The Science of Nature (2020) 107: 34
https://doi.org/10.1007/s00114-020-01690-1

REVIEW

The dynamic eggs of the Phasmatodea and their apparent convergence with plants

James C. O'Hanlon[1] · Braxton R. Jones[2] · Matthew W. Bulbert[2]

Received: 9 April 2020 / Revised: 22 July 2020 / Accepted: 23 July 2020 / Published online: 31 July 2020

Abstract
The egg stages of animal life cycles are underappreciated in terms of their capacity for dispersal, protection, and biotic and abiotic interactions. Some of the most intriguing egg morphologies are seen in stick and leaf insects (Phasmatodea). Phasmids are charismatic insects, particularly due to their incredible camouflage, though a lesser-known fact is that their eggs are incredibly diverse in shape and structure, reflecting varying ecological niches. Perhaps most remarkable are those eggs which appear to resemble plant seeds in both their appearance and means of dispersal, such as via water and animal vectors. Numerous hypotheses surrounding the function of these egg morphologies and their apparent convergence with seeds have been proposed; however, empirical evidence remains lacking. Here, we present an initial synthesis of available evidence surrounding the ecology and dispersal strategies of phasmid eggs and weigh up the evidence for convergent evolution between phasmid eggs and seeds. In doing so, we highlight areas where further research is needed and discuss how the ecology of phasmid eggs may interplay with other aspects of phasmid ecology, distribution, and evolution.

Keywords Dispersal · Stick insects · Seeds · Egg · Myrmecochory · Phoresy

Eggs as dynamic entities

The tendency for behavioural and ecological research to focus on mature animals can overlook the majority of behavioural and ecological interactions that can occur. Juvenile stages of animal life histories—including nymphal, larval, and egg (or embryonic) stages—often make up the longest component of animal life cycles, yet their unique ecology may often be overlooked in favour of understanding the ecology and evolution of adult forms (Guerra-Grenier 2019). In the case of eggs, their immobility and inherent vulnerability imply that survival through the egg stage can be heavily dependent on the actions of the parent including oviposition site selection and adult defence (e.g. Montgomerie and Weatherhead 1988; Refsneider and Janzen 2010). Often though, the investment of parents in egg care, especially in insects, is limited (Wong et al. 2013). Thus, the eggs are left to defend themselves without the option of being able to flee.

Eggs are far from being passive entities with selection favouring a broad range of abiotic and biotic interactions crucial for their survival. The colours and patterning of eggs, for example, may transmit visual signals that deter predators, may relay information to parents for assessment of identity and quality, or are used by parents to assess egg load at potential oviposition sites (Cherry and Gosler 2010; Hallman and Griebler 2015; Guerra-Grenier 2019). Some animals even use the egg stage for dispersal, such as in the wind-dispersed eggs of certain crustaceans (Brendonck and Riddoch 1999; Pincel et al. 2016). In insects, diversity in egg morphology has been shown to correlate most strongly with the ecological niche of the egg itself, as opposed to being constrained by the characteristics of the adults that lay the eggs (Church et al. 2019). The diverse survival adaptations and ecological interactions of which eggs are capable no doubt explain some of the staggering diversity of forms seen in animal eggs.

The dynamic life histories of eggs may be most well-appreciated in vertebrates (Kilner 2006; e.g. Altig and McDiarmid 2007; Cherry and Gosler 2010), especially in

Communicated by: José Eduardo Serrão

✉ James C. O'Hanlon
johanlon@une.edu.au

[1] School of Environmental and Rural Science, University of New England, Armidale 2350, Australia

[2] Department of Biological Sciences, Macquarie University, Balaclava Road, North Ryde, NSW 2109, Australia

birds. Extensive research on bird nesting ecology has revealed the importance of factors such as nest defence (Montgomerie and Weatherhead 1988), nest construction and concealment (Mainwaring et al. 2014), and intraspecific communication within the nest (e.g. Katsis et al. 2018). In vertebrates, it is common for eggs to be attended by one or both parents. In stark contrast, parental care of eggs in insects is comparatively rare (Tallamy 2000; Royle et al. 2012). Eggs are often left unattended resulting in them having to contend with the selective pressures imposed by predators and environmental conditions (e.g. Church et al. 2019).

Perhaps the most intriguing examples of dynamic egg life histories are seen in the stick and leaf insects (order Phasmatodea). Phasmid eggs are incredibly diverse in structure across the order and have been the focus of much discussion, particularly for their utility as taxonomic characteristics (Clark 1976; Sellick 1988, 1997a, c; Fig. 1). The oviposition behaviours of phasmids also vary greatly, and the morphology of the eggs correlates highly with the oviposition strategy of the phasmids (Robertson et al. 2018). Despite ongoing interest in phasmid egg morphology, there has been little research into the functional significance of such diverse egg morphologies and oviposition behaviours (Goldberg et al. 2015; but see Robertson et al. 2018). There are, however, numerous hypotheses that relate these morphologies to functional roles in egg dispersal and protection from predators and parasites.

In discussions surrounding the ecology of phasmid eggs, one common theme emerges, which is their apparent similarity to plant seeds. Remarkably, the diverse oviposition strategies and egg morphologies of phasmids often appear to be convergent with seed dispersal and protective adaptations in plants. Most notable is the convergence towards using ants as dispersers of both plant seeds and phasmid eggs (Compton and Ware 1991; Hughes and Westoby 1992; Windsor et al. 1996; Stanton et al. 2015). Additionally, there is evidence for water-based and vertebrate-based dispersal in phasmid eggs with parallels to water- and vertebrate-dispersed seeds (e.g. Kobayashi et al. 2014; Suetsugu et al. 2018).

The similarity of phasmid eggs to seeds has been noted for some time (e.g. Stockard 1908), likely due to broad similarities such as their overall size, ovoid shape, dark colour, and rigid outer shell. Early explanations for these similarities ranged from mere coincidence (Severin 1910) to some form of protective mimicry that avoids the attention of predators

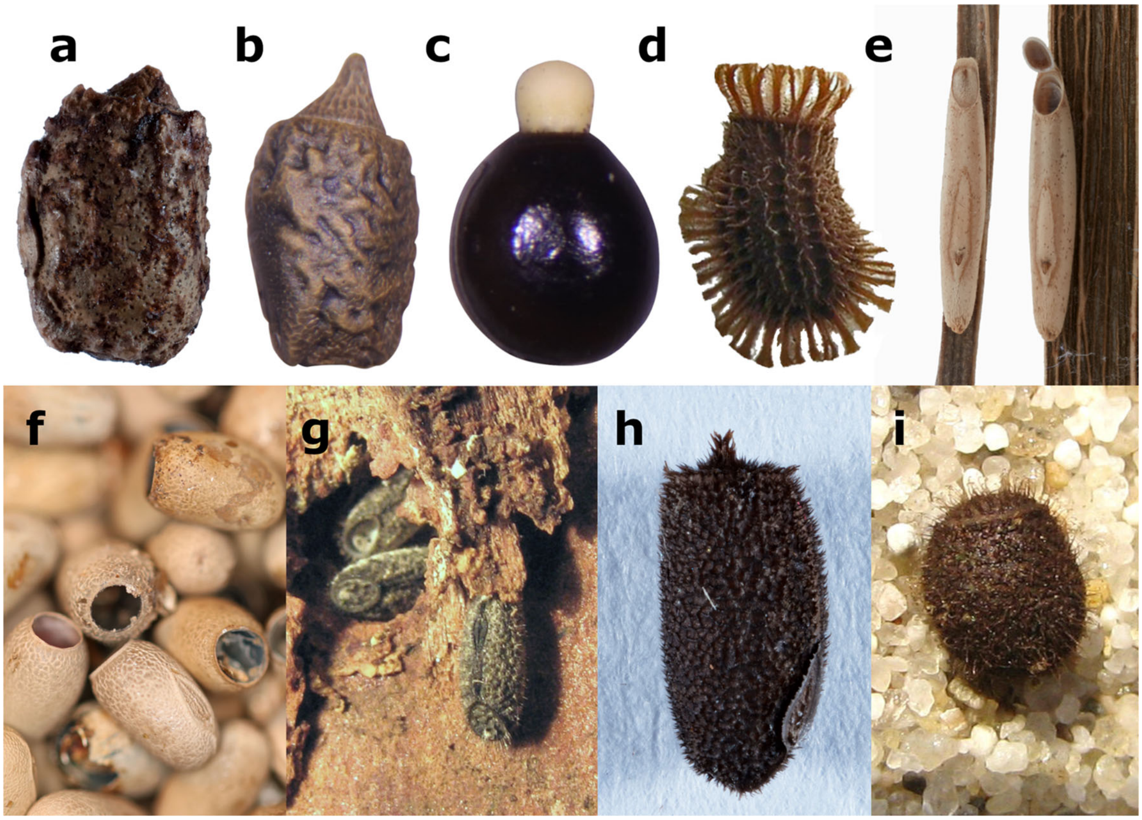

Fig. 1 Examples of the diversity seen in phasmid eggs. **a** *Clitarchus hookeri* (locality: New Zealand, image: Morgane Merien). **b** *Megacrania batesii* (locality: Australia, image: Braxton Jones). **c** *Acrophylla thoon* (locality: Australia, image: Braxton Jones). **d** *Phyllium philippinicum* (locality: Philippines, image modified from Wikimedia Commons: User Drägüs). **e** *Denhama* sp. (locality: Australia, image: Braxton Jones). **f** *Drycocelus australis* (locality: Australia, image: Stephen Fellenberg). **g** *Sipyloidea sipylus* (locality: Southeast Asia, image: Wikimedia commons—user Drägüs). **h** *Spinotectarchus acornutus* (locality: New Zealand, image: Morgane Merien). **i** *Epidares nolimetangere* (locality: Borneo, image: Wikimedia commons—user Drägüs)

and parasites (Stockard 1908). However, little research has explicitly tested these hypotheses. As evidence continues to accumulate surrounding the dynamic behavioural ecology of phasmid eggs and their apparent convergence with plants, it is becoming clear that this order of insects provides an excellent system to study the ecological interactions and evolutionary history of animal eggs.

In this review, we discuss the importance of the egg (or embryonic) stage as a dynamic phase in animal life histories. Rather than presenting an exhaustive list of phasmid egg types and morphologies across the order, we focus on discussing existing hypotheses for the function of phasmid egg morphologies and assess the available evidence surrounding them. We consider the benefits of ancestral 'egg-dropping' behaviours and the evolution of secondary egg-dispersal adaptations. Using insight into the much more substantial literature on the evolution of seed survival and dispersal strategies, we weigh the evidence for convergent evolution between phasmid eggs and plant seeds, and whether this may be driven by niche similarities between the two groups. Following this, we discuss the evolutionary shift to 'specific placement' of eggs and the potential benefits of this oviposition strategy. In consolidating this evidence, we outline where further research is needed to fully understand the ecology of phasmid eggs and hope that this discussion will provide a springboard for future research into this charismatic and elusive group of animals.

Dispersal abilities across life history stages

Dispersal is essentially the relocation of individuals from one location to another for growth and reproduction. It is the fundamental process that facilitates gene flow. It contributes to the maintenance of genetic diversity within populations and reduces competition with parents and intraspecifics (Bohonak 1999). The fundamental process of dispersal is relatively straightforward for organisms that have self-propulsion (e.g. walking, swimming, flying). Relocation to a suitable habitat, for instance, is self-driven and influenced by that organism's ability to find the habitat and survive the journey (e.g. avoiding predators).

Sessile organisms often rely on more stochastic mechanisms for dispersal such as biotic and abiotic vectors. A classic example is sessile marine corals (Anthozoa). In these organisms, long-distance dispersal occurs in the embryonic state where, following mass spawning events, fertilised embryos enter a pelagic stage of their life cycle before settling on the seafloor (Jackson 1986). In sessile organisms, it is advantageous for dispersal to occur at the embryonic stage, as this provides the chance for offspring to explore environments away from parents, and the embryonic forms of organisms are generally smaller and easier to disperse (Wang and Smith 2002; Panov and Caceres 2007). This is common in sessile marine organisms where motile juveniles are spread via an aquatic medium. Embryonic dispersal in terrestrial environments is less prevalent, although there are a number of examples of wind dispersal of eggs in marine and freshwater crustaceans (Brendonck and Riddoch 1999; Pincel et al. 2016). As we discuss below, phasmids have evolved eggs capable of dispersal via a number of means. Whilst phasmids are not entirely sessile, they are generally limited in their mobility. Thus, it is conceivable that the limited dispersal ability of phasmids is a contributing factor towards the evolution of embryonic dispersal methods, as in plants and other sessile organisms.

Whereas the embryonic life stages of animals can be overlooked as dynamic entities, the embryonic stages of plant life histories are much more highly regarded in terms of their diverse survival and dispersal adaptations. Their lack of mobility at maturity means that the embryonic stage is the only opportunity plants have to relocate to a suitable growing habitat away from the parent plant. Seeds may be dispersed locally via gravity or ballistic projection or dispersed far from the parent plant via abiotic couriers such as water and wind, or biotic animal vectors (Murray 1986; Burns 2012). Seeds may have remarkable structural and/or mechanistic innovations such as the 'wings' of wind-dispersed seeds (Horn et al. 2001) or the buoyant chambers and water-resistant coatings of water-dispersed seeds (Smith 1994; Nathan et al. 2008). Plants that rely on animal interactions may encase their seeds in bright fruits that attract animal vectors and can survive passage through animal digestive tracts (endozoochory; Traveset et al. 2007). Others have seeds with elaborate barbs or hooks that adhere to mammalian fur and bird feathers (epizoochory; Kulbaba et al. 2009). Some plants may also use secondary dispersal mechanisms such as those that disperse their seeds locally which are then carried underground by ants, where the seeds are protected from bushfires and predators, and placed in areas of high nutrient availability (myrmecochory; Giladi 2006).

Ecology of the Phasmatodea

Phasmids, commonly known as stick insects, leaf insects, and walking sticks, are generally nocturnal, large-bodied, herbivorous insects. They range from being monophagous, eating only one species of plant, to polyphagous, with multiple food plant options (Bedford 1978). Phasmids are generally characterised as being still or slow-moving, which is often coupled with a lack of functional wings and/or camouflage tactics that rely on limited movement such as crypsis or masquerade (Whiting et al. 2003; Trueman et al. 2004). In many cases, males are smaller and more mobile, whereas females are larger and relatively limited in their mobility (e.g. *Extatosoma tiaratum* (Phasmatidae); Fig. 2). Like most

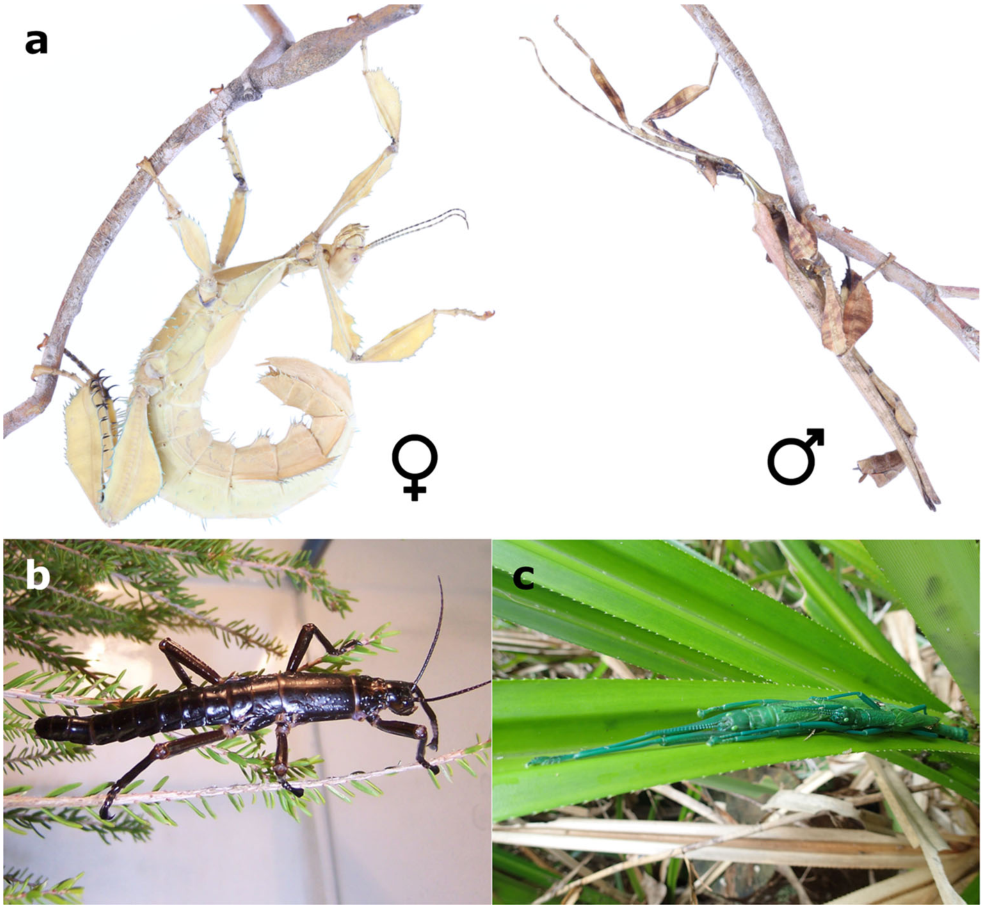

Fig. 2 **a** Adult *Extatosoma tiaratum* female and male (locality: Australia, image: James O'Hanlon). **b** Adult female *Dryococelus australis* (locality: Australia, image: Stephen Fellenberg). **c** *Megacrania batesii* pair (image: Matthew Bulbert)

insects, phasmids do not care for their eggs or their young. Instead, they employ a diversity of egg-dispersal strategies that ultimately lead to the eggs having to fend for themselves.

The eggs of phasmids are diverse in appearance, so much so, they are traditionally used for taxonomic discrimination (Clark 1976; Sellick 1988, 1997c; Fig. 1). Concurrent with a variation in appearance is a diversity in oviposition behaviours, which appears to account for some of the morphological variation (Robertson et al. 2018). It has been long claimed that phasmid eggs either mimic or masquerade as seeds. The convergence in the use of ants to relocate both seeds and eggs certainly provided weight to these claims (Compton and Ware 1991; Hughes and Westoby 1992; Windsor et al. 1996; Stanton et al. 2015). Beyond this, there has been relatively little comparative investigation of the apparent similarities between plant seeds and phasmid eggs, and our understanding of the functional importance of such diverse egg morphologies and oviposition behaviours has yet to be fully resolved (Goldberg et al. 2015; Robertson et al. 2018).

Carlberg (1983) categorised the egg-laying strategies of phasmids into two broad categories: eggs without specific placement (such as those that are dropped or flicked to the ground) and eggs with specific placement (such as those that are buried or adhered to plant surfaces). Within these broad categories, Carlberg (1983) recognised other shared characteristics of species' egg-laying strategies such as those groups that laid eggs in discrete clutches as opposed to individually. Here, we use this framework to explore the selective pressures, which may lead to these various egg management strategies, and discuss the evidence for how the ecological niche of eggs can lead to this diverse suite of egg morphologies. Furthermore, we investigate the concept that the limited dispersal abilities of adult phasmids are a contributing factor towards the evolution of embryonic dispersal methods, in accordance with plants and other sessile organisms.

Eggs without specific placement

Egg dropping

The ancestral egg-laying strategy in phasmids is simply to drop eggs onto the ground (Robertson et al. 2018). The hard outer shell that is a characteristic of phasmid eggs has been suggested to be a major adaptation for this oviposition strategy, protecting the eggs when falling from a height. This further suggests that ancestral phasmids were arboreal in nature as are most extant phasmids. Passively dropped eggs generally have a simple round shape. Fossilised phasmid eggs described from the middle Eocene era (~ 44 Ma) exhibit a similar round shape and share characteristics seen in extant species' eggs such as an operculum and external micropylar plate (Sellick 1994). Many species that drop eggs have a conspicuous 'capitulum' on their eggs, which facilitates secondary dispersal by acting as a food reward for foraging ants (see below).

Dropping eggs requires little movement, and it has been hypothesised that the passive dropping or flicking of eggs has evolved in parallel with, or at least helps facilitate, phasmids' primary camouflage defence (Robertson et al. 2018). This remains to be tested and requires consideration of phasmid activity patterns, including the fact that phasmids are generally nocturnal and more active when feeding at night.

Egg flicking

Many species actively 'flick' their eggs away, by recoiling their abdomen and swiftly 'catapulting' the eggs (Bedford 1978; Robertson et al. 2018). This may act to distance new offspring from parents and conspecifics, reduce spatial clumping of eggs, or increase chances of new offspring reaching yet to be exploited host plants. Ultimately, these strategies are expected to either reduce inbreeding and resource competition, decrease over exploitation of resources, or impede the ability of predators and parasites to locate the eggs (Taylor 1976).

Dropping or flicking of eggs is paralleled in plants. Many plants simply drop their seeds locally but may also disperse them at further distances using 'ballistic' dispersal (van der Pijl 1982; Traveset et al. 2014). Dropping seeds directly below the canopy of a plant creates the risk of the seeds having to compete for resources and may lead to increased risk of inbreeding depression when the seedling matures. Therefore, plants may rely on further mechanisms that increase the distance of the seed to the host plant such as ballistic dispersal where plants' 'shoot' seeds into the air. For example, filaree *Erodium cicutarium* (Geraniaceae) seeds are propelled up to half a metre away from the parent by stored energy within stiff bristle like 'awns' attached to the seed (Evangelista et al. 2011). Perhaps the most extreme example of ballistic dispersal is the sandbox tree *Hura crepitans* (Euphorbiaceae), which has earned the nickname 'dynamite tree' for its round fruits that explode propelling seeds up to 45 m away from the parent plant (Swaine and Beer 1977).

Seeds that are dispersed by gravity or ballistic dispersal can be aided further by the action of wind currents (van der Pijl 1982; Muñoz et al. 2004; Traveset et al. 2014). Often, seeds are morphologically adapted for wind dispersal by being extremely lightweight or having wing-like 'vanes' that catch wind currents (e.g. Augspurger 1986). Within botany, the use of a secondary dispersal agent, such as wind water and animal vectors, is termed 'allochory'. This is opposed to 'autochory', which describes dispersal mechanisms solely reliant on the plant (van der Pijl 1982). We do not know of any research that has considered the interactions between wind and the morphology of dropped or flicked phasmid eggs. However, there are growing bodies of evidence surrounding the use of water and animal vectors as dispersal agents for phasmid eggs.

Ocean dispersal and rafting—hydrochory

The wide distribution patterns of certain phasmids across the globe suggest that oceanic dispersal has occurred, likely during the egg stage. For example, phasmids of the Mascarene islands near Madagascar appear to be nested within the Australian Lanceocercata clade (Cliquennois and Brock 2004; Bradler et al. 2015). The eggs of many of these species are glued to the surface of branches or leaves, which lead Cliquennois and Brock (2004) to hypothesise that the ancestors of modern-day Mascarene stick phasmids may have arrived there from Western Australia as eggs glued to vegetation rafting across east-west currents in the Indian Ocean.

Rafting on vegetation is a potential means of dispersal for many small animals. Terrestrial invertebrates are commonly found inhabiting rafting vegetation in the ocean (Heatwole and Levins 1972; Thiel and Gutow 2005). Whilst a transoceanic journey on flotsam seems like an epic journey for small animals to take, it is not beyond the realms of possibility. The flightless *Pachyrhynchus* weevils (Curculionidae) are wood borers that lay their eggs inside the fruits and stems of a range of plant species. Yeh et al. (2018) showed that the eggs and larvae of *Pachyrhynchus* weevils were resistant to immersion in seawater for a number of days and suggested that rafting on floating vegetation has likely led to their colonisation of islands in South East Asia.

It has been suggested that phasmid eggs may be capable of oceanic dispersal without needing to raft on vegetation. The outer surfaces of *Megacrania* (Phasmatidae) eggs are 'sponge-like' and float in water (Fig. 1c). Kobayashi et al. (2014) showed that *Megacrania* eggs are still viable after floating in saltwater for extended periods of time and can even hatch whilst floating. Again, this highlights another apparent similarity between the dispersal strategies of plants and phasmids. Coastal plants often favour dispersal by ocean currents (Nathan et al. 2008). Familiar examples include coconut and mangrove seeds that use air pockets to stay buoyant above the surface and are carried to new sites via ocean currents (Murray 1986; Smith 1994).

Oceanic dispersal has been hypothesised for the phasmids of the genus *Megacrania* that are dispersed across the western Pacific (Ushirokita 1998). *Megacrania* phasmids are restricted to coastal vegetation zones as they primarily feed on *Pandanus* (Pandanaceae) plants (Yamasaki 1991; Cernak and Hasenpusch 2000; Fig. 2c). Interestingly, *Pandanus* plants bear fruits that float on water, and oceanic dispersal is known to be a major contributor to their current distribution patterns (Gallaher et al. 2015). This raises further questions about the possibility of niche similarities driving the co-evolution of both phasmid and host plant dispersal methods. As *Pandanus* plants are patchily distributed along coastal areas, finding new host plants poses a challenge for the specialist feeding *Megacrania*. As the behaviour of oceanic currents may influence the dispersion of both *Pandanus* seeds and *Megacrania* eggs, it may be speculated that hydrochory is an adaptation that increases the chances of *Megacrania* eggs dispersing to new habitats containing suitable host plants.

Dispersal by ants—myrmecochory

Once laid by the adult, phasmid eggs can be involved in a range of interspecific interactions, including those related to secondary dispersal and defence. As noted above, many species that drop or flick their eggs to the ground have a fatty acid–rich 'capitulum' on the outer surfaces of their eggs (Fig. 3). This appears to be an adaptation for secondary dispersal as the capitulum acts as a food reward for foraging ants that will collect the phasmid eggs and carry them away, even going so far as to carry the eggs into their nests (Compton and Ware 1991; Hughes and Westoby 1992; Windsor et al. 1996; Stanton et al. 2015; Fig. 3g). What makes this dispersal strategy even more remarkable is the fact that it is convergent with the well-studied phenomenon of 'myrmecochory' in plants. Many plants have seeds which harbour a fatty acid–rich 'elaiosome' which acts as a reward for foraging ants that disperse the seed and often deposit the seed within their nests (Giladi 2006; Fig. 3f). A recent study showed that plants and phasmids have converged upon the same chemical signalling strategy to exploit ant behaviour (Stanton et al. 2015). Oleic acid was found to be the primary fatty acid component of both seed elaiosomes and egg capitula and is the major compound involved in eliciting the food-carrying behaviour in ants (Brew et al. 1989; Fischer et al. 2008).

Myrmecochory in plants occurs worldwide but is particularly prevalent in areas such as Australia and the Mediterranean (Lengyel et al. 2010). Whilst ants are able to disperse seeds away from the parent plant, recent research has shown that myrmecochory may actually limit the dispersal potential of tree seeds compared with alternative strategies such as wind and bird dispersal (Lengyel et al. 2009). Furthermore, this may lead to higher rates of speciation in ant-dispersed plant lineages. Thus, it appears that the main benefits of myrmecochory may be related to survival rather than dispersal. Seeds taken into ant nests may be protected from predators and bushfires, and may be placed in a stable environment ideal for germination (for a review see Giladi 2006). Whether the behaviour of ants acts to extend or limit the dispersal potential of phasmids, and whether phasmid eggs also benefit from the protection and stable environments that ant nests provide, remains unknown. As noted above, Hughes and Westoby (1992) showed that *Didymuria violescens* (Phasmatidae) eggs buried underneath the soil were less likely to be parasitised. Thus, it is likely that ant dispersal and placement inside ant nests may function to avoid parasitism and predation. However, the functional benefits of ant-based dispersal in phasmids remain to be studied in earnest.

Ants can be formidable predators, thus forming a symbiotic association with them seems like a risky strategy. It is often assumed that the capitulum of phasmid eggs is consumed by ants and the hard outer shell of the egg is sufficient to prevent the ants from preying upon the developing embryo. Observations have been made of ants carrying phasmid eggs into their nests, but no studies have investigated their long-term fate. This raises many questions about whether eggs persist long term in ants' nests and what adaptations exist that would enable nymphs to emerge within an ants' nest. The first instar nymphs of *Extatosoma tiaratum* (Phasmatidae) are putative ant mimics (Bedford 1978) raising the exciting possibility of complex signalling interactions between juvenile phasmids and potential predators.

The role of the egg capitulum as an ant attractant has been investigated in five species of phasmid thus far, including *Ctenomorpha marginipennis* (Phasmatidae; formerly known as *C. chronus*), *Didymuria violescens* (Hughes and Westoby 1992), *Bacillus coccyx* (Bacillidae; Compton and Ware 1991), *Calynda bicuspis* (Diapheromeridae; Windsor et al. 1996), and *Eurycnema goliath* (Phasmatidae; Stanton et al. 2015) (Fig. 3). However, egg capitula are present in a large number of phasmid species, and this interaction with ants is likely to have played an influential role in the evolution and distribution of phasmids worldwide. Despite a paucity of information on the ecology of ant dispersal, this remains the most studied dispersal mechanisms in phasmids, and it builds the first evidence for egg morphological traits and adaptations converging on those of seeds.

Dispersal by other animals—endozoochory and epizoochory

Seed-dispersal strategies using animal vectors are often characterised as either endozoochorous or epizoochorous (van der Pijl 1982). Endozoochory refers to seeds that are dispersed by animals that consume the seeds whole and then deposit the seeds elsewhere after they have moved through the digestive tract unscathed. Epizoochory refers to seeds that 'hitchhike' on animals, either directly through attachment to an animal's fur or through a secondary intermediatory substance such as seeds attached to plant material that the animal relocates, e.g. nesting material collected by birds. There is no direct evidence of either endozoochory or epizoochory occurring intentionally for the dispersal of phasmid eggs. Some

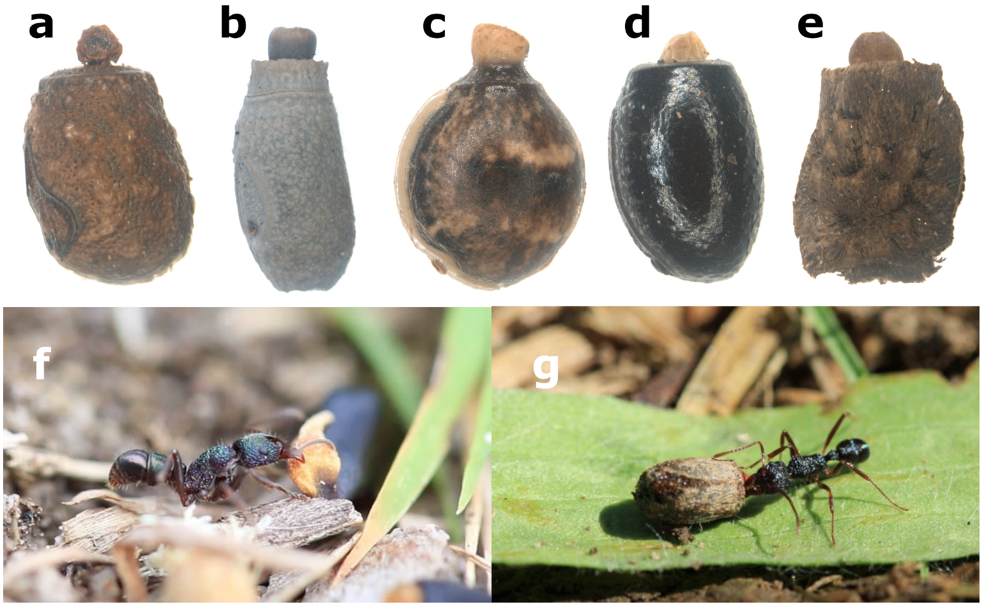

Fig. 3 Capitulate eggs of **a** *Ctenomorpha marginipennis*, **b** *Tropidoderus childrenii*, **c** *Extatosoma tiaratum*, **d** *Anchiale* sp., and **e** *Eurycnema goliath*. **f** *Rhytidoponera* sp. ant holding the elaiosome of an *Acacia* sp. seed. **g** *Rhytidoponera* sp. ant carrying the capitula-bearing egg of a *Eurycnema goliath* stick insect. All species shown here are native to Australia (images: James O'Hanlon)

recent evidence, however, suggests that vertebrate dispersal agents may have the capacity to influence phasmid egg dispersal.

A recent study argued that egg transport via birds may be possible in a manner strangely analogous to the dispersal of seeds ingested in fruit (Suetsugu et al. 2018). The majority of seeds that are dispersed via endozoochory involve frugivores that are physiologically adapted to digest the soft carbohydrate-rich fruit, whilst the hard protein-based seeds remain viable after passing through the digestive tract. Phasmid eggs are not placed in fruits. However, Suetsugu et al. (2018) reasoned that a gravid female phasmid is effectively a 'fruiting' body full of eggs with a hard outer coating that may make them resistant to digestion. Further weight is given to this speculation given that phasmids are parthenogenetic and the eggs inside females can contain viable offspring regardless of their mating status. Suetsugu et al. (2018) fed gravid female *Ramulus irregulariterdentatus* (Phasmatidae) stick insects to captive insectivorous brown-eared bulbuls (*Hypsipetes amaurotis*), and around 5–8% of the eggs that were inside the gravid phasmids survived intact through the digestive tract of the birds. Remarkably, two of these eggs remained viable and later hatched. This led Suetsugu et al. (2018) to suggest that in rare cases, long-distance phasmid dispersal could actually result from bird predation.

Whereas fruits have evolved to attract their animal consumers (e.g. Lomascolo and Schaefer 2010), there is no such suggestion that phasmids are 'intentionally' offering themselves to predators. The work of Suetsugu et al. (2018) was conducted in captivity and is a proof of concept. But whether eggs stored inside predated phasmids survive through the digestive tracts of wild birds, and whether this has contributed to distribution patterns of phasmids, should be taken with caution and is currently speculative.

In plants, seeds may also be dispersed directly by granivores (Orłowski et al. 2016), whereby incomplete digestion can result in seeds being excreted intact and viable. Seeds are known to exhibit some resistance to chemical and mechanical digestion (van der Pijl 1982), yet there is little evidence to show that phasmid eggs are adapted to be similarly resistant. Noting the morphological similarity of some phasmid eggs to seeds, Shelomi (2011) raised the questions of whether they could be dispersed by granivores or are highly susceptible to predation by granivores. In extensive feeding trials, the eggs of *Extatosoma tiaratum*, *Ramulus nematodes*, and *Ramulus artemis* (Phasmatidae) were completely digested following ingestion by quails and domestic chickens. Thus, the possibility of egg dispersal via vertebrates eating 'seed-like' eggs seems unlikely at this stage.

Epizoochory, where plant seeds can adhere to animal fur or feathers and be carried by the animal vector, is one of the least common forms of seed dispersal (Sorensen 1986). It is, however, common in invasive species and, depending on the vector, has the potential to spread seeds over long distances (e.g. Couvreur et al. 2004a). Seeds achieve this adherence through having long hairs and spines that become entangled with the fibres of fur and feathers. The morphology of epizoochorous seeds varies widely, and the presence of complex adherence structures, such as spines with hooks and barbs, greatly increases their chances of staying attached to animal surfaces (e.g. Couvreur et al. 2004b; Kulbaba et al. 2009). A number of phasmid species lay eggs that exhibit long hairs and spines and share a notable resemblance to epizoochorous seeds (e.g. Sellick 1997b; Fig. 1d). For example, the eggs of *Epidares* (Heteropterygidae) species have short coarse hooked hairs

(Fig. 1i), and *Pylaemenes* (Heteropterygidae) eggs have short spines that terminate in a multi-pronged hook (synonym *Datames*; Sellick 1997b). Their similarity to some vertebrate-dispersed plant seeds raises the question of whether they could also function to adhere eggs to mammalian fur or bird feathers.

Whilst no experimental evidence exists for epizoochory in phasmid eggs, the diversity of spines and hairs found on eggs raises an exciting possibility. The potential for stochastic dispersal by animal vectors raises many other possibilities. For example, adherence to plants might lead to dispersal via animals that relocate that plant material. Birds, for instance, are known to relocate seeds when building nests (Dean et al. 1990) and could conceivably also relocate phasmid eggs adhered to plant matter that is collected as nesting material. The attachment of insect eggs to an animal vector is not unprecedented, with aquatic *Daphnia* (Daphniidae) eggs known to hitch a ride with backswimmers that transport the eggs even when in flight (Van de Muetter et al. 2008).

Eggs with specific placement

Attachment to host plant or burial

In contrast to the ancestral 'egg-dropping' strategy, many species have evolved oviposition strategies that involve specific placement of the eggs. The oviposition behaviours associated with specific egg placement can be simple, such as cases where eggs are buried when the ovipositor is simply driven into the soil or a crevice on the host plant, and the eggs are laid in place (Carlberg 1989). *Sipyloidea* and *Orxines* (Lonchodidae) species will frequently wedge eggs into flaky bark and crevices on plants (Bedford 1978; Sellick 1988; Fig. 1g). Alternatively, there can be more elaborate behaviours such as in the case of *Anisomorpha buprestoides* (Pseudophasmatidae) that hold their abdomen upwards and drop eggs into a freshly dug hole below (Hetrick 1949), or *Epidares nolimetangere* (Heteropterygidae) that have been observed to flick their elaborately spined eggs forward where they catch on to female's antennae; the females then proceed to remove the eggs with their forelimbs and place them into the soil (Abercrombie 1992).

Eggs can be glued on the edges of leaves or on the stems of the host plant. These eggs can be elongated, such as in the Australian *Denhama* (Lonchodidae) phasmids that glue long slender eggs to grasses (Fig. 1e). *Spinosipyloidea doddi* (Lonchodidae) lay hairy eggs that have been observed attached to the hairy leaves of their host plant (Brock and Hasenpusch 2009). Generally, phasmid eggs are laid singly, but there are cases of eggs being laid in small discrete clutches (Carlberg 1989). There is one unique case in the Vietnamese subfamily Korinninae (Prisopodidae) of phasmids glueing eggs to surfaces in large ordered groups creating an oval structure reminiscent of the oothecae of praying mantises and tortoise beetles (Goldberg et al. 2015).

Evolutionary ramifications of egg placement

With the possible exception of eggs that are glued to rafting vegetation (described above), eggs that are laid with specific placement are limited in their dispersal abilities. This raises further questions as to what selective pressures have led to the evolution of these strategies across the order. Robertson et al. (2018) showed evidence for multiple independent evolutionary origins of egg burial, or insertion into vegetation as an oviposition strategy, and further suggested that this oviposition strategy is most common in robust-bodied, relatively immobile species. However, the authors do not provide a functional explanation as to how phasmids in this niche would benefit from the specific placement of their eggs. Here, we suggest that the functional benefits of the varied oviposition strategies involving specific placement may include access to host plants and protection from predators and parasites.

Whilst some phasmids have a wide range of host plants they can feed on, those that are species-specific are limited to certain plants that can have patchy distributions. It thus becomes important for insects to remain with their host plant (Cernak and Hasenpusch 2000; Bragg 2001). Specific placement of eggs on or near the host plant may ensure that nymphs emerge close to their required food source (Goldberg et al. 2015). This is particularly important for groups with robust bodies and very limited dispersal abilities, such as the 'tree lobster' groups of phasmids (e.g. Lonchodinae, Fig. 1b).

Egg placement amongst soil or vegetation may provide protective benefits such as simple concealment camouflage from both predators and parasites. It has been hypothesised that *Sipyloidea doddi* (Lonchodidae) could gain chemical protection by adhering their eggs to *Alstonia muelleriana* (Milkwood) plants, which exude a white noxious chemical from any part of the tree that has been exposed (Brock and Hasenpusch 2009), potentially warding off predators.

There are two subfamilies of Chrysididae wasps known to be obligate parasitoids of phasmid eggs, Amiseginae and Lobosceliidinae (Krombein 1956; Baker 2016). It is conceivable that egg burial and oviposition into tight crevices could protect eggs from predators and parasites. Hughes and Westoby (1992) showed that *Didymuria violescens* (Phasmatidae) eggs sampled from leaf litter and soils had reduced rates of parasitism with increasing soil depth. Female Amiseginae and Lobosceliidinae wasps are generally flightless and live amongst leaf litter (Krombein 1983a; Kimsey 2012). As such, it has been hypothesised that adhering eggs to plant surfaces away from the ground may function to keep eggs away from parasites (Goldberg et al. 2015). However, these two groups of parasitoids are elusive and rarely encountered, and little is known about their behaviour and biology, including how they locate eggs. Several specimens of phasmid parasitoids have been sampled from malaise traps, indicating that some species may be capable of inhabiting and locating eggs within arboreal habitats (Krombein 1983b).

Conclusions and future research directions

The morphological similarities between seeds and phasmid eggs have been noted for some time (Henneguy 1890; Severin 1910; Compton and Ware 1991; Hughes and Westoby 1992), and phasmid eggs are often described as ‘seed mimics’. For the eggs to truly mimic a seed, though, it must be shown that they resemble a specific ‘model’ that leads to other animals incorrectly identifying them and behaving towards the eggs in some way that benefits the phasmid. To our knowledge, there has been no real attempt at quantifying visual similarities between phasmid eggs and seeds. Botanists exposed to phasmid eggs have apparently mistaken them for seeds (Severin 1910), and there have been claims of phasmid eggs closely resembling legume seeds (Bedford 1978). However, there remains no evidence that particular phasmid eggs resemble specific ‘model’ species. Suggestions that phasmid eggs may gain protection from egg predators by resembling seeds are difficult to justify, particularly given that resembling seeds could perceivably lead to consumption by granivores.

Even the evidence that ant-dispersed phasmid eggs share chemical similarities with tree seeds does not necessarily imply mimicry but instead may represent a remarkable example of convergence. The chemicals that elicit the carrying behaviour in ants are common fatty acids that may simply reflect the nutritional content of both seed capitula and egg elaiosomes (Stanton et al. 2015). Rather than being ‘seed mimics’, the apparent convergences between phasmid eggs and seeds may be broadly attributable to niche similarities between plants and phasmids, leading to convergence towards similar embryonic survival and dispersal strategies.

The morphological traits of plant seeds are known to correlate strongly with dispersal mechanisms (Thomson et al. 2010). It stands to reason that egg traits may also allow researchers to identify putative dispersal mechanisms in phasmids, allowing for explicit hypothesis testing. For example, multiple independent studies have demonstrated the role of the egg capitula in eliciting ant dispersal (Compton and Ware 1991; Hughes and Westoby 1992; Windsor et al. 1996; Stanton et al. 2015), though the list of species in which this has been investigated is hardly exhaustive. Phasmid eggs appear to display a range of morphological structures that have parallels in seeds, which may indicate further examples of convergence in dispersal strategy.

Whilst there is evidence for oceanic dispersal having had large-scale impacts on the evolution and distribution of phasmids (e.g. Bradler et al. 2015), this evidence is lacking for many other forms of egg dispersal such as the possibility of dispersal via mammalian or bird vectors. The most well-documented animal vector for phasmids is ants that are attracted to egg capitula. The convergent case of ant-based seed dispersal in plants has been shown to have had global impacts on the distribution and species diversity of angiosperm plants (Lengyel et al. 2009, 2010). Given the large number of phasmid species whose eggs have a capitulum, ants have likely had a similar impact on the distribution and evolution of phasmids. Research into the functional benefits of ant-based dispersal in phasmids may reveal whether there are environmental factors, such as bushfires or the presence of suitable ant species as vectors, which can lead to the evolution of ant-based dispersal strategies in both plants and phasmids. Similarly, hypothesis-driven research into the potential for phasmid egg dispersal via both abiotic and biotic vectors is warranted.

Many species eggs have yet to be formally described, and our understanding of egg morphology and ecology is mostly limited to a number of species that are easily reared in captivity. Further exploratory and descriptive work will help to further reveal how egg traits vary based on phylogenetic relationships. As research begins to uncover the functional benefits of the diverse egg morphologies of phasmids, we can begin to address the broader selective pressures and trade-offs influencing evolutionary patterns across the order. More evidence is needed to begin speculating on how the local environment, and the ecology of the adults, may influence the dispersal and protection strategies used by eggs. For example, do species that show host plant specificity use egg-laying strategies that place newly hatched nymphs near suitable food sources? In which case, do niche similarities between phasmids and their host plants exert significant selective pressures to result in co-evolution of both phasmid and host plant dispersal methods, as in the example of oceanic dispersal in *Megacrania* stick insects and their *Pandanus* host plants discussed above? And does the dispersal ability of the adult stage influence whether eggs exhibit dispersal adaptations? With the exception of a few experiments showing that eggs are viable following immersion in seawater (Wang and Chu 1982), we know very little about the physiological ability of eggs to withstand environmental conditions that would make particular protective and dispersal strategies viable. Are eggs specifically adapted to withstand submersion, digestion, and the bite forces of ants that apparently act as their nursery maids? Furthermore, considering that phasmid eggs can lay dormant for years, what environmental conditions may trigger hatching, how do these reflect local conditions, and how may this benefit the hatchlings? The same niche similarities that may have led to convergence in dispersal strategies may have led to convergence in other aspects of plant and phasmid biology and ecology.

Phasmids are renowned for their morphological resemblance to plants and are regarded as highly sophisticated examples of camouflage and masquerade. Their similarity to plants does not stop there, and, as we are learning more about their dynamic life cycles, it appears that the embryonic stages of both plants and phasmids share some uncanny similarities. The incredible diversity seen in phasmid eggs has been a source of fascination for many years. Despite this fascination, our understanding of the dynamic ecology of phasmid eggs is in its infancy. We have showcased here the wealth of existing hypotheses and natural history observations surrounding the ecology and evolution of eggs that we hope will act as a foundation for exciting research in the future.

Code availability Not applicable.

Authors' contributions All authors contributed equally to this work, including the conception, development, and writing of this manuscript.

Data availability Not applicable.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Abercrombie I (1992) Egg laying by *Epidares nolimetangere* (de Haan) and *Dares ulula* (Westwood). Phasmid Stud 1:2–4

Altig R, McDiarmid R (2007) Morphological diversity and evolution of egg and clutch structure in amphibians. Herpetol Monogr 21:1–32

Augspurger CK (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. Am J Bot 73:353–363

Baker E (2016) An online taxonomic database of the stick insect (Phasmida) egg-parasitising subfamilies Amiseginae and Loboscelidiinae (Hymenoptera: Chrysididae). Biodivers Data J 4: e7441

Bedford G (1978) Biology and ecology of the Phasmatodea. Annu Rev Entomol 23:125–149

Bohonak AJ (1999) Dispersal, gene flow, and population structure. Q Rev Biol 74:21–45

Bradler S, Cliquennois N, Buckley T (2015) Single origin of the Mascarene stick insects: ancient radiation on sunken islands? BMC Evol Biol 15:196

Bragg PE (2001) Phasmids of Borneo. Natural History Publications, Kota Kinabalu

Brendonck L, Riddoch BJ (1999) Wind-borne short range egg dispersal in anostracans (Crustacea: Branchiopoda). Biol J Linn Soc 67:87–95

Brew CR, O'Dowd J, Rae ID (1989) Seed dispersal by ants: behaviour-releasing compounds in elaiosomes. Oecologia 80:490–497

Brock PD, Hasenpusch JW (2009) The complete field guide to Australian stick and leaf insects. CSIRO Publishing, Collingwood

Burns K (2012) Seed dispersal: the blind bomb maker. Curr Biol 22: R535–R537

Carlberg U (1983) A review of different types of egglaying in the Phasmida in relation to the shape of the eggs and with a discussion on their taxonomic importance (Insecta). Biol Zentralblatt 102:587–602

Carlberg U (1989) Group effect during postembryonic development in *Eurycantha calcarata* Lucas (Insecta: Phasmida). Fauna Nor 46: 101–106

Cernak M, Hasenpusch J (2000) Distribution, biology and conservation status of the peppermint stick insect, *Megacrania batesii* (Kirby) (Phasmatodea: Phasmatidae), in Queensland. Mem Qld Mus 46: 67–68

Cherry M, Gosler A (2010) Avian eggshell coloration: new perspectives on adaptive explanations. Biol J Linn Soc 100:753–762

Church S, Donoghue S, de Medeiros B, Extavour C (2019) Insect egg size and shape evolve with ecology but not developmental rate. Nature 571:58–64

Clark JT (1976) The eggs of stick insects (Phasmida): a review with descriptions of the eggs of eleven species. Syst Entomol 1:95–105

Cliquennois N, Brock PD (2004) Phasmids of Mauritius: *Mauritiophasma* n. gen., *Monognoisis* n. gen., *Epicharmus* Stal 1875 and discussion on their remarkable eggs (Phasmatodea). J Orthop Res 13:1–13

Compton SG, Ware AB (1991) Ants disperse the elaiosome-bearing eggs of an African stick insect. Psyche (Stuttg) 98:207–214

Couvreur M, Christiaen B, Verheyen K, Hermy M (2004a) Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. Appl Veg Sci 7:229–236

Couvreur M, Vandenberghe B, Verheyen K, Hermy M (2004b) An experimental assessment of seed adhesivity on animal furs. Seed Sci Res 14:147–159

Dean W, Milton S, Siegfried W (1990) Dispersal of seeds as nest material by birds in semiarid karoo shrubland. Ecology 71:1299–1306

Evangelista D, Hotton S, Dumais J (2011) The mechanics of explosive dispersal and self-burial in the seeds of the filaree, *Erodium cicutarium* (Geraniaceae). J Exp Biol 214:521–529

Fischer RC, Richter F, Hadacek F, Mayer V (2008) Chemical differences between seeds and elaiosomes indicate an adaptation to nutritional needs of ants. Oecologia 155:539–547

Gallaher T, Callmander M, Buerki S, Keeley S (2015) A long distance dispersal hypothesis for the Pandanaceae and the origins of the *Pandanus tectorius* complex. Mol Phylogenet Evol 83:20–32

Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos 112:481–429

Goldberg J, Bresseel J, Constant J, Kneubühler B, Leubner F, Michalik P, Bradler S (2015) Extreme convergence in egg-laying strategy across insect orders. Sci Rep 5:7825

Guerra-Grenier E (2019) Evolutionary ecology of insect egg coloration: a review. Evol Ecol 33:1–9

Hallman K, Griebler E (2015) Eggshell types and their evolutionary correlation with life-history strategies in squamates. PLoS ONE 10: e0138785

Heatwole H, Levins R (1972) Biogeography of the Puerto Rican Bank: flotsam transport of terrestrial animals. Ecology 53:112–117

Henneguy LF (1890) Note sur la structure de l'enveloppe de l'oeuf des Phyllies. Bull Société Philomanthique Paris 2:18–25

Hetrick LA (1949) The oviposition of the two-stiped walkingstick *Anisomorpha buprestoides* (Stoll). Proc Entomol Soc Wash 51: 103–104

Horn H, Nathan R, Kaplan S (2001) Long distance dispersal of tree seeds by wind. Ecol Res 16:877–885

Hughes L, Westoby M (1992) Capitula on stick insect eggs and elaiosomes on seeds: convergent adaptations for burial by ants. Funct Ecol 6:642–648

Jackson J (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull Mar Sci 39:588–606

Katsis A, Davies M, Buchanan K et al (2018) Prenatal exposure to incubation calls affects song learning in the zebra finch. Sci Rep 8:15232

Kilner R (2006) The evolution of egg colour and patterning in birds. Biol Rev 81:383

Kimsey LS (2012) Review of the odd chrysidid genus *Loboscelidia* Westwood, 1874 (Hymenoptera, Chrysididae, Loboscelidiinae). ZooKeys 213:1–40

Kobayashi S, Usui R, Nomoto K, Ushirokita M, Denda T, Izawa M (2014) Does egg dispersal occur via the ocean in the stick insect *Megacrania tsudai* (Phasmida: Phasmatidae)? Ecol Res 29:1025–1032

Krombein KV (1956) A generic review of the Amiseginae, a group of Phasmatid egg parasites, and notes on the Adelphinae (Hymenoptera, Bethyloidea, Chrysididae). Trans Am Entomol Soc 82:147–215

Krombein KV (1983a) Biosystematic studies of Ceylonese wasps, XI: a monograph of the Amiseginae and Loboscelidiinae (Hymenoptera: Chrysididae). Smithson Contrib Zool

Krombein KV (1983b) Three new egg parasites of South African walking sticks (Hymenoptera: Chrysididae, Amiseginae). J Entomol Soc S Afr 46:139–146

Kulbaba M, Tardif J, Staniforth R (2009) Morphological and ecological relationships between burrs and furs. Am Midl Nat 161:380–392

Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR (2009) Ants sow the seeds of global diversification in flowering plants. PLoS ONE 4: e5480

Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR (2010) Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants. Perspect Plant Ecol Evol Syst 12:43–55

Lomascolo S, Schaefer HM (2010) Signal convergence in fruits: a result of selection by frugivores? J Evol Biol 23:614–624

Mainwaring M, Hartley I, Lambrechts M, Deeming C (2014) The design and function of birds' nests. Ecol Evol 20:3909–3928

Montgomerie R, Weatherhead P (1988) Risks and rewards of nest defence by parent birds. Q Rev Biol 63:167–187

Muñoz J, Felicísimo ÁM, Cabezas F, Burgaz AR, Martínez I (2004) Wind as a long distance dispersal vehicle in the Southern Hemisphere. Science 304:1144–1147

Murray DR (1986) Seed dispersal. Academic Press, Sydney

Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long-distance seed dispersal. Trends Ecol Evol 23:638–647

Orłowski G, Czaranecka J, Goławski A et al (2016) The effectiveness of endozoochory in three avian seed predators. J Ornithol 157:61–73

Panov V, Caceres C (2007) Role of diapause in dispersal of aquatic invertebrates. In: Diapause in Aquatic Invertebrates Theory and Human Use. Springer

Pincel T, Brendonck L, Vanschoenwinkel B (2016) Propagule size and shape may promote local wind dispersal in freshwater zooplankton-a wind tunnel experiment. Limnol Oceanogr 61:122–131

Refsneider J, Janzen FJ (2010) Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. Annu Rev Ecol Evol Syst 41:39–57

Robertson J, Bradler S, Whiting MF (2018) Evolution of oviposition techniques in stick and leaf insects (Phasmatodea). Front Ecol Evol 6:216

Royle N, Smiseth N, Kölliker M (2012) The evolution of parental care. Oxford University Press, Oxford

Sellick J (1988) The capitula of phasmid eggs: an update with a review of the current state of phasmid ootaxonomy. Zool J Linnean Soc 93: 273–282

Sellick J (1994) Phasmida (stick insect) eggs from the Eocene of Oregon. Palaeontology 37:913–922

Sellick J (1997a) The range of egg capsule morphology within the Phasmatodea and its relevance to the taxonomy of the order. Ital J Zool 64:97–104

Sellick J (1997b) The "umbrella" spines and other surface projections of some phasmid eggs and some comments on phasmid taxonomy. Phasmid Stud 6:15–20

Sellick J (1997c) Descriptive terminology of the phasmid egg capsule, with an extended key to the phasmid genera based on egg structure. Syst Entomol 22:97–122

Severin HHP (1910) A study on the structure of the egg of the walking-stick, *Diapheromera femorata* Say; and the biological significance of the resemblance of phasmid eggs to seeds. Ann Entomol Soc Am 111:83–89

Shelomi M (2011) Phasmid eggs do not survive digestion by quails and chickens. J Orthop Res 20:159–162

Smith J (1994) Patterns of disseminule dispersal by drift in the north-west Coral Sea. N Z J Bot 32:435–461

Sorensen A (1986) Seed dispersal by adhesion. Annu Rev Ecol Syst 17: 443–463

Stanton A, Dias D, O'Hanlon JC (2015) Egg dispersal in the Phasmatodea: convergence in chemical signaling strategies between plants and animals? J Chem Ecol 41:689–695

Stockard CR (1908) Habits, reactions, and mating instincts of the 'walking-stick', *Aplopus mayeri*. Publ Carnegie Inst Wash 103:43–59

Suetsugu K, Funaki S, Takahashi A, Ito K, Yokoyama T (2018) Potential role of bird predation in the dispersal of otherwise flightless stick insects. Ecology 99:1504–1506

Swaine MD, Beer T (1977) Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytol 78:695–708

Tallamy D (2000) Sexual selection and the evolution of exclusive paternal care in arthropods. Anim Behav 60:559–567

Taylor J (1976) The advantage of spacing-out. J Theor Biol 59:485–490

Thiel M, Gutow L (2005) The ecology of rafting in the marine environment. I. The floating substrata. Oceanogr Mar Biol Annu Rev 42: 181–264

Thomson FJ, Moles AT, Auld TD, Ramp D, Ren S, Kingsford RT (2010) Chasing the unknown: predicting seed dispersal mechanisms from plant traits. J Ecol 98:1310–1318

Traveset A, Robertson A, Rodríguez-Pérez A (2007) A review on the role of endozoochory in seed germination. Seed Dispersal Theory Its Appl Chang World 78–103

Traveset A, Heleno R, Nogales M (2014) The ecology of seed dispersal. Seeds Ecol Regen Plant Communities 3:62–93

Trueman J, Pfeil B, Kelchner S, Yeates D (2004) Did stick insects really regain their wings? Syst Entomol 29:138–139

Ushirokita M (1998) Eggs of stick insect drifting in the wake of screw pine's seed. Insectarium 35:108–115

Van de Muetter F, Stoks R, De Meester L (2008) Size selective dispersal of Daphnia resting eggs by backswimmers (*Notonecta maculata*). Biol Lett 4:494–496

van der Pijl L (1982) Principles of dispersal in higher plants, 3rd edn. Springer-Verlag, Berlin

Wang C-H, Chu Y-I (1982) The morphological study of the egg shell of the Tsuda's giant stick insect *Megacrania alpheus* Westwood. NTU Phytopathol Entomol 9:98–109

Wang B, Smith TB (2002) Closing the seed dispersal loop. Trends Ecol Evol 17:379–386

Whiting MF, Bradler S, Maxwell T (2003) Loss and recovery of wings in stick insects. Nature 421:264–267

Windsor DM, Trapnell DW, Amat G (1996) The egg capitulum of a neotropical walkingstick, *Calynda bicuspis*, induces aboveground egg dispersal by the ponerine ant, *Ectatomma ruidum*. J Insect Behav 9:353–367

Wong J, Meunier J, Kölliker M (2013) The evolution of parental care in insects: the roles of ecology, life history and the social environment. Ecol Entomol 38:123–137

Yamasaki T (1991) Occurrence of *Megacrania alpheus* (Cheleutoptera: Phasmatidae) in Iriomote-jima Island, Ryukyus. Proc Jpn Soc Syst Zool 44:49–56

Yeh H, Tseng H, Lin CP et al (2018) Rafting of floating fruit is effective for oceanic dispersal of flightless weevils. J Exp Biol 221:jeb190488