity. At the same time, parental care is associated with increased survival of offspring to the adult stage, again consistently with previous findings at the individual level. Future work should aim to incorporate the effects of error in the data. Additionally, I have demonstrated that controlled experiments on individual species show a consistent difference between carer-provisioners and carer-guarders: carer-provisioners, which invest more in their current brood, have an accordingly larger effect upon their brood's survival. In future, further experiments and a careful meta-analysis may show a similar disparity in costs between the two types of care.

Thus my results show that the synthesis of inter- and intraspecific studies can be used to infer more information than is available to either method in isolation, and can pinpoint the most interesting areas for further research. In this case the most obviously interesting area for future research is in the Scarabaeidae, a group with a great variety of parental care strategies, and whose members lie way outside the normal relationship between body size and fecundity. There is already a body of literature on the Scarabaeidae (see, for example, Halffter & Matthews, 1966; Huerta *et al.*, 2003; Monteith & Storey, 1981; Sato, 1998), and several phylogenetic comparisons of various behaviours (Philips *et al.*, 2004; Villalba *et al.*, 2002), but to date no comparative study has addressed the evolutionary function of their spectacularly low rate of egg-laying.

Research should now also focus on incorporating egg size, an important

determinant of offspring fitness, into a comparative analysis. One theory that has come under much scrutiny is the 'safe harbour hypothesis' (Shine, 1978), that egg size should increase in response to the evolution of parental care to take advantage of the resulting low juvenile mortality. However, an alternative hypothesis based on the trade-offs suggested by this study might predict that egg size might decrease with parental care. Although the total proportion of resources allocated to offspring biomass does not necessarily influence the best resolution of the egg size-egg number trade-off, between species egg size may still decrease with parental care as a result of generally reduced allocation to offspring biomass, and should by the same token decrease by more with increasing amounts of parental investment. This information could be relatively easily incorporated into the analyses outlined here. Also of particular interest would be how male-only parental care affects lifetime fecundity. If care is done by the male, we might expect that the female could therefore lay *more* rather than fewer eggs as proposed by Tallamy & Wood (1986).

Chapter 4

Male-caring *Rhinocoris* and *Stylosanthes*: an unlikely preference?

4.1 Abstract

The evolution of exclusive male parental care is predicted to depend partly upon factors that reduce the mating costs of care. One such factor is high population density, such that caring males encounter many females despite being stationary. In Uganda, male-caring assassin bugs *Rhinocoris tristis* and *R. albopilosus* are reported to live at high density on the plant *Stylosanthes*, suggesting that aggregation on this plant may have favoured the evolution of male care. I found *R. tristis* as predicted at high density on *Stylosanthes*. In this chapter, I investigate what benefit *R. tristis* get from living on this plant. The plant's sticky hairs provide protection from ants, potential egg predators, and *Stylosanthes* also harbours a favourable distribution of prey compared to that available on mixed vegetation. However, the *Stylosanthes* species favoured by *R. tristis* was only recently (c.

1950) introduced to Africa. Therefore, if the evolution of male care was favoured by high density through aggregation on a plant, *R. tristis* probably originally aggregated on a different plant species. In contrast to *R. tristis*, I found *R. albopilosus* at lower density, and on mixed vegetation, and I discuss possible reasons for the difference in ecology. My findings suggest that the costs and benefits affecting parental care can be affected by a range of ecological factors not usually implicated in its evolution.

4.2   Introduction

In species where offspring require care at a cost to one or other parent, anisogamy usually predisposes the female to care. This is because her gametes are more expensive, and so by incurring the cost of caring she foregoes fewer potential offspring than would the male if he were to care (e.g. Clutton-Brock, 1991; Trivers, 1972). This bias is further increased in species with internal fertilization (Gross & Shine, 1981), which physically separates males from fertilized eggs. In insects, the majority of species are internal fertilizers, and so uniparental male care is predicted to be very rare (see chapter 2). Generally, this is found to be the case (Tallamy, 2001). However, there are a few examples of exclusive male care, mostly from within the Hemiptera, for example giant water bugs (Smith, 1997); golden egg bugs (Katvala & Kaitala, 2003, but see Gomendio & Reguera, 2001), and assassin bugs (Thomas, 1994).

There has been much debate over why males should care in these groups (e.g. Manica & Johnstone, 2004; Tallamy, 2001; Tallamy & Wood, 1986). The evolution of male care has been been predicted to depend mainly on the conjunction

of (1) males caring for 'overlapping' egg clutches i.e. simultaneous clutches from more than one female, (2) high female reproductive rate, and (3) high population density (Manica & Johnstone, 2004; Thomas, 1994), which together lead to a high number of females likely to encounter a stationary caring male. Here, I explore some factors promoting the evolution of male parental care in assassin bugs.

Population density is therefore predicted to be central to the evolution of male care. In Uganda, male-caring assassin bugs *Rhinocoris tristis* and *R. albopilosus* are reported to live at high density on *Stylosanthes guianensis* (Bequaert, 1935; Nyiira, 1970; Odhiambo, 1959; Thomas, 1994). Specialization on, or a preference for, a resource can lead to increased local population density (Takahashi *et al.*, 2001), which could drive the evolution of paternal care as predicted by Manica & Johnstone (2004). Host plant specialization in plant-feeding insects has been extensively studied (reviewed in Bernays & Graham, 1988; Jaenike, 1990; Stamp, 2001). However, specialization by *predators* such as assassin bugs is much rarer (e.g. Beard & Walter, 2001; Gilbert, 2005; Wheeler, 2001). Predators and plants are, by definition, separated by at least one trophic level, and are therefore unlikely to co-evolve directly. But predators can also respond to plant traits indirectly through the plant's effect on the distribution of their prey. This "tri-trophic interaction" (Price *et al.*, 1980) depends on the predator's dietary range: specialist predators are often restricted to their prey's host plant (Gilbert, 2005), and are sometimes attracted to this plant as a prey-location cue (Agelopoulos & Keller, 1994; Bargen *et al.*, 1999, but see Walde, 1995). However, generalist predators are much less likely to evolve such a plant preference. Here, a preference might evolve because the predator

gets supplementary nutrients from the plant (e.g. Coll, 1996), because of a preponderance of suitable types of prey on one plant (Beard & Walter, 2001), or because the plant is a refuge ("enemy-free space"; Stamp, 2001) from the predator's own natural enemies (Schellhorn & Andow, 1999). Enemy-free space in particular has the potential to lead to host-plant specialization. If insects can get protection for their eggs from one kind of host plant, they may reduce investment in other forms of defence such as a protective egg wall, which can increase their dependency on the plant's protection (Eberhard, 1975).

In this chapter, I investigate what benefit *Rhinocoris* assassin bugs might get from living on *Stylosanthes*. I look at possible benefits related to food, and to protection from predators. With regard to food, I ask firstly 'do *R. tristis* directly feed from *Stylosanthes*?', and secondly 'does *Stylosanthes* harbour a favourable distribution of prey for *R. tristis*?'. Thirdly, since *Stylosanthes* is covered in sticky trichomes, I ask 'do *R. tristis* nymphs feed from miniscule prey stuck to *Stylosanthes*' sticky hairs?'. With regard to predators, I ask 'does *Stylosanthes* protect *Rhinocoris* eggs from ant predators, and hence create enemy-free space?'. Finally, I discuss possible roles of *Stylosanthes* in the evolution of assassin bug male parental care.

4.3 Methods

4.3.1 Study species and site

Assassin bugs of the genus *Rhinocoris* (Hemiptera: Reduviidae) are generalist, predatory bugs native to Africa. The genus contains several hundred species (Capriles,

1990), almost all of which lay small clutches of eggs but do not care for them (Cobben, 1996). In three known cases, though, males guard overlapping egg broods against parasitoids until hatching; *R. tristis* Stål (Thomas, 1994), *R. albopilosus* Signoret (Bequaert, 1935; Odhiambo, 1959) and *R. albopunctatus* Stål (Nyiira, 1970). Male-caring *Rhinocoris* occur sympatrically in Uganda, breed continuously and aseasonally (e.g. Thomas, 1994), and all appear strongly to prefer to forage and oviposit on plants of the genus *Stylosanthes*, on which they are reported at high population densities. In Uganda, *R. tristis* and *R. albopunctatus* have both been recorded on *S. guianensis* (Nyiira, 1970; Thomas, 1994, respectively); *R. albopilosus* has been recorded both on *S. guianensis* (Thomas, 1994) and on *S. mucronata* (Odhiambo, 1959). They will attack and eat any insect up to their own size (Ambrose, 1999), a mean of 9.89±0.08mm (male, n=48) and 11.94±0.08mm (female, n=59) for *R. tristis*, and 11.54±0.17mm (male, n=23) and 13.66±0.13mm (female, n=30) for *R. albopilosus*.

Stylosanthes spp. (Fabaceae) are leguminous pasture crops grown for their high protein content and ability to withstand variability in soil nutrients. While *S. mucronata* is native to Uganda, agriculturalists have found other South American species to be more productive, and most commercially-grown *Stylosanthes* spp., including *S. guianensis*, were introduced to Africa recently, from the 1950s onwards (Lazier, 1984). They became much more abundant than *S. mucronata* until *Stylosanthes* was almost all destroyed in Uganda by the anthracnose fungus (Irwin *et al.*, 1984) from which populations are now recovering.

Field and laboratory studies were conducted at NAARI (Namulonge Agriculture and Agronomy Research Institute) near Gayaza, approximately 40km north of Kampala, Uganda, with permission from NARO (National Agriculture Research Organization) and UNCST (Uganda National Council of Science and Technology). Data were collected between October 2003 and June 2005.

For laboratory studies, assassin bugs were collected from mixed vegetation around the field station and maintained in cylindrical glass Dietz petrol-lamp hoods ('bottles') measuring 25cm (height) $\times$ 20cm (diameter), at room temperature and humidity and natural hours of daylight (6am – 6pm). They were fed once a day with medium-sized insects (0.5 – 1 $\times$ the bugs' body length) collected by sweep-net from surrounding vegetation. Both ends of the bottles were sealed with thin cotton material held in place by rubber bands, and the material was soaked in water once a day to provide drinking water. Three split bamboo canes of approximately 20cm length and 5mm diameter were provided in each bottle for oviposition substrate.

For field studies, eight field sites of 100m^2, measuring either 10$\times$10m or 20$\times$5m according to spatial constraints at the field station, were monitored for a maximum of 16 weeks under a mark-release-recapture protocol. Four sites consisted of *S. guianensis* grown in monoculture, while the other four ('grass' sites) had mixed vegetation (e.g. *Panicum* spp., *Dolichos* spp., *Calliandra* spp.) which also included small amounts of wild *S. guianensis*. The protocol consisted of searching the site intensively for 3h each day, starting at a pseudorandomly-chosen time during daylight hours. Each bug seen was captured and either (1) captured, marked on its thorax and the leathery parts of its wings using student's acrylic paint (Allman) applied with a cocktail stick, and released, (2) noted as a recapture, or (3) marked *in situ* if guarding, without being captured, to reduce the chance of abandonment. Nymphs were not recorded since the mark would disappear when the nymph moulted; and also because of the difficulty of identification in the field; while adult *R. tristis* and *R. albopilosus* are only barely distinguishable (*R. albopilosus* adults are slightly larger and thinner, and have more distinct white patches on the underside of their abdomen), nymphs are virtually identical. Monitoring was continued for periods of 6 days (the 'observation period') at two sites before shifting to two others, in a rotating pattern.

4.3.2 Population density

Adult population density was calculated as the mean number of different adults encountered during half an hour's collecting (during mark-release-recapture studies) on a 100m^2 site.

4.3.3 Food

Adults

To see whether bugs fed directly from *Stylosanthes*, I recorded any instance of plant-feeding by *R. tristis* or *R. albopilosus* that I saw. To look at whether *Stylosanthes* harboured the right kind of prey for *R. tristis*, I investigated what species the bugs were eating compared to what was available. To assess the bugs' diet, any prey seen being consumed by assassin bugs was collected for identification and classification. Prey items were identified to order and sorted into size categories according to what size of meal they represented for an assassin bug: 'small' (0–5mm; suitable prey for an early-instar nymph), 'medium' (5–15mm; suitable prey for an adult assassin bug) and 'large' (over 15mm, usually as big or bigger than the assassin bug itself, and representing a large meal). Insects much larger than the assassin bugs (over 30mm) were ignored, since they were assumed to be unsuitable as prey items.

To assess what prey were available, sweep-net samples were taken from 22 patches of *Stylosanthes* and 22 from grass (i.e. from on and around the grass mark-release-recapture sites). The exact locations for sampling were chosen pseudorandomly from across mark-release-recapture sites. Sampling was done by the same observer to reduce bias. Each sample consisted of ten seconds of sweep-netting with a strong, fine net (Watkins & Doncaster; mesh size 1.5mm), after which the entire contents were placed in 96% ethanol for later identification.

To test for differences in availability of prey, firstly I used a simple χ^2 test to compare abundances of insects in the different size classes. To test further for differences in taxonomic composition between samples, I divided each size class up further into taxonomic orders. I then compared the insects caught in the sweep-net samples on *Stylosanthes* and grass sites using an analysis of similarity (ANOSIM). This compares the median Bray-Curtis distance (a measure of sample heterogeneity) between samples for all permutations of *Stylosanthes*/grass pairings with the median distances between all grass/grass and all *Stylosanthes*/*Stylosanthes* pairings.

To look at differences between what the assassin bugs were actually eating and what was available, I compared each species' prey records on both types of vegetation with the sweep-net samples using 'χ^2 distance' (e.g. Gilbert & Owen, 1990). This is a one-way measure of similarity that assesses whether specimens present in one sample are also present in another. This is appropriate in this case because I am only interested in whether insects that are present in the bugs' diet are also present in the vegetation, and not *vice versa*. The χ^2 distances from the prey records to the sweep-net samples on each type of vegetation were compared using Wilcoxon rank sum tests.

Nymphs

To investigate whether nymphs survive longer on *Stylosanthes*, or exploit tiny prey items stuck to its sticky hairs, I divided six newly-hatched broods from laboratory females of *R. tristis* into three groups of nymphs, which were placed in separate bottles. Into the first bottle of each brood I placed a bare split-bamboo stem. Into the second I placed a freshly-cut stem of *Stylosanthes* from the field. Into the third I placed a similar stem which had been washed thoroughly under a tap for two minutes and shaken dry. If nymphs eat tiny prey items immobilized by the sticky hairs, they should develop more quickly when the stem is not washed clean, so the null hypothesis was that

nymphs should develop at equal rates on unwashed and washed *Stylosanthes* stems. Any effect washing might have on the humidity was reduced by adding water to the cloth covering the bottles in all treatments (as was usual practice, in supplying the insects with water). The stems in each bottle were replaced every day. Otherwise, the bottles were not supplied with food. Each day the number of nymphs remaining alive, and the number moulting, were counted.

To avoid pseudoreplication from nymphs sharing bottles, I used the mean time-to-death for each bottle, and analysed the data with a linear mixed effects model, with 'Natal brood' included as a random factor.

4.3.4 Predators

To investigate whether *Stylosanthes* confers protection from ant predators, I chose eight ant nests located around *Stylosanthes* fields, pseudorandomly with regard to location and ant morphospecies. I then placed a reward (a freshly-killed medium-sized cricket) to the top of (1) a 20cm stem of *Stylosanthes* from which hairs had been removed from the *branches alone* by rubbing ('Intact' group), (2) a 20cm stem of *Stylosanthes* from which the sticky hairs had been removed from the *stem* by rubbing (making a clear, hair-free path to the reward; 'Shaved' group), and (3) a 20cm split bamboo stem (Control group). Five replicates of each treatment were placed c. 1m from each ant nest and c. 50cm apart. Within each group, stems were c. 10cm apart. I noted the presence or absence of ants, 3 hours and 18 hours after the start of the experiment. I also noted whether or not the reward had disappeared.

Since the data had a binomial error structure (counts of presence/absence) and also a random factor (site), I analysed them with generalized linear mixed models using penalised quasi-likelihood (glmmPQL) using the MASS package in R.

All data were analysed using R 2.2.1 (R Development Core Team, 2005).

4.4 Results

4.4.1 Population density

Adult *R. tristis* were found at densities of 2.225 ± 0.168 individuals/100m^2/$\frac{1}{2}$-hour on *Stylosanthes* sites, and of 0.830 ± 0.101 individuals/100m^2/$\frac{1}{2}$-hour on grass sites. By contrast, adult *R. albopilosus* were found at much lower densities on *Stylosanthes*: 0.020 ± 0.007 individuals/100m^2/$\frac{1}{2}$-hour, and higher densities on grass: 1.575 ± 0.105 individuals/100m^2/$\frac{1}{2}$-hour (ANOVA, interaction between 'species' and 'vegetation type', $F_{1,231} = 159.9, p < 0.001$; see figure 4.1).

4.4.2 Food

Adults

No adult *R. tristis* or *R. albopilosus* was ever observed feeding directly on *Stylosanthes*. By contrast, they were commonly seen eating arthropods. Prey items recorded for *R. tristis* and *R. albopilosus* spanned seven and five orders respectively. Grouped by size classes alone, *Stylosanthes* samples had similar numbers of 'medium' and 'large' prey items, but more prey in the 'small' category than did the grass samples ($\chi^2_2 = 6.711, p = 0.035$; see figure 4.4.2). When I divided them further into taxonomic orders, *Stylosanthes* sweep-net samples were significantly different from grass samples (ANOSIM based on 1000 permutations; R-statistic$= 0.088, p = 0.011$; figure 4.4.2). *Stylosanthes* samples
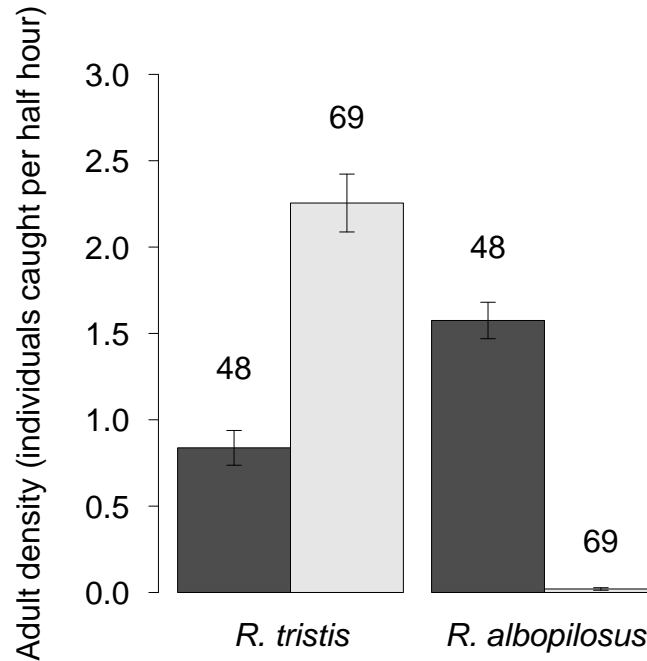
Figure 4.1: Mean (± s.e.) Adult population density on grass (dark bars) and *Stylosanthes* (light bars) sites for *R. tristis* and *R. albopilosus*. Sample sizes are indicated above the bars; data are taken from daily counts during mark-release-recapture studies.

were richer in spiders, Orthoptera and large Heteroptera, while grass samples contained more medium-sized Heteroptera. The Bray-Curtis distances were significantly shorter between grass-grass sample pairs than both the distances between *Stylosanthes-Stylosanthes* pairs and those between *Stylosanthes*-grass pairs. This indicates both that grass samples were different from *Stylosanthes* and that they were also less variable in taxonomic composition.

To compare the bugs' prey records with the prey available in the sweep-net samples, I looked at the similarity (i.e. the χ^2-distances) between the frequencies of each taxon in the prey records and the frequencies in each sweep-net

sample on the appropriate type of vegetation. *R. tristis*' diet was closer to the prey available in the environment when it was on *Stylosanthes* than when on grass. The χ^2-distances from *R. tristis*' prey items on *Stylosanthes* to the sweep-net samples on *Stylosanthes* were much smaller than the distances from the grass prey records for *R. tristis* to the grass samples (Wilcoxon rank sum test, $W = 445, p \ll 0.001$, n=44; figure 4.4).

Although prey records for *R. albopilosus* on *Stylosanthes* were too scarce to permit a statistical comparison, the distance between *R. albopilosus*' diet on grass sites and the prey available on grass sites was similar to the distance between *R. tristis*' diet on *Stylosanthes* and the prey available on *Stylosanthes* ($W = 296, p = 0.212$, n=44), and was significantly smaller than the distance between *R. tristis*' diet on grass and the prey available on grass, even after correcting for non-orthogonality of contrasts ($W = 439, p \ll 0.001$, n=44; see figure 4.4). Comparing the two species' total prey records directly using a simple χ^2 test, there was no difference (χ^2_7=6.285, p=0.507).

Nymphs

Although *R. tristis* nymphs raised on only a bare stem did not die earlier than nymphs on untreated and washed *Stylosanthes* (figure 4.5), there was a marginal trend in this direction ($F_{2,10} = 3.823, p = 0.058$; linear mixed-effects model, see table 4.1). No nymphs were ever observed feeding from the plant, and they did not congregate around any part of the *Stylosanthes* stem placed in the bottle. Nor were nymphs ever seen with a prey item (except for other nymphs; a very small number of nymphs cannibalized their siblings). Furthermore, no nymphs survived until the first moult, indicating that none of
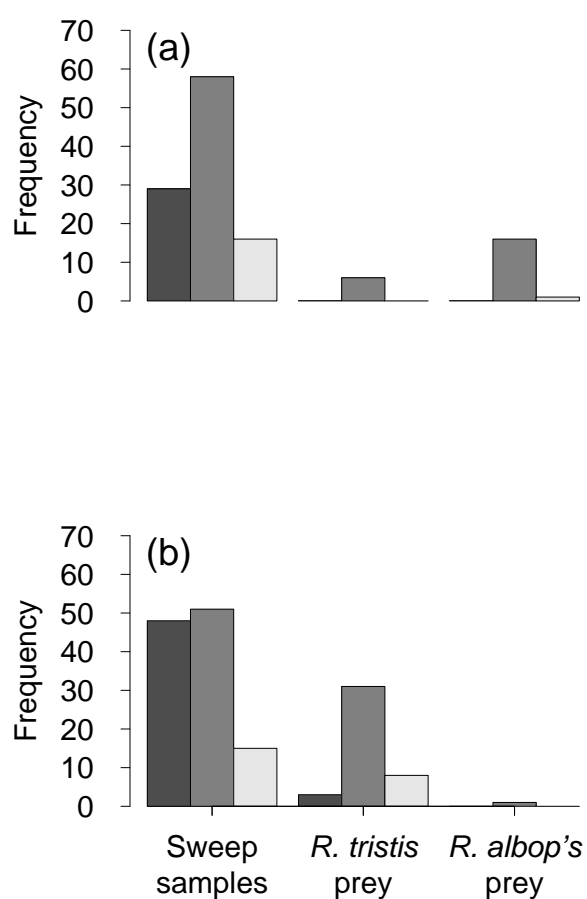
Figure 4.2: Raw counts of small (dark bars), medium (medium bars) and large (light bars) prey items (a) on *Stylosanthes* and (b) on grass sites, as estimated from sweep-net samples, and in *R. tristis* and *R. albopilosus* prey records.
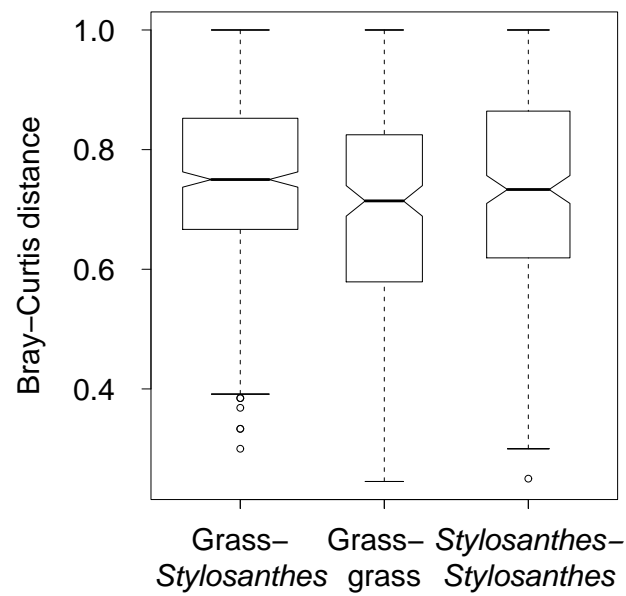
Figure 4.3: Median (± IQR) Bray-Curtis distances for all possible pairings of grass-*Stylosanthes* samples (n=528), grass-grass samples (n=231) and *Stylosanthes-Stylosanthes* samples (n=276). Boxes show inter-quartile range; whiskers show range of data. Notches represent $\pm 1.58 \times \text{IQR}/\sqrt{n}$ and are given for clarity; non-overlapping notches indicate statistically different distributions (McGill *et al.*, 1978, cited in R Development Core Team, 2005).
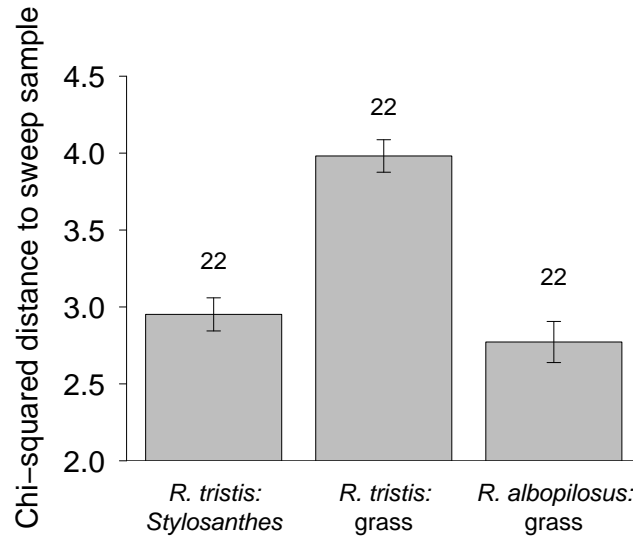
Figure 4.4: Mean ($\pm$ s.e.) χ^2 distance from the prey records of *R. tristis* and *R. albopilosus* to the sweep-net samples on their respective vegetation types. Sample sizes (i.e. number of χ^2-distances computed) are given above the bars.

the treatments was sufficient to sustain nymphal growth or survival.

4.4.3 Predators

Ants were less likely after 3 hours to have reached rewards on top of intact *Stylosanthes* stems than on top of shaved stems or bare cane controls (glmmPQL; $F_{2,110} = 15.228, p < 0.001$; figure 4.6a). After 18 hours, there was no difference between treatments ($F_{2,110} = 1.685, p = 0.190$). The rewards on intact stems were also less likely to have disappeared than on shaved stems or bare cane controls, after 3h ($F_{2,110} = 10.831, p < 0.001$) and 18h ($F_{2,110} = 8.811, p < 0.001$; figure 4.6b). Breakdown of models is given in table 4.2.
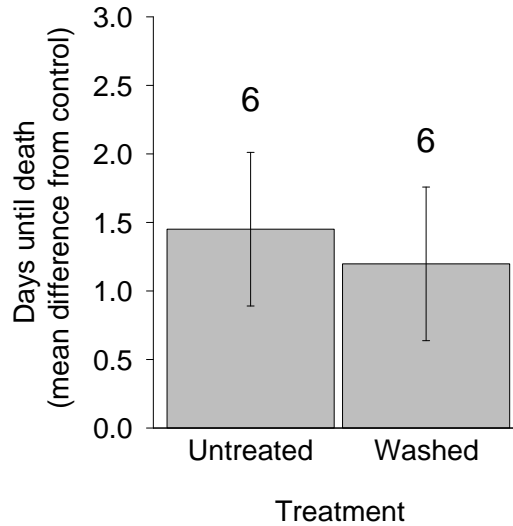
Figure 4.5: Mean (± s.e.) survival time of *R. tristis* nymphs, expressed as the difference between treatment (Untreated or Washed) and control (Cane).

R. tristis **nymph survival** Source of variation	Effect size	SE	df (Δ/resid.)	F-value	p-value
Fixed factors					
Intercept (Control)	6.724	0.550	1/10		
Treatment	—	—	2/10	3.822	0.058
Untreated	1.450	0.560			
Washed	1.207	0.560			

Table 4.1: Factors affecting the mean survival time of nymphs (Linear mixed-effects model fit by REML). The random factor 'Natal brood' had a significant effect and was retained in the model (Likelihood ratio test versus model without 'Natal brood'; LR=6.271, p=0.012).

4.5 Discussion

The elevated population density on *Stylosanthes* described here for *R. tristis* supports previous findings for this species (Thomas, 1994) and I have further shown that the bugs occur at much lower density elsewhere. Generalist preda-
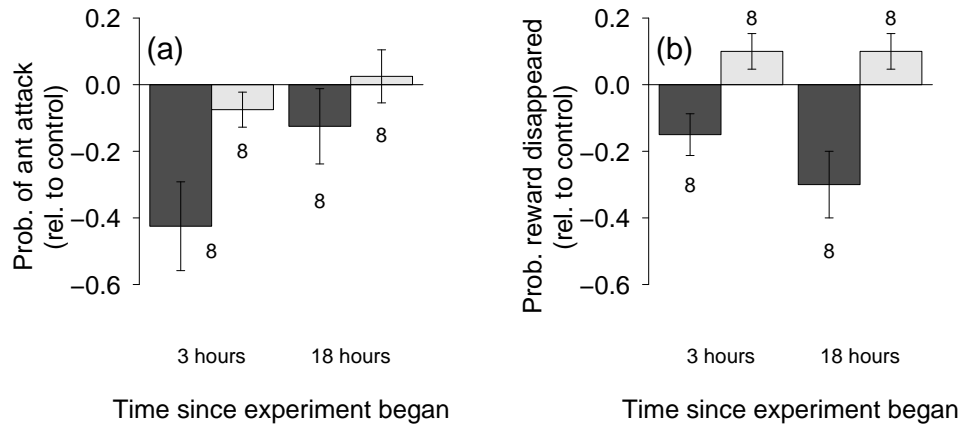
Figure 4.6: (a) Mean ($\pm$ s.e.) probability of ant attack for 'Intact' stems (dark bars) and 'Shaved' (light bars) expressed as the difference from the 'Cane' control. (b) Mean ($\pm$ s.e.) probability of reward disappearance for 'Intact' stems (dark bars) and 'Shaved' (light bars) expressed as the difference from the 'Cane' control.

tory arthropods preferring to forage on one plant species are rare, and reasons for such preferences are sometimes unclear (e.g. Beard & Walter, 2001; Wheeler, 2001). Neither adults nor nymphs got a nutritional benefit from *Stylosanthes*, but prey distribution on *Stylosanthes* was more closely matched to *R. tristis*' diet than on grass, and its trichomes impeded potential egg predators. By contrast, I found *R. albopilosus* at lower density than previously reported (Odhiambo, 1959), and on mixed vegetation. Here I discuss possible reasons for this difference, going on to discuss my findings in the context of the evolution of parental care in *Rhinocoris*.

Ant attack (3h) Source of variation	Effect size	SE	df (Δ/resid.)	F-value	p-value
Intercept (Control)	0.043	0.033	1/110		
Treatment	—	—	2/110	15.228	<0.001
Shaved	-0.007	0.008			
Intact	-0.037	0.003			
Ant attack (18h)					
Intercept (Control)	0.043	0.018	1/110		
Treatment	—	—	2/110	1.685	0.190
Shaved	0.004	0.017			
Intact	-0.020	0.010			
Disappearance (3h)					
Intercept (Control)	0.011	.005	1/110		
Treatment	—	—	2/110	10.831	<0.001
Shaved	0.005	0.006			
Intact	-0.007	0.002			
Disappearance (18h)					
Intercept (Control)	0.115	0.029	1/110		
Treatment	—	—	2/110	8.811	<0.001
Shaved	0.019	0.021			
Intact	-0.056	0.012			

Table 4.2: GlmmPQL tables showing probability of ant attack and reward disappearance after three and 18 hours. In each case the random factor, Replicate group, had a significant effect and was retained in the model, since the standard error of its estimate was larger than the residual deviance for the model.

4.5.1 Food

Adults

It is unsurprising that *R. tristis* gets no direct nutritional benefit from *Stylosanthes*. Feeding on plants is not unknown for a predator (Coll, 1996; Coll & Guer-

shon, 2002), but is rare. I could not replicate Thomas's (1994) observation that *R. tristis* adults would insert their rostra into *Stylosanthes* flowers, presumably to suck the nectar. Furthermore, since flowers are a seasonal resource on *Stylosanthes*, this is unlikely to represent a major source of nutrients for *R. tristis*, which breeds all year round.

It is also unsurprising that *R. tristis* appears not to be specialized to a particular type of prey on *Stylosanthes*: I found its diet to encompass seven orders of insects. This reflects the typically generalist diet of assassin bugs: almost all known assassin bugs are generalist predators, including *Rhinocoris* (e.g. Parker, 1969). Previous authors have found the diet of *R. tristis* (Thomas, 1994) and *R. albopilosus* (Odhiambo, 1959) to span many orders of arthropods (and likewise for *R. albopunctatus*; Nyiira, 1970).

However, there were different distributions of prey items available to *R. tristis* on *Stylosanthes* and grass sites; and, perhaps reflecting this, *R. tristis* chose abundant prey on *Stylosanthes*, but chose rarer prey on grass. Chesson (1978) hypothesized that predator choosiness may impose costs of prey selection; hence, on grass *R. tristis* may incur larger costs of selecting its prey. Prey distribution has well-documented effects on predator activity and distribution (e.g. Begon *et al.*, 1990; Dell'Arte & Leonardi, 2005; Venzon *et al.*, 1999; Winder *et al.*, 2005). However, from this correlative evidence the causality is unclear: *R. tristis* may prefer to live on *Stylosanthes* because of a more suitable range of prey, or may have had a preference for *Stylosanthes* and later adapted its diet to suit the prey available.

Nymphs

R. tristis nymphs did not live longer on either *Stylosanthes* treatment, washed or unwashed, than on bare canes. There was a trend in this direction, though, which is unlikely to reflect a nutritional benefit since nymphs were never seen feeding from the plant. *Stylosanthes* may have provided a microclimate in the laboratory that was slightly more favourable than the bare cane treatment; for example, *Stylosanthes*' hairs may have slightly elevated humidity around the stems.

We can eliminate the hypothesis that early-instar *Rhinocoris* nymphs feed from minute prey items stuck to the sticky trichomes of *Stylosanthes*, since nymphs survived no longer on untreated than on washed stems. Predators can sometimes benefit from prey immobilization by plants (especially carnivorous plants; Anderson & Midgley, 2002; Clarke & Kitching, 1995; Zamora, 1990). Furthermore Nyiira (1970) suggested that *R. albopunctatus* nymphs could feed on tiny prey that inhabit *Stylosanthes*. However, if there are such prey, they are not immobilized by *Stylosanthes*' sticky hairs.

4.5.2   Predators

Ants and other egg predators of *Rhinocoris* were substantially impeded in reaching a reward by *Stylosanthes* trichomes. Even though the reward was generally eventually reached, the delay caused by trichomes is predicted to increase the costs to the egg predator of pursuing the reward (the role of trichomes is well-documented in tri-trophic interactions; Price *et al.*, 1980). Trichomes can sometimes provide 'enemy-free space' (Price *et al.*, 1980; Stamp, 2001), and even for a

predator, the distribution of enemies can sometimes affect the choice of oviposition site (e.g. *Adalia* spp.; Schellhorn & Andow, 1999). Assuming that potential egg predators would be deterred from reaching eggs by trichomes in the same way as they are deterred from reaching the reward in this experiment, this could provide a source of protection for *Rhinocoris* eggs, even more so since *Stylosanthes* generally grows as a tangled mass of interwoven branches, as opposed to the single stems used in my experiment.

However, the fact that *S. guianensis* was only recently introduced to Africa suggests that it is only recently that *R. tristis* has begun living on this plant at high density. *R. tristis'* distribution is limited to Africa (Capriles, 1990), so it is highly improbable that this species was introduced to Africa alongside *S. guianensis*. *R. tristis* may originally have lived on the native but less hairy *S. mucronata* as has been reported for *R. albopilosus* (Odhiambo, 1959). For *R. tristis*, *S. guianensis* may be indistinguishable from *S. mucronata*, and so may be an acceptable substitute at NAARI, or *R. tristis* could have shifted in preference to the hairier species. Alternatively, *R. tristis* may originally have simply preferred hairy plants in general, and this preference may have led to a specialization on *Stylosanthes* since its introduction. This generates a testable prediction: that general "hairiness" would be used by *R. tristis* females as a cue for laying.

4.5.3 *R. albopilosus*

In contrast to *R. tristis*, the low density of *R. albopilosus* on *Stylosanthes* conflicts with previous studies, which find *R. albopilosus* on *Stylosanthes* at just as high, or even higher densities than *R. tristis* (Odhiambo, 1959; Thomas, 1994).

Why should *R. tristis* and not *R. albopilosus* live at elevated densities on *S. guianensis* at NAARI? *R. albopilosus* may be out-competed by *R. tristis*. The two species are morphologically and behaviourally almost identical and in this study I have shown that their diet was statistically similar, so it is likely that they occupy similar ecological niches, which may lead to competitive exclusion (Begon *et al.*, 1990), although why this should happen at NAARI and not at other authors' field sites is not yet known. What determines the outcome of competition between *R. tristis* and *R. albopilosus* on various species of *Stylosanthes* remains to be investigated. Alternatively, *R. albopilosus* may not have evolved to prefer *S. guianensis* in the same way as *R. tristis* and still prefers *S. mucronata* as reported by Odhiambo (1959). I did not find *S. mucronata* anywhere at NAARI, or indeed anywhere in Uganda at the time of the study (this was assumed to be due to the anthracnose fungus outbreak), so at NAARI *R. albopilosus* may not have its preferred substrate, and so may be forced to forage on mixed vegetation.

4.5.4   Evolution of parental care

Although the protection afforded by trichomes on *S. guianensis* combined with a favourable distribution of prey may increase local population density of *R. tristis* to high levels, the recency of introduction of *S. guianensis* suggests that this event did not precede the evolution of parental care in *R. tristis*. Prior to the evolution of parental care, a preference may have existed for features of either native *Stylosanthes* spp., e.g. *S. mucronata*, or of other hairy plants. This may have been the precursor to increased population density that brought about

conditions for care as predicted by Manica & Johnstone's (2004) model. Furthermore, the potential enemy-free space created by *Stylosanthes* may have led to *R. tristis* falling into Eberhard's (1975) trap: having found an effective form of egg protection from predators (*Stylosanthes*), *R. tristis* may subsequently have reduced investment in other forms of egg protection (e.g. the egg wall), which both increased dependency on the plant, and also necessitated a means of defence against *parasitoids* (parental care). Further dependency on the plant might have come about through *R. tristis* modifying its diet preferences to correspond to the prey available on *Stylosanthes*.

This study shows that the ecological factors which contribute to the costs and benefits affecting the evolution of parental care can be multiple and complex. At NAARI, I found *R. tristis* at high population density on *S. guianensis* while *R. albopilosus* lived at lower density on mixed vegetation sites. On *Stylosanthes*, *R. tristis* may have gained protection from egg predators owing to the plant's sticky trichomes, but there is no evidence that adults or nymphs gained direct nutritional benefit, or exploited a special type of prey. However, *R. tristis* ate prey which were abundant on *Stylosanthes* but chose rarer prey on grass, as shown by a comparison between its recorded prey and the prey available, implying that *R. tristis* may suffer less cost of prey selectivity on *Stylosanthes*. Although the egg protection afforded by *S. guianensis*, as studied, is unlikely to have been a selective pressure for *R. tristis* because of the recency of the plant's introduction to Africa, existing preferences based on adaptation to *S. mucronata* as seen in *R. albopilosus*, or on other hairy plants, may have led to specialization on *S. guianensis*. This hypothesized preference may have

preceded the evolution of male parental care by elevating population density. The beneficial effects of protection from trichomes, a favourable distribution of prey and, potentially, decreased investment in egg defences following the evolution of parental care, may have combined to increase *R. tristis*' dependency on *Stylosanthes*, producing the patterns of population density described here.

Chapter 5

Not over there, dear: sexual conflict over egg placement in assassin bugs

5.1 Abstract

If males gain sexually-selected benefits by caring for eggs, there may be potential conflict over offspring conspicuousness. Females should lay in positions that minimize egg mortality, so we would expect them to favour hidden over conspicuous locations. However, males should favour caring in conspicuous positions if they thereby gain additional matings. Conflict over egg conspicuousness has rarely been studied. I investigate female choice for caring males and the costs and benefits of conspicuousness in two African assassin bugs, *Rhinocoris tristis* and *R. albopilosus*, where males care for overlapping broods. In both species, females chose to lay eggs with caring over non-caring males, but unexpectedly laid *more* eggs for non-caring males. Females could be under pressure to lay quickly for caring males to synchronize hatching; or, alternatively, could lay more

for non-caring males as an 'incentive' not to abandon. Male *R. tristis* occur more often on exposed stems, which are conspicuous, than under leaves where they are hidden. In this species, males can accumulate more eggs on stems than on leaves, so males should prefer stems. However, stem broods suffer four times more parasitism, so females should favour leaves. Thus, males appear to be 'winning' this conflict. By contrast, male *R. albopilosus* only occur under leaves. Parasitism under leaves is ten times that in *R. tristis*, so for *R. albopilosus*, stems may suffer unfeasibly high parasitism, despite potential benefits to males. Here, it seems females are winning. My results show that the evolutionary consequences of parental care can depend upon subtle differences in ecological context.

5.2 Introduction

In species with anisogamy, it is usually the case that females, producing expensive gametes, are limited by resources, whereas males, producing cheap gametes, are limited by access to females (Bateman, 1948; Emlen & Oring, 1977; Trivers, 1972). This means that all else being equal, females are able to choose between a number of males who want to mate, and can profit greatly by making a good choice. The benefits of choosing the right male can be direct, like a nuptial gift (Thornhill, 1976; Vahed, 1998), or indirect, by choosing a male of good genetic quality who will either produce offspring of correspondingly high quality (e.g. Andersson, 1994; Petrie, 1994) or which at least will be more attractive to females sharing the same preference (Fisher, 1958).

To reap these benefits, though, a female must choose correctly, and so she

must have a reliable way of distinguishing good quality from poor quality males. To prevent exploitation by poor quality males masquerading as good quality males, it pays the female to use a criterion trait for choosing between males which is an 'honest signal', i.e. costly for the males to maintain (Johnstone, 1995; Zahavi, 1975), such that only good quality males can display a good quality trait. In these circumstances, it will pay the males to maximize the conspicuousness of this trait to females, while minimizing its costs to themselves (Lindstrøm, 2000; Manica, 2002; Scheffer *et al.*, 1996).

In species where males mainly provide direct benefits to females by enhancing offspring survival through paternal care, the trait females use to choose between males should indicate the willingness of the male to care for offspring, and the quality of that care. This can involve signals relevant to a male's intentions, like preparing a nest and displaying it to females (e.g. sticklebacks, Barber *et al.*, 2001; pipefish, Östlund & Ahnesjö, 2005; bowerbirds, Borgia, 1985). However, since caring parents (of either sex) commonly increase their parental effort when caring for bigger broods (reviewed in Clutton-Brock, 1991), and often abandon smaller broods (e.g. scissortail sergeant damselfish, Manica, 2002), it can often pay females to choose males based on whether or not they already have eggs (e.g. sand gobies, Forsgren *et al.*, 1996, Östlund & Ahnesjö, 2005; assassin bugs, Thomas & Manica, 2005).

Where females prefer to lay eggs with males who are already caring, we might expect that males would evolve to exploit that preference. Firstly, males should be willing to care for eggs to which they are not related, if by doing so they can sufficiently increase their mating success (Mora, 1990; Nyiira, 1970). If this selection pressure is strong enough, males should also compete over

unrelated broods (Thomas, 1994). Secondly, we might expect males to favour egg broods that are conspicuous, since by doing so they would stand to attract more females (Candolin, 2004). Thirdly, we might expect this exploitation to lead to a conflict of interest. Males, while expected to maximize their total number of surviving offspring, are also expected to trade off the survival of the existing brood against potential future reproduction, and so should sacrifice some of the existing brood if this results in increased mating success. This could be, for example, through increased conspicuousness to females and its associated mortality risks (Zuk & Kolluru, 1998), or by filial cannibalism to make up for the energetic costs of caring (Lindstrøm, 2000; Manica, 2002). The female has nothing to gain from the male's future reproduction, however (except potentially as a dilution of risk for her own brood), so the female is expected to evolve to reduce such exploitation by the male (Lindstrøm, 2000).

In assassin bugs of the genus *Rhinocoris* (Hemiptera: Reduviidae), generalist, predatory bugs native to Africa, such a potential conflict may exist. The genus contains several hundred species (Capriles, 1990), almost all of which lay small batches of eggs but do not care for them (Cobben, 1996). Egg mortality is primarily through attack by parasitoid wasps of the family Scelionidae (Ambrose, 1999; Cobben, 1996; Thomas, 1994). In three species, though, males guard the eggs against parasitoids until hatching; *R. tristis* Stål (Thomas, 1994), *R. albopilosus* Signoret (Bequaert, 1935; Odhiambo, 1959) and *R. albopunctatus* Stål (Nyiira, 1970), which all occur sympatrically in Uganda (Thomas, 1994). *R. tristis* males care for overlapping broods (Manica & Johnstone, 2004). As predicted, females prefer to lay eggs for caring males (Thomas & Manica, 2005), and as a consequence males compete to guard unrelated eggs (Thomas,

1994), and partially cannibalize broods, compensating for the energetic costs of care suffered by other caring but non-cannibalistic species (Thomas & Manica, 2003). Following the reasoning outlined above, we might therefore expect males to benefit from conspicuousness to females, and for that conspicuousness to carry a cost to eggs, creating a sexual conflict. In the congeneric *R. albopilosus*, males show a care pattern similar to *R. tristis* (Odhiambo, 1959), but sexual selection has not been investigated, and the potential for sexual conflict is therefore unknown.

In this chapter I investigate female preference for caring males in *R. tristis* and *R. albopilosus*, its effect upon male behaviour, and the resulting costs and benefits to males and females. Using field and lab studies, I first sought to establish whether females prefer caring males in *R. albopilosus* using a simultaneous choice experiment. Then I looked at the number of eggs laid and latency to lay for caring males in *R. tristis* and *R. albopilosus*. I asked three questions about the effect that a female preference should have upon male behaviour: (1) do males compete to care for unrelated eggs, (2) do males cannibalize some eggs, and (3) do males benefit from conspicuousness to females? I then asked specifically whether males in conspicuous places incur increased predation, making conspicuousness costly to maintain, and whether conspicuousness carries a cost to eggs in terms of increased parasitism, creating the potential for sexual conflict over the placement of eggs. To do this, I looked at eggs in two kinds of location: either hidden under leaves or on exposed plant stems, a difference in laying pattern which was noted by Thomas & Manica (2005) and which I hypothesized may lead to a difference in conspicuousness.

5.3 Methods

5.3.1 Study species and site

Rhinocoris spp. are Harpactorine assassin bugs (Heteroptera: Reduviidae, subfamily Harpactorinae) which breed continuously and aseasonally (e.g. Nyiira, 1970; Thomas, 1994). All known Harpactorinae lay discrete batches of eggs; however, where almost all of them including *Rhinocoris* abandon these batches, in *R. tristis* and *R. albopilosus* along with one other known species, *R. albopunctatus*, males care for eggs until hatching. They are generalist predators which will attack and eat any insect up to their own size (Ambrose, 1999), a mean of 9.89±0.08mm (male, n=48) and 11.94±0.08mm (female, n=59) for *R. tristis*, and 11.54±0.17mm (male, n=23) and 13.66±0.13mm (female, n=30) for *R. albopilosus*. They inhabit low-lying vegetation and in Uganda occur at high density on the pasture legume *Stylosanthes* (Nyiira, 1970; Thomas, 1994).

Field and laboratory studies were conducted at NAARI (Namulonge Agriculture and Agronomy Research Institute) near Gayaza, approx. 40km north of Kampala, Uganda, with the kind permission of NARO (National Agriculture Research Organization) and UNCST (Uganda National Council of Science and Technology). Data were collected between October 2003 and June 2005.

For laboratory studies, assassin bugs were collected from mixed vegetation around the field station and maintained in cylindrical glass Dietz petrol-lamp hoods ('bottles') measuring 25cm (height) × 20cm (diameter), at room temperature and humidity and natural hours of daylight (6am – 6pm). They were fed once a day with medium-sized insects (0.5 – 1 × the bugs' body length) collected by sweep-net from surrounding vegetation. Both ends of the bottles were sealed with thin cotton material held in place by rubber bands, and the material was soaked in water once a day to provide drinking water. Three split bamboo canes of approximately 20cm length and 5mm

diameter were provided in each bottle for oviposition substrate.

For field studies, eight field sites of 100m^2, measuring either 10×10m or 20×5m according to spatial constraints at the field station, were monitored for a maximum of 16 weeks under a mark-release-recapture protocol. This consisted of searching the site intensively for 3h each day, starting at a pseudorandomly-chosen time during daylight hours. Each bug seen was captured and either (1) marked on its thorax and the leathery parts of its wings using student's acrylic paint (Allman) applied with a cocktail stick, (2) noted as a recapture, or (3) marked *in situ* if caring, to reduce the chance of abandonment. The number of eggs laid and hatched in each brood was counted and the brood lightly brushed with coloured ink so as easily to identify subsequently added batches of eggs. Monitoring was continued for periods of 6 days (the 'observation period') at two sites before shifting to two others, in a rotating pattern.

Following hatching, egg broods were also examined in the laboratory to count the number of parasitized and cannibalized eggs. This was done using a Heerbrugg Wild M3B binocular microscope at 6x magnification. Parasitized eggs are easily told apart from hatched eggs, since hatched eggs have their operculum open and their chorion intact, while parasitized eggs have an intact operculum and a hole in the chorion near the base of the egg through which the Scelionid parasitoid has emerged (Thomas & Manica, 2003). Cannibalized eggs are easily identified because they (1) have an intact operculum, showing they have not hatched, and (2) are empty, meaning they have been sucked dry by the male, and have not simply failed to hatch.

5.3.2 Female choice

To test whether female *R. albopilosus* choose to mate with caring males, I followed Thomas & Manica's (2005) laboratory procedure. I placed a single, non-caring male and a

gravid female together in a bottle until they mated (n=10). After mating, the male was allowed to assume the post-copulatory riding position for 1h, after which a second male, already caring for eggs, was introduced to the bottle. I observed the female until she laid eggs, and recorded the ID of the male with which the female eventually chose to lay eggs. This was easy, since the female would either lay eggs directly adjoining the already-caring male's batch, whereupon this male would care for them, or she would lay elsewhere in the bottle with the male on her back closely attending the eggs, and he would then care for them. The resulting frequency table for all females I analysed using a χ^2 test, alongside general observations of behaviour during the test period.

To test whether females lay more eggs, or lay more quickly, for caring males, I paired females with non-caring males (*R. tristis*: n=39, *R. albopilosus*: n=15) until eggs were laid. In a second group, each female received a male already caring for one batch of eggs (*R. tristis*: n=12, *R. albopilosus*: n=5). Both sets of males had been isolated and fed the day prior to the experiment. The size and age of the single batch that the male was caring for were uncontrolled (range 12–48 eggs, age 1–4 days). The number of eggs laid by the females and the latency to lay (in days) were recorded and the results analysed using unpaired t-tests. A paired experimental design was attempted, comparing the same female laying for caring and non-caring males, but was found to be impractical due to females' reluctance to lay twice in the laboratory.

One potential source of selection for female choice might be a difference in egg viability in broods of different sizes. Whether eggs are on average more viable in smaller or larger broods may determine whether females are better off initiating broods or adding to them, which could drive selection for a preference for or against caring males. I examined the effect of parasitism on the viability of eggs in differently sized broods using field data on total brood sizes and parasitism. I analysed the viability

per egg in a brood (counted simply as the number of eggs in the brood minus the number parasitized, divided by the total number of eggs) using a linear model (LM) with 'brood size' as a predictor (Crawley, 2002).

5.3.3 Male behaviour

To investigate whether *R. albopilosus* will care for unrelated eggs as has been reported for *R. tristis* (Thomas, 1994), 13 male *R. albopilosus* were tested with unrelated eggs by the simple procedure of introducing a single, non-caring male from the field to a brood laid by a female in the laboratory. All broods tested in this way were between one and two days old (i.e. they had been laid the previous day). The male was left with the eggs for three hours, after which his behaviour was recorded as 'caring' or not 'caring'. 'Caring' was defined as standing over eggs and (1) attacking a mock 'parasitoid' (a globe-headed pin mounted on a dissection probe) directed towards the eggs, and (2) not attacking the same parasitoid when held at a similar distance but away from the eggs. If he was caring after this period, he was left to care for another hour before another non-caring male was introduced. The behaviour of this male was then observed for three hours. The frequency of fights observed was analysed using a simple χ^2 test.

To test for cannibalism, seven *R. albopilosus* broods and 39 *R. tristis* broods were examined, and the number of cannibalized eggs in each brood was counted. I tested for differences between the species in the probability of cannibalism using simple χ^2 tests, and for differences in the rate of cannibalism using t-tests.

5.3.4   Costs and benefits of conspicuousness

For each brood found in the field, the position (under leaf or on exposed stem) was recorded. Total brood sizes were recorded as the maximum number of eggs in broods whose eggs were observed to hatch during the observation period. Broods that disappeared during the observation period were assumed to have been predated. I compared the total brood sizes on stems and under leaves using t-tests, and the number of broods that were predated on stems and under leaves using χ^2 tests.

Batch sizes were recorded as the number of eggs by which broods were observed to increase between daily observations, easily counted by the number of new, unmarked eggs. Increases in egg numbers of more than 10% over the maximum batch size observed in the laboratory were treated as two batches and excluded from the analysis, since the size of each batch was unknown. Since there were multiple batches of eggs per brood, I first controlled for the effect of brood ID using a linear mixedeffects model, including 'position' and 'batch order' as fixed factors and 'brood ID' as a random factor. If the random factor did not have a significant effect, it was dropped from the model and an LM was used. Batch sizes were included in the analysis regardless of whether the brood was eventually eaten.

The way my data were collected meant that I could not count directly the number of batches added to a brood, since sites were only monitored for 6d each, while the mean duration of caring is approximately 15d (Thomas, 1994, and pers. obs.). This meant that most broods were encountered after several batches had been laid. I produced a conservative estimate of the number of batches by dividing the size of the brood when I initially discovered it by the maximum recorded field batch size (44) and rounding the result down. I analysed these data using a generalized linear model (GLM) with poisson error structure, with response variable 'estimated number of batches per brood' and predictor variable 'brood position'.

In a smaller subset of broods (*R. tristis*, n=39; *R. albopilosus*, n=7) the number of eggs parasitized was counted. I looked at factors affecting the probability and the rate of parasitism using GLMs and LMs respectively.

All data were analysed using R 2.2.1 (R Development Core Team, 2005).

5.4 Results

5.4.1 Female choice

In the simultaneous choice experiment, nine out of ten female *R. albopilosus* chose to mate with the caring male ($\chi^2_1 = 6.40, p = 0.011$). The behaviour was unmistakable: the female walked directly up to the caring male and presented him with the riding male, as if to encourage a fight between the males. In all cases the caring male was the winner of the fight, displacing the riding male and then mating with the female, who subsequently added eggs to his brood.

Females laid more quickly for caring males by 1.6 days in *R. tristis* ($t_{30} = 3.137, p = 0.004$) and by 3.0 days in *R. albopilosus* ($t_8 = 2.572, p = 0.033$; figure 5.1a). However, females laid fewer, not more, eggs for caring males (figure 5.1b), by a mean of 11 eggs in *R. tristis* ($t_{22} = 3.470, p = 0.002$) and 15 eggs in *R. albopilosus* ($t_{12} = 3.617, p = 0.003$), in both cases an increase of about half the mean batch size.

There was no association between the mean viability per egg in a brood and the size of the brood ($F_{1,40} = 0.018, p = 0.894$; figure 5.2).
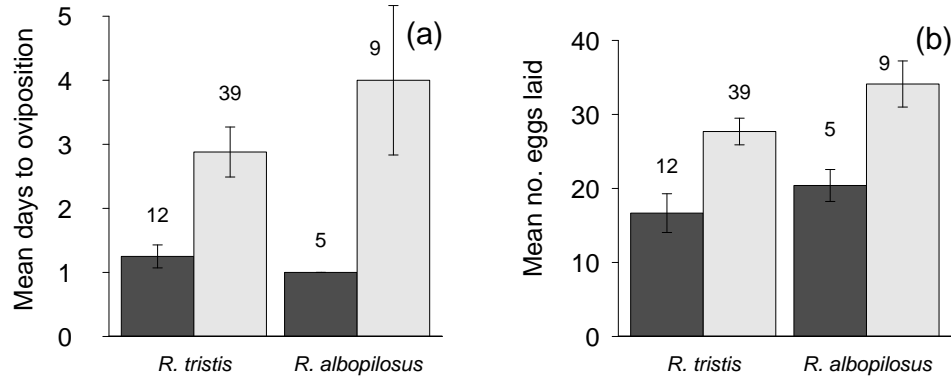
Figure 5.1: (a) Mean ($\pm$ s.e.) time taken by *R. tristis* and *R. albopilosus* females to lay for caring (dark bars) and non-caring males (light bars). Both species laid more quickly for caring males. All five *R. albopilosus* females laying for caring males did so in one day: hence there is a standard error of zero days. (b) Mean ($\pm$ s.e.) number of eggs laid by *R. tristis* and *R. albopilosus* females for caring and non-caring males. Both species laid more eggs for non-caring males. Sample sizes are shown above the bars.

5.4.2 Male behaviour

Of thirteen males tested, all thirteen began guarding the unrelated eggs ($\chi_1^2 = 13.000, p < 0.001$). Twelve subsequently-introduced males initiated fights with the resident male ($\chi_1^2 = 9.308, p = 0.002$).

Twenty-nine out of 39 *R. tristis* broods contained cannibalized eggs, as did all seven *R. albopilosus* broods. There was no difference between the two species in probability of cannibalism ($\chi_1^2 = 0.350, p = 0.554$). Neither was there a difference in the mean proportion of the brood cannibalized between the two species ($t_{33} = 0.821, p = 0.404$), which was 0.14$\pm$0.02 in *R. albopilosus* and 0.12$\pm$0.02 in *R. tristis*.
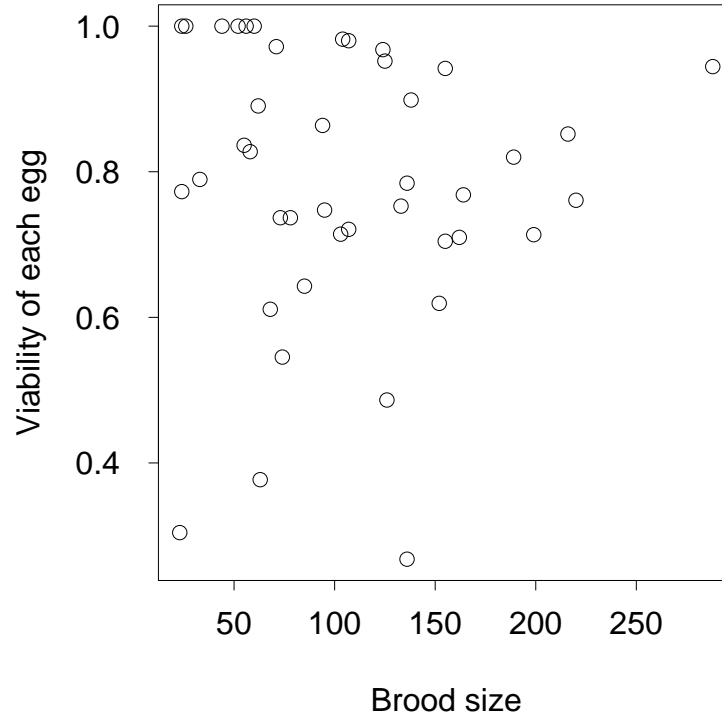
Figure 5.2: Mean viability per egg in field *R. tristis* broods, measured as (number of unparasitized eggs / total number of eggs), plotted against total number of eggs. There was no association between the variables.

5.4.3 Costs and benefits of conspicuousness

The distribution of eggs between leaves and stems of *R. tristis* and *R. albopilosus* were very different ($\chi^2_1 = 27.726, p < 0.001$): *R. tristis* broods were found more than twice as often on stems (136 broods) as on leaves (58 broods), whereas *R. albopilosus* were found more often under leaves (28 broods) than on stems (8 broods), and did not lay frequently enough on stems to permit a statistical comparison. Therefore, I compared *R. albopilosus* leaf broods with *R. tristis* leaf broods. *R. albopilosus* leaf broods were significantly smaller than those of *R. tristis* by about 20 eggs ($t_{72} = -2.139, p = 0.036$; figure 5.3a). They were

also parasitized more often, and at a much higher rate: all seven *R. albopilosus* broods examined were parasitized, which was significantly more than seven out of 17 in *R. tristis* leaf broods ($\chi^2_1 = 4.846, p = 0.027$). Within each brood, the rate of parasitism in *R. albopilosus* was approximately four times higher than in *R. tristis* ($t_7 = 3.567, p = 0.008$, figure 5.3b).

The following stem/leaf comparisons are for *R. tristis* only, since *R. albopilosus* did not lay on stems. *R. tristis* broods were about 25% larger on stems than under leaves ($t_{125} = -1.985, p = 0.049$; figure 5.4a) and tended to be more variable, although the difference did not reach significance: a variance of 3745.5 (stems) vs. 2485.5 (leaves; Bartlett's test for homogeneity of variances; $K^2_1 = 3.124, p = 0.070$). Following a similar pattern, individual batches were also bigger on stems by about 25% (linear mixed-effects model, breakdown in table 5.1; $F_{1,45} = 5.785, p = 0.02$), and were significantly more variable in size, with a variance of 236.9 as opposed to 65.3 for leaves (Bartlett's test for homogeneity of variances; $K^2_1 = 8.938, p = 0.002$; figure 5.4b). There was no difference between the estimated number of batches on leaves (2.57 ± 0.17), and that on stems (2.99 ± 0.13), only a marginal trend (GLM; $F_{1,189} = 3.67, p = 0.055$).

There was no difference between leaves and stems in the number of *R. tristis* broods of known fate which disappeared during the monitoring period: nine out of 26 (leaves) versus thirteen out of 54 (stems; $\chi^2_1 = 0.232$, p=0.630). In total, approx. 27% of broods disappeared.

The distribution of parasitized eggs was bimodal, with one peak at zero parasitism, and another at about 15%, as shown in figure 5.5a. This distribution suggests two separate processes: discovery by parasitoids, determining

whether or not a brood is parasitized, and, once a brood is discovered, the number of eggs a parasitoid is able to lay. First, the peak at zero is likely to represent broods that were never discovered by parasitoids. I analysed the probability of discovery (i.e. whether or not a brood was parasitized) using a generalized linear model with binomial error structure (breakdown in table 5.2a). While the brood's position (leaf/stem) had no effect, the probability of discovery was found to covary negatively with the adult population density, as assessed by the mean number of adult insects caught in half an hour during mark-release-recapture observations: broods laid at higher population density were less likely to be parasitized ($\chi^2_1 = 4.532, p = 0.033$; figure 5.5b). By contrast, brood size had a positive effect, the likelihood of discovery being higher in bigger broods ($\chi^2_1 = 5.518, p = 0.019$; figure 5.5c).

Secondly, the peak above zero parasitism in figure 5.5a corresponds to broods that were discovered by parasitoids. Since the parasitism rate was normally-distributed (following square-root transformation), I analysed the data using a linear model (breakdown in table 5.2b). Neither brood size nor population density affected the rate of parasitism, but brood position had a clear positive effect: broods on stems are more parasitized than broods under leaves ($F_{1,19} = 8.292, p = 0.010$; figure 5.5d).

Do males still get a benefit after the differential effect of parasitism? Making the simplistic assumption that the measured factors are the only ones acting, we can roughly quantify the costs and benefits for males with some simple arithmetic. A males total success will be the number of viable eggs he gets from a brood. This we can calculate as the mean number of eggs laid minus the mean number that are parasitized, discounted by the chance that the whole

brood will be predated. If a brood has probability d of disappearing, and probability p of being discovered by parasitoids, but when it is discovered, a mean proportion r of the eggs are parasitized, we can calculate the mean number of viable eggs a male gets from a brood as follows:

Viable eggs = (1-probability of predation) × [(1-p)(eggs if not parasitized) + p(eggs if parasitized)]

= (1-d) × [(1-p) × total eggs + p((1-r) × total eggs)]

To assess differences between leaves and stems incorporating the risk of predation and parasitism, I used a Monte Carlo simulation to generate 100000 leaf-stem pairs of estimates using parameters and standard errors from the models constructed above, shown in the table below:

R. tristis	Parameter	Value	± s.e.
Leaf	probability of predation*	0.11	0.02
	brood size	89.02	8.36
	parasitism probability	0.54	0.08
	parasitism rate	0.07	0.03
Stem	probability of predation*	0.11	0.02
	brood size	107.95	9.89
	parasitism probability	0.54	0.08
	parasitism rate	0.170	0.05

*obtained using a GLM with binomial error structure, of the form "p(predated) = brood position + error". Leaves and stems did not differ, so I used the same estimate for each.

For *R. tristis*, stem estimates (52.8 eggs, 95% c.i.:34.8, 73.1 eggs) were consistently larger than corresponding leaf estimates (38.9 eggs, 95% c.i. 25.7, 53.9 eggs; binomial test with 100000 runs, p<0.001) by a mean of 13.8 eggs (95% c.i.:

3.4, 25.7 eggs). Hence, male *R. tristis* got a net benefit on stems after accounting for parasitism costs.

R. albopilosus hardly laid on stems, so data were too sparse to measure the costs and benefits of doing so. However, I generated preliminary estimates by assuming that (1) the proportional increase in brood size and in parasitism rate on stems relative to leaves would be the same as for *R. tristis*, (2) that standard errors would be similar from leaves to stems as is estimated for *R. tristis*, and (3) that *R. albopilosus* would suffer similar predation rates to *R. tristis*:

R. albopilosus	Parameter	Value	± s.e.
Leaf	probability of predation	0.11	0.02
	brood size	67.00	8.62
	parasitism probability	1∗	0.00
	parasitism rate	0.26	0.05
Stem	probability of predation	0.11	0.02
	brood size†	81.30	8.62
	parasitism probability	1	0.00
	parasitism rate‡	0.63	0.05

∗(all 7 broods parasitized, hence probability 1 with no error)

†(multiplied by same factor as *R. tristis*, 108/89=1.21)

‡(multiplied by same factor as *R. tristis*, 0.17/0.07=2.42)

Using these parameters, stem estimates (16.5 eggs, 95% c.i.:0, 63.9 eggs) were consistently *smaller* than leaf estimates (43.9 eggs, 95% c.i.: 31.9, 56.8 eggs; binomial test with 100000 runs, $p < 0.001$) by a mean of 27.5 eggs (95% c.i.: -20.4, 51.5 eggs).
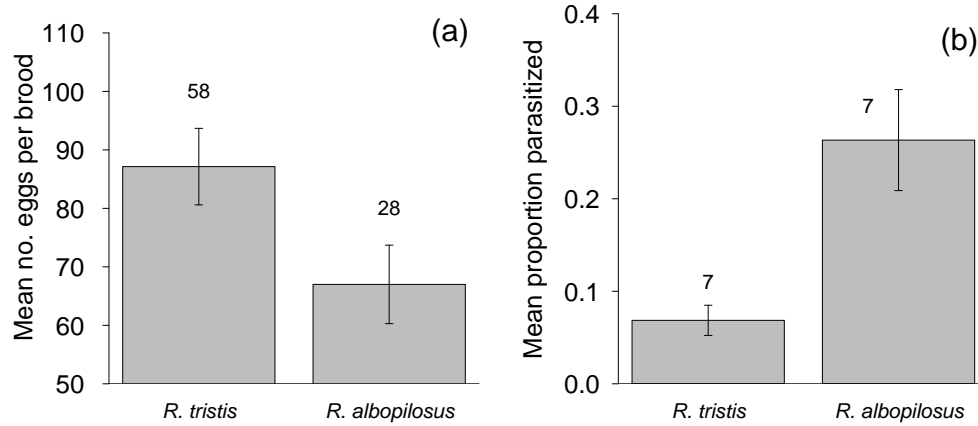
Figure 5.3: (a) Mean ($\pm$ s.e.) number of eggs in *R. albopilosus* and *R. tristis* leaf broods. *R. tristis* broods were bigger. (b) Mean ($\pm$ s.e.) *R. albopilosus* and *R. tristis* parasitism under leaves. *R. albopilosus* broods were parasitized more heavily. Sample sizes are shown above the bars.
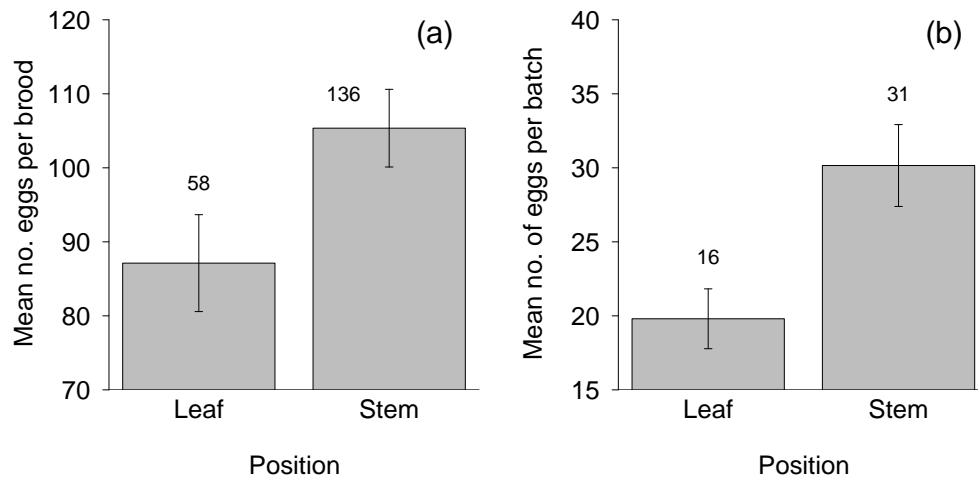
Figure 5.4: (a) Mean ($\pm$ s.e.) brood sizes on leaves and stems for *R. tristis*. Broods on stems were larger than broods on leaves. Broods were not more variable on stems, although there was a non-significant trend. Sample sizes are shown inside the bars. (b) Mean ($\pm$ s.e.) batch sizes on leaves and stems for guarding male *R. tristis*. Batches were bigger and also more variable on stems. Sample sizes are shown above the bars. Breakdown of the linear mixed-effects model is given in table 5.1

111

R. tristis **batch sizes** Source of variation	Effect size	SE	df (Δ/resid.)	F-value	p-value
Intercept (Leaf)	4.433	0.289	1/61		
Position	—	—	1/61	5.785	0.019
(Stem)	0.852	0.354			
Batch order	0.246	0.324	1/60	0.578	0.450

Table 5.1: Factors affecting batch sizes in *R. tristis* (Linear model). Egg batches on stems are significantly larger (figure 5.4b). Brood ID was initially included as a random factor due to multiple batches per brood, but did not have a significant effect and so was dropped from the model. Statistics for non-significant terms show the marginal effect of each term on the minimal model.

(a) Probability of discovery Source of variation	Effect size	SE	df (Δ/resid.)	F-value	p-value
Intercept	-0.239	1.397			
Population density	-0.483	0.344	1/37	4.532	0.033
Brood size	0.014	0.007	1/37	5.518	0.019
Brood position	0.379	0.760	1/36	0.247	0.619
(b) Parasitism rate					
Intercept (Leaf)	0.245	0.051			
Brood position	—	—	1/19	8.292	0.010
(Stem)	0.180	0.062			
Brood size	<0.001	<0.001	1/18	0.414	0.527
Population density	<0.001	0.026	1/18	<0.001	0.991

Table 5.2: (a) Factors affecting probability of discovery in *R. tristis* broods (GLM with binomial error structure). (b) Factors affecting rate of parasitism in *R. tristis* broods (LM with normal error structure). Statistics for non-significant terms show the marginal effect of each term on the minimal model.
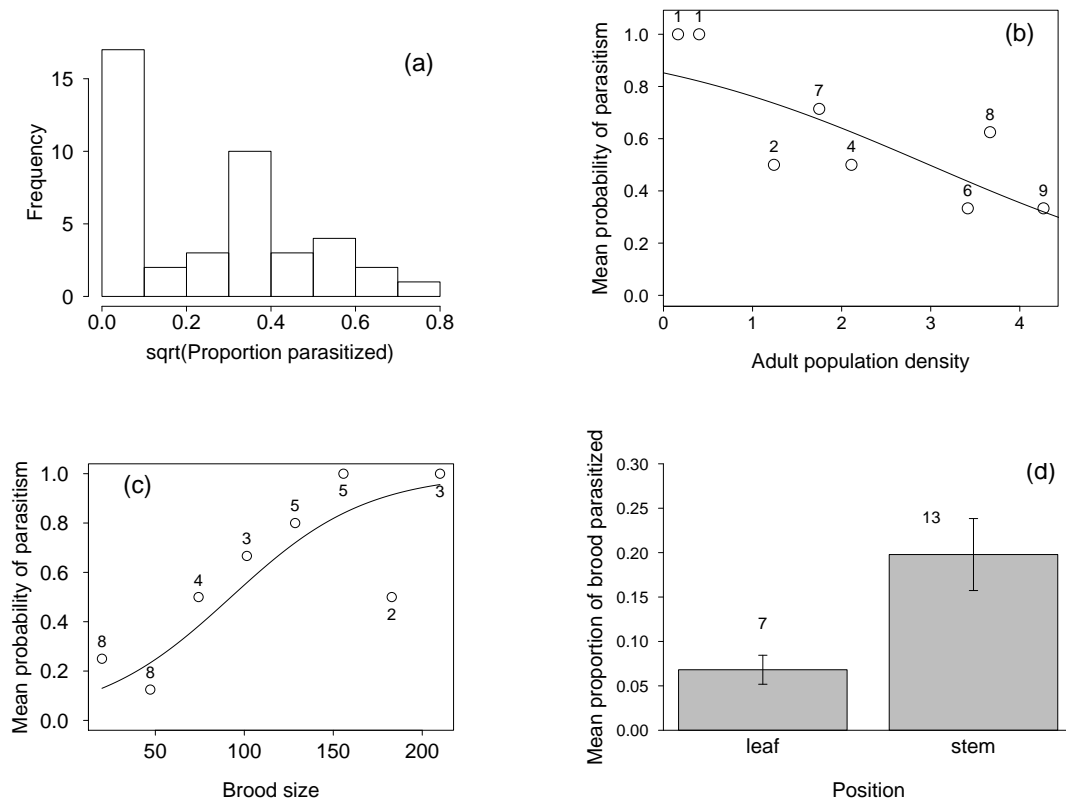
Figure 5.5: (a) Histogram of percent parasitism for both *R. tristis* and *R. albopilosus*, square-root transformed. The relatively large number of zeros corresponds to broods not discovered by parasitoids, whereas the normally-distributed set of non-zero values corresponds to broods which were parasitized. (b) Mean probability of discovery by parasitoids against adult population density (no. of adults discovered per half-hour collecting) in *R. tristis*, with fitted line from the GLM. Probability of discovery decreased with adult population density. The number of broods is shown above each point. (c) Mean probability of discovery by parasitoids against brood size in *R. tristis*, with fitted line from the GLM. Larger broods were more likely to be parasitized. (d) Mean ($\pm$ s.e.) proportion parasitized for parasitized broods (i.e. broods with above zero parasitism). Stem broods were approximately 18% more parasitized. Sample sizes are given above the bars. Breakdowns of the models are given in table 5.2

5.5   Discussion

Like *R. tristis* (Thomas & Manica, 2005), female *R. albopilosus* chose to mate with and lay for caring males. This makes sense if, as in *R. tristis*, caring males are less likely to abandon (Thomas, 1994). Additionally, the risk of cannibalism and/or parasitism may be diluted in larger broods (Manica, 2002, 2003; Rohwer, 1978), so cannibalism may facilitate the evolution of such a preference (Lindstrøm, 2000).

Females of both species laid more quickly for caring than for non-caring males. If females prefer caring males, a female paired to a non-caring male (who is therefore riding on her back) may delay oviposition while wandering in the hope of finding a caring male. It is also possible that females that add to a brood early may benefit from reproductive synchrony within the brood. Communally-laying burying beetles are known to benefit from reproductive synchrony because it reduces the risk that cobreeders will cannibalize their offspring (Eggert & Muller, 2000). In *Rhinocoris*, females who lay late run the risk of the male abandoning their eggs once the existing brood has hatched. Consequently they may have evolved a tendency to lay as quickly as possible for caring males. Furthermore, in *R. tristis*, parasitoids preferentially attack peripheral eggs (Thomas, 1994), and larger broods are more likely to be parasitized (this study), which means it is costly to lay at the edge of a brood, and advantageous to have eggs surrounding one's own. This favours females who add to a brood early. Egg cannibalism could also select for early-laying females, since cannibalism is predicted to target younger eggs (Manica, 2002).

If it benefits females to prefer caring males, females should avoid initiating

114

broods. However, counter-intuitively, *R. tristis* females consistently laid larger batches for non-caring males. In some other taxa, females may lay *fewer* eggs for non-caring males as a test of their willingness to care (Kraak & van den Berghe, 1992; Smith, 1997). It is possible that differences in male ejaculate may affect female laying patterns: caring males may suffer from sperm depletion. However, assassin bug males can mate frequently, up to three times a day (Thomas, 1994, and pers. obs.) and in this study, males had not mated for at least a day prior to experiment, probably ample time to replenish sperm reserves. Non-caring males may also facultatively adjust their ejaculate to manipulate females into laying larger batches, although it is unclear why a male should do this only when he has no eggs.

If females benefit from hatching synchrony, then a female paired with a caring male may be forced to oviposit before enough of her eggs have matured for her to lay her optimal batch size. With a non-caring male, however, her eggs can develop during the post-copulatory riding period, and so she can lay a larger batch. Under this hypothesis, females should prefer to lay *large* batches and are forced to lay *under* their optimal batch size for caring males. This hypothesis is also consistent with there being no relationship between brood size and egg viability, as shown in figure 5.2: a large first batch followed by smaller subequent batches would be a passive effect of female egg depletion. There is also a clear prediction: females who have been experimentally isolated for longer periods of time should lay correspondingly larger batches for caring males.

In the light of males abandoning smaller broods and in the absence of an inherent advantage for the female who initiates a brood, we could view the ex-

tra eggs laid for non-caring males as a 'staying incentive', to reduce the male's probability of abandoning them. Staying incentives have been proposed in co-operatively breeding species as one means of persuading non-reproductive helpers to stay at the nest (Reeve & Ratnieks, 1993; Vehrencamp, 1983), although evidence is scarce (e.g. Heg *et al.*, 2006; Liebert & Starks, 2006). This would suggest that female assassin bugs are forced to lay *over* their optimal batch size for non-caring males, and that their optimum strategy may be to lay smaller batches. A female may lay a bigger incentive for a non-caring male depending on the perceived risk of him abandoning the eggs, which might include factors like his quality, female density, and food availability, all of which generate testable predictions.

Consistently with prediction, both *R. tristis* (Thomas, 1994) and *R. albopilosus* (this study) competed to guard unrelated eggs, and both partially cannibalized their brood. Also as predicted, male *R. tristis* had a reproductive advantage from caring for eggs on exposed stems, in terms of larger broods and larger batches. The finding that males do not get more batches on stems than they do on leaves is consistent with the result that both broods and batches are bigger on stems by a similar amount , about 25% (figures 5.4a and 5.4b), which implies that males get more eggs from *each female* on stems, not more females overall. Males had higher *variance* in success on stems, suggesting that sexual selection among males in conspicuous places is more intense, as has also been found for male-caring fish (Candolin, 2004). However, this was not accompanied by the predicted cost to males of an increase in predation. Although this does not rule out male care as an honest indicator of quality (Tallamy, 2000),

two factors make this explanation unlikely *a priori*. First, the potential indicator trait is the egg brood, so any benefit accruing to males must be traded off against associated costs to the eggs (Lindstrøm, 2000), and second, the initiating female decides whether or not a male receives the costly trait, since she decides where to lay the first batch. Hence, we should not be surprised if a straightforward cost in terms of predation risk to males is not in evidence.

Male *R. tristis* should prefer stems, despite the parasitism costs, since they got a net increase in number of viable eggs. By contrast, females should prefer leaves, since they are not interested in the potential total size of the brood, and so the costs of higher parasitism on stems are not offset by the increased number of eggs. Therefore, male and female *R. tristis* seem to have conflicting interests over the positioning of the egg broods.

Since *R. tristis* laid more on stems than under leaves, this conflict seems to have been resolved in favour of the male. However, females decide where to initiate broods; so why did females lay on stems, to their apparent cost? I tested whether females are forced to oviposit by riding males using a quick experiment; nine out of ten *lone*, mated females in the laboratory still laid on stems. But males could also manipulate female costs by selectively abandoning leaf broods. Although my data show no difference between leaves (10 out of 22) and stems (14 out of 36) in the frequency of males seen to abandon broods in the field, it could still be that females place males differentially according to their quality. Females could easily assess males' quality by gauging their weight during postcopulatory riding, as in some biparental beetles (Rasa *et al.*, 1998). Whether females place males in different positions according to their weight could be easily tested by pairing them with males of varying weight in

the laboratory.

The effect of brood size on the probability of discovery by parasitoids is most likely explained by variation in conspicuousness, as in many insects (reviewed by Gross, 1993). *R. tristis* and *R. albopilosus* eggs have bright white caps in stark contrast to their black chorions, rendering them much more visible than eggs of other species, whose chorions are light brown (pers. obs.), hence it is very possible that parasitoids would use them as visual cues. The negative effect of population density may represent a dilution effect (Hamilton, 1971), that may partially explain why *R. tristis* is found at such high densities. Aggregation is a known defence against parasitoids (Gross, 1993), as it is against many enemies (see e.g. Begon *et al.*, 1990).

Whether a brood was on a leaf or a stem, i.e. its conspicuousness, affected not the probability of discovery but the *rate* of parasitism, saying effectively that males are less good at caring on stems. It is unlikely that males on stems spend a disproportionate amount of time trying to attract females, since I did not observe any form of display behaviour. However, males may be incapacitated while mating, which takes a mean of about 6 minutes in *R. tristis* (pers. obs.), during which time the male is locked to the female and almost certainly unable to pursue parasitoids. Incapacity during mating has been invoked to explain lapses in male golden egg bug defences against parasitic females laying eggs on their backs (Katvala & Kaitala, 2003, but see Gomendio & Reguera, 2001). I found a non-significant trend for males on stems to receive slightly more egg batches than those under leaves, which warrants further investigation.

Although the estimates reported here were tentative, *R. albopilosus* males may not get the same benefits from guarding on stems due to prohibitively high rates of parasitism. If this is true, males' interests may coincide with those of the females, both preferring broods laid under leaves, and so there may be less opportunity for sexual conflict over egg placement. However, this estimate is based on low initial sample sizes leading to unrepresentative errors (cf. zero error in probability of parasitism); consequently the error in the estimate is large (indicated by wide 95% confidence intervals) and so should be treated as uncertain until more data can be obtained for *R. albopilosus*. Interestingly, Nyiira (1970) reports that *R. albopunctatus*, the other known male-caring *Rhinocoris*, also prefers to lay eggs under leaves, and may thus be in a similar situation to *R. albopilosus*.

Thus, in *R. tristis* there may be a double conflict between the male and the female who together initiate a brood. Firstly the female may be forced to lay over her preferred batch size to provide a staying incentive to that male. Secondly, she may be manipulated by him in some way into laying in a conspicuous position, where he will get future benefits from increased mating success, but her eggs will be more parasitized due to the male's reduced effectiveness. In *R. albopilosus*, the first source of conflict was evident in the form of increased batch sizes for non-caring males, but there may be no opportunity for conflict over conspicuousness since even inconspicuous eggs suffered high rates of parasitism, making it potentially unfeasible to lay in conspicuous locations.

Chapter 6

Discussion

In this thesis I set out to investigate how different patterns of insect behaviour and life-history can influence the costs and benefits leading to the evolution of parental care, and how the evolution of parental care can in turn influence patterns of insect behaviour. I used between-species comparisons and phylogenetic methods to test large-scale evolutionary hypotheses, and then used field studies in assassin bugs to test proximate hypotheses. Specifically, the evolutionary questions I wanted to ask were 'what are the major transitions in insect parental care evolution' (chapter 2), and 'do insects incur a general trade-off between parental care and future reproduction?' (chapter 3). The proximate questions I wanted to ask were 'what factors lead *Rhinocoris tristis* to aggregate on one species of plant, bringing about conditions for the evolution of male parental care?' (chapter 4) and 'is there a sexual conflict over egg placement in male-caring *Rhinocoris*?' (chapter 5).

6.1 Findings of this thesis

6.1.1 Parental care in insects

In chapter 2, looking at the transitions in the sex performing parental care, I found that most of the transitions predicted by existing hypotheses were present in insects' evolutionary history. The earliest insects lost the parental care that is widespread in their ancestors, probably at the same time as they evolved a well-protected egg and an ovipositor. In their subsequent diversification, insects have either (1) re-evolved female care, and then in some, biparental care, or (2) evolved male care. This goes some way towards clarifying the debate surrounding the evolution of male care in insects; my results indicate that male care arises out of no care, but not out of female or biparental care. Further tests can now address explicitly directional hypotheses of association, for example that the evolution of a predatory lifestyle tends to precede the evolution of male care (Tallamy, 2001; Tallamy & Wood, 1986), and can also look at more fine-grained analyses of transitions within taxa – particularly the Hemiptera, which contains most examples of male care in insects. Additionally, transitions within the Dictyoptera should be investigated, since my results suggested surprisingly that their ancestor was a male-carer, a strategy that no modern Dictyopterans exhibit.

In chapter 3, I looked at the effects of parental care upon life history among insect species, and found that while parental care was positively associated with offspring survival to adulthood, insects incurred a trade-off between parental care and lifetime fecundity, consistently with the findings of many studies on single species. Further, comparative analysis revealed that increased invest-

ment in parental care was associated with correspondingly lower fecundity. Although increased investment in care was not associated with higher absolute values of offspring survival in the comparative analysis, a separate analysis of experimental manipulations measuring the benefits of parental care showed that insect parents that care and provision their offspring have a greater effect upon survival than insects that care alone. We are therefore justified in making the generalization that insects incur a trade-off between parental care and future reproduction. Further work should now address the relationship between investment in egg number and egg size, since egg number alone is not a truly comprehensive measure of investment in reproduction. Studies should also investigate the unusual negative association I found between provisioning behaviour and the body size-fecundity relationship. The Scarabaeidae in particular offer an excellent opportunity to study the parental care-fecundity relationship in detail, owing to their large range of care strategies and the especially rich data available for this group. Additionally, hypotheses about the direction of evolution, such as those addressed in chapter 2, can be incorporated into comparative analyses (see, for example, Kolm *et al.*, 2005a,b) to test for causal relationships between variables rather than merely for nondirectional associations.

The phylogeny of insects I have compiled for these comparative studies is necessarily a preliminary hypothesis of insect relationships owing to the extreme diversity of insect species. Further comparative work on insects should now aim to increase confidence in the insect phylogeny, inasmuch as this is possible. Firstly, alternative hypotheses for relationships within controversial taxa such as the Dictyoptera should be considered separately, to test whether

this affects the results of comparative analyses. Secondly, a phylogenetic supertree should be constructed as soon as it becomes feasible.

6.1.2 Parental care in assassin bugs

In chapter 4, I investigated factors influencing the unusual preference of male-caring *Rhinocoris* assassin bugs for a single genus of plant, *Stylosanthes*, leading them to live at high population density, which is implicated in the evolution of male care (Manica & Johnstone, 2004). The plant protects the bugs' eggs against ants, potential egg predators, and also provides a favourable distribution of prey compared to that available on mixed vegetation. Thus *Stylosanthes* could have provided favourable conditions for the evolution of male care in *Rhinocoris*. What remains unexplained is why *R. tristis* should have been found on my *Stylosanthes* plots at much higher density than *R. albopilosus*, which tended to live elsewhere – a finding contrary to previous studies, which recorded the opposite pattern (e.g. Thomas, 1994). Studies should now address the historical association between geographical radiations of male-caring *Rhinocoris* and different species of *Stylosanthes* to test formally the relationship between host plant specialization, population density and male care. Additionally, the population dynamics and interactions of *R. tristis* and *R. albopilosus* should be investigated, to help understand the contrasting patterns of abundance that I and other authors have found in the field.

In chapter 5, I investigated the potential for sexual conflict over egg conspicuousness in *Rhinocoris* assassin bugs. I found that in *R. tristis* males and females do indeed have different interests with regard to the conspicuousness

of eggs. Males can accumulate more eggs in conspicuous locations than in inconspicuous ones, but at the cost of a higher proportion being parasitized. Over the many batches that a male can accumulate, this represents a worthwhile trade-off for the male; but for a female adding her individual batch, the payoff is greater when eggs are inconspicuous, to reduce the proportion parasitized. Since *R. tristis* broods are much more commonly laid on conspicuous stems than hidden under leaves, males appear to be winning this conflict. In their congener, *R. albopilosus*, parasitism was too high for males to get any benefit from guarding in conspicuous places, and there was correspondingly no evidence of a sexual conflict, since broods are always hidden under leaves. Whether this conflict exists in other male-caring insects should now be investigated. Male-caring Belostomatid bugs would be a potential target, although males may stand to gain less from conspicuousness in some members of this group if successive females tend to cannibalize existing eggs before laying themselves (Ichikawa, 1990). Other arthropods could also be addressed, for example male-caring *Zygopachylus* harvestmen (Mora, 1990). In this group, males build special nests explicitly to attract the attention of females, so this conflict may be particularly evident.

The two species of male-caring assassin bug, *R. tristis* and *R. albopilosus*, showed important ecological differences in both the factors affecting the evolution of male care (population density) and the evolutionary consequences arising from male care (potential for sexual conflict over conspicuousness); these differences could eventually help us understand reasons behind the adaptive radiation of this group of male-carers, and could also have implications for their further evolution. Of particular interest will be subsequent studies on *R.*

albopunctatus, the remaining male-caring *Rhinocoris*. I did not find this species at NAARI, but they have been recorded in Uganda (Nyiira, 1970); their relationship with *Stylosanthes*, and the potential for sexual conflict in this species, should now be addressed. Molecular studies could also now investigate the monophyly of male-caring *Rhinocoris* as well as their placement with regard to the female-caring *R. carmelita* and *R. erythropus*. I have constructed a preliminary molecular phylogeny based on two loci which suggests that the male carers are indeed monophyletic, and have a separate origin from female care in *R. carmelita*, supporting the hypothesis proposed by (Manica & Johnstone, 2004) and tested in chapter 2 of this thesis, that male care should evolve out of no care. Behavioural studies on assassin bugs could now address the predictions about the bugs' ecology arising from Manica & Johnstone's model. Initial results I gathered from the field for ten species of *Rhinocoris* suggest that the model correctly predicts a bug's parental care strategy based on features of its ecology, paticularly its population density and the time taken for females to replenish their eggs following oviposition.

6.2 Conclusions

In investigating parental care evolution in insects, I have taken both a 'top-down' approach by looking comparatively between species, and also a 'bottom-up' approach using field studies on individual species. My results show that on a large scale, parental care evolution in insects largely confirms predictions arising from existing theory, while on a small scale, the causes and consequences of parental care evolution can be very subtly influenced by an an-

imal's ecology. The next step in integrating the two approaches should be formal meta-analysis of factors affecting the evolution of parental care across insects, incorporating the results of multiple manipulation experiments in a phylogenetic-comparative context. In chapter 3 of this study I began this process; many more tests are possible given the availability of data. In particular, multiple experiments across species of sympatric assassin bugs with different care strategies, coupled with a phylogeny of the group, would offer excellent opportunities for testing fine-grained hypotheses about the ecological causes and consequences of parental care evolution.

While there is no shortage of in-depth intraspecific studies on the behavioural ecology of parental care in insects, large-scale comparative studies are very rare. Now that a preliminary insect phylogeny is available, I have shown that we can use this approach to test the general theories about insect parental care evolution that arise from trends observed across single-species studies. Indeed, because there is such a wealth of life history and behavioural data for insects, not merely related to parental care (e.g. Cornell & Hawkins, 1995; Eickwort, 1981; Garcia-Barros, 2000; Hinton, 1981; Wilson, 1971), the advent of a workable insect tree for phylogenetic-comparative studies means that such results can be viewed as 'low-hanging fruit' for the student willing to gather this kind of data. Particularly promising areas include the factors affecting the evolution of sociality in insects, about which there is a wealth of hypotheses (e.g. Crespi & Choe, 1997; Gadagkar, 1990; Wilson, 1971), and the evolution of insect mating systems, which are extremely diverse and much debated (see reviews in Choe & Crespi, 1997), but with few formal comparative tests. Phylogenetic-comparative tests can also be used to link insect behavioural ecology to other

fields for which data are rich, for example more traditional insect ecology and population dynamics, along with fields that are currently emerging, such as molecular-stoichiometric constraints on insect ecology (e.g. Fagan *et al.*, 2002), along with more applied areas such as conservation (the uses of phylogeny in conservation is a growing interest; see Purvis *et al.*, 2005).

Appendix A

Measuring insect body size

There is no consensus on a standard measure of body size in insects, at least among comparative studies, despite attempts to standardize it (Rogers *et al.*, 1976; Sample *et al.*, 1993; Smock, 1980). The best measure is dry weight (Blair Hedges, 1985; Western, 1979; Western & Ssemakula, 1982). Its usual alternative, body length, is a poor predictor of mass, especially for sets of species with highly different morphologies, and often produces less tight allometric curves (Blair Hedges, 1985). However, the procedure for obtaining dry weight is time-consuming, so few studies use it (e.g. Rasa *et al.*, 1998); it is especially rarely used in comparative studies that require a range of species from many locations (but see Addo-Bediako *et al.*, 2002). Dry weight is also recorded less often than body length in the literature. Here, I develop a technique for measuring insect dry weight from large numbers of pinned museum specimens, which is relatively quick and easy compared to its alternative (locating, catching, killing, drying and weighing field specimens; see e.g. Sample *et al.*, 1993), and with a relatively small loss of accuracy.

Methods

I measured dry weight using pinned museum specimens from the collections at the University of Cambridge, UK (Insect Room, Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ) and the British Museum of Natural History (Cromwell Road, London SW7 5BD). I weighed the whole, pinned specimen to a precision of 0.001g, using a balance accurate to 0.0001g (Cambridge: Ohaus® Adventurer Pro balance; London: Sartorius® GD503 balance), then estimated the weight of the pin and subtracted it. Museum pins were non-standardized, so to estimate pin weight I first weighed 100 pins of different kinds, and recorded the length and diameter (using calipers precise to 0.05mm), head type (visually assessed as 'none', 'small' (< 0.5mm diameter), 'medium' (< 1mm diameter) and 'large' (> 1mm diameter) and material ('brass' or 'steel' assessed using a magnet). I then constructed a linear model with 'volume', 'material' and 'head type' as predictor variables. Pin volume was calculated as $\pi \times (\frac{diameter}{2})^2 \times length$.

Depending upon availability, I weighed up to six specimens for each species. Loss of mass over time due to wear and tear, museum beetle activity, corrosion of the pin, repairs using glue, and different preservation methods might be expected to affect the weight. Hence, for a given species I chose the youngest and best condition specimens with no outward evidence of museum beetle infestation, 'verdigris' (copper corrosion that affects brass pins) or glue. I recorded the specimen's age if given. In the Dictyoptera, specimens were often coated in a shellac-style preservative, while members of the Orthoptera were frequently found to be stuffed with cotton wool. Such specimens were excluded. I also

chose specimens on the smallest possible pin, to minimize unexplained variance in pin weight.

To compare my estimates of dry weight with measurements from other authors (e.g. Radtke & Williamson, 2005; Rogers *et al.*, 1976; Sage, 1982; Sample *et al.*, 1993), I also measured body length (anterior-most part of labrum or frons, excluding projections such as pronotal spurs, to the posterior-most part of abdomen, excluding projections such as cerci, ovipositors or forceps) and pronotum width (distance between humeral angles at widest point). I compared my estimates with other authors by comparing the parameters of the allometric equation: $W = e^b.(L)^a$. I also compared my allometric regression of dry weight upon body area (calculated as body length × pronotum width) with that of Sample *et al.* (1993) who made the same measure.

Results

I measured body weight for 891 museum specimens from 263 species, 110 families and 14 orders. Museum specimens weighed from an estimated 0.004g (Lepidoptera: *Cryptoblabes*) to 9.546g (Blattaria: *Macropanesthia*) after subtraction of the pin weight. Pin weight was estimated from pin volume, head size, and metal type with an r^2 of 98.7% (p<0.0001; n=100, data not shown).

The age of the museum specimen had a very small positive effect on dry weight (Slope estimate= $0.007, r^2 = 0.015, F_{1,356} = 6.67, p < 0.05$) which disappeared after the nine specimens from before 1860 were excluded (Slope estimate= $0.003, r^2 = 0.001, F_{1,347} = 1.54, p = 0.214$). These individuals were therefore excluded from subsequent analyses.

Dry weight (W) scaled with length (L) according to the equation $W = e^{-3.155}.(L)^{2.575}, r^2 = 0.74$ (figure A.1). These parameters are comparable to those of Sample *et al.* (1993, $W = e^{-3.628}.(L)^{2.494}$) and Rogers *et al.* (1976, $W = e^{-3.490}.(L)^{2.62}$) both of whom used oven-dried specimens. When I took pronotum width into account, dry weight (W) scaled with body area (A) according to the following equation: $W = e^{-1.987}.(L)^{1.369}, r^2 = 0.85$. The dry weights I report here were consistently heavier than those found by Sample *et al.* (1993), by a factor of about 13.5%, calculated as the ratio of the two fitted lines at the midpoint for body length ($(\frac{94.7-2.2}{2}) = 46.25$mm), equal to $\frac{e^{-3.155}.(46.25)^{2.575}}{e^{-3.628}.(46.25)^{2.494}} = 1.135$.

Slopes differed between orders significantly (length-weight slope: $F_{12,865} = 12.54, p < 0.0001$; area-weight slope: $F_{12,865} = 13.35, p < 0.0001$; table A.1, estimates from other authors given for comparison); the steepest length-weight relationship was in the Lepidoptera ($a = 3.461 \pm 0.130$), the shallowest in the Ephemeroptera ($a = 1.269 \pm 0.316$). In general, body area explained more variation than body length, although the reverse was true for Trichoptera (also found by Sample *et al.*, 1993), Neuroptera, and Dermaptera.

Generally, the degree of accuracy to which length and pronotum width explained variation in dry weight of museum specimens (i.e. the r^2 for the regression line of one on the other) was about 10% less than that with which Sample *et al.* (1993) could explain variation in the dry weights of their field-collected specimens (table A.1). Interestingly, in the case of the Diptera, I could explain much less variation in museum specimen weight than Sample *et al.* (1993) explained in their freshly dried specimens (my $r^2 = 0.50$, their $r^2 = 0.94$).

		Range		Length			Length × pronotum width		
Taxon	Ref	(mm)	n	b±s.e.	a±s.e.	r²	b±s.e.	a±s.e.	r²
Insecta	TS	2.2–94.7	891	-3.155±0.134	2.575±0.051	0.74	-1.987±0.081	1.369±0.019	0.85
	S&al	2.13–54.51	1673	-3.628±0.073	2.494±0.032	0.88	-2.140±0.036	1.331±0.011	0.94
	S	1.1–68.1	1362	-3.963	2.46	0.89			
	R&al	0.5–36	500	-3.490	2.62	0.94			
Coleoptera	TS	3.6–68.7	232	-1.112±0.167	2.126±0.062	0.86	-0.168±0.120	1.052±0.026	0.87
	S&al	3.34–34.82	330	-3.247±0.175	2.492±0.081	0.86	-1.857±0.095	1.296±0.030	0.92
	S	2.2–25	161	-1.878±0.348	2.18±0.13	0.94			
Hemiptera	TS	2.2–92.0	151	-2.206±0.254	2.194±0.102	0.76	-1.867±0.187	1.256±0.046	0.84
	S&al	3.20–40.23	70	-4.784±0.313	3.075±0.147	0.93	-2.765±0.135	1.423±0.041	0.97
	S	1.7–34.0	114	-3.461±0.311	2.40±0.21	0.93			
Lepidoptera	TS	4.9–38.6	139	-6.074±0.337	3.461±0.130	0.84	-3.461±0.215	1.659±0.056	0.87
	S&al	2.76–44.62	196	-5.909±0.257	2.959±0.085	0.93	-3.138±0.129	1.483±0.031	0.96
Hymen-optera	TS	3.0–28.3	87	-3.812±0.470	2.643±0.185	0.77	-2.202±0.240	1.386±0.065	0.84
	S&al	2.81–34.91	274	-4.284±0.183	2.696±0.083	0.89	-2.375±0.080	1.456±0.028	0.95
Diptera	TS	2.4–24.3	83	-1.612±0.407	1.644±0.201	0.44	-0.822±0.282	0.909±0.100	0.50
	S&al	2.90–23.65	257	-3.184±0.184	2.213±0.085	0.85	-3.976±0.306	1.682±0.073	0.94
	S	2.3–68.1	136	-5.221±0.588	2.43±0.15	0.96			
Orthoptera	TS	14.4–64.6	63	-0.223±0.383	1.815±0.113	0.81	-0.511±0.339	1.210±0.064	0.85
Neuroptera	TS	2.60–11.25	7	-1.469±0.502	1.371±0.254	0.82	-0.887±0.499	0.892±0.207	0.74
	S&al	3.45–54.51	70	-4.483±0.204	2.570±0.073	0.97	-1.684±0.146	1.172±0.033	0.98
Trichoptera	TS	5.2–12.9	16	-5.403±0.682	3.386±0.308	0.89	-3.076±0.746	1.783±0.258	0.76
	S&al	3.25–19.34	90	-4.610±0.184	3.044±0.097	0.96	-2.369±0.132	1.501±0.055	0.95
	S	3.2–25.0	232	6.266±0.693	3.12±0.29	0.83			
Dictyoptera	TS	13.1–94.7	51	-1.368±0.761	2.018±0.217	0.63	-2.492±0.351	1.436±0.061	0.92
Ephemer-optera	TS	2.9–23.6	32	0.402±0.660	1.269±0.316	0.33	-0.504±0.460	0.690±0.178	0.31
	S	1.1–24.1	459	-5.021±0.095	2.88±0.07	0.94			
Dermaptera	TS	4.25–19.90	19	-3.057±0.939	2.365±0.382	0.68	-2.137±0.918	1.462±0.274	0.60

Table A.1: Parameter estimates for regressions of dry specimen weight on length and on length × pronotum width for different orders. Sources are as follows: TS, this study; S&al, Sample *et al.* (1993); R&al, Rogers *et al.* (1976); S, Smock (1980).

Discussion

A reliable measure of body size is crucial to an interspecific life-history analysis (Blair Hedges, 1985). The dry weights and the length-weight and area-weight slopes that I report here are in agreement with previous findings based
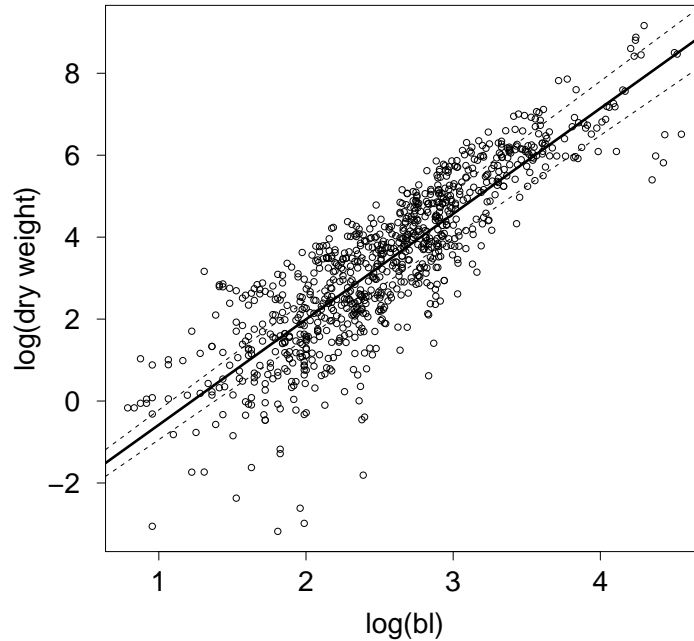
Figure A.1: (a) Log(dry insect weight) against log(body length) with fitted line and 95% confidence limits.

on oven-drying specimens (Rogers *et al.*, 1976; Sample *et al.*, 1993; Smock, 1980). This implies that museum specimens could be a feasible proxy for oven-dried specimens for measuring dry weight, depending upon requirements. My r^2 values were less by about 10% on average than those of other studies, which may reflect the general effects of age and wear-and-tear, although specimen weight was not correlated with specimen age. However, this is a quick, cheap and relatively easy way of obtaining dry weights as opposed to catching and drying specimens from around the world. Studies that do not depend on absolute accuracy in their results, or which require weights in retrospect for existing specimens, may view this as a worthwhile trade-off.

Interestingly my specimens tended to be slightly heavier than Sample *et al.*'s (1993)

and Smock's (1980) curves. Their method of oven drying over a few hours may cause the volatilisation of more material within the specimens than occurred in my specimens, which dried at ambient temperature over many years. This would be consistent with the fact that Sample *et al.* (1993) dried their specimens at 70°C for 48 hours, and their specimens were heavier than those of Smock (1980), who dried his aquatic insects at 105°C for four hours (although Smock attributed the difference in weight to different levels of chitinization between aquatic and terrestrial insects). A systematic study of the loss of weight from volatilization due to drying temperature could help reduce unexplained variance in future studies of insect dry weight. Alternatively, my specimens may have gained weight from verdigris (although I checked externally and chose good quality specimens, some may have been affected internally), or I may have repeatedly and systematically underestimated the weights of the pins, although this is highly unlikely to produce such a consistent discrepancy: at the higher range of specimen size the pins represented only a tiny proportion of specimen weight.

Appendix B

Data tables

Table B1. List of species used in parental care transition analysis (see chapter 2).

Order	Species	Care code	Care
Coleoptera	Abax spp	0	None
Coleoptera	Ablattaria laevigata	1	Female
Coleoptera	Acanthoscelides obtectus	0	None
Coleoptera	Acromis sparsa	1	Female
Coleoptera	Acromis spinifex	1	Female
Coleoptera	Adalia bipunctata	0	None
Coleoptera	Agrilus arcuatus	0	None
Coleoptera	Agriotes mancus	0	None
Coleoptera	Agriotes ponticus	0	None
Coleoptera	Aleochara bilineata	0	None
Coleoptera	Amphicoma vulpes	0	None
Coleoptera	Anachalcos cupreus	2	Biparental
Coleoptera	Anaides simplicicollis	0	None
Coleoptera	Anaides sp	0	None
Coleoptera	Anobium punctatum	0	None
Coleoptera	Anomala horticola	0	None
Coleoptera	Anthrenus museorum	0	None
Coleoptera	Anthrenus verbasci	0	None
Coleoptera	Aphodius ater	0	None
Coleoptera	Aphodius elegans	0	None
Coleoptera	Aphodius fimetarius	0	None
Coleoptera	Aphodius fossor	0	None
Coleoptera	Aphodius haroldianus	0	None
Coleoptera	Aphodius lividus	1	Female
Coleoptera	Aphodius prodromus	0	None
Coleoptera	Aphodius rufipes	0	None
Coleoptera	Aphodius sphacelatus	0	None
Coleoptera	Aploderus caesus	0	None
Coleoptera	Apoderus spp	1	Female
Coleoptera	Astaenomoechus sp1	0	None
Coleoptera	Astaenomoechus sp2	0	None
Coleoptera	Ataenius sp	0	None
Coleoptera	Attagenus pellio	0	None
Coleoptera	Attagenus piceus	0	None
Coleoptera	Attelabus spp	1	Female
Coleoptera	Australoplatypus incompertus	2	Biparental
Coleoptera	Bangasternus fausti	0	None
Coleoptera	Bledius arenoides	0	None
Coleoptera	Bledius bicornis	0	None
Coleoptera	Bledius diota	0	None
Coleoptera	Bledius furcatus	0	None
Coleoptera	Bledius longulus	2	Biparental
Coleoptera	Bledius opacus	0	None
Coleoptera	Bledius pygmaeus	0	None
Coleoptera	Bledius spectabilis	2	Biparental
Coleoptera	Bledius tricornis	0	None
Coleoptera	Bolitotherus cornutus	0	None
Coleoptera	Brachypterolus pulicarius	0	None
Coleoptera	Bruchidius obtectus	0	None
Coleoptera	Bruchus pisorum	0	None
Coleoptera	Bruchus quadrimaculatus	0	None
Coleoptera	Bubas bison	0	None
Coleoptera	Bubas bubalus	0	None
Coleoptera	Byctiscus spp	1	Female
Coleoptera	Byturus tomentosus	0	None
Coleoptera	Calandra oryzae	0	None
Coleoptera	Callineda testudinaria	0	None
Coleoptera	Calosoma sycophanta	0	None
Coleoptera	Canthon bispinus	2	Biparental
Coleoptera	Canthon cyanellus	2	Biparental
Coleoptera	Canthon edentulus	2	Biparental
Coleoptera	Canthon muticus	2	Biparental
Coleoptera	Capnodis tenebrionis	0	None
Coleoptera	Carpophilus hemipterus	0	None
Coleoptera	Carpophilus humeralis	0	None
Coleoptera	Carpophilus obsoletus	0	None
Coleoptera	Carterus calydonus	1	Female
Coleoptera	Cassida canaliculata	0	None
Coleoptera	Cephalodesmius armiger	2	Biparental
Coleoptera	Cephalodesmius laticollis	2	Biparental
Coleoptera	Cephalodesmius quadridens	2	Biparental
Coleoptera	Ceratocanthus relucens	0	None
Coleoptera	Chaetodus sp	0	None
Coleoptera	Chilocorus kuwanae	0	None
Coleoptera	Chilocorus nigritus	0	None
Coleoptera	Chilocorus stigma	0	None
Coleoptera	Chondrocephalus debilis	2	Biparental
Coleoptera	Chondrocephalus granulifrons	2	Biparental
Coleoptera	Chondrocephalus purulensis	2	Biparental
Coleoptera	Chrysomela crotchi	0	None

Order	Species	Care code	Care
Coleoptera	Circellium bacchus	2	Biparental
Coleoptera	Clemora smithi	0	None
Coleoptera	Coccidotrophus socialis	2	Biparental
Coleoptera	Coccinella novemnotata	0	None
Coleoptera	Coccinella septempunctata	0	None
Coleoptera	Coccotrypes carpophagus	2	Biparental
Coleoptera	Copris arizonensis	2	Biparental
Coleoptera	Copris armatus	2	Biparental
Coleoptera	Copris aspericollis	2	Biparental
Coleoptera	Copris boucardi	0	None
Coleoptera	Copris diversus	2	Biparental
Coleoptera	Copris fricator	2	Biparental
Coleoptera	Copris gopheri	2	Biparental
Coleoptera	Copris hispanus	2	Biparental
Coleoptera	Copris incertus	2	Biparental
Coleoptera	Copris laeviceps	0	None
Coleoptera	Copris lugubris	2	Biparental
Coleoptera	Copris lunaris	2	Biparental
Coleoptera	Copris minutus	2	Biparental
Coleoptera	Copris remotus	1	Female
Coleoptera	Copris sp	0	None
Coleoptera	Copris tullius	2	Biparental
Coleoptera	Coptodactyla sp	2	Biparental
Coleoptera	Coptorhina sp	2	Biparental
Coleoptera	Coraebus rubi	0	None
Coleoptera	Corthylus spp	0	None
Coleoptera	Crossotarsus saundersi	2	Biparental
Coleoptera	Cryptogenius fryi	0	None
Coleoptera	Cryptolaemus montrouzieri	0	None
Coleoptera	Cybocephalus semiflavus	0	None
Coleoptera	Cycloneda limbifer	0	None
Coleoptera	Cyphocleonus achates	0	None
Coleoptera	Cyphopisthes descarpertriesi	0	None
Coleoptera	Cyptochirus distinctus	2	Biparental
Coleoptera	Dendroctonus brevicomis	0	None
Coleoptera	Dendroctonus piceaperda	2	Biparental
Coleoptera	Dendroctonus ponderosae	2	Biparental
Coleoptera	Dendroctonus pseudotsugae	2	Biparental
Coleoptera	Dendroctonus valens	2	Biparental
Coleoptera	Deporaus spp	1	Female
Coleoptera	Dermestes frischi	0	None
Coleoptera	Dermestes lardarius	0	None
Coleoptera	Dermestes maculatus	0	None
Coleoptera	Dichotomius anaglypticus	2	Biparental
Coleoptera	Dichotomius haroldi	2	Biparental
Coleoptera	Dichotomius micans	2	Biparental
Coleoptera	Dichotomius semiaeneus	2	Biparental
Coleoptera	Dichotomius torulosus	2	Biparental
Coleoptera	Dinoderus minutus	0	None
Coleoptera	Doliopygus contradti	2	Biparental
Coleoptera	Drilus flavescens	0	None
Coleoptera	Enoclerus barri	0	None
Coleoptera	Enoclerus lecontei	0	None
Coleoptera	Epepeotus luscus	0	None
Coleoptera	Epilachna chrysomelina	0	None
Coleoptera	Eugenysa columbiana	1	Female
Coleoptera	Euoniticellus intermedius	2	Biparental
Coleoptera	Eurysternus balachowskyi	2	Biparental
Coleoptera	Eurysternus caribaeus	2	Biparental
Coleoptera	Eurysternus deplanatus	0	None
Coleoptera	Eurysternus foedus	2	Biparental
Coleoptera	Eurysternus inflexus	0	None
Coleoptera	Eurysternus jessopi	0	None
Coleoptera	Eurysternus magnus	2	Biparental
Coleoptera	Eurysternus marmoreus	2	Biparental
Coleoptera	Eurysternus mexicanus	2	Biparental
Coleoptera	Exochomus flavipes	0	None
Coleoptera	Galerucella calmariensis	0	None
Coleoptera	Galerucella pusilla	0	None
Coleoptera	Geotrupes mutator	0	None
Coleoptera	Geotrupes spiniger	1	Female
Coleoptera	Geotrupes stercorarius	0	None
Coleoptera	Geotrupes vernalis	0	None
Coleoptera	Germarostes aphodioides	0	None
Coleoptera	Germarostes globosus	0	None
Coleoptera	Germarostes macleayi	0	None
Coleoptera	Gnathotrichus materiarius	2	Biparental
Coleoptera	Gonioctena americana	0	None
Coleoptera	Gonioctena japonica	1	Female
Coleoptera	Gonioctena nigroplagiata	0	None
Coleoptera	Gonioctena olivacea	0	None
Coleoptera	Gonioctena rubripennis	0	None
Coleoptera	Gonioctena sibirica	1	Female

Order	Species	Care code	Care
Coleoptera	Gonioctena springlovae	0	None
Coleoptera	Gymnetron antirrhini	0	None
Coleoptera	Gymnetron linariae	0	None
Coleoptera	Gymnetron netum	0	None
Coleoptera	Harmonia axyridis	0	None
Coleoptera	Heliocopris andersoni	2	Biparental
Coleoptera	Heliocopris dilloni	2	Biparental
Coleoptera	Heliocopris hamadryas	2	Biparental
Coleoptera	Heliocopris japetus	2	Biparental
Coleoptera	Heliocopris neptunus	2	Biparental
Coleoptera	Heliocopris sp	2	Biparental
Coleoptera	Heliscus tropicus	2	Biparental
Coleoptera	Helochares lividus	1	Female
Coleoptera	Heterocerus flexuosus	1	Female
Coleoptera	Hippodamia convergens	0	None
Coleoptera	Hoplocerambyx spinicornis	0	None
Coleoptera	Hybosorus illigeri	0	None
Coleoptera	Hylobius transversovittatus	0	None
Coleoptera	Hypera brunnipennis	0	None
Coleoptera	Ips pini	2	Biparental
Coleoptera	Ips typographus	2	Biparental
Coleoptera	Kheper aegyptiorum	2	Biparental
Coleoptera	Kheper aeratus	2	Biparental
Coleoptera	Kheper clericus	2	Biparental
Coleoptera	Kheper cupreus	2	Biparental
Coleoptera	Kheper lamarcki	2	Biparental
Coleoptera	Kheper nigroaeneus	2	Biparental
Coleoptera	Kheper platynotus	2	Biparental
Coleoptera	Kheper subaeneus	2	Biparental
Coleoptera	Labidomera suturella	1	Female
Coleoptera	Lamprophorus tenebrosus	0	None
Coleoptera	Laricobius erichsonii	0	None
Coleoptera	Larinus minutus	0	None
Coleoptera	Larinus obtusus	0	None
Coleoptera	Lasioderma serricorne	0	None
Coleoptera	Lebia grandis	0	None
Coleoptera	Leis conformis	0	None
Coleoptera	Leptaulax bicolor	2	Biparental
Coleoptera	Leptochirus sp	0	None
Coleoptera	Lethrus apterus	0	None
Coleoptera	Lethrus jacobsoni	0	None
Coleoptera	Lichnanthe vulpina	0	None
Coleoptera	Lyctus brunneus	0	None
Coleoptera	Lyctus linearis	0	None
Coleoptera	Madrasostes sculpturatum	0	None
Coleoptera	Madrasostes variolosum	0	None
Coleoptera	Mecinus janthinus	0	None
Coleoptera	Melanotus fuscipes	0	None
Coleoptera	Melanotus longulus	0	None
Coleoptera	Melolontha melolontha	0	None
Coleoptera	Mesomorphus villiger	0	None
Coleoptera	Minarthrum sp	2	Biparental
Coleoptera	Mormolyce phyllodes	0	None
Coleoptera	Myelophilus piniperda	0	None
Coleoptera	Mylabris pustulatus	0	None
Coleoptera	Necrobia rufipes	0	None
Coleoptera	Necrophilus hidrophiloides	0	None
Coleoptera	Necrophilus subterraneus	0	None
Coleoptera	Neochetina bruchi	0	None
Coleoptera	Neochetina eichhorniae	0	None
Coleoptera	Nicrophorus americanus	2	Biparental
Coleoptera	Nicrophorus defodiens	2	Biparental
Coleoptera	Nicrophorus germanicus	2	Biparental
Coleoptera	Nicrophorus humator	2	Biparental
Coleoptera	Nicrophorus interruptus	2	Biparental
Coleoptera	Nicrophorus investigator	2	Biparental
Coleoptera	Nicrophorus mexicanus	2	Biparental
Coleoptera	Nicrophorus nigrita	2	Biparental
Coleoptera	Nicrophorus orbicollis	2	Biparental
Coleoptera	Nicrophorus pustulatus	2	Biparental
Coleoptera	Nicrophorus quadripunctatus	2	Biparental
Coleoptera	Nicrophorus tomentosus	2	Biparental
Coleoptera	Nicrophorus vespillo	2	Biparental
Coleoptera	Nigidius sp	0	None
Coleoptera	Oberia erythrocephala	0	None
Coleoptera	Odonteus darlingtoni	0	None
Coleoptera	Odontotaenius disjunctus	2	Biparental
Coleoptera	Odontotaenius striatopunctatus	2	Biparental
Coleoptera	Odontotaenius zodiacus	2	Biparental
Coleoptera	Ogyges adamsi	2	Biparental
Coleoptera	Ogyges championi	2	Biparental
Coleoptera	Ogyges crassulus	2	Biparental
Coleoptera	Ogyges furcillatus	2	Biparental

Order	Species	Care code	Care
Coleoptera	Ogyges hondurensis	2	Biparental
Coleoptera	Oileus sargi	2	Biparental
Coleoptera	Omaspides pallidipennis	1	Female
Coleoptera	Oniticellus cinctus	2	Biparental
Coleoptera	Oniticellus egregius	2	Biparental
Coleoptera	Oniticellus formosus	2	Biparental
Coleoptera	Oniticellus pictus	2	Biparental
Coleoptera	Oniticellus planatus	2	Biparental
Coleoptera	Oniticellus pseudoplanatus	2	Biparental
Coleoptera	Oniticellus rhadamistus	2	Biparental
Coleoptera	Onitis belial	2	Biparental
Coleoptera	Onitis ion	2	Biparental
Coleoptera	Onthophagus binodis	2	Biparental
Coleoptera	Onthophagus gazella	2	Biparental
Coleoptera	Onthophagus hirculus	2	Biparental
Coleoptera	Onthophagus taurus	2	Biparental
Coleoptera	Onthophagus vacca	0	None
Coleoptera	Oryctes boas	0	None
Coleoptera	Oryctes elegans	0	None
Coleoptera	Oryctes rhinoceros	0	None
Coleoptera	Oxyops vitiosa	0	None
Coleoptera	Parastizopus armaticeps	2	Biparental
Coleoptera	Paroplapoderus spp	1	Female
Coleoptera	Passalus caelatus	2	Biparental
Coleoptera	Passalus coniferus	2	Biparental
Coleoptera	Passalus cornutus	2	Biparental
Coleoptera	Passalus guatemalensis	2	Biparental
Coleoptera	Passalus interstitialis	0	None
Coleoptera	Passalus morio	2	Biparental
Coleoptera	Passalus punctatostriatus	2	Biparental
Coleoptera	Passalus punctiger	2	Biparental
Coleoptera	Passalus spiniger	2	Biparental
Coleoptera	Passalus spp	2	Biparental
Coleoptera	Passalus unicornis	2	Biparental
Coleoptera	Paulianostes acromialis	0	None
Coleoptera	Paxillus leachi	2	Biparental
Coleoptera	Paxillus recticarinatus	0	None
Coleoptera	Pedaria sp	2	Biparental
Coleoptera	Petrejoides guatemalae	2	Biparental
Coleoptera	Petrejoides michoacanae	2	Biparental
Coleoptera	Petrejoides reyesi	2	Biparental
Coleoptera	Petrejoides tenuis	2	Biparental
Coleoptera	Phaeochrous emarginatus	0	None
Coleoptera	Phanaeus daphnis	2	Biparental
Coleoptera	Phanaeus spp	2	Biparental
Coleoptera	Phloeosimus sp	1	Female
Coleoptera	Phosphuga atrata	0	None
Coleoptera	Phrenapates bennetti	2	Biparental
Coleoptera	Phymatapoderus spp	1	Female
Coleoptera	Phytodecta rufipes	1	Female
Coleoptera	Platypus compositus	2	Biparental
Coleoptera	Platypus severini	2	Biparental
Coleoptera	Platystethus arenarius	1	Female
Coleoptera	Poecilips spp	0	None
Coleoptera	Polydrusus mollis	1	Female
Coleoptera	Polyporus sp	2	Biparental
Coleoptera	Popilius disjunctus	2	Biparental
Coleoptera	Popilius eclipticus	2	Biparental
Coleoptera	Popilius haagi	2	Biparental
Coleoptera	Prionus californicus	0	None
Coleoptera	Proculejus brevis	2	Biparental
Coleoptera	Proculus burmeisteri	2	Biparental
Coleoptera	Proculus goryi	2	Biparental
Coleoptera	Proculus jicaquei	2	Biparental
Coleoptera	Proculus mniszechi	2	Biparental
Coleoptera	Proculus opacipennis	2	Biparental
Coleoptera	Proculus opacus	2	Biparental
Coleoptera	Prosopocoilus inclinatus	0	None
Coleoptera	Pseudacanthus grannulipennis	2	Biparental
Coleoptera	Pseudoarrox karreni	2	Biparental
Coleoptera	Pseudomesomphalia thallassina	1	Female
Coleoptera	Pseudoscymnus tsugae	0	None
Coleoptera	Pterorthochaetes insularis	0	None
Coleoptera	Pterostichus multipunctatus	0	None
Coleoptera	Ptinus fur	0	None
Coleoptera	Ptinus sexpunctatus	0	None
Coleoptera	Rhinocyllus conicus	0	None
Coleoptera	Rhizopertha dominica	0	None
Coleoptera	Rhynchites auratus	1	Female
Coleoptera	Rodolia cardinalis	0	None
Coleoptera	Saperda carcharias	0	None
Coleoptera	Scarabaeus aesculapius	2	Biparental
Coleoptera	Scarabaeus bennigseni	2	Biparental

Order	Species	Care code	Care
Coleoptera	Scarabaeus catenatus	2	Biparental
Coleoptera	Scarabaeus cicatricosus	2	Biparental
Coleoptera	Scarabaeus cristatus	2	Biparental
Coleoptera	Scarabaeus denticollis	2	Biparental
Coleoptera	Scarabaeus endroedyi	2	Biparental
Coleoptera	Scarabaeus fitzsimoni	2	Biparental
Coleoptera	Scarabaeus funebris	2	Biparental
Coleoptera	Scarabaeus galenus	2	Biparental
Coleoptera	Scarabaeus gariepinus	2	Biparental
Coleoptera	Scarabaeus glentoni	2	Biparental
Coleoptera	Scarabaeus hippocrates	2	Biparental
Coleoptera	Scarabaeus laevistriatus	2	Biparental
Coleoptera	Scarabaeus proboscideus	2	Biparental
Coleoptera	Scarabaeus rodriguesi	2	Biparental
Coleoptera	Scarabaeus rugosus	2	Biparental
Coleoptera	Scarabaeus rusticus	2	Biparental
Coleoptera	Scarabaeus sacer	2	Biparental
Coleoptera	Scarabaeus schinzi	2	Biparental
Coleoptera	Scarabaeus semipunctatus	2	Biparental
Coleoptera	Scarabaeus striatum	2	Biparental
Coleoptera	Scarabaeus valeflorae	2	Biparental
Coleoptera	Scarabaeus westwoodi	2	Biparental
Coleoptera	Scolytus rugulosus	2	Biparental
Coleoptera	Sisyphus sp	2	Biparental
Coleoptera	Sitophilus granarius	0	None
Coleoptera	Spercheus emarginatus	1	Female
Coleoptera	Sphenoptera jugoslavica	0	None
Coleoptera	Spurius bicornis	2	Biparental
Coleoptera	Stephanoderes hampei	2	Biparental
Coleoptera	Stethorus punctum	0	None
Coleoptera	Sulcophanaeus batesi	2	Biparental
Coleoptera	Sulcophanaeus carnifex	2	Biparental
Coleoptera	Sulcophanaeus imperator	2	Biparental
Coleoptera	Sulcophanaeus menelas	2	Biparental
Coleoptera	Synapsis tmolus	2	Biparental
Coleoptera	Tachyporus hypnorum	0	None
Coleoptera	Taeniocerus bicanthatus	2	Biparental
Coleoptera	Taeniocerus platypus	2	Biparental
Coleoptera	Tenebrio molitor	0	None
Coleoptera	Tenebrio obscurus	0	None
Coleoptera	Tenebroides mauritanicus	0	None
Coleoptera	Tragiscus dimidiatus	2	Biparental
Coleoptera	Tribolium castaneum	0	None
Coleoptera	Trichosirocalus horridus	0	None
Coleoptera	Trinodes rufescens	0	None
Coleoptera	Trogoderma granarium	0	None
Coleoptera	Trogoderma varium	0	None
Coleoptera	Trogoderma versicolor	0	None
Coleoptera	Typhaeus hiostius	0	None
Coleoptera	Typhaeus typhoeus	0	None
Coleoptera	Verres cavicollis	2	Biparental
Coleoptera	Verres corticicola	2	Biparental
Coleoptera	Verres furcilabris	2	Biparental
Coleoptera	Verres hageni	2	Biparental
Coleoptera	Veturius boliviae	2	Biparental
Coleoptera	Vindex sp	2	Biparental
Coleoptera	Xyleborus fornicatus	0	None
Coleoptera	Zabrotes subfasciatus	0	None
Crustacea	Dyopedos monacanthus	1	Female
Crustacea	Gammarus pseudolimnaeus	1	Female
Crustacea	Leptocheirus pinguis	1	Female
Dermaptera	Anechura bipunctata	1	Female
Dermaptera	Anisolabis littorea	1	Female
Dermaptera	Chelidura pyrenaica	1	Female
Dermaptera	Chelidurella acanthopygia	1	Female
Dermaptera	Chelisoches morio	1	Female
Dermaptera	Diplatys sp	1	Female
Dermaptera	Forficula auricularia	1	Female
Dermaptera	Forficula pubescens	1	Female
Dermaptera	Forficula tomis	1	Female
Dermaptera	Labidura riparia	1	Female
Dermaptera	Marava arachidis	1	Female
Dermaptera	Pseudochelidura sinuata	1	Female
Dictyoptera	Anchiale maculata	0	None
Dictyoptera	Anisomorpha buprestoides	0	None
Dictyoptera	Bactrododema krugeri	0	None
Dictyoptera	Blaberus craniifer	1	Female
Dictyoptera	Blaberus giganteus	1	Female
Dictyoptera	Blatta orientalis	0	None
Dictyoptera	Blattella germanica	1	Female
Dictyoptera	Blattella humbertiana	1	Female
Dictyoptera	Blattella vaga	1	Female
Dictyoptera	Byrsotria fumigata	1	Female

Order	Species	Care code	Care
Dictyoptera	Carausius morosus	0	None
Dictyoptera	Cryptocercus clevelandi	2	Biparental
Dictyoptera	Cryptocercus kyebangensis	2	Biparental
Dictyoptera	Cryptocercus punctulatus	2	Biparental
Dictyoptera	Ctenomorphodes tessulatus	0	None
Dictyoptera	Cyphocrania gigas	0	None
Dictyoptera	Didymuria violescens	0	None
Dictyoptera	Diploptera punctata	1	Female
Dictyoptera	Ectobius panzeri	0	None
Dictyoptera	Epilampra wheeleri	0	None
Dictyoptera	Eurycantha calcarata	0	None
Dictyoptera	Eurycnema goliath	0	None
Dictyoptera	Eurycotis floridana	0	None
Dictyoptera	Extatosoma tiaratum	0	None
Dictyoptera	Galepsus sp	1	Female
Dictyoptera	Geoscapheus dilatatus	0	None
Dictyoptera	Graeffia crouani	0	None
Dictyoptera	Gromphadorhina laevigata	1	Female
Dictyoptera	Gromphadorhina portentosa	1	Female
Dictyoptera	Hierodula crassa	0	None
Dictyoptera	Hierodula parviceps	0	None
Dictyoptera	Ischnoptera deropeltiformis	0	None
Dictyoptera	Leucophaea maderae	1	Female
Dictyoptera	Macropanesthia rhinoceros	1	Female
Dictyoptera	Macropanesthia spp	1	Female
Dictyoptera	Mantis religiosa	0	None
Dictyoptera	Megacrania alpheus	0	None
Dictyoptera	Megacrania wegneri	0	None
Dictyoptera	Metriotes diocles	0	None
Dictyoptera	Nauphoeta cinerea	1	Female
Dictyoptera	Necroscia sparaxes	0	None
Dictyoptera	Neogeoscapheus spp	1	Female
Dictyoptera	Ophicrania leveri	0	None
Dictyoptera	Orxines macklotti	0	None
Dictyoptera	Palophus episcopalis	0	None
Dictyoptera	Palophus sp	0	None
Dictyoptera	Palophus tiaratus	0	None
Dictyoptera	Panesthia australis	2	Biparental
Dictyoptera	Panesthia cribrata	0	None
Dictyoptera	Panesthia laevicollis	2	Biparental
Dictyoptera	Parapanesthia spp	1	Female
Dictyoptera	Paratenodera sinensis	0	None
Dictyoptera	Parcoblatta pennsylvanica	0	None
Dictyoptera	Periplaneta americana	0	None
Dictyoptera	Periplaneta australasiae	0	None
Dictyoptera	Perisphaerus glomeriformis	1	Female
Dictyoptera	Perisphaerus sp	1	Female
Dictyoptera	Phalces longiscaphus	0	None
Dictyoptera	Phlebonotus pallens	1	Female
Dictyoptera	Phyllium bioculatum	0	None
Dictyoptera	Podacanthus typhon	0	None
Dictyoptera	Pseudophoraspis nebulosa	1	Female
Dictyoptera	Pseudosermyle truncata	0	None
Dictyoptera	Pycnoscelus surinamensis	1	Female
Dictyoptera	Salganea esakii	2	Biparental
Dictyoptera	Salganea gressiti	2	Biparental
Dictyoptera	Salganea raggei	2	Biparental
Dictyoptera	Salganea taiwanensis	2	Biparental
Dictyoptera	Supella longipalpa	1	Female
Dictyoptera	Supella supellectilium	0	None
Dictyoptera	Tarachodes afzelii	1	Female
Dictyoptera	Tarachodes maurus	1	Female
Dictyoptera	Thanatophyllum akinetum	1	Female
Dictyoptera	Thorax porcellana	1	Female
Dictyoptera	Timema californica	0	None
Dictyoptera	Trichoblatta sericea	1	Female
Dictyoptera	Tropidoderus childreni	0	None
Diplura	Dipljapyx humberti	1	Female
Diptera	Aedes aegyptii	0	None
Diptera	Anabremia inquilina	0	None
Diptera	Anopheles atroparvus	0	None
Diptera	Aphidoletes aphidimyza	0	None
Diptera	Baccha elongata	0	None
Diptera	Baccha obscuripennis	0	None
Diptera	Bradysia impatiens	0	None
Diptera	Calliphora erythrocephala	0	None
Diptera	Chaetorellia acrolophi	0	None
Diptera	Chironomus plumosus	0	None
Diptera	Chironomus tentans	0	None
Diptera	Chironomus tepperi	0	None
Diptera	Chrysomya bezziana	0	None
Diptera	Chrysotoxum cautum	0	None
Diptera	Contarinia nasturtii	0	None

141

Order	Species	Care code	Care
Diptera	Corynoneura scutellata	0	None
Diptera	Cricotopus trifasciatus	0	None
Diptera	Ctenophora guttata	0	None
Diptera	Culex fatigans	0	None
Diptera	Cyzenis albicans	0	None
Diptera	Dacus tryoni	0	None
Diptera	Delia antiqua	0	None
Diptera	Drino munda	0	None
Diptera	Drosophila melanogaster	0	None
Diptera	Erioischia brassicae	0	None
Diptera	Erioptera lutea	0	None
Diptera	Exorista flaviceps	0	None
Diptera	Goniops chrysacoma	1	Female
Diptera	Harmolita tritici	0	None
Diptera	Leschenaultia adusta	0	None
Diptera	Leschenaultia exul	0	None
Diptera	Lucilia cuprina	0	None
Diptera	Lucilia sericata	0	None
Diptera	Merodon equestris	0	None
Diptera	Musca domestica	0	None
Diptera	Platycheirus albimanus	0	None
Diptera	Pseudactaeon curvatus	0	None
Diptera	Pterodonta flavipes	0	None
Diptera	Rhagoletis boycei	3	Male
Diptera	Rhagoletis cerasi	0	None
Diptera	Rhagoletis juglandis	3	Male
Diptera	Rhingia campestris	0	None
Diptera	Rhingia rostrata	0	None
Diptera	Rhipidia maculata	0	None
Diptera	Sciara coprophila	0	None
Diptera	Sepedon neili	0	None
Diptera	Sepedon sphegea	0	None
Diptera	Sericomyia silentis	0	None
Diptera	Simulium pinctipes	0	None
Diptera	Simulium spp	0	None
Diptera	Smittia gracilis	0	None
Diptera	Spurgia esulae	0	None
Diptera	Stomoxys calcitrans	0	None
Diptera	Stomoxys sitiens	0	None
Diptera	Sturmia harrisinae	0	None
Diptera	Sturmia scutellata	0	None
Diptera	Syrphus ribesii	0	None
Diptera	Syrphus vitripennis	0	None
Diptera	Tabanus macer	0	None
Diptera	Tabanus rubidus	0	None
Diptera	Tabanus tenens	0	None
Diptera	Terellia virens	0	None
Diptera	Tipula flavolineata	0	None
Diptera	Tipula luna	0	None
Diptera	Trichopoda pennipes	0	None
Diptera	Urophora affinis	0	None
Diptera	Urophora quadrifasciata	0	None
Diptera	Vermileo vermileo	0	None
Diptera	Voria ruralis	0	None
Diptera	Winthemia fumiferanae	0	None
Embioptera	Anisembia texana	1	Female
Embioptera	Clothoda urichi	1	Female
Embioptera	Embia major	1	Female
Embioptera	Monotylota ramburi	1	Female
Embioptera	Oligotoma ceylonica	1	Female
Embioptera	Oligotoma greeniana	1	Female
Embioptera	Oligotoma humbertiana	1	Female
Embioptera	Oligotoma nigra	1	Female
Ephemeroptera	Baetis pumilus	0	None
Ephemeroptera	Binoculus pennigerus	0	None
Ephemeroptera	Caenis horaria	0	None
Ephemeroptera	Caenis moesta	0	None
Ephemeroptera	Centroptilum luteolum	0	None
Ephemeroptera	Cloeon dipterum	0	None
Ephemeroptera	Cloeon simile	0	None
Ephemeroptera	Ecdyonurus fluminum	0	None
Ephemeroptera	Ecdyonurus helviticus	0	None
Ephemeroptera	Ephemerella ignita	0	None
Ephemeroptera	Ephoron virgo	0	None
Ephemeroptera	Habrophlebia modesta	0	None
Ephemeroptera	Heptagenia lateralis	0	None
Ephemeroptera	Hexagenia limbata	0	None
Ephemeroptera	Leptophlebia vespertina	0	None
Ephemeroptera	Siphlonurus lacustris	0	None
Geophilomorpha	Dicellophilus carniolensis	1	Female
Hemiptera	Abedus herberti	3	Male
Hemiptera	Acanthosoma griseum	1	Female
Hemiptera	Aconophora compressa	1	Female

Order	Species	Care code	Care
Hemiptera	Aconophora femoralis	1	Female
Hemiptera	Aconophora laminata	1	Female
Hemiptera	Aconophora marginata	1	Female
Hemiptera	Aconophora mexicana	1	Female
Hemiptera	Aconophora nigricornis	1	Female
Hemiptera	Aconophora pallescens	1	Female
Hemiptera	Aconophora robusta	1	Female
Hemiptera	Adomerus triguttulus	1	Female
Hemiptera	Aepophilus bonnairei	1	Female
Hemiptera	Aepophilus sp	1	Female
Hemiptera	Agapophyta viridula	0	None
Hemiptera	Alchisme apicalis	1	Female
Hemiptera	Alchisme grossa	1	Female
Hemiptera	Alchisme sp	1	Female
Hemiptera	Alchisme virescens	1	Female
Hemiptera	Aleyrodes singularis	1	Female
Hemiptera	Amblypelta sp	3	Male
Hemiptera	Anthocoris confusus	0	None
Hemiptera	Antiteuchus amplus	0	None
Hemiptera	Antiteuchus innocens	0	None
Hemiptera	Antiteuchus macraspis	1	Female
Hemiptera	Antiteuchus mixtus	1	Female
Hemiptera	Antiteuchus piceus	1	Female
Hemiptera	Antiteuchus sepulcralis	1	Female
Hemiptera	Antiteuchus tripterus	1	Female
Hemiptera	Antiteuchus variolus	1	Female
Hemiptera	Aphis fabae	0	None
Hemiptera	Aphrophora flavipes	0	None
Hemiptera	Aquarius remigis	0	None
Hemiptera	Aradus cinnamomeus	0	None
Hemiptera	Arvelius atropunctatus	0	None
Hemiptera	Aspongopus sp	0	None
Hemiptera	Atopozelus pallens	1	Female
Hemiptera	Augocoris sp	1	Female
Hemiptera	Bagauda lucifugus	3	Male
Hemiptera	Belostoma malkini	3	Male
Hemiptera	Bilimekia broomfieldi	1	Female
Hemiptera	Bilimekia styliformis	1	Female
Hemiptera	Bolbonota aspidistrae	0	None
Hemiptera	Bolbonota sp	0	None
Hemiptera	Brachypelta aterrima	1	Female
Hemiptera	Calloconophora caliginosa	1	Female
Hemiptera	Calloconophora sp	1	Female
Hemiptera	Campylenchia latipes	0	None
Hemiptera	Campylenchia nutans	0	None
Hemiptera	Campylenchia sp	0	None
Hemiptera	Cantao ocellatus	1	Female
Hemiptera	Carbula humerigera	0	None
Hemiptera	Caternaultiella rugosa	1	Female
Hemiptera	Chlorocoris sp	1	Female
Hemiptera	Cimex lectularius	0	None
Hemiptera	Cladonota biclavata	0	None
Hemiptera	Ctenoneurus hochstetteri	1	Female
Hemiptera	Cyclopelta sp	1	Female
Hemiptera	Cymbomorpha sp	0	None
Hemiptera	Darnis partita	0	None
Hemiptera	Deraeocoris nebulosus	0	None
Hemiptera	Dinocoris tripterus	1	Female
Hemiptera	Dysdercus obscuratus	0	None
Hemiptera	Dysdercus ruficollis	0	None
Hemiptera	Edessa sp	1	Female
Hemiptera	Elasmostethus interstinctus	0	None
Hemiptera	Elasmucha dorsalis	1	Female
Hemiptera	Elasmucha fieberi	1	Female
Hemiptera	Elasmucha grisea	1	Female
Hemiptera	Elasmucha putoni	1	Female
Hemiptera	Elasmucha signoreti	1	Female
Hemiptera	Enchenopa bifenestrata	0	None
Hemiptera	Enchenopa caruata	0	None
Hemiptera	Enchenopa ignidorsum	0	None
Hemiptera	Enchenopa sericea	0	None
Hemiptera	Enchophyllum sp	0	None
Hemiptera	Endochus inornatus	0	None
Hemiptera	Erechtia abbreviata	1	Female
Hemiptera	Erechtia gibbosa	1	Female
Hemiptera	Erechtia pruinosa	1	Female
Hemiptera	Erechtia sp	1	Female
Hemiptera	Eumecopus sp	1	Female
Hemiptera	Euphyonarthex phyllostoma	1	Female
Hemiptera	Euschistus heros	0	None
Hemiptera	Eysarcoris inconspicous	0	None
Hemiptera	Gargara citrea	0	None
Hemiptera	Gargara semibrunnea	0	None

Order	Species	Care code	Care
Hemiptera	Geocoris pallens	0	None
Hemiptera	Geocoris punctipes	0	None
Hemiptera	Gerris buenoi	0	None
Hemiptera	Gerris odontogaster	0	None
Hemiptera	Ghilianella sp	1	Female
Hemiptera	Guayaquila emarginata	1	Female
Hemiptera	Guayaquila pallescens	1	Female
Hemiptera	Guayaquila sp	1	Female
Hemiptera	Halyomorpha mista	0	None
Hemiptera	Hotea subfasciata	0	None
Hemiptera	Hypsoprora sp	0	None
Hemiptera	Irantha armipes	0	None
Hemiptera	Kronides incumbens	0	None
Hemiptera	Lecanium nigrofasciatum	1	Female
Hemiptera	Legnotus limbatus	1	Female
Hemiptera	Leioscyta nitida	1	Female
Hemiptera	Leioscyta spiralis	1	Female
Hemiptera	Lethocerus deyrollei	3	Male
Hemiptera	Lethocerus griseus	3	Male
Hemiptera	Lethocerus maximus	3	Male
Hemiptera	Lethocerus mazzai	3	Male
Hemiptera	Lygaeus pandurus	0	None
Hemiptera	Meadorus griseus	1	Female
Hemiptera	Membracis caguetaensis	0	None
Hemiptera	Membracis dorsata	0	None
Hemiptera	Membracis flava	0	None
Hemiptera	Membracis foliata	0	None
Hemiptera	Membracis mexicana	0	None
Hemiptera	Membracis orteguazaensis	0	None
Hemiptera	Membracis tectigera	0	None
Hemiptera	Membracis trimaculata	0	None
Hemiptera	Metcalfiella monogramma	1	Female
Hemiptera	Nabis alternatus	0	None
Hemiptera	Nabis rugosus	0	None
Hemiptera	Neomaskellia bergii	1	Female
Hemiptera	Neomegalotomus parvus	0	None
Hemiptera	Nerthra fuscipes	0	None
Hemiptera	Neuroctenus elongatus	1	Female
Hemiptera	Neuroctenus hochstetteri	1	Female
Hemiptera	Neuroctenus pseudonymus	3	Male
Hemiptera	Neuroctenus simplex	1	Female
Hemiptera	Nezara viridula	0	None
Hemiptera	Notocera sp	0	None
Hemiptera	Nysius huttoni	0	None
Hemiptera	Occamus typicus	1	Female
Hemiptera	Ochropepla inaequalis	1	Female
Hemiptera	Ochropepla sp	1	Female
Hemiptera	Oebalus pognax	0	None
Hemiptera	Oncopeltus fasciatus	0	None
Hemiptera	Orius insidiosus	0	None
Hemiptera	Orius tristicolor	0	None
Hemiptera	Pachycoris fabricii	1	Female
Hemiptera	Pachycoris klugii	1	Female
Hemiptera	Pachycoris stallii	1	Female
Hemiptera	Pachycoris torridus	1	Female
Hemiptera	Panstrongylus geniculatus	0	None
Hemiptera	Parastrachia japonensis	1	Female
Hemiptera	Parastrachia nagaensis	0	None
Hemiptera	Perillus bioculatus	0	None
Hemiptera	Philya sp	0	None
Hemiptera	Phloea paradoxa	1	Female
Hemiptera	Phloea sp	1	Female
Hemiptera	Phloeophana corticata	1	Female
Hemiptera	Phloeophana longirostris	1	Female
Hemiptera	Phloeophana sp	1	Female
Hemiptera	Phyllomorpha laciniata	3	Male
Hemiptera	Physomerus grossipes	1	Female
Hemiptera	Picromerus bidens	0	None
Hemiptera	Piezodorus guildinii	0	None
Hemiptera	Pisilus tipuliformis	1	Female
Hemiptera	Platycotis minax	1	Female
Hemiptera	Platycotis sp	1	Female
Hemiptera	Platycotis tuberculata	1	Female
Hemiptera	Platycotis vittata	1	Female
Hemiptera	Platymeris biguttata	0	None
Hemiptera	Plunentis porosus	3	Male
Hemiptera	Plunentis yurupucu	3	Male
Hemiptera	Podisus maculiventris	0	None
Hemiptera	Podisus modestus	0	None
Hemiptera	Polyglypta dispar	1	Female
Hemiptera	Polyglypta dorsalis	1	Female
Hemiptera	Polyglypta lineata	1	Female
Hemiptera	Porphyrophora polonica	0	None

Order	Species	Care code	Care
Hemiptera	Potnia gladiator	1	Female
Hemiptera	Potnia sp	1	Female
Hemiptera	Procyrta pectoralis	0	None
Hemiptera	Psallus ambiguus	0	None
Hemiptera	Publilia concava	1	Female
Hemiptera	Publilia modesta	1	Female
Hemiptera	Publilia reticulata	1	Female
Hemiptera	Pyrgauchenia brunnea	1	Female
Hemiptera	Pyrgauchenia tristaniopsis	1	Female
Hemiptera	Pyrrhocoris apterus	0	None
Hemiptera	Ramosella thalli	1	Female
Hemiptera	Rhaphidosoma circumvagans	0	None
Hemiptera	Rhinocoris albopilosus	3	Male
Hemiptera	Rhinocoris albopunctatus	3	Male
Hemiptera	Rhinocoris bicolor	0	None
Hemiptera	Rhinocoris carmelita	1	Female
Hemiptera	Rhinocoris fuscipes	0	None
Hemiptera	Rhinocoris marginatus	0	None
Hemiptera	Rhinocoris rapax	0	None
Hemiptera	Rhinocoris segmentarius	0	None
Hemiptera	Rhinocoris tristis	3	Male
Hemiptera	Rhodnius neivai	0	None
Hemiptera	Rhodnius pictipes	0	None
Hemiptera	Rhodnius prolixus	0	None
Hemiptera	Sastragala esakii	1	Female
Hemiptera	Sastragala scutellata	1	Female
Hemiptera	Schizolachnus piniradiatae	0	None
Hemiptera	Scolopocerus uhleri	3	Male
Hemiptera	Scotinophora sp	1	Female
Hemiptera	Sehirus albonotatus	1	Female
Hemiptera	Sehirus bicolor	1	Female
Hemiptera	Sehirus biguttatus	1	Female
Hemiptera	Sehirus cinctus	1	Female
Hemiptera	Sehirus luctuosus	1	Female
Hemiptera	Sehirus niveimarginatus	1	Female
Hemiptera	Sehirus sexmaculatus	1	Female
Hemiptera	Smynthurodes betae	1	Female
Hemiptera	Sphedanolestes signatus	0	None
Hemiptera	Stalotypa fairmairii	1	Female
Hemiptera	Stenolemus arachniphagus	3	Male
Hemiptera	Stictopelta sp	0	None
Hemiptera	Sycanus collaris	0	None
Hemiptera	Tectocoris diophthalmus	1	Female
Hemiptera	Thalia bimaculata	0	None
Hemiptera	Thyanta perditor	0	None
Hemiptera	Triatoma infestans	0	None
Hemiptera	Triatoma maculata	0	None
Hemiptera	Triatoma pallidipennis	0	None
Hemiptera	Trioza erytreae	0	None
Hemiptera	Tritomegas bicolor	1	Female
Hemiptera	Tritropidia sp	1	Female
Hemiptera	Tylopelta sp	0	None
Hemiptera	Umbonia ataliba	1	Female
Hemiptera	Umbonia crassicornis	1	Female
Hemiptera	Umbonia reducta	1	Female
Hemiptera	Umbonia spinosa	1	Female
Hemiptera	Urentius echinus	0	None
Hemiptera	Vanduzea arquata	0	None
Hemiptera	Zelus armillatus	1	Female
Hemiptera	Zelus exsanguis	0	None
Hemiptera	Zelus sp	1	Female
Hymenoptera	Aglaostigma occipitosa	0	None
Hymenoptera	Alloxysta pleuralis	0	None
Hymenoptera	Amblymerus bruchophagi	0	None
Hymenoptera	Ammophila campestris	0	None
Hymenoptera	Ammophila pubescens	0	None
Hymenoptera	Ammophila sabulosa	0	None
Hymenoptera	Anacharis immunis	0	None
Hymenoptera	Anaphes flavipes	0	None
Hymenoptera	Andricus quercusradicis	0	None
Hymenoptera	Angitia fenestralis	0	None
Hymenoptera	Apharaeta genevensis	0	None
Hymenoptera	Aphelinus asychis	0	None
Hymenoptera	Aphelinus mali	0	None
Hymenoptera	Aphelinus semiflavus	0	None
Hymenoptera	Apis mellifera	1	Female
Hymenoptera	Aptesis nigrocincta	0	None
Hymenoptera	Arpactophilus mimi	1	Female
Hymenoptera	Athalia rosae	0	None
Hymenoptera	Aulacidea tragoponis	0	None
Hymenoptera	Austrogorytes bellicosus	0	None
Hymenoptera	Barbotinia oraniensis	0	None
Hymenoptera	Bathyplectes anurus	0	None

Order	Species	Care code	Care
Hymenoptera	Bathyplectes curculionis	0	None
Hymenoptera	Bembecinus antipodum	0	None
Hymenoptera	Bembecinus egens	0	None
Hymenoptera	Bembecinus hirtulus	0	None
Hymenoptera	Bembix mareeba	0	None
Hymenoptera	Bembix promontorii	0	None
Hymenoptera	Brachymeria femorata	0	None
Hymenoptera	Callaspidia sp	0	None
Hymenoptera	Campoplex haywardi	0	None
Hymenoptera	Catolaccus grandis	0	None
Hymenoptera	Cedria paradoxa	1	Female
Hymenoptera	Cephalcia fuscipennis	0	None
Hymenoptera	Cephalonomia gallicola	0	None
Hymenoptera	Cerceris truncata	0	None
Hymenoptera	Clitemnestra plomleyi	0	None
Hymenoptera	Cotesia glomerata	0	None
Hymenoptera	Diadegma insulare	0	None
Hymenoptera	Dielocerus diasi	1	Female
Hymenoptera	Digelasinus diversipes	1	Female
Hymenoptera	Diplolepis rosae	0	None
Hymenoptera	Dirhicnus alboannulatus	0	None
Hymenoptera	Dynatus nigripes	2	Biparental
Hymenoptera	Encarsia formosa	0	None
Hymenoptera	Encarsia inaron	0	None
Hymenoptera	Eretmocerus eremicus	0	None
Hymenoptera	Eriborus terebrans	0	None
Hymenoptera	Eupteromalus nidulans	0	None
Hymenoptera	Eurytoma amygdali	0	None
Hymenoptera	Exeristes roborator	0	None
Hymenoptera	Exoneurella eremophila	0	None
Hymenoptera	Figites sp	0	None
Hymenoptera	Habrocytus cerealellae	0	None
Hymenoptera	Halictus marginatus	1	Female
Hymenoptera	Helorus paradoxus	0	None
Hymenoptera	Hoplocampa crataegi	0	None
Hymenoptera	Hyposoter disparis	0	None
Hymenoptera	Ibalia rufipes	0	None
Hymenoptera	Isocolus lichtensteini	0	None
Hymenoptera	Kapala terminalis	0	None
Hymenoptera	Kleidotoma dolichocera	0	None
Hymenoptera	Leptopilina boulardi	0	None
Hymenoptera	Lysiphlebus testaceipes	0	None
Hymenoptera	Megalopta genalis	1	Female
Hymenoptera	Melittobia acasta	0	None
Hymenoptera	Melittobia australica	0	None
Hymenoptera	Melittobia clavicornis	0	None
Hymenoptera	Melittobia digitata	0	None
Hymenoptera	Mesoleius tenthredinis	0	None
Hymenoptera	Metaphycus alberti	0	None
Hymenoptera	Microstigmus comes	1	Female
Hymenoptera	Mischnocyttarus mexicanus	1	Female
Hymenoptera	Moniaecera asperata	0	None
Hymenoptera	Muscidifurax raptor	0	None
Hymenoptera	Nealiolus curculionis	0	None
Hymenoptera	Neralsia sp	0	None
Hymenoptera	Nythobia insularis	0	None
Hymenoptera	Ooencyrtus kuwanai	0	None
Hymenoptera	Osmia papaveris	0	None
Hymenoptera	Osmia rufa	0	None
Hymenoptera	Pamphilus betulae	0	None
Hymenoptera	Pamphilus latifrons	0	None
Hymenoptera	Parnips nigripes	0	None
Hymenoptera	Pediobius foveolatus	0	None
Hymenoptera	Perga affinis	1	Female
Hymenoptera	Perga lewisi	1	Female
Hymenoptera	Periclistus brandtii	0	None
Hymenoptera	Peristenus digoneutis	0	None
Hymenoptera	Phaenoglyphis viliosa	0	None
Hymenoptera	Phaeogenes nigridens	0	None
Hymenoptera	Phanurus beneficiens	0	None
Hymenoptera	Philanthus triangulum	0	None
Hymenoptera	Pholetesor ornigis	0	None
Hymenoptera	Pison spinolae	0	None
Hymenoptera	Podagritus parrotti	0	None
Hymenoptera	Pristocera rufa	1	Female
Hymenoptera	Prosaspicera sp	0	None
Hymenoptera	Prosierola bicarinata	1	Female
Hymenoptera	Prospaltella perniciosa	0	None
Hymenoptera	Psenulus concolor	0	None
Hymenoptera	Psenulus interstitialis	0	None
Hymenoptera	Sceliphron assimile	0	None
Hymenoptera	Sceliphron laetum	0	None
Hymenoptera	Scolia manilae	0	None

Order	Species	Care code	Care
Hymenoptera	Sphecius pectoralis	0	None
Hymenoptera	Sphecius speciosus	0	None
Hymenoptera	Stilbula cynipiformis	0	None
Hymenoptera	Synergus albipes	0	None
Hymenoptera	Thermos olfersii	1	Female
Hymenoptera	Tiphia popilliavora	0	None
Hymenoptera	Trichiocampus viminalis	0	None
Hymenoptera	Trichogramma cacoeciae	0	None
Hymenoptera	Trichogramma embryophagum	0	None
Hymenoptera	Trichogramma evanescens	0	None
Hymenoptera	Trichogramma minutum	0	None
Hymenoptera	Trichogramma ostriniae	0	None
Hymenoptera	Trichogramma semblidis	0	None
Hymenoptera	Trichrysis cyanea	0	None
Hymenoptera	Trigonopsis cameronii	2	Biparental
Hymenoptera	Trissolcus basalis	0	None
Hymenoptera	Trypoxylon attenuatum	0	None
Hymenoptera	Trypoxylon beaumonti	0	None
Hymenoptera	Trypoxylon lactitarse	2	Biparental
Hymenoptera	Trypoxylon palliditarse	0	None
Hymenoptera	Trypoxylon politum	2	Biparental
Hymenoptera	Trypoxylon rogenhoferi	2	Biparental
Hymenoptera	Trypoxylon subimpressum	2	Biparental
Hymenoptera	Trypoxylon superbum	2	Biparental
Hymenoptera	Trypoxylon tenoctitlan	2	Biparental
Hymenoptera	Trypoxylon xanthandrum	2	Biparental
Hymenoptera	Xestophanes potentillae	0	None
Hymenoptera	Xyalaspis sp	0	None
Hymenoptera	Xyalophora sp	0	None
Isoptera	Kalotermes flavicollis	2	Biparental
Isoptera	Zootermopsis nevadensis	2	Biparental
Lepidoptera	Actebia fennica	0	None
Lepidoptera	Aegeria pictipes	0	None
Lepidoptera	Aglia tau	0	None
Lepidoptera	Agrotis repleta	0	None
Lepidoptera	Agrotis segetum	0	None
Lepidoptera	Anagasta kuhniella	0	None
Lepidoptera	Antheraea pernyi	0	None
Lepidoptera	Antheraea yamamai	0	None
Lepidoptera	Archips rosanus	0	None
Lepidoptera	Azygophleps scalaris	0	None
Lepidoptera	Bombyx mori	0	None
Lepidoptera	Caligula lindia	0	None
Lepidoptera	Calophasia lunula	0	None
Lepidoptera	Celama sorghiella	0	None
Lepidoptera	Chamaesphecia hungarica	0	None
Lepidoptera	Chilo auricilia	0	None
Lepidoptera	Chilo suppresalis	0	None
Lepidoptera	Corcyra cephalonica	0	None
Lepidoptera	Cossus cossus	0	None
Lepidoptera	Crambus laqueatellus	0	None
Lepidoptera	Cryptoblabes gnidiella	0	None
Lepidoptera	Diacrisia virginica	0	None
Lepidoptera	Diatraea lineolata	0	None
Lepidoptera	Diatraea saccharalis	0	None
Lepidoptera	Ectomyelois ceratoniae	0	None
Lepidoptera	Enarmonia formosana	0	None
Lepidoptera	Epiphyas postvittana	0	None
Lepidoptera	Eteobalea intermediella	0	None
Lepidoptera	Eteobalea serratella	0	None
Lepidoptera	Etiella zinckenella	0	None
Lepidoptera	Eulophonotus myrmeleon	0	None
Lepidoptera	Euproctis chrysorrhoea	0	None
Lepidoptera	Graellsia isabellae	0	None
Lepidoptera	Heliothis armigera	0	None
Lepidoptera	Heliothis zea	0	None
Lepidoptera	Heliothis zeae	0	None
Lepidoptera	Hepialus humuli	0	None
Lepidoptera	Herpystis cuscutae	0	None
Lepidoptera	Hyles euphorbiae	0	None
Lepidoptera	Hypolimnas anomala	1	Female
Lepidoptera	Hypolimnas antilope	1	Female
Lepidoptera	Laphygma frugiperda	0	None
Lepidoptera	Lithophane laticinerea	0	None
Lepidoptera	Lymantria ampla	0	None
Lepidoptera	Lymantria dispar	0	None
Lepidoptera	Malacosoma disstria	0	None
Lepidoptera	Margaronia unionalis	0	None
Lepidoptera	Metzneria paucipunctella	0	None
Lepidoptera	Neoris huttoni	0	None
Lepidoptera	Nomophila noctuella	0	None
Lepidoptera	Oiketicus kirbyi	0	None
Lepidoptera	Orgyia postica	0	None

Order	Species	Care code	Care
Lepidoptera	Orthosia hibisci	0	None
Lepidoptera	Othreis materna	0	None
Lepidoptera	Oxycanus cervinata	0	None
Lepidoptera	Pammene juliana	0	None
Lepidoptera	Pandemis ribeana	0	None
Lepidoptera	Papilio demoleus	0	None
Lepidoptera	Papilio polyxenes	0	None
Lepidoptera	Pelochrista medullana	0	None
Lepidoptera	Perisomena caecigena	0	None
Lepidoptera	Phalera bucephala	0	None
Lepidoptera	Phthorimaea operculella	0	None
Lepidoptera	Pieris napi	0	None
Lepidoptera	Pieris rapae	0	None
Lepidoptera	Plodia interpunctella	0	None
Lepidoptera	Polygonia c-album	0	None
Lepidoptera	Protoparce maculata	0	None
Lepidoptera	Protoparce sexta	0	None
Lepidoptera	Pterolonche inspersa	0	None
Lepidoptera	Quinta cannae	0	None
Lepidoptera	Samia cynthia	0	None
Lepidoptera	Saturnia atlantica	0	None
Lepidoptera	Saturnia cephalariae	0	None
Lepidoptera	Saturnia pavonia	0	None
Lepidoptera	Saturnia pavoniella	0	None
Lepidoptera	Saturnia pyri	0	None
Lepidoptera	Saturnia spini	0	None
Lepidoptera	Spilonota ocellana	0	None
Lepidoptera	Stilpnotia salicis	0	None
Lepidoptera	Thaumetopoea processionea	0	None
Lepidoptera	Tineola bisselliella	0	None
Lepidoptera	Tiracola plagiata	0	None
Lepidoptera	Trichoplusia ni	0	None
Lepidoptera	Vitula edmandsii	0	None
Lepidoptera	Zeuzera coffeae	0	None
Lepidoptera	Zeuzera pyrina	0	None
Mecoptera	Boreus sp	0	None
Mecoptera	Hylobittacus apicalis	0	None
Mecoptera	Panorpa helena	0	None
Mecoptera	Panorpa pryeri	0	None
Megaloptera	Sialis lutaria	0	None
Neuroptera	Chrysopa formosana	0	None
Neuroptera	Chrysopa madestes	0	None
Neuroptera	Chrysopa oculata	0	None
Neuroptera	Chrysopa perla	0	None
Neuroptera	Chrysopa plorabunda	0	None
Neuroptera	Chrysopa rufilabris	0	None
Neuroptera	Chrysoperla carnea	0	None
Neuroptera	Climaciella brunnea	0	None
Neuroptera	Hemerobius humuli	0	None
Neuroptera	Hemerobius stigma	0	None
Neuroptera	Mantispa interrupta	0	None
Neuroptera	Symperobius amicus	0	None
Odonata	Gomphus externus	0	None
Odonata	Megaloprepus coerulatus	0	None
Odonata	Platycnemis pennipes	0	None
Orthoptera	Acheta domesticus	0	None
Orthoptera	Aeropus sibericus	0	None
Orthoptera	Anurogryllus arboreus	1	Female
Orthoptera	Anurogryllus muticus	1	Female
Orthoptera	Brachytrupes achatinus	1	Female
Orthoptera	Conocephalus ensiferum	0	None
Orthoptera	Conocephalus fuscus	0	None
Orthoptera	Conocephalus saltator	0	None
Orthoptera	Euthypoda acutipennis	0	None
Orthoptera	Gryllodes sigillatus	0	None
Orthoptera	Gryllotalpa africana	1	Female
Orthoptera	Gryllotalpa gryllotalpa	1	Female
Orthoptera	Gryllotalpa hexadactyla	1	Female
Orthoptera	Gryllulus domesticus	0	None
Orthoptera	Gryllus campestris	0	None
Orthoptera	Gymnogryllus humeralis	0	None
Orthoptera	Isophya pyrenaea	0	None
Orthoptera	Locusta migratoria	0	None
Orthoptera	Locusta migratorioides	0	None
Orthoptera	Locustana pardalina	0	None
Orthoptera	Miogryllus lineatus	0	None
Orthoptera	Nemobius sylvestris	0	None
Orthoptera	Nomadacris septemfasciata	0	None
Orthoptera	Phaneroptera pistillata	0	None
Orthoptera	Scapsipedus aspersus	0	None
Orthoptera	Schistocerca gregaria	0	None
Orthoptera	Tachycines asynomorus	0	None
Orthoptera	Tettigonia viridissima	0	None

Order	Species	Care code	Care
Orthoptera	Tridactylus apicalis	0	None
Phthiraptera	Haematopinus eurysternus	0	None
Phthiraptera	Pediculus humanus	0	None
Phthiraptera	Phthirus pubis	0	None
Phthiraptera	Trichodectes canis	0	None
Phthiraptera	Trichodectes scalaris	0	None
Plecoptera	Dinocras cephalotes	0	None
Plecoptera	Perlodes mortoni	0	None
Polyzoniida	Bacillozonium nodulosum	3	Male
Polyzoniida	Brachycybe lecontei	3	Male
Polyzoniida	Brachycybe producta	3	Male
Polyzoniida	Brachycybe rosea	3	Male
Psocoptera	Liposcelis bostrychophilus	0	None
Psocoptera	Liposcelis divergens	0	None
Psocoptera	Liposcelis granicola	0	None
Psocoptera	Peripsocus nitens	1	Female
Psocoptera	Peripsocus quadrifasciatus	0	None
Scolopendrida	Otostigmus scabricauda	0	None
Scolopendrida	Scolopendra heros	1	Female
Siphonaptera	Ctenocephalides felis	0	None
Siphonaptera	Hystrichopsylla dippiei	0	None
Siphonaptera	Nosopsyllus fasciatus	0	None
Siphonaptera	Pulex irritans	0	None
Thysanoptera	Bactridothrips brevitubus	0	None
Thysanoptera	Dunatothrips aneurae	2	Biparental
Thysanoptera	Elaphrothrips tuberculatus	2	Biparental
Thysanoptera	Frankliniella occidentalis	0	None
Thysanoptera	Frankliniella schultzei	0	None
Thysanoptera	Frankliniella tenuicornis	0	None
Thysanoptera	Hercinothrips femoralis	0	None
Thysanoptera	Hoplothrips karnyi	3	Male
Thysanoptera	Idolothrips sp	3	Male
Thysanoptera	Sporothrips sp	3	Male
Thysanoptera	Suocerathrips linguis	2	Biparental
Thysanoptera	Tiarothrips subramanii	2	Biparental
Thysanura	Lepisma saccharina	0	None
Thysanura	Thermobia domestica	0	None
Trichoptera	Athripsodes cinereus	0	None
Trichoptera	Athripsodes senilis	0	None
Trichoptera	Bereodes minuta	0	None
Trichoptera	Brachycentrus subnubilus	0	None
Trichoptera	Drusus annulatus	0	None
Trichoptera	Hydropsyche angustipennis	0	None
Trichoptera	Limnephilus flavicornis	0	None
Trichoptera	Limnephilus lunatus	0	None
Trichoptera	Mystacides longicornis	0	None
Trichoptera	Notidobia ciliaris	0	None
Trichoptera	Oecetis lacustris	0	None
Trichoptera	Phryganaea grandis	0	None
Trichoptera	Potamophylax stellatus	0	None

Table B2. List of species used in phylogenetic-comparative analysis (see chapter 3). References are available from the author on request.

Order	Family	Species	Dry weight (g)	Lifetime fecundity (eggs)	Survival in field (%)
Coleoptera	Anobiidae	Anobium punctatum	1.43	55	
Coleoptera	Bruchidae	Acanthoscelides obtectus	5.65	68	
Coleoptera	Buprestidae	Capnodis tenebrionis	234.52	279	
Coleoptera	Buprestidae	Coraebus rubi	33.16	56	
Coleoptera	Byturidae	Byturus tomentosus	5.90	83.5	
Coleoptera	Carabidae	Calosoma sycophanta	305.90	1959	
Coleoptera	Carabidae	Lebia grandis	21.58	1300	
Coleoptera	Cerambycidae	Oberia erythrocephala	20.48	40	
Coleoptera	Chrysomelidae	Ambrostoma quadriimpressum	53.93	500	
Coleoptera	Chrysomelidae	Galerucella calmariensis	5.65	350	
Coleoptera	Chrysomelidae	Galerucella pusilla	4.76	350	
Coleoptera	Chrysomelidae	Gonioctena japonica	21.51	40.6	
Coleoptera	Chrysomelidae	Gonioctena olivacea	16.91	600	2.88
Coleoptera	Chrysomelidae	Leptinotarsa decemlineata	49.63	1000	30.87
Coleoptera	Cleridae	Necrobia rufipes	8.05	89.59	
Coleoptera	Coccinellidae	Adalia bipunctata	7.51	537	
Coleoptera	Coccinellidae	Chilocorus nigritus	5.79	289.5	
Coleoptera	Coccinellidae	Coccinella septempunctata	26.38	700	9.2
Coleoptera	Coccinellidae	Coleomegilla maculata	3.44	600	7
Coleoptera	Coccinellidae	Cryptolaemus montrouzieri	1.07	439	
Coleoptera	Coccinellidae	Exochomus flavipes	7.26	137	
Coleoptera	Coccinellidae	Harmonia axyridis	27.17	560.5	
Coleoptera	Coccinellidae	Hippodamia convergens	3.44	221	
Coleoptera	Coccinellidae	Leis conformis	17.03	904	
Coleoptera	Coccinellidae	Rodolia cardinalis	0.89	165	
Coleoptera	Curculionidae	Anthonomus pomorum	4.62	53	
Coleoptera	Curculionidae	Cyphocleonus achates	76.49	65	
Coleoptera	Curculionidae	Gymnetron antirrhini	2.89	54	
Coleoptera	Curculionidae	Gymnetron netum	4.37	45	
Coleoptera	Curculionidae	Hylobius transversovittatus	37.39	200	
Coleoptera	Curculionidae	Hypera nigrirostris	4.37	83	
Coleoptera	Curculionidae	Neochetina bruchi	8.62	200	
Coleoptera	Curculionidae	Neochetina eichhorniae	11.98	200	
Coleoptera	Curculionidae	Oxyops vitiosa	38.42	470	
Coleoptera	Curculionidae	Phytonomus meles	7.88	252	
Coleoptera	Curculionidae	Rhinocyllus conicus	14.29	150	
Coleoptera	Curculionidae	Sitophilus granarius	3.44	231	
Coleoptera	Curculionidae	Sitophilus oryzae	3.57	62	
Coleoptera	Curculionidae	Trichosirocalus horridus	16.02	800	
Coleoptera	Dermestidae	Anthrenus museorum	2.69	22	
Coleoptera	Dermestidae	Anthrenus verbasci	2.94	60	
Coleoptera	Dermestidae	Attagenus pellio	9.85	50	
Coleoptera	Dermestidae	Attagenus piceus	8.62	83	
Coleoptera	Dermestidae	Dermestes lardarius	19.77	138	
Coleoptera	Dermestidae	Trogoderma granarium	1.88	40	
Coleoptera	Dermestidae	Trogoderma versicolor	8.74	108.5	
Coleoptera	Derodontidae	Laricobius erichsonii	0.71	50	
Coleoptera	Drilidae	Drilus flavescens	5.76	475	
Coleoptera	Dytiscidae	Dytiscus marginalis	469.20	1000	
Coleoptera	Elateridae	Agriotes mancus	15.59	105	
Coleoptera	Elateridae	Melanotus longulus	46.05	173	
Coleoptera	Lampyridae	Lamprophorus tenebrosus	42.76	66	
Coleoptera	Lyctidae	Lyctus brunneus	4.03	17	
Coleoptera	Lyctidae	Lyctus linearis	1.94	15	
Coleoptera	Nitidulidae	Carpophilus hemipterus	2.86	1071	
Coleoptera	Nitidulidae	Carpophilus humeralis	4.83	882	
Coleoptera	Nitidulidae	Carpophilus obsoletus	0.72	80	
Coleoptera	Ptinidae	Ptinus fur	3.13	38.6	
Coleoptera	Ptinidae	Ptinus sexpunctatus	6.54	21	
Coleoptera	Rhipiceridae	Macrosiagon tricuspidata	26.26	550	
Coleoptera	Scarabaeidae	Amphimallon caucasium	82.89	18	
Coleoptera	Scarabaeidae	Amphimallon majalis	71.70	22	
Coleoptera	Scarabaeidae	Anomala horticola	36.84	17.7	
Coleoptera	Scarabaeidae	Aphodius ater	2.69	48	
Coleoptera	Scarabaeidae	Bubas bison	223.78	60	
Coleoptera	Scarabaeidae	Cephalodesmius armiger	42.02	5	
Coleoptera	Scarabaeidae	Copris diversus	463.00	3.5	76
Coleoptera	Scarabaeidae	Copris incertus	53.74	11	76
Coleoptera	Scarabaeidae	Copris remotus	40.79	41	
Coleoptera	Scarabaeidae	Eurysternus marmoreus	56.60	10	75
Coleoptera	Scarabaeidae	Melolontha melolontha	346.04	19	
Coleoptera	Scarabaeidae	Onitis belial	453.52	20	
Coleoptera	Scolytidae	Ips pini	6.47	146	
Coleoptera	Scolytidae	Scolytus rugulosus	1.92	55	
Coleoptera	Scolytidae	Xyleborus germanus	2.25	35	
Coleoptera	Silphidae	Phosphuga atrata	103.80	159	
Coleoptera	Staphylinidae	Aleochara bilineata	3.44	700	
Coleoptera	Staphylinidae	Tachyporus hypnorum	5.74	94.6	
Coleoptera	Tenebrionidae	Bolitotherus cornutus	61.18	10.5	
Coleoptera	Tenebrionidae	Tenebrio molitor	55.49	276	

Order	Family	Species	Dry weight (g)	Lifetime fecundity (eggs)	Survival in field (%)
Coleoptera	Tenebrionidae	Tenebrio obscurus	63.66	463	
Coleoptera	Tenebrionidae	Tribolium castaneum	3.28	360	
Coleoptera	Trogositidae	Tenebroides mauritanicus	17.45	1190	
Dermaptera	Anisolabididae	Euboriella annulipes	20.91	52.7	
Dermaptera	Forficulidae	Anechura bipunctata	22.14	55	
Dermaptera	Forficulidae	Chelidurella acanthopygia	5.93	55	
Dermaptera	Forficulidae	Forficula auricularia	18.14	40	
Dermaptera	Labiduridae	Labidura riparia	73.17	440	
Dictyoptera	Blaberidae	Diploptera punctata	75.44	29	
Dictyoptera	Blaberidae	Nauphoeta cinerea	100.25	193	
Dictyoptera	Blaberidae	Pycnoscelus surinamensis	66.88	70	
Dictyoptera	Blattellidae	Blattella germanica	22.62	242	
Dictyoptera	Blattidae	Eurycotis floridana	672.51	104	
Dictyoptera	Blattidae	Periplaneta australasiae	187.55	180	
Dictyoptera	Cryptocercidae	Cryptocercus punctulatus	164.51	73	49
Dictyoptera	Mantidae	Mantis religiosa	441.52	1100	
Dictyoptera	Phasmatidae	Didymuria violescens	410.00	357	
Dictyoptera	Phasmatidae	Extatosoma tiaratum	4966.64	1011	
Dictyoptera	Phasmatidae	Phyllium bioculatum	530.56	92.5	
Dictyoptera	Phasmatidae	Podacanthus typhon	1447.48	428	
Dictyoptera	Phasmatidae	Tropidoderus childreni	1662.94	468	
Diptera	Calliphoridae	Calliphora erythrocephala	21.88	2500	
Diptera	Calliphoridae	Chrysomya bezziana	11.30	175	
Diptera	Calliphoridae	Lucilia cuprina	14.66	1000	
Diptera	Calliphoridae	Lucilia sericata	14.66	151	28.7
Diptera	Cecidomyiidae	Aphidoletes aphidimyza	0.45	70	
Diptera	Cecidomyiidae	Spurgia esulae	0.28	140	
Diptera	Chironomidae	Chironomus plumosus	3.31	1750	
Diptera	Chironomidae	Chironomus tentans	9.75	2350	
Diptera	Chironomidae	Corynoneura scutellata	0.11	22	
Diptera	Chironomidae	Cricotopus trifasciatus	1.01	350	
Diptera	Muscidae	Delia antiqua	3.90	123	
Diptera	Muscidae	Erioischia brassicae	3.76	115	2.95
Diptera	Muscidae	Musca domestica	6.53	2387	
Diptera	Muscidae	Stomoxys calcitrans	10.22	147.5	
Diptera	Sciomyzidae	Sepedon sphegea	9.30	274	
Diptera	Simuliidae	Simulium spp	2.84	350	
Diptera	Syrphidae	Rhingia campestris	6.17	156.5	
Diptera	Tabanidae	Tabanus macer	10.50	250	
Diptera	Tabanidae	Tabanus rubidus	31.24	600	
Diptera	Tachinidae	Cyzenis albicans	3.89	1373	
Diptera	Tachinidae	Voria ruralis	8.36	169	
Diptera	Tephritidae	Chaetorellia acrolophi	0.85	69	
Diptera	Tephritidae	Terellia virens	1.03	80	
Diptera	Tipulidae	Erioptera lutea	1.16	105	
Diptera	Tipulidae	Tipula flavolineata	26.04	369	
Diptera	Trypetidae	Rhagoletis juglandis	1.91	126	59
Embioptera	Embiidae	Monotylota ramburi	1.54	80	
Embioptera	Oligotomidae	Oligotoma nigra	1.04	220	
Ephemeroptera	Baetidae	Baetis pumilus	2.82	1104.5	
Ephemeroptera	Baetidae	Centroptilum luteolum	2.66	1236.5	
Ephemeroptera	Baetidae	Cloeon dipterum	3.30	904	
Ephemeroptera	Baetidae	Cloeon simile	7.13	2896.5	
Ephemeroptera	Caenidae	Caenis horaria	1.05	556	
Ephemeroptera	Caenidae	Caenis moesta	1.58	934	
Ephemeroptera	Ephemerellidae	Ephemerella ignita	1.42	1006.5	
Ephemeroptera	Ephemeridae	Hexagenia limbata	18.90	4000	
Ephemeroptera	Heptageniidae	Ecdyonurus fluminum	4.72	1798.5	
Ephemeroptera	Heptageniidae	Ecdyonurus helviticus	2.31	4222.5	
Ephemeroptera	Heptageniidae	Heptagenia lateralis	3.66	2014	
Ephemeroptera	Leptophlebiidae	Habrophlebia modesta	1.51	1628	
Ephemeroptera	Leptophlebiidae	Leptophlebia vespertina	3.41	1314	
Ephemeroptera	Polymitarcidae	Ephoron virgo	5.42	750	
Ephemeroptera	Siphlonuridae	Siphlonurus lacustris	7.48	2105.5	
Hemiptera	Acanthosomatidae	Elasmostethus interstinctus	11.98	200	
Hemiptera	Acanthosomatidae	Elasmucha grisea	7.99	45	
Hemiptera	Acanthosomatidae	Elasmucha putoni	25.72	49.9	
Hemiptera	Acanthosomatidae	Elasmucha signoreti	5.19	33.79	
Hemiptera	Anthocoridae	Anthocoris confusus	0.91	48.8	
Hemiptera	Anthocoridae	Cimex lectularius	2.35	541	
Hemiptera	Anthocoridae	Orius insidiosus	0.12	129	
Hemiptera	Anthocoridae	Orius tristicolor	0.14	129	
Hemiptera	Jassidae	Acinopterus angulatus	2.76	188	
Hemiptera	Lygaeidae	Geocoris punctipes	1.28	178	
Hemiptera	Lygaeidae	Nysius huttoni	0.59	87.5	
Hemiptera	Lygaeidae	Oncopeltus fasciatus	6.63	849	
Hemiptera	Membracidae	Publilia concava	3.40	145	
Hemiptera	Membracidae	Thalia bimaculata	35.86	28	
Hemiptera	Membracidae	Umbonia crassicornis	46.50	32.5	38
Hemiptera	Miridae	Deraeocoris nebulosus	1.32	240	
Hemiptera	Miridae	Psallus ambiguus	1.65	34	
Hemiptera	Pentatomidae	Nezara viridula	87.28	907	38.2
Hemiptera	Pentatomidae	Podisus maculiventris	18.81	300	

Order	Family	Species	Dry weight (g)	Lifetime fecundity (eggs)	Survival in field (%)
Hemiptera	Reduviidae	Endochus inornatus	37.24	90.7	
Hemiptera	Reduviidae	Irantha armipes	6.43	30.6	
Hemiptera	Reduviidae	Panstrongylus geniculatus	131.54	61.6	76
Hemiptera	Reduviidae	Rhinocoris fuscipes	22.11	340	
Hemiptera	Reduviidae	Rhinocoris marginatus	47.45	154.7	
Hemiptera	Reduviidae	Rhodnius neivai	67.11	885.5	
Hemiptera	Reduviidae	Sphedanolestes signatus	5.38	41	
Hemiptera	Reduviidae	Sycanus collaris	67.63	229	
Hemiptera	Reduviidae	Triatoma infestans	215.97	150	
Hemiptera	Reduviidae	Triatoma maculata	215.97	502	
Hemiptera	Reduviidae	Triatoma pallidipennis	215.97	499	24
Hemiptera	Scutelleridae	Pachycoris klugii	72.93	81	
Hemiptera	Tingidae	Corythucha ciliata	0.42	166	31
Hemiptera	Tingidae	Corythucha marmorata	0.23	136.7	20
Hemiptera	Tingidae	Corythucha pruni	0.53	160.7	33
Hemiptera	Tingidae	Gargaphia solani	0.65	127.8	23
Hemiptera	Tingidae	Urentius echinus	0.78	74	
Hymenoptera	Aphelinidae	Encarsia inaron	0.01	129	
Hymenoptera	Argidae	Dielocerus diasi	59.06	75	
Hymenoptera	Argidae	Digelasinus diversipes	50.92	75	
Hymenoptera	Argidae	Thermos olfersii	77.04	27	
Hymenoptera	Bethylidae	Pristocera rufa	1.95	21.5	
Hymenoptera	Braconidae	Apanteles melanoscelus	0.40	1000	
Hymenoptera	Braconidae	Apharaeta genevensis	0.15	175	
Hymenoptera	Braconidae	Cotesia glomerata	0.15	175	
Hymenoptera	Braconidae	Pholetesor ornigis	0.08	370	
Hymenoptera	Cynipidae	Diplolepis rosae	0.33	408	
Hymenoptera	Cynipidae	Periclistus brandtii	0.04	73	
Hymenoptera	Cynipidae	Synergus albipes	0.10	35	
Hymenoptera	Cynipidae	Xestophanes potentillae	0.03	88	
Hymenoptera	Figitidae	Anacharis immunis	0.03	20	
Hymenoptera	Figitidae	Callaspidia sp	0.72	20	
Hymenoptera	Figitidae	Figites sp	0.23	90	
Hymenoptera	Figitidae	Phaenoglyphis viliosa	0.03	80	
Hymenoptera	Ichneumonidae	Angitia fenestralis	1.43	540	
Hymenoptera	Ichneumonidae	Aptesis nigrocincta	3.54	20.2	
Hymenoptera	Ichneumonidae	Bathyplectes curculionis	1.23	200	
Hymenoptera	Ichneumonidae	Campoplex haywardi	1.10	87	
Hymenoptera	Ichneumonidae	Diadegma insulare	0.18	150	
Hymenoptera	Mymaridae	Anaphes flavipes	0.02	20	
Hymenoptera	Pamphilidae	Cephalcia fuscipennis	8.65	23	
Hymenoptera	Pamphilidae	Cephalcia isshikii	63.41	51	
Hymenoptera	Sphecidae	Sceliphron assimile	104.09	20	38.7
Hymenoptera	Sphecidae	Sceliphron laetum	104.09	8	
Hymenoptera	Sphecidae	Trypoxylon palliditarse	50.78	9.5	70.6
Hymenoptera	Tenthredinidae	Athalia rosae	3.87	51	
Hymenoptera	Tenthredinidae	Hoplocampa crataegi	1.78	69	
Hymenoptera	Tenthredinidae	Trichiocampus viminalis	12.03	85	
Hymenoptera	Tiphiidae	Tiphia popilliavora	6.78	36	
Hymenoptera	Trichogrammatidae	Trichogramma cacoeciae	0.01	14	
Hymenoptera	Trichogrammatidae	Trichogramma embryophagum	0.01	2.5	
Hymenoptera	Trichogrammatidae	Trichogramma evanescens	0.00	57	
Hymenoptera	Trichogrammatidae	Trichogramma minutum	0.01	29	
Hymenoptera	Trichogrammatidae	Trichogramma ostriniae	0.01	54	
Hymenoptera	Trichogrammatidae	Trichogramma semblidis	0.01	0.1	
Lepidoptera	Cosmopterygidae	Eteobalea intermediella	10.54	180	
Lepidoptera	Cosmopterygidae	Eteobalea serratella	14.04	180	
Lepidoptera	Cossidae	Cossus cossus	675.91	1000	
Lepidoptera	Cossidae	Zeuzera pyrina	240.82	851	
Lepidoptera	Gelechiidae	Metzneria paucipunctella	4.30	80	
Lepidoptera	Geometridae	Chiasmia clathrata	4.34	325	
Lepidoptera	Gracilariidae	Lithocolletis blancardella	0.07	12	
Lepidoptera	Hepialidae	Hepialus humuli	76.01	600	
Lepidoptera	Lasiocampidae	Malacosoma disstria		183	1.36
Lepidoptera	Lymantriidae	Euproctis chrysorrhoea	27.29	175	
Lepidoptera	Lymantriidae	Lymantria dispar	29.96	680	1.67
Lepidoptera	Lymantriidae	Stilpnotia salicis	89.99	350	
Lepidoptera	Noctuidae	Agrotis segetum	49.92	2788	
Lepidoptera	Noctuidae	Calophasia lunula	41.60	250	
Lepidoptera	Noctuidae	Heliothis armigera	36.90	800	52.77
Lepidoptera	Noctuidae	Heliothis zea	36.90	80	4.5
Lepidoptera	Noctuidae	Trichoplusia ni		507	10.7
Lepidoptera	Notodontidae	Phalera bucephala	208.04	270	
Lepidoptera	Nymphalidae	Hypolimnas anomala		565	61
Lepidoptera	Pieridae	Pieris napi	21.03	362.5	
Lepidoptera	Pieridae	Pieris rapae	23.96	350	10.03
Lepidoptera	Pyralidae	Chilo suppresalis	9.68	85	5.5
Lepidoptera	Pyralidae	Corcyra cephalonica	2.59	116	
Lepidoptera	Pyralidae	Cryptoblabes gnidiella	1.47	150	
Lepidoptera	Pyralidae	Ectomyelois ceratoniae	10.04	125	
Lepidoptera	Pyralidae	Etiella zinckenella	2.27	33	
Lepidoptera	Pyralidae	Margaronia unionalis	14.39	590	
Lepidoptera	Pyralidae	Nomophila noctuella	8.93	258	

Order	Family	Species	Dry weight (g)	Lifetime fecundity (eggs)	Survival in field (%)
Lepidoptera	Pyralidae	Plodia interpunctella	3.23	250	
Lepidoptera	Saturniidae	Antheraea yamamai	649.63	114	
Lepidoptera	Saturniidae	Samia cynthia	169.59	400	
Lepidoptera	Sesiidae	Chamaesphecia hungarica	25.62	150	
Lepidoptera	Tineidae	Tineola bisselliella	1.06	80	
Lepidoptera	Tortricidae	Agapeta zoegana	4.18	49.5	
Lepidoptera	Tortricidae	Archips rosanus	2.00	147	
Lepidoptera	Tortricidae	Enarmonia formosana	3.78	49	
Lepidoptera	Tortricidae	Epiphyas postvittana	2.27	309.5926	0.98
Lepidoptera	Tortricidae	Pammene juliana	2.14	180	
Lepidoptera	Tortricidae	Pandemis ribeana	1.47	313	
Lepidoptera	Tortricidae	Pelochrista medullana	9.02	120	
Lepidoptera	Tortricidae	Spilonota ocellana	1.33	180	2.77
Megaloptera	Sialidae	Sialis lutaria	7.96	725	
Neuroptera	Chrysopidae	Chrysopa madestes	3.09	42.5	
Neuroptera	Chrysopidae	Chrysopa oculata	6.61	185	
Neuroptera	Chrysopidae	Chrysopa rufilabris	2.71	31	
Neuroptera	Sympherobiidae	Sympherobius amicus	0.93	250	
Orthoptera	Acrididae	Locusta migratorioides	799.64	497	
Orthoptera	Acrididae	Locustana pardalina	380.59	320	
Orthoptera	Acrididae	Nomadacris septemfasciata	943.76	388	
Orthoptera	Acrididae	Schistocerca gregaria	1016.53	317	
Orthoptera	Gryllidae	Anurogryllus muticus	109.29	22.5	
Orthoptera	Gryllidae	Gryllodes sigillatus	110.22	138	
Orthoptera	Gryllidae	Gryllulus domesticus	116.85	2636	
Orthoptera	Gryllidae	Gryllus campestris	404.21	850	
Orthoptera	Gryllidae	Gymnogryllus humeralis	172.78	285	
Orthoptera	Gryllotalpidae	Gryllotalpa gryllotalpa	809.91	250	
Orthoptera	Tettigoniidae	Conocephalus fuscus	93.90	65	
Orthoptera	Tettigoniidae	Euthypoda acutipennis	595.94	69	
Orthoptera	Tettigoniidae	Isophya pyrenaea	203.85	37.5	
Orthoptera	Tettigoniidae	Tettigonia viridissima	536.26	70	
Phthiraptera	Pediculidae	Pediculus humanus	0.25	250	
Phthiraptera	Phthiridae	Phthirus pubis	0.04	26	
Siphonaptera	Pulicidae	Pulex irritans	0.52	450	
Trichoptera	Leptoceridae	Mystacides longicornis	1.77	237.5	
Trichoptera	Limnephilidae	Drusus annulatus	3.24	240	
Trichoptera	Limnephilidae	Limnephilus flavicornis	18.61	343	
Trichoptera	Limnephilidae	Limnephilus lunatus	14.01	328.5	

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