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Effects of host plant growth form on dropping behaviour in leaf beetles

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Many leaf-eating insects drop from their host plants to escape predators. However, they must return to the leaves of the host plant after dropping, which represents a cost associated with this behaviour. In woody plants, the positioning of leaves is generally higher than that of herbaceous plants, which suggests that dropping from woody plants might be costlier for leaf-eating insects than dropping from herbaceous plants. Therefore, we predicted that dropping behaviour would be observed less frequently in insects that feed on woody plant leaves than in those that feed on herbaceous plant leaves. To test this prediction, we investigated dropping behaviour experimentally in larvae (23 species) and adults (112 species) of leaf beetles (Coleoptera: Chrysomelidae) on their host plants (86 species of 44 families) in field conditions. Larvae on woody plants exhibited dropping behaviour less frequently than those on herbaceous plants. However, this pattern was not detected in adults. Thus, host plant growth form might affect the evolution of dropping behaviour in leaf beetle larvae, but not in winged adults, perhaps owing to their higher mobility.

ADDITIONAL KEYWORDS: adults – anti-predator defences – behavioural costs – chemical defences – Chrysomelidae – Coleoptera – herbaceous plants – larvae – woody plants.

INTRODUCTION

Animals defend themselves against predators in various ways (Edmunds, 1974; Sugiura, 2020). The evolution of anti-predator defences can be driven by benefits gained from protection against predators and by the associated costs (Bowers, 1992; Camara, 1997; Zevereva *et al.*, 2017). The benefits and costs of defences are closely associated with habitat. For example, phytophagous insects sequester host plant chemicals in their bodies to defend against predators (Nishida, 2002); the effectiveness of chemical defences can vary among host plant species because they have different enemies and access to different chemical components (Denno *et al.*, 1990; Singer & Stireman, 2003). Although studies have investigated the effects of host plants on the effectiveness of anti-predator defences (Denno *et al.*, 1990; Singer & Stireman, 2003), few studies have clarified the effects of host plants on the costs associated with anti-predator defences in phytophagous insects (Matsubara & Sugiura, 2018).

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Dropping behaviour for rapid escape from predators is among the simplest of anti-predator defences (Humphreys & Ruxton, 2019). This behaviour has been reported in various animal groups, such as mammals, lizards and insects (Edmunds, 1974; Lima, 1993; Losey & Denno, 1998a, b; Vitt *et al.*, 2002; Martins *et al.*, 2005; Sato *et al.*, 2005; Castellanos *et al.*, 2011; Greeney *et al.*, 2012; Barnett *et al.*, 2015, 2017; Humphreys & Ruxton, 2019; Sugiura, 2020). Therefore, dropping behaviour has evolved convergently in diverse animal groups (Humphreys & Ruxton, 2019). Dropping is frequently associated with other defensive behaviours; for example, some phytophagous insects feign death (i.e. exhibit thanatosis) as they drop from host plants (Ohno & Miyatake, 2007; Matsubara & Sugiura, 2018). Although dropping allows rapid escape from predators (Day *et al.*, 2006; Francke *et al.*, 2008), sudden departure from the food resources and microhabitat can reduce feeding efficiency and reproduction and increase development time (Roitberg *et al.*, 1979; Loughridge & Luff, 1983; Dill *et al.*, 1990; Losey & Denno, 1998c; Nelson, 2007; Perović *et al.*, 2008; Agabiti *et al.*, 2016). These are considered to be costs associated with dropping behaviour.

Host plants can affect the cost of dropping behaviour in phytophagous insects (Matsubara & Sugiura, 2018). When phytophagous insects drop to the ground, they must then return to an appropriate feeding position on the host plant. Underlying leaves can prevent phytophagous insects from dropping to the ground, thereby reducing the costs of dropping behaviour. For example, leaf beetles are much less likely to drop to the ground from large, oval leaves than from cleft leaves because the former can act as safety nets for the falling beetles (Matsubara & Sugiura, 2018). Given that the leaf positions on woody plants are generally higher than those on herbaceous plants, insects require more time and energy to move from the ground to their feeding position on woody plants. Consequently, the costs associated with dropping from woody plants are expected to be higher than those associated with dropping from herbaceous plants. Some arthropods that inhabit woody plants reportedly avoid dropping to the ground by gliding (Yanoviak *et al.*, 2005, 2009, 2015; Meresman *et al.*, 2017) or using silk lifelines (Brackenbury, 1996; Sugiura & Yamazaki, 2006). Therefore, dropping behaviour is expected to occur less frequently in insects that feed on woody plant leaves than in those that feed on herbaceous plant leaves. However, this prediction has never been tested. Clarification of the relationships between host plants and dropping behaviour would contribute to our understanding of the evolution of defensive behaviours and host plant selection in phytophagous insects.

To elucidate the effects of host plant growth form (i.e. herbaceous vs. woody plants) on dropping behaviour in phytophagous insects, we investigated the anti-predator defences of leaf beetles (Coleoptera: Chrysomelidae) on their host plants in field conditions in Japan. The species diversity of leaf beetles is high; the family Chrysomelidae includes ~41 000 extant species (Jolivet *et al.*, 2008), ~700 of which are recorded in Japan (Kimoto & Takizawa, 1994). Most leaf beetle species are dietary specialists that feed on particular families and genera of plants (Kimoto & Takizawa, 1994; Jolivet & Verma, 2002). Although closely related beetle species frequently use the same plant families, some congeneric species feed on different plant families (Kimoto & Takizawa, 1994). Leaf beetles defend themselves against predators in various ways, including dropping, flying, jumping, clinging, having spines and self-mimicking of feeding damage (Kimoto & Takizawa, 1994; Jolivet & Verma, 2002; Konstantinov *et al.*, 2018; Shinohara & Takami, 2020; Sugiura, 2020). The secretion of chemical liquids from the body is well documented in some leaf beetle larvae as a chemical defence against predators such as ants (Sugawara *et al.*, 1979; Pasteels *et al.*, 1982; Pasteels *et al.*, 1984; Kimoto & Takizawa, 1994). Thus, leaf beetles are an appropriate insect group for investigating the effects of host plant growth form on dropping behaviour and other anti-predator defences in phytophagous insects. Larvae and adults of many leaf beetle species are found on host plant leaves, making it possible to compare the effects of host plant growth form on dropping behaviour in larvae and adults.

In this study, we investigated experimentally the defensive behaviour of larvae (23 species) and adults (112 species) of leaf beetles on their host plants in field conditions in Japan. We examined whether larvae and adults showed dropping or other defensive behaviours in response to artificial stimuli on their host plants and explored the effects of host plant growth form (herbaceous or woody plants) on the evolution of dropping behaviour in leaf beetles.

MATERIAL AND METHODS

Study site and species

Field experiments were conducted at 102 sites in Japan (Matsubara & Sugiura, 2021; 25°51′–41°22′N, 127°42′–141°22′E, 1–1090 m a.s.l.). The study sites included various environments, such as forest, grassland and farm. Leaf beetle larvae are external leaf feeders, leaf/stem miners, seed borers, detritus feeders or root-feeders (Jolivet, 1988). In this study, we focused on external leaf feeders that potentially drop from host plant leaves. Early instar larvae were not included in this study because they were too small to be investigated in field conditions. Therefore, larvae with body length ≥ 5 mm were used for subsequent experiments.

Leaf beetles and their host plants were identified based on their morphological characteristics (Kimoto & Takizawa, 1994; Azegami *et al.*, 2013a, b; Hayashi, 2014). The growth form (woody or herbaceous) of each plant species was determined based on the presence or absence of woody tissues in the stems (Clapham *et al.*, 1987; Azegami *et al.*, 2013a, b; Hayashi, 2014).

Field experiments

To explore the effects of host plant growth form (woody or herbaceous) on the defensive behaviours of leaf beetles, we investigated the responses of beetles to simulated attacks in field conditions, following the procedure of Matsubara & Sugiura (2018). When larval or adult leaf beetles fed externally on plant leaves, we measured the feeding elevation (i.e. vertical distance from the ground to the feeding position). Individuals on leaves higher than 3.0 m were not included in our experiments because they could not be reached. We randomly selected beetles on leaves (height, ≤ 3.0 m) and poked the larval dorsal abdomen or adult elytra with forceps to simulate attacks by predacious insects (e.g. ants). Forceps have been used frequently to simulate predator attacks (e.g. Miyatake *et al.*, 2008; Müller *et al.*, 2016; Matsubara & Sugiura, 2018). To standardize the stimuli, the same researcher used the same forceps in all the field experiments. The same degree of stimulus was provided to all leaf beetles in this study. When beetles did not respond to a stimulus, they were poked repeatedly at 2 s intervals, up to five times. Beetles on the lowest leaves are more likely to drop to the ground than those on the overlying leaves, because underlying leaves can prevent beetles from reaching the ground (Matsubara & Sugiura, 2018). Therefore, to evaluate the effects of underlying leaves on dropping behaviour, we did not use beetles found on the lowest leaves in our experiments.

Initially, we recorded whether beetles exhibited dropping behaviour in response to artificial stimuli. Dropping behaviour was defined as departure from the feeding position attributable to gravity. When insects dropped from the host plant leaves, we also recorded the place to which they dropped (i.e. leaves or ground/water) or whether they flew before landing (Fig. 1). Dropping behaviour is frequently accompanied by thanatosis (Humphreys & Ruxton, 2018); for example, some adults of a leaf beetle species fold their legs and antennae to feign death as they drop from host plants (Matsubara & Sugiura, 2018). We included such death feigning as dropping behaviour in this study, because it was difficult to observe whether each leaf beetle feigned death during dropping. We also recorded other defensive behaviours, such as emission of visible liquids, flying, jumping and running.

Field experiments were conducted on sunny or cloudy days (08:30–18:00 h) from April 2016 to May 2020, at temperatures of 16.2–35.4 °C.

Data analysis

The defensive behaviours of some beetle species were observed at several sites. However, site effects were not included in following models because our preliminary analysis detected no site effects on dropping behaviour.

Generalized linear mixed models (GLMMs) with binomial error distribution and logit link were used to determine the effects of host plant growth form on dropping and other behaviours of leaf beetles. As response variables, we used whether each individual exhibited dropping behaviour or not (one or zero), whether each individual dropped to the ground or not (one or zero), whether each larva exhibited chemical defence or not (one or zero) and whether each adult flew during dropping or not (one or zero). In all analyses, host plant growth form (woody or herbaceous) was used as a fixed factor. Leaf beetle tribe and species were fitted as nested random effects to account for phylogenetic constraints (Hiraiwa & Ushimaru, 2017).

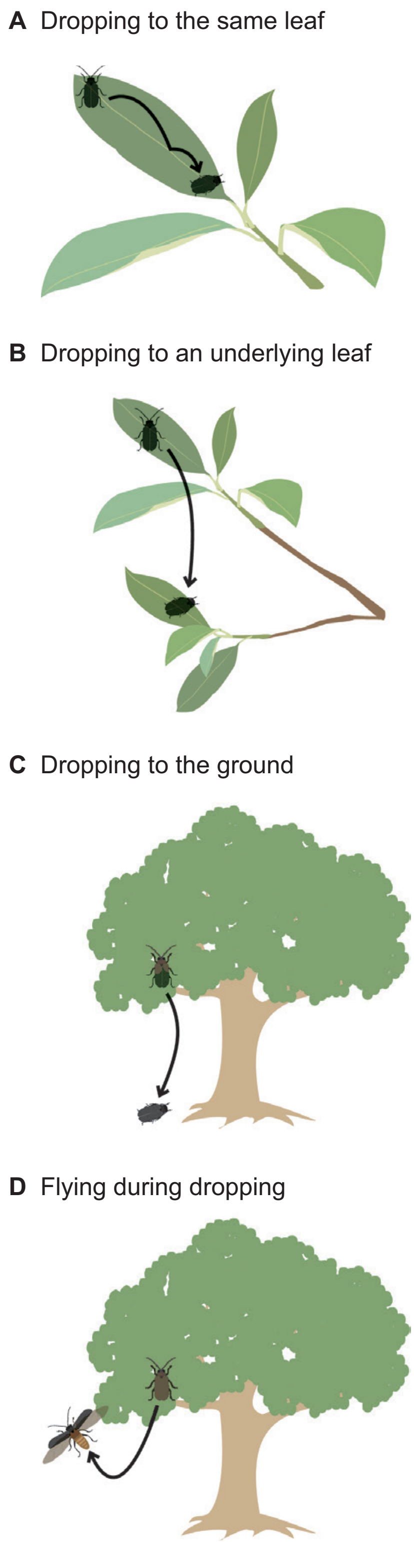

Figure 1. Four patterns of dropping behaviour in leaf beetles: A, dropping to the same leaf; B, dropping to an underlying leaf; C, dropping to the ground or water; and D, flying during during dropping.

All analyses were performed using the software R v.3.5.2 (R Core Team, 2018). The GLMMs were run using the *lme4* package 1.1.13 (Bates *et al.*, 2017).

RESULTS

A total of 286 leaf beetle larvae (23 species from six tribes) on host plants (23 species from 16 families) were investigated in field conditions; 15 and eight beetle species fed on the leaves of woody and herbaceous plants, respectively (Appendix 1). The larval feeding elevations were 1501.2 ± 36.9 mm (mean ± SEM, $N = 186$) on woody plants and 315.6 ± 14.1 mm ($N = 100$) on herbaceous plants. When poked with forceps, 2.2% of 186 larvae (13.3% of 15 species) on woody plants and 36.0% of 100 larvae (87.5% of eight species) on herbaceous plants exhibited dropping behaviour (Fig. 2A; Table 1). Larvae on herbaceous plants dropped to the ground more frequently compared with those on woody plants (Fig. 2B; Table 1). Other defensive behaviours were also observed. For example, 52.2% of 186 larvae (60.0% of 15 species) on woody plants and 56.0% of 100 larvae (87.5% of eight species) on herbaceous plants secreted visible chemicals, with no significant difference between woody and herbaceous plants (Fig. 2C; Table 1). Other larvae (1.4%) raised their faecal shields in response to artificial stimuli.

A total of 809 leaf beetle adults (112 species from 22 tribes) on host plants (86 species from 44 families) were investigated; 57 and 55 beetle species fed on the leaves of woody and herbaceous plants, respectively (Appendix 1). The feeding elevations of adult beetles were 1207.7 ± 26.9 mm ($N = 393$) on woody plants and 524.6 ± 18.5 mm ($N = 416$) on herbaceous plants. When poked with forceps, 37.7% of 393 leaf beetle adults (64.9% of 57 species) on woody plants and 39.2% of 416 adults (58.2% of 55 species) on herbaceous plants exhibited dropping behaviour (Fig. 3A; Table 2). Host plant growth form did not significantly affect dropping behaviour in leaf beetle adults (Fig. 3A, B; Table 2). In addition, significantly more adults flew after dropping from woody (9.4%) than from herbaceous plants (2.9%; Fig. 3C; Table 2). Beetles that did not drop ran (22.1%), jumped (14.2%), flew (7.3%) or secreted visible chemical liquids from their bodies (0.6%) in response to stimuli. Other beetles (1.9%) used their legs to hold tenaciously to leaf surfaces.

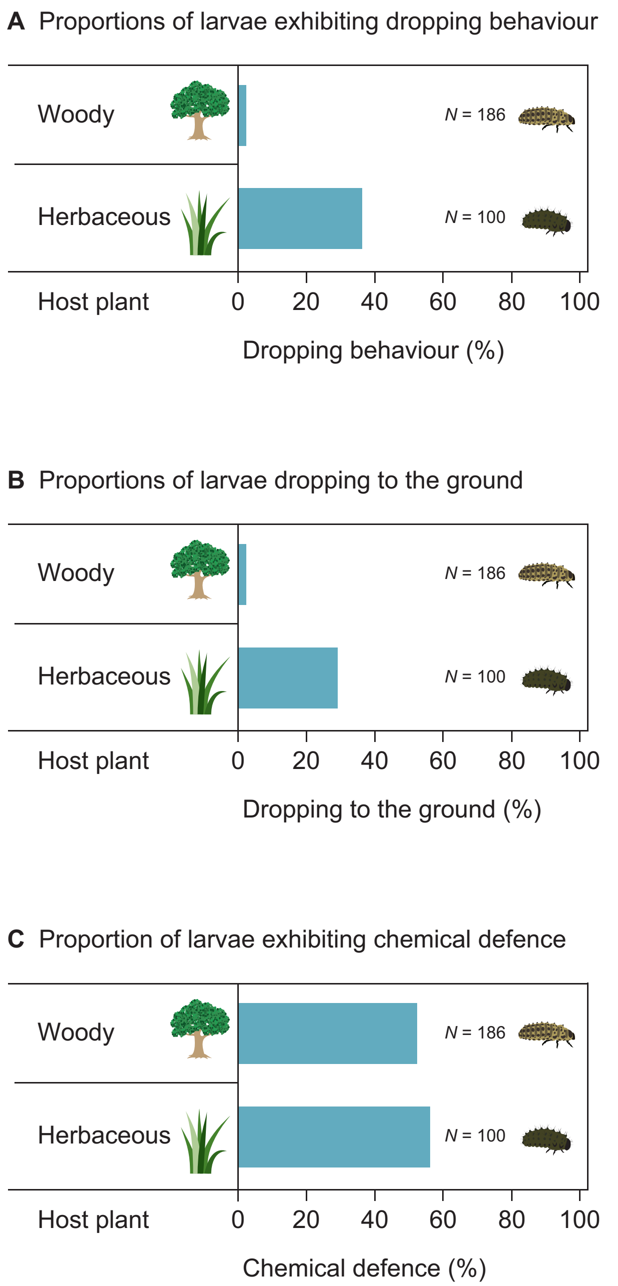

Figure 2. Dropping and other defensive behaviours of leaf beetle larvae. Proportions of leaf beetle larvae: A, exhibiting dropping behaviour; B, dropping to the ground; and C, exhibiting chemical defence. Sample size: 186 individuals (15 species) on woody plants and 100 individuals (eight species) on herbaceous plants.

DISCUSSION

Previous studies have investigated the effects of host plants on anti-predator defences in phytophagous insects (Denno *et al.*, 1990). However, few studies have focused on host plant architecture as a factor that affects dropping behaviour in leaf-feeding insects (Matsubara & Sugiura, 2018). In the present study, we conducted field experiments to test the prediction that dropping behaviour would be observed less frequently among

Table 1. Results of generalized linear mixed models for defensive behaviours by leaf beetle larvae

Response variable	Fixed factor	Coefficient estimate	SE	*Z*-value	*P*-value
Dropping behaviour	Intercept	−0.61	0.27	−2.28	0.02
	Host plant growth form*	−3.26	0.58	−5.63	< 0.01
Dropping to the ground	Intercept	−0.92	0.26	−3.57	< 0.01
	Host plant growth form*	−2.93	0.57	−5.15	< 0.01
Chemical defence	Intercept	−0.16	1.15	−0.14	0.89
	Host plant growth form*	−0.99	1.39	−0.72	0.47

*Herbaceous plants were used as a reference.

Table 2. Results of generalized linear mixed models for defensive behaviours by leaf beetle adults

Response variable	Fixed factor	Coefficient estimate	SE	*Z*-value	*P*-value
Dropping behaviour	Intercept	−0.39	0.56	−0.70	0.48
	Host plant growth form*	−0.53	0.51	−1.05	0.29
Dropping to the ground	Intercept	−1.48	0.46	−3.23	< 0.01
	Host plant growth form*	−0.76	0.44	−1.73	0.08
Flying during dropping	Intercept	−4.58	0.70	−6.50	< 0.01
	Host plant growth form*	1.54	0.55	2.80	< 0.01

*Herbaceous plants were used as a reference.

insects that feed on woody plant leaves than among those that feed on herbaceous plant leaves. Leaf beetle larvae on woody plants exhibited dropping behaviour less frequently than those on herbaceous plants (Fig. 2A; Table 1), supporting our prediction. However, this pattern was not detected in adults (Fig. 3A; Table 2).

Defensive strategies in leaf beetles

Leaf beetle larvae exhibited chemical defence more frequently than dropping behaviour in our experiments (Fig. 2C; Table 1). Thus, larvae frequently avoided leaving their feeding sites. Most larvae that dropped from host plants ultimately landed on the ground (Fig. 2B), necessitating a return to the host plant leaves by walking. Given that leaf positions on woody plants are generally higher than those on herbaceous plants, dropping from woody plants might be costlier compared with dropping from herbaceous plants. Therefore, larvae that feed on woody plants were more likely to avoid leaving their feeding sites than those that feed on herbaceous plants (Fig. 2A). However, larvae that feed on woody plants did not use chemical defences more frequently than those that feed on herbaceous plants (Fig. 2C). Given that chemicals emitted by leaf beetle larvae can effectively repel predators such as ants and spiders (Sugawara *et al.*, 1979; Pasteels *et al.*, 1982, 1988; Kimoto & Takizawa, 1994), the larvae of many leaf beetle species prefer to adopt chemical defences. However, we might have overestimated the importance of chemical defences in larval leaf beetles because our study was limited to the larvae of 23 species (six tribes of Chrysomelidae).

Leaf beetle adults exhibited dropping behaviour more frequently than larvae (Figs 2A, 3A). However, the drop rates of adult beetles did not differ significantly between woody and herbaceous plants (Fig. 3A; Table 2). Dropped adults frequently returned to host plant leaves by flying before landing on the ground, suggesting that the costs associated with dropping behaviour are lower for adults that can fly. The results of our previous study showed that larvae of the leaf beetle *Phaedon brassicae* Baly required more time than did adults to return to feeding sites (i.e. leaves) on host plants (Matsubara & Sugiura, 2018). Given that the costs associated with dropping to the ground are lower for adults than for larvae, adults might not avoid leaving their host plants in response to predator attacks. Alternative defensive behaviours of adults included running, jumping and flying. Although very few adults emitted visible chemical liquids from their bodies, adults of some leaf beetle species reportedly secrete small amounts of defensive chemicals (Pasteels *et al.*, 1988). Thus, our study might have underestimated the importance of chemical defences in adult leaf beetles.

Effects of plant growth form on dropping behaviour

We observed effects of host plant growth form (i.e. woody or herbaceous plants) on dropping behaviour

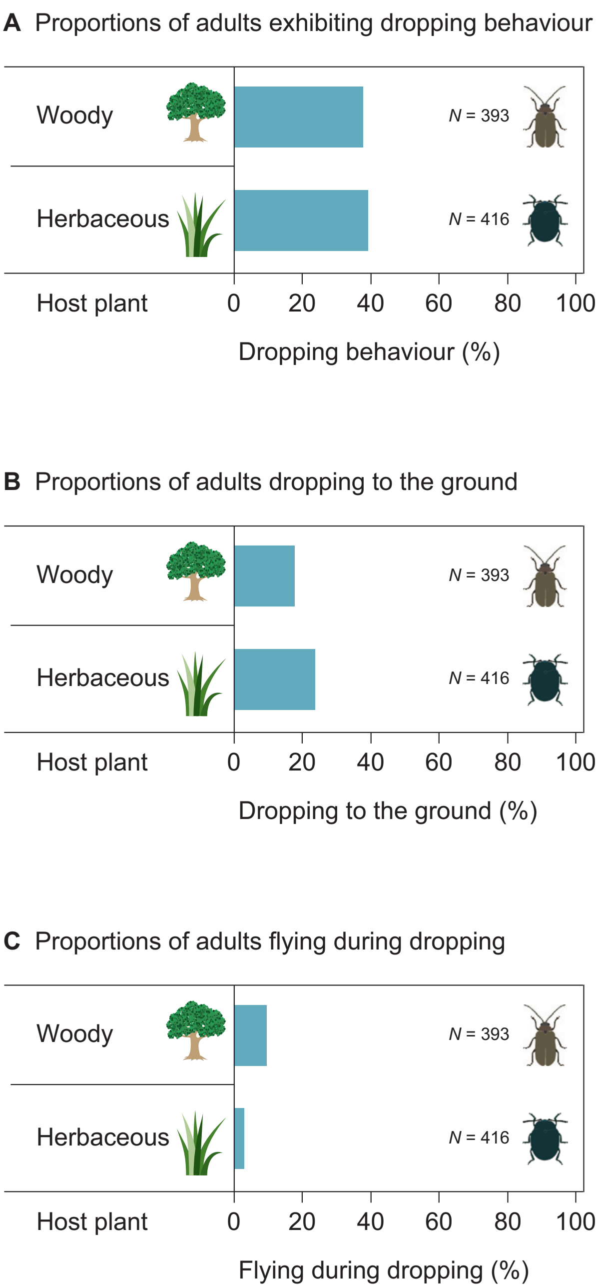

Figure 3. Dropping and other defensive behaviours of leaf beetle adults. Proportions of leaf beetle adults: A, exhibiting dropping behaviour; B, dropping to the ground; C, flying during dropping. Sample size: 393 individuals (57 species) on woody plants and 416 individuals (55 species) on herbaceous plants.

in leaf beetle larvae (Fig. 2A) but not in the adults (Fig. 3A). Given that few leaf beetle larvae can move among host plants, host plants can strongly influence their survival. The costs associated with dropping from woody plants might be higher than those associated with dropping from herbaceous plants, and differential costs between woody and herbaceous plants should be higher in leaf beetle larvae than in flying adults.

Dropping behaviour in leaf beetle larvae might have evolved via at least one of four potential processes: (1) species that feed on herbaceous plants acquiring dropping behaviour; (2) species that feed on woody plants losing dropping behaviour; (3) species that exhibit dropping behaviour shifting from woody to herbaceous host plants; or (4) species that do not exhibit dropping behaviour shifting from herbaceous to woody host plants. The drop rate can vary among larvae of the same leaf beetle species (Appendix 1; Matsubara & Sugiura, 2018), which suggests that this behaviour is frequently acquired or lost among species (i.e. hypothetical process 1 or 2). We did not observe whether oviposition site preferences (e.g. woody or herbaceous plants) varied among adults of the same leaf beetle species in the present study. However, oviposition preferences for host plant species reportedly vary among adult females of the same leaf beetle species (Vencl & Srygley, 2013; Vencl *et al.*, 2011, 2013), suggesting that shifts in host plant occur frequently among species (i.e. hypothetical process 3 or 4). Molecular phylogenetic analyses (e.g. ancestral reconstruction) of defensive behaviours and host plants would help to elucidate the selective processes promoting the evolution of dropping behaviour in leaf beetles.

Conclusion

The results of this study indicate that host plant growth form affected the evolution of dropping behaviour in leaf beetle larvae but not in winged adults. However, the evolution of dropping behaviour in phytophagous insects can be influenced by other factors, such as host plant range. When generalist species drop from the host plant to the ground, they can find other plants to eat more easily than can specialist species (Bernays & Graham, 1988). Therefore, the costs associated with dropping from host plants might be higher for specialists than for generalists. In addition, primary defences, such as body colour, might affect the evolution of dropping behaviour in phytophagous insects. Insect species with cryptic body colour are less easily detected by predators compared with those having aposematic body colour when they drop to the ground. Consequently, dropping from host plants might have evolved more frequently in cryptic species than in aposematic species. Further studies are needed to test these effects on the evolution of dropping behaviour in phytophagous insects.

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SHARED DATA

The data from the study are available from the Figshare Digital Repository (Matsubara & Sugiura, 2021).

Appendix 1. Host plants and dropping behaviour of leaf beetles used in this study

Leaf beetles						Host plants	
	Subfamily		Dropping*				
Code	Tribe	Species	Adult	Larva	Type†	Species	Growth form
	Alticinae						
1	Alticini	*Altica caerulescens*	7 (7)	2 (6)	ELF	*Acalypha australis*	Herbaceous
2	Alticini	*Altica cyanea*	0 (10)	–	ELF	*Ludwigia epilobioides*	Herbaceous
3	Alticini	*Altica oleracea*	3 (4)	3 (10)	ELF	*Trapa japonica*	Herbaceous
4	Alticini	*Altica* sp.	0 (1)	–	RF	*Isodon* sp.	Herbaceous
5	Alticini	*Aphthona formosana*	1 (8)	–	RF	*Mallotus japonicus*	Woody
6	Alticini	*Aphthona perminuta*	0 (4)	–	RF	*Castanea crenata*	Woody
7	Alticini	*Aphthonalitica angustata*	4 (10)	–	UK	*Akebia trifoliata*	Woody
8	Alticini	*Argopus balyi*	0 (2)	–	LM	*Clematis apiifolia*	Herbaceous
9	Alticini	*Chaetocnema* sp.	2 (3)	–	RF	*Digitaria ciliaris*	Herbaceous
10	Alticini	*Clitea metallica*	0 (5)	0 (8)	ELF	*Citrus unshiu*	Woody
11	Alticini	*Epitrix hirtipennis*	0 (10)	–	RF	*Solanum melongena*	Herbaceous
12	Alticini	*Hemipyxis cinctipennis*	0 (11)	–	ELF	*Clerodendrum trichotomum*	Woody
13	Alticini	*Hemipyxis flavipennis*	2 (3)	–	ELF	*Clematis apiifolia*	Herbaceous
14	Alticini	*Lanka fulva*	0 (1)	–	UK	*Piper kadsura*	Woody
15	Alticini	*Longitarsus scutellaris*	0 (5)	–	RF	*Plantago asiatica*	Herbaceous
16	Alticini	*Longitarsus* sp.	0 (10)	–	ELF	*Heliotropium arboreum*	Woody
17	Alticini	*Mantura clavareaui*	0 (5)	–	LM	*Rumex acetosa*	Herbaceous
18	Alticini	*Nonarthra cyanea*	0 (2)	–	UK	*Cerasus* × *yedoensis*	Woody
19	Alticini	*Philopona vibex*	0 (2)	–	ELF	*Plantago asiatica*	Herbaceous
20	Alticini	*Phyllotreta striolata*	0 (15)	–	RF	*Brassica rapa*	Herbaceous
21	Alticini	*Psylliodes punctifrons*	0 (10)	–	RF	*Brassica rapa*	Herbaceous
22	Alticini	*Sphaeroderma nigricolle*	2 (8)	–	LM	*Smilax china*	Woody
23	Alticini	*Sphaeroderma quadrimaculatum*	0 (8)	–	LM	*Clematis apiifolia*	Herbaceous
24	Alticini	*Sphaeroderma tarsatum*	0 (10)	–	LM	*Sasa kurilensis*	Herbaceous
25	Alticini	*Sphaeroderma unicolor*	0 (8)	–	LM	*Clematis terniflora*	Herbaceous
	Bruchinae						
26	Amblycerini	*Spermophagus rufiventris*	0 (2)	–	SEB	*Ipomoea indica*	Herbaceous
	Cassidinae						
27	Aspidimorphini	*Laccoptera quadrimaculata*	0 (8)	–	LM	*Ipomoea cairica*	Herbaceous
						Ipomoea indica	Herbaceous
28	Cassidini	*Cassida circumdata*	2 (6)	–	LM	*Ipomoea indica*	Herbaceous
29	Cassidini	*Cassida nebulosa*	0 (1)	–	ELF	*Chenopodium album*	Herbaceous
30	Cassidini	*Cassida piperata*	0 (3)	0 (5)	ELF	*Amaranthus blitum*	Herbaceous
31	Cassidini	*Cassida versicolor*	0 (6)	0 (2)	ELF	*Cerasus* × *yedoensis*	Woody
						Cerasus campanulata	Woody

Appendix 1. Continued

Leaf beetles						Host plants	
	Subfamily		Dropping*				
Code	Tribe	Species	Adult	Larva	Type†	Species	Growth form
32	Cassidini	*Cassida vespertina*	0 (1)	–	ELF	*Clematis apiifolia*	Herbaceous
33	Cassidini	*Thlaspida cribrosa*	0 (9)	0 (8)	ELF	*Callicarpa japonica*	Woody
34	Cassidini	*Thlaspida lewisii*	0 (1)	–	ELF	*Fraxinus lanuginosa*	Woody
35	Hispini	*Dactylispa subquadrata*	2 (3)	–	LM	*Castanea crenata*	Woody
						Quercus serrata	Woody
36	Hispini	*Rhadinosa nigrocyanea*	4 (11)	–	LM	*Miscanthus sinensis*	Herbaceous
37	Notosacanthini	*Notosacantha ihai*	0 (4)	–	LM	*Turpinia ternata*	Woody
	Chrysomelinae						
38	Chrysomelini	*Chrysolina aurichalcea*	9 (21)	–	ELF	*Artemisia indica*	Herbaceous
39	Chrysomelini	*Chrysolina exanthematica*	5 (15)	–	ELF	*Lycopus lucidus*	Herbaceous
40	Chrysomelini	*Chrysolina virgata*	5 (20)	–	ELF	*Lycopus lucidus*	Herbaceous
41	Chrysomelini	*Chrysomela populi*	0 (16)	0 (7)	ELF	*Populus tremula*	Woody
42	Chrysomelini	*Chrysomela vigintipunctata*	0 (6)	0 (10)	ELF	*Salix triandra*	Woody
43	Chrysomelini	*Gastrolina depressa*	0 (10)	0 (20)	ELF	*Juglans mandshurica*	Woody
44	Chrysomelini	*Gastrolinoides japonicus*	0 (2)	2 (15)	ELF	*Viburnum plicatum*	Woody
45	Chrysomelini	*Gastrophysa atrocyanea*	18 (20)	4 (10)	ELF	*Rumex japonicus*	Herbaceous
46	Chrysomelini	*Gonioctena rubripennis*	0 (9)	0 (12)	ELF	*Wisteria floribunda*	Woody
47	Chrysomelini	*Linaeidea aenea*	0 (2)	–	ELF	*Alnus pendula*	Woody
48	Chrysomelini	*Linaeidea formosana*	0 (15)	0 (16)	ELF	*Alnus japonica*	Woody
49	Chrysomelini	*Phaedon brassicae*	12 (12)	8 (30)	ELF	*Raphanus sativus*	Herbaceous
50	Chrysomelini	*Phola octodecimguttata*	5 (14)	2 (8)	ELF	*Vitex rotundifolia*	Woody
51	Chrysomelini	*Plagiodera versicolora*	1 (20)	0 (14)	ELF	*Salix chaenomeloides*	Woody
	Criocerinae						
52	Criocerini	*Lilioceris formosana*	8 (11)	–	ELF	*Smilax china*	Woody
53	Criocerini	*Lilioceris merdigera*	1 (3)	–	ELF	*Lilium longiflorum*	Herbaceous
54	Criocerini	*Lilioceris subpolita*	2 (2)	–	ELF	*Smilax china*	Woody
55	Lemini	*Lema cirsicola*	0 (1)	–	ELF	*Commelina communis*	Herbaceous
56	Lemini	*Lema decempunctata*	0 (1)	–	ELF	*Solanum melongena*	Herbaceous
57	Lemini	*Lema diversa*	0 (4)	–	ELF	*Commelina communis*	Herbaceous
58	Lemini	*Oulema tristis*	0 (3)	–	ELF	*Carex* sp.	Herbaceous
	Cryptocephalinae						
59	Chlytrini	*Physosmaragdina nigrifrons*	1 (1)	–	DF	*Fallopia japonica*	Herbaceous
60	Chlytrini	*Smaragdina nipponensis*	3 (3)	–	DF	*Celtis sinensis*	Woody
61	Chlytrini	*Smaragdina semiaurantiaca*	2 (11)	–	DF	*Carpesium divaricatum*	Herbaceous
62	Cryptocephalini	*Cryptocephalus approximatus*	8 (10)	–	UK	*Wisteria floribunda*	Woody
						Castanea crenata	Woody

Appendix 1. Continued

Leaf beetles						Host plants	
	Subfamily		Dropping*				
Code	Tribe	Species	Adult	Larva	Type†	Species	Growth form
						Quercus serrata	Woody
						Rosa multiflora	Woody
63	Cryptocephalini	*Cryptocephalus nigrofasciatus*	2 (2)	–	UK	*Salix triandra*	Woody
64	Cryptocephalini	*Cryptocephalus perelegans*	3 (9)	–	UK	*Leucaena leucocephala*	Woody
						Quercus serrata	Woody
						Morus australis	Woody
65	Cryptocephalini	*Cryptocephalus signaticeps*	1 (2)	–	UK	*Castanea crenata*	Woody
						Quercus serrata	Woody
66	Fulcidacini	*Chlamisus geniculatus*	1 (1)	–	UK	*Rubus sieboldii*	Woody
67	Fulcidacini	*Chlamisus spilotus*	1 (1)	–	UK	*Quercus serrata*	Woody
	Donaciinae						
68	Donaciini	*Donacia lenzi*	0 (8)	–	RF	*Nymphaea tetragona*	Herbaceous
69	Donaciini	*Donacia ozensis*	0 (3)	–	RF	*Nuphar japonica*	Herbaceous
70	Donaciini	*Donacia vulgaris*	1 (5)	–	RF	*Nuphar japonica*	Herbaceous
						Sparganium sp.	Herbaceous
71	Haemoniini	*Donacia japana*	4 (16)	–	RF	*Sparganium* sp.	Herbaceous
	Eumolpinae						
72	Bromiini	*Acrothinium gaschkevitchii*	7 (10)	–	RF	*Vitis ficifolia*	Woody
						Vitis sp.	Woody
73	Bromiini	*Demotina decorata*	2 (3)	–	UK	*Quercus glauca*	Woody
74	Bromiini	*Demotina fasciculata*	0 (2)	–	UK	*Quercus serrata*	Woody
75	Bromiini	*Lypesthes ater*	2 (2)	–	UK	*Juglans mandshurica*	Woody
76	Bromiini	*Lypesthes fulvus*	1 (2)	–	UK	*Cinnamomum yabunikkei*	Woody
77	Bromiini	*Lypesthes japonicus*	2 (2)	–	UK	*Camellia japonica*	Woody
78	Bromiini	*Scelodonta lewisii*	4 (11)	–	UK	*Rumex japonicus*	Herbaceous
79	Bromiini	*Trichochrysea japana*	3 (3)	–	UK	*Quercus crispula*	Woody
80	Bromiini	*Trichochrysea okinawana*	1 (1)	–	UK	*Quercus crispula*	Woody
81	Euryopini	*Colasposoma auripenne*	2 (2)	–	RF	*Ipomoea cairica*	Herbaceous
82	Euryopini	*Colasposoma dauricum*	2 (3)	–	RF	*Calystegia pubescens*	Herbaceous
83	Typophorini	*Basilepta fulvipes*	21 (29)	–	UK	*Artemisia indica*	Herbaceous
84	Typophorini	*Basilepta ruficollis*	2 (2)	–	UK	*Cerasus × yedoensis*	Woody
85	Typophorini	*Pagria* sp.	10 (12)	–	STB	*Rhaphiolepis indica*	Woody
	Galerucinae						
86	Galerucini	*Galeruca vicina*	11 (15)	–	ELF	*Petasites japonicus*	Herbaceous

Appendix 1. Continued

Leaf beetles						Host plants	
	Subfamily		Dropping*				
Code	Tribe	Species	Adult	Larva	Type†	Species	Growth form
87	Galerucini	*Galerucella grisescens*	5 (15)	2 (7)	ELF	*Rumex japonicus*	Herbaceous
88	Galerucini	*Galerucella nipponensis*	1 (4)	–	ELF	*Trapa japonica*	Herbaceous
89	Galerucini	*Ophraella communa*	4 (8)	4 (7)	ELF	*Xanthium occidentale*	Herbaceous
90	Galerucini	*Pyrrhalta fuscipennis*	0 (1)	–	UK	*Acer pictum*	Woody
91	Galerucini	*Pyrrhalta humeralis*	2 (6)	0 (20)	ELF	*Viburnum odoratissimum*	Woody
92	Galerucini	*Pyrrhalta lineola*	0 (10)	–	ELF	*Salix dolichostyla*	Woody
93	Hylaspini	*Agelastica coerulea*	2 (9)	0 (20)	ELF	*Alnus japonica*	Woody
94	Hylaspini	*Arthrotus niger*	9 (10)	–	ELF	*Wisteria floribunda*	Woody
						Castanea crenata	Woody
						Alnus japonica	Woody
95	Hylaspini	*Gallerucida bifasciata*	5 (5)	13 (25)	ELF	*Fallopia japonica*	Herbaceous
96	Hylaspini	*Morphosphaera coerulea*	5 (8)	0 (11)	ELF	*Ficus erecta*	Woody
						Morus australis	Woody
97	Luperini	*Atrachya menetriesi*	2 (3)	–	ELF	*Vicia* sp.	Herbaceous
98	Luperini	*Aulacophora bicolor*	6 (8)	–	RF	*Diplocyclos palmatus*	Herbaceous
99	Luperini	*Aulacophora indica*	13 (21)	–	RF	*Cucumis sativus*	Herbaceous
						Cucurbita maxima	Herbaceous
						Lagenaria siceraria	Herbaceous
100	Luperini	*Aulacophora loochooensis*	2 (2)	–	RF	*Diplocyclos palmatus*	Herbaceous
101	Luperini	*Aulacophora nigripennis*	5 (9)	–	RF	*Diplocyclos palmatus*	Herbaceous
102	Luperini	*Epaenidea elegans*	1 (2)	–	UK	*Ehretia dicksonii*	Woody
103	Luperini	*Fleutiauxia armata*	18 (20)	–	RF	*Morus australis*	Woody
104	Luperini	*Liroetis coeruleipennis*	1 (10)	–	UK	*Quercus acutissima*	Woody
105	Luperini	*Monolepta kurosawai*	2 (2)	–	UK	*Hovenia trichocarpa*	Woody
106	Luperini	*Monolepta nojiriensis*	6 (12)	–	UK	*Styrax japonicus*	Woody
107	Luperini	*Monolepta pallidula*	2 (2)	–	UK	*Quercus variabilis*	Woody
108	Luperini	*Paridea angulicollis*	1 (1)	–	RF	*Gynostemma pentaphyllum*	Herbaceous
109	Luperini	*Paridea quadriplagiata*	1 (1)	–	RF	*Aster sugimotoi*	Herbaceous
110	Oidini	*Oides bowringii*	10 (15)	0 (15)	ELF	*Kadsura japonica*	Woody
	Lamprosomatinae						
111	Lamprosomatinae	*Oomorphoides cupreatus*	8 (22)	–	UK	*Aralia elata*	Woody
112	Lamprosomatinae	*Oomorphoides loochooensis*	8 (8)	–	UK	*Schefflera heptaphylla*	Woody

*Numbers of individuals dropping from host plants. Values in parentheses indicate the total numbers of individuals investigated in this study.
†Larval feeding type: DF, detritus feeder; ELF, external leaf feeder; LM, leaf miner; RF, root feeder; SEB, seed borer; STB, stem borer; UK, unknown. All adults feed externally on leaves.