Phasmid Eggs Do Not Survive Digestion by Quails and Chickens

Author: Shelomi, Matan

Source: Journal of Orthoptera Research, 20(2) : 159-162

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.020.0203

Phasmid eggs do not survive digestion by quails and chickens

Matan Shelomi

Department of Entomology, University of California Davis, 1 Shields Ave., Davis, CA 95616. Email: mshelomi@ucdavis.edu

Abstract

The eggs of several Phasmatodea (stick insects) species bear strong resemblances to plant seeds. Such mimicry could increase predation on the eggs by vertebrate granivores, especially on eggs that are not buried by ants. In contrast, predation could be beneficial to the insects if the eggs can survive the digestive tract and hatch afterwards. This experiment tests the hypothesis that granivorous birds can act as dispersal agents for phasmid eggs. The eggs of three walking stick species—*Extatosoma tiaratum*, *Ramulus nematodes*, and *R. artemis*—were offered to two species of terrestrial, granivorous bird: quail (*Coturnix japonica*) and chickens (*Gallus gallus domestica*). The birds consumed the eggs eagerly. Examination of the resulting manure showed that most eggs were completely digested. Only one unbroken egg was recovered out of nearly one thousand eggs fed, suggesting that these bird species could not disperse phasmid eggs. Seed-mimicry's fitness costs must be mitigated in nature to explain its prevalence in the Phasmatodea.

Key words

Phasmatodea, egg, mimicry, capitulum, dispersal, bird, *Extatosoma*, *Ramulus*

Introduction

Entomologists and botanists alike have long remarked on the similarity of the eggs of several Phasmatodea (stick insects) to plant seeds (Henneguy 1890, Sharp 1898, Severin 1910, Bedford 1978, Stockard 2006). Many resemble the toxic seeds of lupins (*Lupinus* sp., Fabaceae), but others resemble the seeds of other, nontoxic legumes (Bedford 1978, Hinton 1981). The similarity in size, coloration, toughness, and structure is strong enough that some botanists have mistaken phasmid eggs for the seeds of specific plant species (Brongniart 1887, Severin 1910). Severin (1910) dismissed the resemblance as having "no bionomic importance", but others have disagreed. Phasmid eggs are most often dropped or ejected onto the ground with little care, exposing them to many terrestrial predators (Hinton 1981, Carlberg 1984, Hughes & Westoby 1992). One hypothesis is that phasmid eggs evolved to resemble seeds because such eggs were ignored by egg-feeding birds and parasitoids (Goeldi 1886), although the latter are known to detect eggs through chemoreception and are unlikely to be fooled by physical mimicry (Severin 1910, Grimpe 1921).

A second hypothesis is that seed mimicry facilitates dispersal and protection of phasmid eggs by ants. Ants collect the eggs of many phasmid species (Compton & Ware 1991, Hughes & Westoby 1992). Furthermore, the eggs of some phasmid species possess on their crown a hard, non-respiratory, knob-like structure called a capitulum (Hughes & Westoby 1992), which can be removed without damage to the egg (Clark 1979). Capitula often resemble the lipid-rich elaiosomes that are present on the seeds of some plants, and which are a favorite food of ants (Compton & Ware 1991). Both the capitula and elaiosomes may have convergently evolved to facilitate removal and burial of the eggs by ants (Hughes & Westoby 1992). Ants more frequently reject eggs that lack capitula (Compton & Ware 1991) or which have had the capitula artificially removed (Hughes & Westoby 1992). Inside the nest, the phasmid eggs are kept safe not only from egg parasitoids, but also from insectivorous birds.

This myrmecochory has been well documented in the phasmid *Extatosoma tiaratum*, whose first instar nymphs go further by mimicking the ants of the genus *Leptomyrmex* (Mayr) in appearance and behavior (Key 1970): this presumably facilitates escape from the nest to the surface after hatching. Some ant species remove (and possibly eat) the capitulum, and then discard the egg (Hughes & Westoby 1992). Phasmid eggs seem to survive and hatch with or without this structure (Hughes & Westoby 1992).

However, not all phasmids are associated with ants. While capitula are consistently absent on the eggs of phasmids that bury or glue their eggs — in which case predation by birds and retrieval by ants is less likely—capitula are also missing in several species and genera that do drop their eggs, such as *Ramulus* (Hughes & Westoby 1992). These eggs still resemble seeds: *R. nematodes* eggs' micropilar plates strongly resemble a seed's hilum (the scar on the seed coat from attachment to the ovary wall), for example (Sharp 1898). This similarity, without the benefits of myrmecochory, puts these eggs at risk: while insectivorous birds may avoid seed-shaped eggs, granivorous birds should be more likely to eat them (Goeldi 1886). This risk of predation is highest for eggs that do not attract ants, as they have no known protection against granivorous birds. The prevalence of seed-mimicking phasmid eggs suggests the cost of predation is either minimal or offset by other advantages. Especially for eggs that are not carried by ants, if they are able to survive passage through a granivorous bird's gut and remain viable, then not only would there be no penalty from bird predation, but also the birds would become a method of dispersal.

Support for the hypothesis that phasmid eggs can be dispersed via digestion and elimination by a vertebrate predator is that phasmid eggs possess a distinct layer of calcium oxalate in the outer exochorion layer of their eggshells (Pantel 1919, Robertson 1941, Moscona 1950, Clark 1958) that requires a pH of 2 to dissolve (Moscona 1950). While some other insects have calcium oxalate crystals in their eggs (Clark 1958), phasmids appear to be unique among insects in possessing a distinct layer of this substance in the outer layer of the egg shell. The calcium oxalate layer has no known function in regards to the ant-burying hypothesis, unless it protects the eggs from omnivorous ants, ant inquilines, or generalist predators and parasites. In addition, this layer is found in both capitulum-free and capitulum-bearing eggs, suggesting that the chemical is not specific to phasmid species whose eggs are buried by ants. Evidence that the eggs of *Extatosoma tiaratum* (Macleay) can survive submergence of over two hours in hydrochloric acid without any disruption of the outer walls (Hinton 1981), suggests eggs may have evolved the layer as a means to withstand a bird's digestive system. However, at this time, it is unknown if birds will consume phasmid eggs and if such eggs can survive passage through their guts.

This experiment marks the first time live birds have been used to test the concept of granivorous birds as a phasmid dispersal agent. The two hypotheses are that grain-feeding birds will accept and consume phasmid eggs, and that the eggs will survive passage through the gut and remain viable. To test these ideas, eggs from three different phasmid species were offered to two species of terrestrial, granivorous birds, whose manure was later examined for the presence of unbroken eggs.

Material and methods

The walking sticks used in this experiment were laboratory-reared specimens from the Bohart Museum of Entomology in the University of California, Davis. Eggs were collected from tank bottoms within three days of oviposition. Three species were used: *E. tiaratum*, an Australian phasmid known to fling its robust eggs up to 2 m horizontally when ovipositing (Carlberg 1984) and whose capitulum-bearing eggs are known to be dispersed by ants (Hughes & Westoby 1992); *Ramulus nematodes* (de Haan), an apterous species from Thailand with long and thin eggs with no capitulum; and *Ramulus artemis* (Westwood), an apterous and parthenogenetic species from Vietnam with flaxseed-shaped eggs and no capitulum (Fig. 1).

The birds used in the experiment were reared and kept in the Hopkins Avian Sciences Research Facility at UC Davis. All were healthy and kept indoors in cages with wire bottoms that allowed manure to fall through. Two species were used: the Japanese quail, *Coturnix japonica* (Temminck & Schlegel) and the chicken, *Gallus gallus domesticus* (Linnaeus). Both species are terrestrial grain-feeders, the type of bird expected to encounter and possibly consume a phasmid egg in the field. Hinton (1981) believed phasmid eggs were very likely to pass through quail guts unharmed and *C. japonica* has also been reported in the same geographical locations as the *Ramulus* species (Madge *et al.* 2002, Brock 2003). Grimpe (1921) showed that chickens will eat phasmid eggs, but he did not report on the passage of eggs into the droppings. Four female and one male quail 8 to 9 weeks old, and five 16 to 18-month old, single-comb White Leghorn hens were each put into separate cages. Quails and chickens were reared in separate henhouses. All birds were fed Purina Mills® Layena® crumbles, broken into medium sized bits. No birds had grit added to their diet at any point in their lifetime.

On the date of the experiment, food was put in a trough in front of the cages as per the birds' standard daily care. For the quails, the food was placed at a depth of < 2 cm to ensure the birds did not use the food to dust themselves and to minimize flinging. Feeding troughs were divided to ensure no bird could access food that was not assigned to it. A total of 140 *R. nematodes* and 170 *R. artemis* eggs were divided evenly among each quail and sprinkled on top of the quails' diet. A total of 145 *R. nematodes* and 480 *E. tiaratum* eggs were divided among the chickens. The eggs of *E. tiaratum* were not given to the quail as they were too large and posed a choking hazard. A plastic sheet was spread underneath each cage to collect any manure. Birds were observed a few hours after feeding and each morning after to see if the eggs had been consumed, ignored, or dropped onto the plastic sheet from the trough. No additional food was provided after the eggs were added for the duration of the experiment, as the food provided was more than sufficient. The sheets were collected after 72 h, which far exceeds the maximum time needed for food to pass through these birds' digestive system (Farner 1960), and the manure manually searched for any sign of insect eggs.

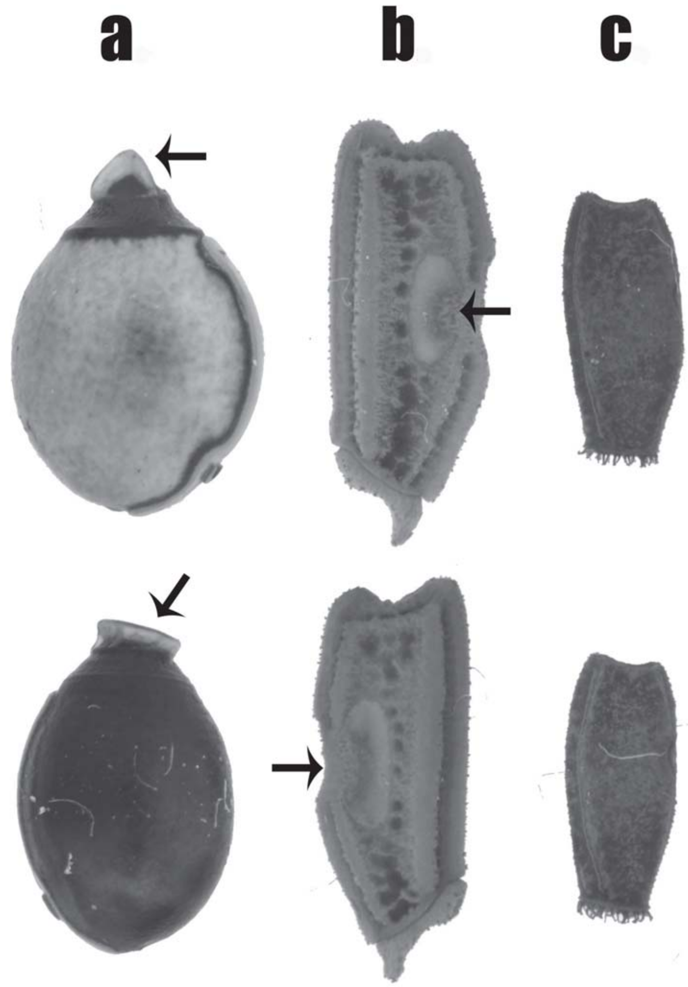

Fig. 1. Whole eggs of three species of Phasmatidae: a) *Extatosoma tiaratum* (arrows point to capitulum), b) *Ramulus nematodes* (arrows point to micropilar plate) and c) *Ramulus artemis*. (Photos by Andrew Richards).

Results

The birds appeared to prefer phasmid eggs. When presented with eggs mixed with their normal food, both the quail and the chickens immediately began to select and eat the eggs, and consumed most or all of them within a few hours. Two quail and one chicken ate every egg presented to them. A total of two *E. tiaratum* eggs were recovered from the uneaten chicken feed, and a total of twenty-four *R. artemis* and twenty-five *R. nematodes* eggs were left in the quails' feed. No eggs were dropped or thrown out of the cage. The manure of both birds was almost devoid of any distinctive solid particles. Only a single, unbroken egg was recovered from the entire experiment: an *E. tiaratum* egg found in the chicken manure (Fig. 2). Otherwise, two badly-damaged *R. nematodes* eggs and one damaged *E. tiaratum* egg were recovered from the chicken manure; five shells

Fig. 2. The single, unbroken *E. tiaratum* egg collected from the manure of a chicken. (Photos by Andrew Richards).

or shell halves of the *R. artemis* eggs and three whole but crushed, *R. nematodes* eggs were recovered from the quail manure (Fig 3). All other eggs had been digested beyond recognition. In total, out of 935 eggs fed to the birds, 884 were eaten (94.5%), and of these, only one (0.11%) passed the gut whole enough to remain viable.

Discussion

This experiment shows that chickens and quail will not only eat phasmid eggs, but may prefer them over their normal laboratory food. Whether this is due to novelty or the birds being fooled by the seed mimicry is unknown. Nearly all of the eggs were digested beyond recognition. The presence of the one whole egg and some relatively intact but hollow eggs suggests that phasmid eggshells are somewhat resistant to the digestive acids of the bird's gut, as predicted by Hinton (1981). The damage patterns and the dearth of recovered fragments suggest that the eggs had been mechanically broken by the beaks and/or the gizzards of the bird. Once the eggshell is broken, the digestive enzymes of the birds can digest the phasmid embryo even if the eggshell passes through the gut. The one egg that survived must therefore have been swallowed whole. Bird-dispersed seeds are usually consumed along with a protective fruit, while phasmid eggs have no protection beyond their shells.

Though even a low percentage of successful passage of eggs through the gut can be enough to disperse a species, this experiment suggests that dispersal of phasmid eggs by quails and chickens is highly unlikely. The combination of biting, mechanical grinding by the bird's gut, and the action of any grit the bird has consumed (grit was not a factor in this experiment) would lead to the complete destruction of any eggs consumed. Thus, at least with chickens and quail, seed mimicry of the egg is demonstrated to have a cost that cannot be offset by bird-related dispersal.

Our results suggest that the evolution of myrmecophory by *E. tiaratum* and other capitulum-bearing phasmids may serve to protect the phasmid egg from consumption by granivorous birds, or at least offset the loss of fitness due to this predation. For capitulum-free eggs however, no known system exists to reduce the fitness cost. Field studies comparing the rate of consumption by birds to that of ant burial in capitulum-free eggs are needed. It is important to note that we tested only chickens and quail; other bird species could produce different results. Other small, granivorous birds such as finches and sparrows, omnivorous birds such as starlings, and waterfowl may also consume phasmid eggs, but give different results. The phasmid eggs tested here can float in water (unpub. data), so the possibility exists that the eggs are washed into bodies of water and consumed by ducks (Brochet *et al.* 2009) and other migratory shorebirds or waders (Green *et al.* 2002, Sánchez *et al.* 2006), whose beaks are less efficient at breaking seeds and who are known to internally transport and disperse seeds of fruitless plants (Sánchez *et al.* 2006) as well as invertebrates (Green & Sánchez 2006, Frisch *et al.* 2007). However, the likelihood of phasmids depending on aquatic birds for dispersal is low. A field study identifying the proportion of a phasmid female's total egg output that is consumed by birds or other organisms will provide further information.

In conclusion, our results demonstrate that phasmid eggs cannot survive ingestion by quail and chickens. However, there is still the possibility that they can survive transit through the guts of some other bird species. We also have shown that quails and chickens are eager to consume phasmid eggs. Bird predation on phasmid eggs would select for egg-defense mechanisms, such as burial by ants.

Acknowledgements

The author thanks Lynn Kimsey, Steve Heydon, and the staff at the Bohart Museum of Entomology, and the Facility Manager of the Hopkins Avian Facility, Jacqueline Pisenti. Egg photographs were taken by Andrew Richards, UC Davis.

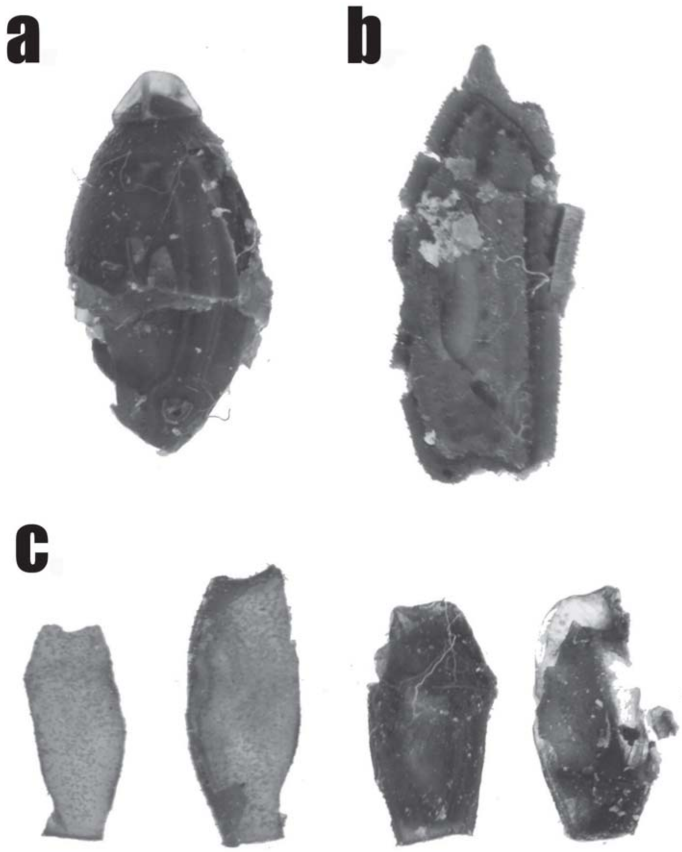

Fig. 3. Fragments of phasmid eggs recovered from bird manure: a) Smashed *E. tiaratum* egg passed by a chicken. b) Cracked and damaged *R. nematodes* egg passed by a quail. c) *R. artemis* egg shell halves or hollows passed by the quails. (Photos by Andrew Richards).

References

Bedford G.O. 1978. Biology and ecology of the Phasmatodea. Annual Review of Entomology 23: 125-149.

Brochet A.L., Guillemain M., Fritz H., Gauthier-Clerc M., Green A.J. 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. Ecography 32: 919-928.

Brock P.D. 2003. Rearing and Studying Stick and Leaf Insects. Cravitz Printing Company Ltd, Orpington, UK.

Brongniart C. 1887. [No title]. Bulletin de Société Entomologique de France 7: 84-87.

Carlberg U. 1984. Oviposition behavior in the Australian stick insect *Extatosoma tiaratum*. Experientia 40: 888-889.

Clark E.W. 1958. A review of literature on calcium and magnesium in insects. Annals Entomological Society of America 51: 142-154.

Clark J.T. 1979. The capitulum of phasmid eggs (Insecta: Phasmida). Zoological Journal Linnean Society 59: 365-375.

Compton S.G., Ware A.B. 1991. Ants disperse the elaiosome-bearing eggs of an African stick insect. Psyche 98: 207-214.

Farner D.S. 1960. Digestion and the digestive system, pp. 411-464. In: Marshall A.J. (Ed.). Biology and Comparative Physiology of Birds. Academic Press, London.

Frisch D., Green A.J., Figuerola J. 2007. High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds. Aquatic Sciences 69: 568-574.

Goeldi E.A. 1886. Die Eier zweier brasilianischen Gespenstheuschrecken. Zoologische Jahrbücher 1: 724-729.

Green A.J., Figuerola J., Sánchez M.I. 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. Acta Oecologica 23: 177-189.

Green A.J., Sánchez M.I. 2006. Passive internal dispersal of insect larvae by migratory birds. Biology Letters 2: 55-57.

Grimpe G. 1921. Beitrage zur Biologie von *Phyllium bioculatum* G. R. Gray (Phasmidae). Zoologische Jahrbücher 44: 227-266.

Henneguy L.F. 1890. Note sur la structure de l'enveloppe de l'oeuf des Phyllies. Bulletin de Société Philomanthique de Paris 2: 18-25.

Hinton H.E. 1981. Biology of Insect Eggs. Pergamon Press Ltd, Oxford.

Hughes L., Westoby M. 1992. Capitula on stick insect eggs and elaiosomes on seeds: convergent adaptations for burial by ants. Functional Ecology 6: 642-648.

Key J.H.L. 1970. Phasmatodea, pp. 348-359. In: CSIRO (Ed.) The Insects of Australia. Melbourne University Press, Melbourne, Australia.

Madge S., McGowan P., Kirwan, G.M. 2002. Pheasants, Partridges, and Grouse. Christopher Helm, London.

Moscona A. 1950. Studies of the egg of *Bacillus libanicus* (Orthoptera, Phasmidae) I. The egg envelopes. Quarterly Journal of Microscopical Science 91: 183-193.

Pantel J. 1919. Le calcium dans la physiologie normale des Phasmides (Orth.): oeuf et larve eclosante. Comptes Rendus de l'Académie des Sciences, Paris 168: 127-129.

Robertson J.D. 1941. The function and metabolism of calcium in the invertebrates. Biological Reviews 16: 106-133.

Sánchez M.I., Green A.J., Castellanos E.M. 2006. Internal transport of seeds by migratory waders in the Odiel marshes, south-west Spain: consequences for long-distance dispersal. Journal of Avian Biology 37: 201-206.

Severin H.H.P. 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. Annals Entomological Society of America 111: 83-93.

Sharp D. 1898. Account of the Phasmidae with notes on the eggs. In: Willey A. (Ed.). Zoological Results Based on Material Collected in New Britain, New Guinea, Loyalty Islands and Elsewhere, Part I. Cambridge University Press, Cambridge, UK.

Stockard C.R. 2006. Habits, reactions, and mating instincts of the 'walking-stick', *Aplopus mayeri*. Publications Carnegie Institute of Washington 2: 43-59.