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Providing care to offspring is a costly, but effective strategy of parents to increase the fitness of their descendants. In insects, parental care has repeatedly evolved in a wide range of taxa. It can take a great diversity of forms, occur at different times during offspring development, last from a few minutes to several years and involve either the mother, the father or both parents. In this chapter, we detail the astounding diversity of parental care in insects. We start by presenting forms of parental care that occur before oviposition, then move to forms occurring between oviposition and egg hatching and conclude with forms of post-hatching parental care occurring before and/or after nutritional independence. This comprehensive review demonstrates overall insects represent a perfect example of the diversity of parental care that can be found in animals, and thus emphasizes why they are excellent biological models for improving our general understanding of its evolution, diversification and underlying physiological and genetic mechanisms.

Parental care, Biparental care, Family life, Cooperation, Conflict, Insects

1 Introduction

Among the multiple strategies that males and females can adopt to ensure the proper development of their offspring, an important one is the expression of parental care. Following Smiseth et al. (2012), parent care is defined as ‘any parental trait that enhances the fitness of a parent’s offspring, and that is likely to have originated and/or is currently maintained for this function’. This broad definition of parental care encompasses behavioural (e.g. egg grooming) as well as non-behavioural (e.g. provisioning of gametes) traits that may be expressed both before and after oviposition but excludes traits whose bearers are individuals other than the parents (e.g. adult siblings). In nature, parental care can take a broad diversity of forms, ranging from egg provisioning and nest construction over brood attendance to food provisioning (Clutton-Brock, 1991; Costa, 2006; Smiseth et al., 2012; Wong et al., 2013). The diverse forms of care can be provided by either the mother, the father, or both parents; they can last from only few minutes to several years; and can range from mildly beneficial to absolutely essential for offspring survival (Klug et al., 2012; Trumbo, 2012; Kramer and Meunier, 2019).

Regardless of its form, parental care often has a profound impact on the fitness of both offspring and parents. On one hand, parental care is beneficial to offspring, as it can improve their quality and increase their survival by neutralizing environmental hazards (Alonso-Alvarez & Velando, 2012; Klug & Bonsall, 2014). On the other hand, investing into parental care often comes with costs to parents. This is because its expression negatively impacts the condition and survival of the tending parents (due to an increased energy loss or elevated risk of predation), and thus reduces their lifetime reproductive success (Trivers, 1972; Alonso-Alvarez & Velando, 2012). Moreover, parental care can entail consequential costs to both parents and offspring that may arise from evolutionary conflicts of interest among the family members over the expression of parental care (Parker et al., 2002; Royle et al., 2004). Because of relatedness asymmetries among the family members, offspring often behave more selfishly than their parents desire, both by trying to manipulate their parents into increasing their parental investment (parent-offspring conflict; Trivers 1974; Kilner and Hinde 2012; Kölliker et al. 2015), and by trying to monopolize limited parental resources at the expense of their (current or future) siblings (sibling rivalry; Mock and Parker 1997; Roulin and Dreiss 2012). For the same reason, one parent might often try to reduce its parental effort at the other parent’s expense (sexual conflict; Trivers 1972; Lessells 2012). Investigating the conditions that allow parents to gain sufficient benefits to offset these costs of parental care (Hamilton, 1964; Smiseth et al., 2012) has thus long been considered of key importance to improve our general understanding of its evolution as a reproductive strategy in animals (Clutton-Brock, 1991; Gross, 2005; Kramer and Meunier, 2019).

Even though not as ubiquitous as in mammals and birds, parental care occurs in many insect taxa. In the vast majority of cases, these examples describe pre-ovipositional traits, with less than 5% of known genera exhibiting post-ovipositional care behaviours (Table 1). For instance, post-ovipositional parental care can be found in 78.9% and 21.7% of the Strepsiptera and Blattodea genera (not taking into account eusocial species), respectively, whereas it has never been reported in seven insect orders (Grylloblattidae,

Mantophasmatodea, Mecoptera, Neuroptera, Phasmatodea, Siphonaptera and Zoraptera; Table 1; Machado and Trumbo 2018). These numbers, however, need to be taken with caution. Insect orders encompass very different numbers of genera and species, and the biology of a vast majority of these species remains poorly known (Footitt and Adler, 2018). This notwithstanding, the most common forms of post-ovipositional parental care in insects are internal egg carrying, as well as egg and offspring attendance (Machado and Trumbo, 2018).

In this book chapter, we aim to give an introduction to parental care as a reproductive strategy in insects by providing a broad overview of the different forms of parental care that can be found in insects. We will detail these different traits in the chronological order in which they take effect on offspring during their development (Figure 1). We begin with parental care before oviposition, when parents may select a site to lay their eggs or build a nest to protect the future clutch. Such pre-ovipositional care also includes females adjusting the quantity and nature of substances provisioned to the eggs to enhance the fitness of the resulting offspring. We then move to forms of parental care occurring between oviposition and egg hatching, when parents may guard and/or brood their eggs. We subsequently present forms of post-hatching parental care, when parents may tend, brood or food-provision their juveniles until they reach nutritional independence, and even later. Finally, we discuss the possibility for 'unconventional' forms of parental care and how it calls for further experimental studies exploring their occurrence in insects.

Note that even if eusocial insects such as ants, termites and some bees and wasps exhibit extended family groups with multiple forms of care towards eggs and/or juveniles (Wilson, 1971; Kramer and Meunier, 2019), most of these forms of care are provided by adult offspring (workers). Such alloparental care does not fall under the definition of parental care introduced above. We therefore did not include care provided by individuals other than the parents in this chapter, and refer readers interested in the nature of family interactions in eusocial insects to the existing comprehensive reviews of this topic (Wilson, 1971; Bourke and Franks, 1995; Choe and Crespi, 1997). The few forms of care provided by the parents (mostly queens) of eusocial species to young offspring, i.e. parental care *sensu stricto*, are typically limited to egg provisioning and some forms of nest construction and egg care during colony foundation and fall within the framework outlined below.

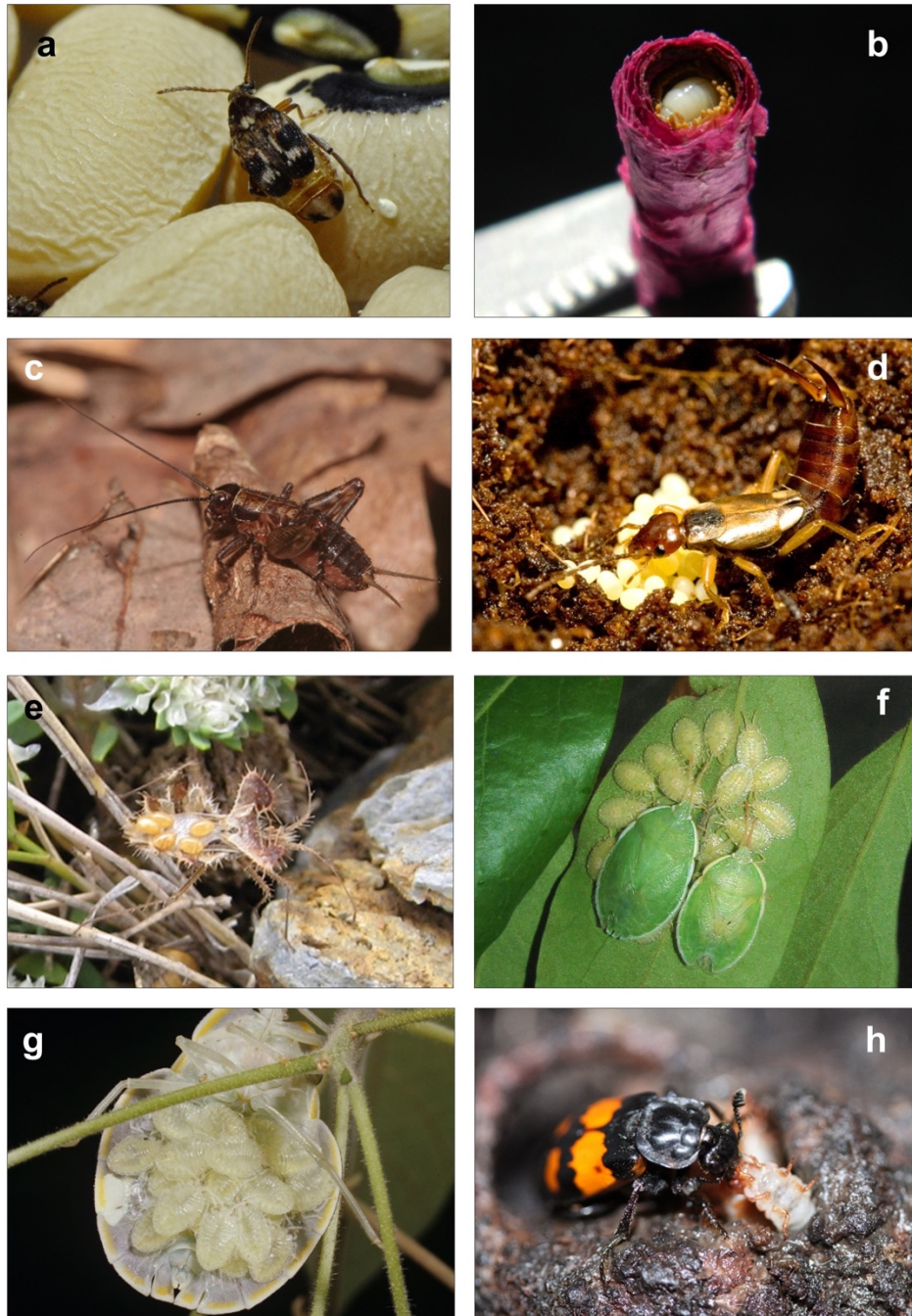


Figure 1 – Examples of the different forms of parental care in insects. (a) Site selection for oviposition in the bean weevil *Callosobruchus maculatus*. A female has laid an egg on a seed (Photo: J. Ritchey). (b) Nest building in the mason bee *Osmia* spp. The nest is built out of flower petals to form a tube – here held with scissors (Photo: A. Mallewick). (c) Egg provisioning in the house cricket *Acheta domesticus*. In this species, mothers adjust the quantity of hormones transferred to their eggs to better fit to their future environment (Photo: S. Pincebourde). (d) Egg attendance in the European earwig *Forficula auricularia*. A female grooms her eggs to remove fungal spores present on its surface (Photo: J. Meunier). (e) Egg brooding in the golden egg bug *Phyllomorpha laciniata*. A male carries conspecific eggs on its back (Photo: D. Carrasco). (f) Offspring attendance in the shield bug *Cumare pallida*. A male and a female guard their nymphs (Photo: G Monteith). (g) Offspring brooding in the shield bug *Peltocopta crassiventris*. A female carrying its nymphs under the abdomen (Photo: J. Wright). (h) Food provisioning in the burying beetle *Nicrophorus vespilloides*. A female regurgitates pre-digested carrion to a begging larva (Photo: P.T. Smiseth).

2 Pre-oviposition Care

2.1 Site Selection for Oviposition

Females can influence the survival and phenotype of their offspring by selecting where to lay their eggs, a process called oviposition-site selection (Refsnider and Janzen, 2010). Across species and taxa, oviposition-site selection can be defined as a form of parental care if it (1) maximizes embryo survival, (2) induces adaptive modifications of offspring phenotype, and/or (3) offers proximity to suitable habitat for the resulting offspring. First, oviposition-site selection can enhance the chances of offspring survival by limiting the risk of egg desiccation or competition with conspecifics after egg hatching. In the bean weevil *Callosobruchus maculatus*, for instance, females avoid laying eggs on beans that already contain conspecific eggs, and thus prevent high levels of within-bean competition that would otherwise increase the development time and mortality of their offspring (Mitchell, 1975). Conversely in the damselfly *Lestes macrostigmata*, females prefer to lay their eggs on plant species growing in the deeper parts of temporary ponds in order to minimize the risk of egg desiccation at the end of the drought season (Lambret et al., 2018). Second, oviposition site selection may lead to adaptive modifications of offspring phenotypes. An example of such modification has been reported in the monarch butterflies *Danaus plexippus*, where mothers infected by the protozoan parasite *Ophryocystis elektroscirrha* improve the resistance of their future offspring against this parasite by selectively laying their eggs on specific food plants (Milkweed species). The resulting offspring therefore only have access to this plant as a food source, and feeding on this plant has been shown to modify offspring physiology in a way that improves their resistance against this parasite (Lefèvre et al., 2012). Finally, oviposition-site selection can favour the proximity of future offspring to a suitable habitat such as one providing direct access to nutrients for growth and development. This is the case in many phytophagous insects, such as the lichenivorous moth *Cleorodes lichenaria* (Pöykkö, 2006). In this species, females prefer host lichens that ensure the shortest developmental period at the expense of higher growth rates at the beginning of the larval period. Similarly, females of the mosquitoes *Culiseta longiareolata* and *Anopheles punctipennis* avoid laying eggs in pools containing predators or competitors of their future larvae (Petranka and Fakhoury, 1991; Spencer et al., 2002; Silberbush and Blaustein, 2011). Finally, this benefit may also involve the production of eggs on or within living animals to allow their future carnivorous offspring to feed on these hosts. Parasitoid wasps are textbook examples of this phenomenon. In these species, females typically evolved an ovipositor (up to 10 cm long, such as in *Megarhyssa macrurus*) to pierce the skin of the host and lay their eggs into its body, or to pierce wood pieces or fruits skins to reach hosts hidden within (Heatwole and Davis, 1965; Vinson, 1976; Elias et al., 2018).

Note that oviposition-site selection may also exclusively favour the survival of the egg-laying mothers and does therefore not necessarily reflect a form of parental care. This is the case in the orange tip butterfly *Anthocharis cardamines*. In this species, females feed extensively on the nectar of the plant they select for oviposition, whereas this plant only has a poor nutritional value – compared to other neighbouring plants – for its larvae (Courtney, 1981). Similarly in the water strider *Aquarius paludum insularis*, females avoid ovipositing in

sites where the backswimmer *Notonecta triguttata*, a predator that only attacks adults, is present (Hirayama and Kasuya, 2013).

2.2 Nest Building

Nests typically serve as a protection against environmental hazards, either of an abiotic source such as (too high or too low) temperature and humidity, or of a biotic source such as predators and pathogenic microbes (Fialho et al., 2018). For instance, in the beewolf *Philanthus triangulum*, females protect their offspring against microbial pathogens by incorporating elements with antipathogenic properties into the nest. To this end, females cultivate *Streptomyces* bacteria in their antenna and apply them to the brood cell prior to oviposition. The bacteria are then taken up by the larva and integrated into the walls of the cocoon where they offer protection against fungal infection and thus enhance larva survival (Kaltenpoth et al., 2005). This protection results from the production of nine antibiotic substances by the bacteria (Kroiss et al., 2010).

A broad diversity of materials can be used by insects to build their nest, such as silk in web spinners and in some bark lice, mud and wax in wasps and bees, and modified plant tissues in the form of galls in some thrips (Machado and Trumbo, 2018). In other species, females directly use unmodified plant parts as nest material. For instance, female mason bees (*Osmia avosetta*) smear the inside of their underground nest with petals from surrounding flowers, probably to safeguard the nest from flooding, as well as to help retaining moisture and thus avoid desiccation (Sedivy et al., 2010). Specifically, the *O. avosetta* female first digs a main tunnel, then brings in large pieces of petals to line the chamber, next carries in fine moist soil to plaster the inner surface of this lining and finally imports new petals to completely line the cell cavity (Sedivy et al., 2010). She then lays a single egg in this chamber, provisions it with a sticky mixture of pollen and nectar and seals the chamber. The use of petals as nest material can also be found in other osmiine bees, such as *Wainia atrorufa*, *W. gessorum* and *W. sexsignata*, where mothers nest in empty snail shells and use petals to partition brood cells within shells (Müller et al., 2018).

Parentally-built nests can exhibit a broad diversity of architectures. The nest can be simple and take the form of a small chamber or tunnel, such as in the necrophagous beetle *Coprophanæus bellicosus* (Fialho et al., 2018) and the European earwig *Forficula auricularia* (Meunier et al., 2012; Diehl and Meunier, 2018). It can also take the form of a silken gallery spun from parental silk glands, such as in the webspinner *Anisembia texana* (Choe, 1994). Conversely, parents can build sophisticated nests, composed of a several chambers dedicated to different functions. In the short tailed cricket *Anurogryllus muticus*, for instance, females built nests with a brood chamber to maintain the eggs and larvae, and a defecation chamber to store feces (West and Alexander, 1963). Note that in some species of ants with independent colony foundation - i.e. where queens found new colonies by themselves - the foundations of the future colony are typically build by the mother (queen) and take the form of a simple nest with only few chambers (Hölldobler and Wilson, 1990). The architecture of the colony then becomes more and more complex when the first adult offspring (workers) take the lead of colony construction.

2.3 Egg Provisioning

Another pre-ovipositional, ancestral form of parental care consists in transferring hormones, energy, nutrients, or other substances into and/or onto the eggs to enhance the fitness of the resulting offspring (Smiseth et al., 2012). Interestingly, many females can vary the nature and amount of the substances they transfer, and such adaptive plasticity in egg provisioning typically facilitates egg development, and helps protecting the eggs against environmental risks such as desiccation, drowning, predation and parasitism (Zeh et al., 1989). In insects, multiple examples of adaptive egg provisioning can be found and reflect responses to future social constraints, food availability and temperature. The level of maternal hormone deposition to eggs reflects social constraints, for instance, in the house cricket *Acheta domesticus*. Mothers of this species provision their eggs with lower doses of ecdysteroid hormones when they are reared under high (as compared to low) social density. This has been suggested to be an adaptive strategy, as it allows mothers to program the production of slow-growing hatchlings (which is often associated with a reduced metabolic budget) in environments with high levels of resource competition, and therefore to enhance the likelihood of offspring survival (Crocker and Hunter, 2018). On the other hand, egg provisioning in the seed beetle *Stator limbatus* is driven by food availability. Here, mothers adaptively change their investment into egg size depending on the type of host plant on which their eggs are laid. Females produce large but few eggs when laying on *Cercidium floridum*, where larvae need to be large and strong enough to penetrate the tough seed coat to feed. By contrast, they produce small but numerous eggs when laying on *Acacia greggii*, as the resulting small larvae can easily penetrate the softer seed coat of this host plant (Fox et al., 1997). Finally, expected future temperatures drive egg provisioning in the butterfly *Bicyclus anynana*. In this species, Fischer and colleagues (2003) demonstrated that it pays off for females to produce larger but fewer eggs at a lower temperature, but more and smaller eggs at a higher temperature.

Egg provisioning may also involve defensive chemicals that are either produced by the mothers themselves or obtained from food via sequestration (Blum and Hilker, 2002). In the European earwig *F. auricularia*, mothers regularly apply self-produced hydrocarbons onto the surface of their eggs, probably to reduce the risk of mould germination and growth (Boos et al., 2014). Females of the chrysomelid beetle *Cryptophalus hypochaeridis* also coat their eggs with a mixture of secretions and faecal materials, which together form a hard defensive structure protecting the eggs against predators (Ang et al., 2008). Performing such an egg coating is costly to *C. hypochaeridis* mothers, and equivalent to producing half an extra egg (Ang et al., 2008).

It is noteworthy that the adaptive effects of egg provisioning may not always be apparent, as they can be masked or altered when other forms of parental care are expressed later during offspring development. In the burying beetle *Nicrophorus vespilloides*, for instance, egg size has a positive effect on offspring body mass in absence of post-hatching care, whereas this effect is absent in presence of post-hatching care (Monteith et al., 2012). By contrast, in the European earwig *F. auricularia*, it is the amount of pre-hatching care that masks the effects of egg size: the mean egg mass is positively associated with offspring

number only in clutches receiving high levels (and not in such receiving low levels) of pre-hatching care (Koch and Meunier, 2014).

3 Pre-hatching Care

3.1 Egg Attendance and Egg Guarding

After egg deposition, parents can remain in the vicinity to physically protect the eggs against biotic and abiotic threats, a phenomenon called egg attendance or egg guarding. Egg attendance is the most common form of post-ovipositional pre-hatching parental care in insects. It has been reported in almost all Dermaptera, as well as many Embiidina, Hemiptera, Membracidae and a few Diptera (Lounibos and Machado-Allison, 1983; Tallamy and Wood, 1986; Edgerly, 1997; Matzke and Lass, 2005). Egg attendance can provide multiple benefits to the eggs and/or the mother offering protection against predators, pathogens, and social parasites. The protection against predators can be found in the nymphalid butterfly *Hypolimnas anomala*, where females straddle their eggs to exclude predatory ants (Nafus and Schreiner, 1988). This behaviour, however, does not deter all types of predators, as it appears to be non-effective against parasitoid wasps (Nafus and Schreiner, 1988). In the coreid bug *Physomeris grossipes*, egg guarding females do not deter predators with body movements, but by discharging chemicals from anal glands (Tallamy and Wood, 1986). Egg guarding may also protect against conspecific predators, such as in the maritime earwig *Anisolabis maritima*, where maternal egg guarding reduces the risk of egg cannibalism by conspecifics (Miller et al., 2011). Egg guarding may also be associated with protection against pathogens. This has been reported in two earwig species, *F. auricularia* and *Labidura riparia*, where mothers frequently groom their eggs to remove fungal spores that otherwise grow and ultimately kill the entire clutch (Shepard et al., 1973; Boos et al., 2014).

3.2 Egg Brooding

After laying, insect parents can carry eggs and provide care to these eggs during carrying, a phenomenon called egg brooding. Note that egg brooding has a different definition in birds, where it is defined as the act of sitting on eggs to incubate them. Insect egg brooding can be found in several insect orders, such as Coleoptera and Hemiptera (Machado and Trumbo, 2018). In the water bug *Abedus herbeti*, for instance, females lay their eggs on the males' back. The males then take over egg brooding and ensure that the eggs receive a proper level of oxygenation (Smith, 1997). Similarly in the golden egg bug *Phyllomorpha laciniata*, females can lay their eggs on plants, but mainly use conspecific males and females as egg-laying substrates. This surprising habit comes with no apparent costs to the recipient individual, whereas it generally improves egg survival when parasitoids are present in the environment (Carrasco and Kaitala, 2009). Interestingly, mothers may also evolve specific morphological traits for egg brooding. In the lobster cockroach *Nauphoeta cinera*, for instance, eggs are extruded, rotated by 90 degrees, and then retracted into a specialized brood sac, where development proceeds until the larvae are ready to hatch (Moore et al., 2007). Similarly, females of the florida woods cockroach *Eurycotis floridana* and the brown-banded cockroach

Supella longipalpa briefly carry their eggs in an extruded ootheca as they travel (Tallamy and Wood, 1986).

4 Post-hatching and Post-birth Care

4.1 Offspring Attendance

Once the eggs have hatched, parents can remain with and provide care to their offspring either at a fixed location or by escorting them. This offspring attendance is a taxonomically widespread phenomenon in insects and can last from a few hours, such as in the cockroaches *Blaberus craniifer*, *Gromphadorhina protentosa* and *Thanatophyllum akinetum* (Bell et al., 2007), to several days or weeks, such as in burying beetles (Scott and Traniello, 1990) and earwigs (Lamb, 1976; Wong and Kölliker, 2012). Offspring attendance typically enhances offspring protection against predators and improves the ability of newly hatched juveniles to defend against microbes and pathogens. The protection of juveniles against predation can be found in the lacebug *Gargaphia solani*. In this species, mothers aggressively protect their newly hatched offspring against predatory coccinellid adults by showing offensive movements towards the predator and/or expressing wing fanning (Tallamy and Denno, 1981). Similarly in the earwig *Anisolabis maritima*, mothers have been shown to fiercely defend their brood of nymphs with their forceps (Suzuki, 2010). Parental defences against microbes have been well studied in the burying beetle *N. vespilloides*. In this species, parents apply antimicrobial anal and oral secretions to the carcass used for breeding to limit the growth of microbes that could infect the larvae or compete with them over food access (Rozen et al., 2008; Arce et al., 2012). Mothers of the European earwig *F. auricularia* also line their nest with feces exhibiting antimicrobial properties (Diehl et al., 2015).

4.2 Offspring Brooding

Similar to egg brooding, offspring brooding consists of carrying juveniles after egg hatching – a phenomenon also called ‘nymphal phoresy’. Just like egg brooding, offspring brooding is a rare phenomenon in insects. It has been reported in the aquatic cockroach *Phlebotomus pallens*, where mothers carry their nymphs under their wing covers (Bell et al., 2007). Offspring brooding is also well documented in the peculiar pentatomoid family Phloeidae, which includes the Australian shield bugs *Peltocopta crassiventris* and *Cumare pallida*. In these species, adults have a flattened body whereby all their covering body part are remarkably expanded into flattened lobes under which mothers typically carry their first instar nymphs (Monteith, 2006).

4.3 Food Provisioning to Offspring

Insect parents exhibit multiple ways of providing food to their newly hatched offspring: the production of trophic eggs, the production of milk-like substances and other feeding secretions, the regurgitation of food, as well as the progressive and non-progressive (i.e. mass) provisioning of food items.

4.3.1 Trophic Egg Production

Trophic eggs (also called 'nurse eggs') are ovariole-produced structures that often exhibit morphological or biochemically specialized phenotypes (Perry and Roitberg, 2006). The production of trophic eggs can be found from solitary to social insects (Perry & Roitberg, 2006), and exhibits great temporal variation during a species' life-cycle, ranging from a production synchronised with that of the fertilized eggs to a delayed production during egg development or even long after the first eggs have hatched (Kudo and Nakahira, 2004, 2005; Filippi et al., 2008). This latter option is quite unusual but can be found in the Passalid beetle *Cylindrocaulus patalis*. In this species, third instar larvae trigger the production of a trophic egg by their mothers through a series of behavioural solicitations in the form of head-rubbing and stridulation (Ento et al., 2008).

Because they are typically non-fertile, the nutritional resources contained in trophic eggs are fully available for offspring (Crespi, 1992; Perry and Roitberg, 2006; Filippi et al., 2008). Having access to and consuming trophic eggs may thus offer crucial nutritional benefits to newly hatched juveniles. These benefits have, for instance, been demonstrated in the Asian cydnid *Canthophorus niveimarginatus*, where the experimental removal of trophic eggs came with a significant decrease in the nymphs' body weight and survival rate (Filippi et al., 2008; Baba et al., 2011). Similarly, the consumption of trophic eggs improved larval nutritional condition and the subsequent expression of anti-predator responses in the beetle *Leptinotarsa decemlineata* (Tigreros et al., 2017). The benefits of trophic egg consumption are not only associated with the eggs' nutritional value, as they can also protect viable eggs from predators (Kudo and Nakahira, 2004) or mediate the vertical transfer of essential symbionts to juveniles. Such a transfer occurs in the stinkbug *Parastrachia japonensis*, where mothers cover trophic eggs with symbiont-containing white mucus so that their juveniles can obtain symbionts while consuming these trophic eggs (Hosokawa et al., 2012). This use of trophic eggs to transfer symbionts to offspring resembles the use of symbiont capsules (which look like small eggs) in the Japanese common plastaspid stinkbug *Megacopta punctatissima* (Fukatsu and Hosokawa, 2002). However, it is important to note that the role of trophic eggs in the transfer of symbionts is not universal among insects (Baba et al., 2011).

The evolution of trophic eggs might be favoured if they allow parents to provide offspring with resources that would be hard or impossible to access for newly hatched individuals (Crespi, 1992). In line with this hypothesis, mothers of the Asian ladybird *Harmonia axyridis* increase the quantity of trophic eggs when the amount of resources available for their future offspring decreases in the environment (Perry and Roitberg, 2005). Similarly, newly hatched nymphs of the burrower bug *C. niveimarginatus* are still unable to feed on the tough vessels of seeds, their primary food source, and therefore require trophic eggs to obtain their first energetic resources (Baba et al., 2011). Alternatively, the production of trophic eggs may also help mothers to increase their investment into offspring quality by provisioning each of their young with more resources than can be contained in one egg (Crespi, 1992). For this reason, it has been suggested that the evolution of trophic egg production should be favoured in species where egg size is subject to strong mechanical and/or physiological constraints, e.g. due to the size of the ovipositor (Mock and Parker, 1997; Noriyuki et al., 2012). Such a

constraint would prevent females from producing larger eggs and would thus only allow females to increase their investment into offspring quality by offering them additional eggs as food sources (Mock and Parker, 1997). This hypothesis, however, received only little attention in the literature and has no clear empirical support (Noriyuki et al., 2012). Overall, this suggests that maternal adaptations to environmental changes rather than morphological constraints on egg size are sufficient to explain the evolution of trophic egg-laying.

Interestingly, the consumption of maternally produced eggs may not only reflect an extended form of parental investment (Alexander, 1974), but also the outcome of sibling competition over parental resources in family-living species (Elgar and Crespi, 1992; Mock and Parker, 1997) or the outcome of queen-worker competition over male production in eusocial insects (Ratnieks and Visscher, 1989; Ratnieks et al., 2006). In family-living species, the difference of genetic relatedness among offspring is expected to generate competition between siblings to monopolise parental resources (Trivers, 1974; Mock and Parker, 1997), so that the consumption of sibling eggs immediately after hatching could be a solid and efficient method to win such a competition. The consumption of fertile eggs has been reported in several insect species (Frechette and Coderre, 2000; López-Ortega and Williams, 2018), making it difficult to understand what is the main driver of egg cannibalism. In other species such as in the cricket *Velarifictorus asperses*, however, nymphs have been shown to discriminate between fertile and non-fertile eggs and to selectively consume the latter (Zeng et al., 2017).

4.3.2 Milk and Other Feeding Secretions

While feeding offspring with milk is a well-known example of maternal care in mammals, it only occurs in a few insects exhibiting adenotrophic vivipary (Ostrovsky et al., 2016). Contrary to mammals, however, this milk feeding typically occurs within the mother's body and involves poorly developed larvae or embryos. The larva typically feed orally from secretions (milk) produced by accessory glands (milk glands) consisting of tubular organs opening into the mother's uterus. Milk feeding is a characteristic of several Diptera families, such as the Glossinidae (tsetse flies), Hippoboscidae (louse or wallaby flies, keds), Nycteribiidae and the Streblidae (bat flies) (Meier et al., 1999). It has also been reported in the Pacific beetle cockroach *Diploptera punctata*, which is the only known species of cockroach where females possess milk glands (Stay and Coop, 1974; Bell et al., 2007; Tobe et al., 2013). Finally, a recent study suggests that milk-feeding could occur in the viviparous earwig *Hemimerus talpoides* (Dermaptera). In this species, the transformed follicular/ovarian cells of mothers and the invaginated dorsal vessel of embryos indeed converge to form a cephalic vesicle analogous to a placenta (Biliński et al., 2018). Just like with mammals, insect milk typically contains a large proportion of proteins as well as some symbionts that can be essential to food digestion by offspring (Tobe et al., 2013; Nováková et al., 2015).

Insect mothers can also feed juveniles outside of their body with non-milk-like secretions. This is the case in several cockroaches, such as *Trichoblatta sericea*, *Thorax porcellana* or *Gromphadorhina oxyhaloinae* (Nalepa and Bell, 1997). In these species, mothers produce feeding secretions either ventrally, under their tegmina, in their abdominal tip, or in their mouthparts. The food source provided to the juveniles can either consist of

hemolymph, sternal and tergal exudates, or secretion from the brood sac (Nalepa and Bell, 1997). In non-viviparous earwig species such as *F. auricularia* and *L. riparia*, young nymphs were also observed actively gnawing at the pleural region of their mother's abdomen (Meunier J, pers. obs.)(Shepard et al., 1973). The function of this behaviour and whether it mediates the transfer of feeding substances from earwig parents to offspring remains, however, unknown.

4.3.3 Food Regurgitation

Food regurgitation (also called stomodeal trophallaxis) typically occurs through mouth-to-mouth contact between parents and offspring. This process allows parents to soften food, add and transfer digestive enzymes, as well as to transfer symbionts to their offspring (Trumbo, 2012). Known cases of parental food regurgitation are scarce in non-eusocial insects. One clear example can be found in the European earwig *F. auricularia*, a species where mothers and nymphs frequently show mouth-to-mouth contact (Mas and Kölliker, 2011). Making use of the relative transparency of newborn earwig nymphs, Staerkle and Kölliker (2008) demonstrated that earwig nymphs become green if they are tended by mothers previously fed with green-colored food. In another earwig species, the striped earwig *L. riparia*, Shepard and colleagues (1973) used radioactive labelling of food, and came to the same conclusion: nymphs showed radioactivity after they had been tended by mothers previously fed with radioactive food. Other well-known examples of food regurgitation in insects are present in burying beetles, such as *Nicrophorus orbicollis*, *N. vespilloides* and *N. quadripunctatus* (Milne and Milne, 1976; Eggert et al., 1998; Suzuki, 2015). In these species, adults have been suggested to regurgitate pre-digested carrion to the young larvae on the carcass. Contrary to earwigs, however, the claim that food regurgitation occurs in burying beetles mostly relies on behavioural observations of mouth-to-mouth contacts between parents and larvae, as well as on studies investigating the effects of starvation on the intensity of larval begging behaviours (e.g. Smiseth & Moore, 2002, 2004; Suzuki, 2015) (but see Capodeanu-Nägler et al., 2018). In the same way, food regurgitation has been suggested to occur in the woodroach genus *Salganea* based on the frequent mouth-to-mouth contacts between mothers and offspring (Nalepa et al., 2008).

4.3.4 Provisioning of Small and Large Food Items

Juveniles of many insect species are capable of processing food items but are rarely able to obtain these items by themselves, e.g. due to poor foraging capabilities. Parents can provide care to circumvent this issue in the form of collecting and bringing back food items to or close to the nest. This is the case in the burrower bug *Sehirus cinctus*, where mothers provide *Lamium purpureum* nutlets to newly hatched nymphs until they reach their second developmental instar (Sites and McPherson, 1982). Similarly, *Embia ramburi* females provide pieces of masticated food to their nymphs (Ledoux, 1958), and females of the short tailed cricket *Anurogryllus muticus* provide nymphs with bits of retrieved food (West and Alexander, 1963). In the earwig *Anisolabis maritima*, mothers also carry small food items with their mouth to the nest (Suzuki, 2010) and adapt the amount of food to the number and need of their nymphs (Suzuki, 2018).

Parents can also provision their offspring with larger food items that simultaneously serve as nesting material, a phenomenon called mass provisioning. A textbook example can be found in burying beetles of the genus *Nicrophorus*. Here, parents provide a carcass of small vertebrates to their larvae, on which they subsequently feed either directly, or indirectly through parental regurgitations (see above)(Scott, 1998). Once *Nicrophorus* females find a carcass of a small vertebrate, they oviposit in its vicinity and start preparing the carcass (alone, or together with the male) by removing the hair or feathers and then creating an opening in the integument of the carcass before or shortly after egg hatching to favour its consumption by the larvae (Eggert et al., 1998; Schrader et al., 2015; Trumbo, 2017). They then apply oral and anal antimicrobial secretions to its surface to help preserving the carcass and allow its use as a food source until the end of larvae development (Suzuki, 2001; Rozen et al., 2008). Another example of brood mass provisioning is found in the dung beetles. In ‘tunneller’ dung beetles, such as the ones found in the genus *Onthophagus*, females pack portions of dung into the end of tunnels excavated beneath the dung pad, and then seal the tunnel after depositing a single egg in each tunnel (Hunt and Simmons, 1997, 2002). Conversely, in ‘roller’ dung beetles, such as the ones found in the family *Scarabaeinae*, females (sometimes together with males) extract a portion of the dung pad, lay one egg on the top of it, and then roll it to form a brood ball that will be tended until hatching (Sato, 1997). Notwithstanding the method, the portion of dung contained in the brood ball varies in size between females (Hunt and Simmons, 2002) and represents the only food source that is available to the larvae during development.

Finally, an extreme form of parental food provisioning occurs when parents provision their offspring with their own body. This rare phenomenon has been reported in the hump earwig, *Anechura harmandi*, where offspring completely consume their mother at the end of post-hatching care (Suzuki et al., 2005). Matrophagy also occurs in the beetle *Micromalthus debilis*, the sole species of the family *Micromalthidae*. In this insect with a very peculiar life-cycle, female offspring feed on fungus-infested rotting wood, whereas male offspring exclusively consume their own mother (Pollock and Normark, 2002; Normark, 2013). Why obligatory matrophagy has only evolved in males and why it is maintained in this species remain yet unclear (Pollock and Normark, 2002; Normark, 2013).

5 Care after Offspring Nutritional Independence

Providing care to offspring after they have reached nutritional independence is a very unusual phenomenon in insects (Clutton-Brock, 1991). It can nevertheless be found in the European earwig *F. auricularia* and the burying beetle *N. vespilloides*. In the European earwig, juveniles attain mobility and can forage for themselves only few days after egg hatching (Wong and Kölliker, 2012). However, earwig mothers remain with their nymphs up to several weeks after their emergence (Lamb, 1976), probably to enhance offspring protection against predators and/or pathogens (Diehl et al., 2015). In the burying beetle *N. vespilloides*, larvae become nutritionally independent about three days after emergence, but mothers remain with the larvae a couple of additional days to defend them against predators and conspecific intruders

(Smiseth et al., 2003). Laboratory experiments of orphaning in this burying beetle reveal that reduced post-hatching care reduces offspring survival rate and mass (Eggert et al., 1998; Capodeanu-Nägler et al., 2016). Finally, in the wood cockroach *Cryptocercus punctulatus* nymphs are nutritionally independent after they reach the third developmental instar, which occurs in several months, but parents remain with their offspring for more than three years (Nalepa, 1990). During this family life, mothers typically provide their offspring with hindgut fluids containing nutrients and hindgut symbionts – two components that are surprisingly not required to ensure offspring survival after their third instar (Nalepa, 1984, 1990).

6 Unconventional Forms of Parental Care

In addition to the ‘classical’ forms of parental care detailed above, it has recently been suggested that other ‘unconventional’ parental behaviours could function as parental care. In particular, Davenport et al. (2019) hypothesised that offspring abandonment and filial cannibalism could be considered (and evolve) as forms of parental care, even in the absence of other classical forms of care. This hypothesis relies on the idea that when within-clutch density negatively affects offspring survival – an effect reported in many species (see in Davenport et al., 2019) – offspring abandonment and filial cannibalism can allow parents to actively reduce the density of their clutch and thus the overall mortality of their young. This benefit would allow classifying these two behaviours as forms of parental care. This hypothesis was supported by their modelling approach (Davenport et al., 2019), particularly when several specific conditions were met: when within-clutch density effects are relatively high, when abandoning or eating some young indeed reduces such density effects, when offspring require care and when eggs are laid at higher than optimal densities. However, this quite limited set of conditions suggests that offspring abandonment and filial cannibalism can only be considered forms of parental care in a very limited number of species and calls for empirical works testing the validity of this interpretation in insects.

7 Conclusions

Insects represent a prime illustration of the diversity of parental care that can be found in animals. Across species, families and genera, forms of parental care range from the simple provisioning of eggs with nutrients and hormones, over the regurgitation of food to older juveniles, to fierce protection of eggs and newly hatched offspring against intruders. This unique diversity makes insects excellent biological models for improving our general understanding of the evolution, diversification and underlying physiological and genetic mechanisms shaping family life in nature.

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Table 1 – Taxonomic distribution of post-ovipositional parental care in insects. Data gathered from multiple sources (Wong et al. 2013; Footitt and Adler 2018; Machado and Trumbo 2018).

| Order name | Common name | Known species number | Number of genera | Number of genera with known forms of parental care ^a (%) | Most represented form(s) of parental care among genera ^a | |
|------------------|----------------------------------|----------------------|------------------|---|---|---|
| Archaeognatha | Jumping bristletails | 500 | 52 | 1 | 1.9% | Egg and offspring attendance |
| Blattodea | Cockroaches, termites | 7,570 | 775 | 168 ^b | 21.7% | Internal egg carrying |
| Coleoptera | Beetles | 390,000 | 4,722 | 331 | 7.0% | Egg and offspring attendance |
| Dermoptera | Earwigs | 2,000 | 203 | 28 | 13.8% | Egg and offspring attendance |
| Diptera | Flies | 160,000 | 3,175 | 676 | 21.3% | Internal egg carrying |
| Embioptera | Web spinners | 450 | 90 | 6 | 6.7% | Offspring attendance |
| Ephemeroptera | Mayflies | 3,328 | 441 | 3 | 0.7% | Internal egg carrying |
| Grylloblattodea | Ice and rock crawlers | 32 | 5 | 0 | 0.0% | - |
| Hemiptera | True bugs | 106,970 | 6,185 | 599 | 9.7% | Internal & external egg carrying/guarding |
| Hymenoptera | Bees, ants, wasps, sawflies | 115,000 | 1,579 | 85 ^b | 5.4% | Egg and offspring attendance |
| Lepidoptera | Moths, butterflies | 174,250 | 16,298 | 23 | 0.1% | Internal egg carrying |
| Mantodea | Mantids | 2,400 | 426 | 4 | 0.9% | Offspring attendance |
| Mantophasmatodea | heelwalkers, gladiators | 19 | 13 | 0 | 0.0% | - |
| Mecoptera | Scorpionflies | 737 | 38 | 0 | 0.0% | - |
| Neuropteridae | Lacewings, owlflies, antlions | 6,434 | 671 | 0 | 0.0% | - |
| Odonata | Dragonflies, damselflies | 5,680 | 642 | 1 | 0.2% | Internal egg carrying |
| Orthoptera | Grasshoppers, crickets, katydids | 28,000 | 2,687 | 6 | 0.2% | Egg and offspring attendance |
| Phasmatodea | stick insects | 3,000 | 473 | 0 | 0.0% | - |
| Phthiraptera | Lice | 5,316 | 304 | 1 | 0.3% | Internal egg carrying |
| Plecoptera | Stoneflies | 3,497 | 286 | 10 | 3.5% | Internal egg carrying |
| Psocoptera | Book and bark lice | 5,500 | 576 | 3 | 0.5% | Egg attendance |
| Siphonaptera | Fleas | 2,185 | 246 | 0 | 0.0% | - |
| Strepsiptera | Twisted wing parasitoids | 630 | 57 | 45 | 78.9% | Internal egg carrying |
| Thysanoptera | Thrips | 6,339 | 842 | 42 ^b | 5.0% | Egg and offspring attendance |
| Trichoptera | Caddisflies | 14,500 | 380 | 1 | 0.3% | Internal egg carrying |
| Zoraptera | Zorapterans | 50 | 1 | 0 | 0.0% | - |
| | | TOTAL | 41167 | 2033 | 4.9% | |

^a More details on the forms of post-ovipositional care per genera can be found in Machado and Trumbo (2018)

^b This number does not include eusocial species