Hiding in plain sight: leaf beetles (Chrysomelidae: Galerucinae) use feeding damage as a masquerade decoy

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We report on a unique variant of the masquerade strategy, wherein small herbivorous leaf beetles (Chrysomelidae: Galerucinae) have recurrently evolved a close resemblance to innocuous, unprofitable decoy objects of their own manufacture, i.e. their own feeding damage. Our study is based on a worldwide sample of 119 species of leaf beetles in the subfamily Galerucinae. Most species (115) are members of the tribe Alticini, the flea beetles s.s., known for their remarkably swift jumping ability and astonishing diversity. Masquerading beetles are small, ranging in length from 1.4 to 4.2 mm, monochromatically light or dark, and lack contrasting patterns or warning colours. Although many species make shallow, light colored trenches, 53% of the adult feeding damage consists of closely spaced, oval to elongate holes that completely penetrate the host leaf, which gives it a pitted, stippled appearance. Body area was correlated with feeding hole area. Hole area increases by 0.60 mm² for each square millimetre of beetle area. Log–linear modelling showed that beetle body colour was darker when damage was darker and lighter when damage was lighter and when host leaves were broad as opposed to narrow and were oriented horizontally as opposed to vertically. We discuss why masquerade is not a response to induced host plant defences. These findings support the hypothesis that intense selection by visually orienting predators, such as insectivorous birds, has driven small leaf beetles to evolve bodies more closely to resemble their feeding damage and evolve their feeding habits to produce damage that resembles their own bodies.

ADDITIONAL KEYWORDS: camouflage – defence – herbivory – mimicry – predation.

INTRODUCTION

As a consequence of intense selection by natural enemies, insect herbivores that feed exposed on the leaf surfaces of their host plants have evolved an astonishing variety of defences to thwart enemies (reviewed by Ruxton, Sherratt & Speed, 2004). Chief among these anti-predator defences is camouflage, which includes many types of crypsis, disruptive coloration and background matching. Collectively, these strategies reduce the risk of prey being detected by potential predators (Cott, 1940). In an alternative form of camouflage, known as masquerade, protection is achieved through visual fidelity to innocuous, pedestrian objects common to the predator’s surroundings (Endler, 1981; Stevens & Merilaita, 2009), such as a leaf, a twig or a bird dropping. The selective benefit of masquerade is thought to be independent of the background against which prey are viewed; masquerade relies on close fidelity of prey to a worthless, innocuous object. In contrast, the benefit of crypsis lies in the close mimetic relationship between the prey item and the prey’s background or substrate (Endler, 1981). Skelhorn Skelhorn, Rowland & Ruxton, (2010a) propose that masquerade might be expected to occur most frequently in herbivorous insects, whose foraging behaviour is sedentary and
exposed on leaf surfaces, as it is in larval Lepidoptera (butterflies and moths), many Orthoptera (leaf-mimic katydids) and Phasmatodea (stick and leaf insects). For example, caterpillars of the early thorn moth (*Selenia dentaria*) masquerade as twigs and those of the giant swallowtail (*Papilio cresphontes*) as bird droppings (Skelhorn, 2015).

We report here on a unique twist to the masquerade strategy, wherein adult flea beetles (*Chrysomelidae: Galerucinae: Alticini*) have evolved a striking resemblance to an inanimate object of their own manufacture, namely their own leaf-feeding damage. Over many years of collecting, one of us (A.S.K.) often observed that it was very difficult to identify the specific position of these small, round-bodied beetles resting on a leaf when there were a large number of small holes or scrapes nearly the same size as the desired beetle. In addition to their smallness, their monochromatic body coloration produced a kind of ‘background matching’ with the surrounding closely spaced, tiny feeding holes to make a stippled damage field, resembling the pattern produced by a shotgun blast. The size and colour similarities between their feeding damage and the flea beetles themselves made them virtually indistinguishable on the leaf surface, all of which served to heighten the collector’s confusion.

There are thousands of flea beetle species, some generalists, but most are quite host specific. The subject of this study is a subset of flea beetles that is monochromatic and lacks the warning colours (e.g. red, yellow, white, orange), iridescence and contrasting patterns of stripes or spots that are typically displayed by their close relatives. Roughly 75% of these bicoloured flea beetles are small (2–5 mm long), rather rounded, and many species are uniformly dark blue, black, ochre, brown or some combination of these somber colours. The remainder are light coloured, with shades of pale brown or tan. All of these drab species possess the remarkable capacity to jump suddenly for long distances at astonishing velocities, when even slightly disturbed, hence the name ‘flea’ beetle (Furth, 1988; Nadein & Betz, 2016). Adult flea beetles are also noteworthy for their reduced reliance on chemical defences compared with other leaf beetles (Pasteels et al., 1994; Ge et al., 2011). Moreover, these small beetles do not consume the entirety of their host’s leaves, as most caterpillars and grasshoppers do, but instead pulverize leaves with numerous small, closely spaced pits, trenches and holes.

We suspect that all these traits describe a pattern of coincident resemblance between beetles and their feeding damage that represents a hitherto unreported example of masquerade as a defence that reduces predation by visually oriented predators, such as birds. We postulate that these small, leaf-feeding beetles have evolved bodies more closely to resemble their feeding damage and evolved their feeding habits to produce damage that resembles their own bodies. In this scenario, masquerade would function as a primary defence by preventing birds from detecting and/or recognizing a beetle as prey. Jumping would serve as a secondary defence if a beetle were detected as prey. We provide evidence that the correspondence between beetle bodies and their feeding damage is not random, not a case of crypsis, background matching, nor a response to induced plant defences, but instead a *bona fide* instance of masquerade as an anti-predator defence adaptation.

**MATERIAL AND METHODS**

The subjects of this study, the leaf beetles (*Chrysomelidae: Galerucinae*), with >9900 valid—species, have a worldwide distribution and feed on plants in >200 families (Konstantinov, 2016). Although their larvae are predominantly root feeders or leaf miners, flea beetle adults feed exposed on the leaves of their host plants. Adults are well known for their enlarged hind femora, which house a remarkable spring mechanism that enables them to jump at extraordinary speeds (>2 m s⁻¹) when approached (Nadein & Betz, 2016).

Our study is based on two sources of data: (1) 16 years of field observations from all biogeographical regions except Australia and Antarctica; and (2) photographs of beetle damage reported in the literature. Long before we suspected that putative beetle–leaf damage correspondence was probably not random, the same kind of beetle–feeding damage was inadvertently documented in a large trove of photographs in the literature (Heikertinger, 1925a, b, c; 1926). Based on our field work and the Heikertinger literature, our dataset includes 119 leaf beetle species in the subfamily Galerucinae, with four from the tribe Galerucini and 115 observations from the tribe Alticini, the flea beetles s.s. (Supporting Information Appendix S1). Each specific observation represents at least three separate observations of a given beetle damage pattern found on different infected individuals of the same host plant species. Except for those from India, all of the beetle–host plant associations have already been reported in the literature.

We measured beetle size and habitus colour in relationship to the size and colour of the damage created by their feeding. First, we categorized beetle colour as follows: (1) ‘light’ habitus: pronotum and elytra of the same light brown, yellowish, ochre or straw colours (Fig. 1); and (2) ‘dark’ habitus: pronotum and elytra of the same dark brown, blue or black colours (Fig. 2).
Sixteen photographs that captured both a beetle and its leaf damage constituted a subset of focal species, with which we were able to quantify the ‘lightness’ and ‘darkness’ classification made by eye. Specimens of the 16 focal species were re-photographed in standardized light conditions. The photography set-up used a microscope (Zeiss Axio Zoom.V16, Thornwood, NY, USA), fitted with a diffuse LED light dome (MD-BL; Metaphase Technologies, Bristol, PA, USA). Measurements of body length were made.

Figure 1. Flea beetles masquerading as their own feeding damage: light-coloured beetles and light-coloured damage. A, Capraita flavida (Horn) on Chilopsis linearis (Cav.) Big Bend National Park, TX, USA; beetle length 3.14–4.48 mm. B, Centralaphthona sp. and its host plant, Eugenia axillaris (Sw.) Wild. (Myrtaceae), Dominican Republic; beetle length 1.40–1.55 mm. Beetle picture taken separately from the picture of the host plant. C, Haemaltica sp. on Memecylon sp. (Melastomataceae), Karnataka, India; beetle length 3.45–3.87 mm. D, Heikertingerella sp. on Tecoma stans (L.) Juss. ex Kunth (Bignoniaceae), Dominican Republic; beetle length 2.2–2.4 mm. E, Leptophyes hoffmani Bryant and its host plant, tree fern (Cyatheales), Puerto Rico; beetle length 2.10–2.37 mm. Beetle picture taken separately from the picture of the host plant. F, Letzuella sp. on Buddleja sp. (Buddlejaceae), Yunnan, China; beetle length 1.9–2.3 mm. G, Longitarsus sp. on Ageratina sp. (Asteraceae), Yunnan, China; beetle length 1.52–1.54 mm. H, Pyrrhalta sp. on Viburnum japonicum Sprengel (Adoxaceae), Japan; beetle length 3.02–3.25 mm. I, Nesaecrepida rufomarginata Blake on Prosopis or Vachellia (Fabaceae), Puerto Rico; beetle length 2.5–2.12 mm. J, Nesaecrepida rufomarginata on Psidium guajava L. (Myrtaceae), Jamaica; beetle length 2.0–2.1 mm.
from the head apex to the elytral apex to the nearest 0.1 mm and were used to calibrate the quantification of their feeding damage areas using ImageJ (v 1.46r; Schneider, Rasband & Eliceiri, 2012). A 0.5 mm² patch from the middle of each beetle’s habitus was used to obtain an intensity value for each species. Photographs were calibrated with a grey standard (40%). The light beetle colour category had a mean ± SD intensity of 95.2 ± 18.45 and the dark category had a value of 37.64 ± 11.1, which were different (Mann–Whitney U-test, \( P < 0.0001 \)).

Flea beetle feeding damage consists of a complex mixture of species-specific feeding patterns that includes shallow scrapes or trenches that fail to penetrate the leaf and often includes adjacent necrotic tissue and deeper holes that completely penetrate the leaf. We sorted this diversity into two colour categories as follows: (1) ‘light’ feeding damage included scrapes

**Figure 2.** Flea beetles masquerading as their own feeding damage: dark-coloured beetles and dark-coloured damage. A, Agelastica alni (L) on Alnus glutinosa (L.) Gaertn. (Betulaceae), Smolensk region, Russia; beetle length 4.56 mm. B, Chaetocnema sp. on Convolvulaceae, Haitan Island, China; beetle length 1.6–1.8 mm. C, Longitarsus sp. on Mertensia franscana A. Heller (Boraginaceae), Arizona, USA; beetle length 1.62–1.67 mm. D, Chaetocnema discreta (Baly) on Beta vulgaris L. (Chenopodiaceae), Karnataka, India; beetle length 1.70–2.27 mm. E, Diphaulaca sp. on Urticaceae, Bolivia; beetle length 3.1–3.2 mm. F, Sphaeroderma sp. on Urtica sp. (Urticaceae), Yunnan, China; beetle length 2.11–2.18 mm. G, Xuthe aunnanesis Heikertinger on Girardinia sp. (Urticaceae), Yunnan, China; beetle length 4.0–4.3 mm. H, examples of host plant damage illustrated by Heikertinger (1925a, c), Phyllotreta atra (F.) on Sinapis arvensis L. (Brassicaceae), beetle length 1.59–1.72 mm and Psylliodes attenuata Koch on Humulus lupulus L. (Cannabaceae), beetle length 1.67–1.75 mm, Austria.
that penetrated the upper epidermis and only part of the mesophyll (e.g. Fig. 1); and (2) ‘dark’ feeding damage included holes that penetrated the leaf surface, which appeared dark because the shaded background of the forest floor could be seen through them (Fig. 2). The precise photographic quantification of an object’s intensity is operationally problematic in field conditions. Although light conditions varied considerably in our photographic documentation, we made a preliminary estimate of the light and dark damage intensity. A 0.5 mm² patch of feeding damage recorded in field photographs was measured using ImageJ (Figs 1 and 2). The light damage category had a mean ± SD intensity value of 159.8 ± 20.9 and the dark category had a value of 43.3 ± 3.1, which were significantly different (Mann–Whitney U-test, P < 0.0001). To determine whether beetle colour or feeding damage was related to leaf shape or orientation, leaves were categorized as ‘broad’ if their width was ≥¼ their length and ‘horizontal’ if the angle subtended by the leaf was ≤120°.

Associations among categorical variables (body colour, hole colour, leaf shape and leaf orientation) were analysed using contingency tables and χ². The interdependence of these variables was analysed using a log-linear logit model as implemented in the CATMOD procedure (SAS, 2011). The Mann–Whitney U-test was used to compare beetle and damage colours. Pearson’s product–moment correlation was used to estimate correlations between beetle and leaf hole areas. Linear least-squares regression was used to describe the dependence of leaf damage area on beetle body area.

Beetle and host plant vouchers are deposited in the National Museum of Natural History, Smithsonian Institution and the Travancore Insect Collection, College of Agriculture, Vellayani, India. Host plant vouchers from Bhutan and India are deposited in the Calicut University Herbarium, India.

RESULTS

In many cases, tissue damage was only partial, forming pale (light) scrapes or shallow trenches (Fig. 1 and Table 1). However, in the majority (53%) of the field and literature observations, feeding damage took the form of oval to elongate (dark) holes, which completely penetrated the leaf (Fig. 2 and Supporting Information Appendix S1). Beetle body colour was significantly dependent on feeding damage colour (χ² = 65.62; P < 0.0001; Table 1). Using the focal subset of 16 species (Fig. 3), log-linear logit modelling of beetle body colour showed that beetle body colour was darker when damage was darker and lighter when damage was lighter (χ² = 5.85; P < 0.016), leaves were broad as opposed to narrow (χ² = 10.39; P < 0.001) and were oriented horizontally as opposed to vertically (χ² = 30.04; P < 0.0001).

The vast majority (>95%) of leaf beetles feed on the abaxial (upper), sunlit leaf surfaces of their hosts. Of the 111 observations, all but one instance involved diurnal feeding (Supporting Information Appendix S1). Masquerading beetles were observed feeding on >25 different gymnospermous, monocotyledonous and eudicotyledonous plant families (Table 1; Supporting Information Appendix S1).

Masquerading beetles were relatively small, averaging (±SD) 2.2 ± 0.8 mm in length. Based on a subset of 16 species for which we had photographic evidence of both the beetle and its damage, the mean ± SD ratio of body:hole areas was 0.47 ± 0.8 mm². There was a significant positive correlation between body area and feeding hole size (Pearson’s product–moment, R = 0.875; coefficient of determination = 0.765). The least-squares regression of leaf hole area on beetle body area was y = 0.59x – 0.25, with leaf hole area increasing ~0.60 mm² for each square millimetre of beetle area (Fig. 4).

DISCUSSION

We postulate that there is a non-random correspondence between the colour and shape of the feeding damage and the body size and colour of the beetles that produced the damage. Comparisons of congeners provide further evidence that beetle–feeding damage matching is not random. For example, two beetle species of the genus Gioia, one light and one dark, inflict correspondingly light- and dark-coloured damage on the leaves of their taxonomically unrelated host plants. The light-coloured Apraea portaricensis makes light-coloured damage on its host, Tabebuia haemantha, whereas its dark-coloured congener makes dark-coloured damage on its host, Handroanthus capitatus. Two dark-coloured species, Chaetocnema tibialis and Chaetocnema discreta, both make dark holes in the same host, Beta vulgaris from Austria and India, respectively. Alternatively, different dark-coloured Longitarsus species make dark-coloured feeding damage on their various boraginaceous hosts, which represent entirely different plant genera (e.g. Cynoglossum and Mertensia). Likewise, the dark Psylliodes attenuata create dark damage on two different plants in the Cannabaceae (Humulus lupus and Cannabis sativa).

Although some invertebrate predators use vision in searching for prey and have been reported to attack some flea beetle species (Cox 1994, 1996), birds are considered to be the primary selective agents for defences such as camouflage, mimicry and aposematism in insects (Fisher, 1930; Jeffords, Sternberg & Waldbauer, 1979; Bowers, Brown & Wheye, 1985). Birds have therefore had a strong impact on the
Table 1. Diversity of light and dark masquerading leaf beetles in relation to feeding damage color, host plant family, and distribution.

| Genus            | Beetle color | Damage color | Plant family                                                                 | Biogeographic region: Country               |
|------------------|--------------|--------------|------------------------------------------------------------------------------|---------------------------------------------|
|                  | lighta       | darkb        | Light damage colors                                                          |                                             |
|                  |              |              | Light damage colors                                                          |                                             |
| Aedmon           | 1            | 1            | 2                              | Lauraceae, Melastomataceae                  | NEO: Dominican Republic, Puerto Rico        |
| Agelastica       | 1            | 1            | 1                              | Betulaceae                                  | PAL: Russia                                 |
| Altica           | 2            | 2            | 2                              | Onagraceae, Rosaceae                        | AFR: Kenya; ORI: India                      |
| Aphthona         | 5            | 3            | 5                              | Euphorbiaceae, Iridaceae                    | ORI: India; PAL: Russia                     |
| Aphthonoides     | 2            | 2            | 2                              | Urticaceae                                  | ORI: Bhutan                                 |
| Apraea           | 1            | 1            | 1                              | Oleaceae                                    | NEO: Dominican Republic, Puerto Rico        |
| Asphaera         | 1            | 1            | 1                              | Urticaceae                                  | NEO: Bolivia                                |
| Batophila        | 4            | 4            | 4                              | Rosaceae                                    | NEO: India                                  |
| Bonfilsus        | 1            | 1            | 1                              | Fabaceae                                    | NEO: Dominican Republic                     |
| Calomicrus       | 1            | 1            | 1                              | Chloranthaceae                              | PAL: Japan                                  |
| Capraita         | 1            | 2            | 1                              | Bignoniaceae, Oleaceae                      | NEO: USA                                    |
| Centralaphthona  | 2            | 2            | 2                              | Euphorbiaceae, Myrtaceae                    | NEO: Dominican Republic                     |
| Chaetocnema      | 8            | 4            | 4                              | Amaranthaceae, Chenopodiaceae, Combretaceae, Combretaceae, Malvaceae, Rosaceae, Salicaceae | NEA: USA; NEO: Dominican Republic; ORI: China, India; PAL: Austria |
| Chalaenosoma     | 1            | 1            | 1                              | Dioscoreaceae                               | ORI: India                                  |
| Chanealtica      | 1            | 1            | 1                              | Bignoniaceae                                | NEO: Bolivia                                |
| Chillocoristes   | 1            | 1            | 1                              | Smilacaceae                                 | ORI: India                                  |
| Demarchus        | 1            | 1            | 1                              | Loranthaceae                                | ORI: India                                  |
| Dibolia          | 2            | 1            | 1                              | Lamiaceae, Plantaginaceae                   | NEA: USA; ORI: India                        |
| Diosyphraea      | 1            | 1            | 1                              | Solanaceae                                  | NEO: Bolivia                                |
| Diphaulaca       | 1            | 1            | 1                              | Urticaceae                                  | NEO: Bolivia                                |
| Epitrix          | 1            | 1            | 1                              | Solanaceae                                  | NEO: Jamaica                                |
| Galerucella      | 1            | 1            | 1                              | Rosaceae                                    | PAL: Russia                                 |
| Gioia            | 1            | 1            | 1                              | Rubiaceae, Solanaceae                       | NEO: Dominican Republic, Jamaica             |
| Haemaltica       | 1            | 1            | 1                              | Melastomataceae                             | ORI: India                                  |
| Halticorpus      | 1            | 1            | 1                              | Polypodiaceae                               | ORI: India                                  |
| Heikertingerella | 3            | 2            | 1                              | Bignoniaceae, Melastomataceae, Verbenaceae  | NEO: Dominican Republic, Puerto Rico         |
| Hermaeophaga     | 1            | 1            | 1                              | Urticaceae                                  | ORI: Bhutan                                 |
| Hyphasis         | 3            | 3            | 3                              | Bignoniaceae, Oleaceae, Rubiaceae           | ORI: India                                  |
| Lanka            | 2            | 2            | 2                              | Piperaceae                                  | ORI: Bhutan, India                          |
| Leptophysa       | 1            | 1            | 1                              | Cyatheales                                  | NEO: Puerto Rico                            |
| Letzuela         | 2            | 2            | 2                              | Buddlejaceae                                | ORI: China                                  |
| Lipromormpha     | 1            | 1            | 1                              | Vitaceae                                    | ORI: China                                  |
| Longitarsus      | 9            | 7            | 10                             | Asteraceae, Boraginaceae, Lamiaceae, Scrophulariaceae | NEA: USA; NEO: Dominican Republic, Jamaica, Puerto Rico; ORI: China, India, Nepal; PAL: Austria; |
| Mandarella       | 1            | 1            | 1                              | Polygonaceae                                | ORI: Bhutan                                 |
| Mantura          | 2            | 2            | 2                              | Polygonaceae                                | NEA: USA; PAL: Austria                      |
evolution of the masquerade defence. Although a detailed comparison of visual systems is beyond the scope of this study, there are several caveats for our use of human vision as a proxy for birds (Endler & Mielke, 2005). First, ultraviolet reflectance is visible to birds, but not to humans. Second, the data presented here are only suggestive of colour matching, because birds have a different colour vision system. There are, however, some important similarities. Humans and birds are affected by similar visual properties of the background when they are searching for cryptic targets (Xiao & Cuthill, 2016). Furthermore, the density and the shape of non-target ‘distractors’ have been shown to reduce search performance in both birds and humans (Dimitrova & Merilaita, 2014). Finally, birds and humans take significantly longer to find monochromatic insect prey presented on a matching background (Stobbe et al., 2009), although the luminous contrast between target and background seems less important to birds on these backgrounds. In variable and heterogeneous environments that characterize the light conditions of the forest understory, gaps and edge environments where flea beetles reside, luminance might be less reliable in avoidance learning and memory (Osorio & Vorobyev, 2005; Stevens & Ruxton, 2012). To confirm the feeding damage masquerade hypothesis, ultraviolet reflectance and luminosity should be experimentally measured in the field and laboratory, and coloration precisely quantified with more advanced image analyses based on recent insights into avian vision (e.g. Arenas, Troscianko & Stevens, 2014).

Induction of plant chemical defences during herbivore attack is a widespread strategy (Mithöfer & Boland, 2012) and might be an alternative explanation for the stippled damage patterns made by flea beetles. Leaves can suffer random tissue damage (e.g. falling debris, high wind) as well as damage from herbivore attack. The main difference between accidental wounding and herbivory is the duration and extent of the tissue damage event (Mithöfer, Wanner & Boland, 2005). Evidently, plants can somehow integrate, as a product, the size of the damaged area with the duration of the damage event and respond accordingly with defence responses or with repair responses (Bricchi et al., 2010). This means that both short bouts of damage spread across a large area, as inflicted by individual beetles, and long bouts of damage concentrated in a small area, as inflicted by gregarious beetles, would resemble the incidental wounding that might not elicit defensive responses in the plant. We suspect that if the beetles feed in brief bouts that produce restricted areas of damage (<5 mm²), then the plants might not detect their presence, but instead recognize the perturbation simply as a kind of incidental wounding that does not elicit a full induction of chemical defensive responses, such as the jasmonate cascade. The stippled, buckshot-like damage patterns

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**Table 1. Continued**

| Genus             | Light Species | Dark Species | Family                  | Region       |
|-------------------|---------------|--------------|-------------------------|--------------|
| Physimerus        | 1             | 2            | Onagraceae, Solanaceae  | NEO: Bolivia |
| Podagrica         | 1             | 1            | Malvaceae               | AFR: Kenya   |
| Peylioides        | 2             | 2            | Cannabaceae, Solanaceae | PAL: Austria, Russia |
| Pyrrhaltia        | 1             | 1            | Adoxaceae               | PAL: Japan   |
| Sinoecrepis       | 1             | 1            |                         | ORI: Bhutan  |
| Sphaeroderma      | 1             | 1            |                         | ORI: China   |
| Xuthea            | 2             | 2            | Urticaceae              | ORI: Bhutan, China |
| Yaminia           | 1             | 1            | Verbenaceae             | ORI: India   |
| Yetialtica        | 1             | 1            | Primulaceae             | ORI: Nepal   |

*Number of light species;
*Number of dark species;
*Genera in blue have exemplar species in the focal group.
*AFR, Africa; NEA, Nearctic; NEO, Neotropical; ORI, Oriental; PAL, Palearctic; USA, United States of America.
are in sharp contrast to the extensive destruction of leaves generally produced by other herbivorous insects, such as Lepidoptera and Orthoptera, by which they achieve concealment from birds through the destruction of the evidence of their presence (Heinrich, 1979). However, whether the stippled feeding patterns are an attempt to fly under the host's defensive radar or if beetles cluster small holes in order hide themselves, as predicted by the masquerade hypothesis, are not necessary mutually exclusive explanations. Intense selection by birds probably fostered the recurrent evolution of masquerade and jumping as anti-predator defences in several flea beetle lineages. These traits that now constitute a co-evolved defensive suite that has promoted flea beetle diversification. The alticines have higher species richness and faster rates of higher diversification compared with their sister galerucines and other leaf beetle lineages (Ge et al., 2011). The efficacy of feeding masquerade and the astonishing jumping ability of these
plain-coloured beetles might have reduced their reliance on chemical secretions, which characterize other leaf beetle lineages (Pastoels et al., 1994). We predict that feeding masquerade in flea beetles, and in the Galerucinae generally, is a more widespread phenomenon compared with the better-studied aspects of crypsis, mimicry and aposematism.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Appendix S1. Masquerading leaf beetles (Chrysomelidae: Galerucinae).