



# Host plant architecture affects the costs of dropping behaviour in *Phaedon brassicae* (Coleoptera: Chrysomelidae)

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## Abstract

Phytophagous insects escape from predators by dropping. However, if they drop to the ground, they must then return to the host plants. Large oval leaves may serve as safety nets when insects drop from overlying leaves. To clarify the effects of leaf shape on the sites to which insects drop, we investigated the dropping behaviour of *Phaedon brassicae* (Coleoptera: Chrysomelidae) on three host plants (daikon, bok choy, and Chinese cabbage). Daikon plants have cleft leaves, whereas bok choy and Chinese cabbage plants have oval leaves. When poked with forceps, larvae dropped less frequently than adults. The proportions of individuals dropping to the ground also differed among host plants. Both larvae and adults on the ventral (abaxial) leaf surfaces of daikon frequently dropped to the ground via clefts in the underlying leaves. However, larvae and adults on the ventral leaf surfaces of bok choy and Chinese cabbage frequently dropped to underlying leaves. Most larvae and adults that dropped to the ground finally returned to host plants. However, the return times were longer for larvae than adults. Therefore, the cost of dropping from daikon leaves was higher than were the costs of dropping from leaves of other crop species.

**Keywords** Defense · Escape · Leaf shapes · Phytophagous insects

## Introduction

Escape is a defensive behaviour (Edmunds 1974; Ruxton et al. 2004). Some arthropods escape predators by dropping (Castellanos et al. 2011; Day et al. 2006; Losey and Denno 1998a, b; Sato et al. 2005). Dropping allows rapid departure from sites where predators may be encountered (Francke et al. 2008; Sato et al. 2005). However, arthropods dropping to the ground may encounter ground-dwelling predators such as ants (Losey and Denno 1998c; Loughridge and Luff 1983) and may also suffer desiccation; ground temperatures are higher than plant aerial temperatures (Dill et al. 1990; Roitberg et al. 1979). In addition, departure from a feeding site reduces reproductive capacity and feeding efficiency

and increases developmental time (Agabiti et al. 2016; Nelson 2007). Even when dropping to the ground is not lethal, the energy used to return to feeding sites and the prolonged growth period can be considered costs of dropping behaviour (Agabiti et al. 2016; Nelson 2007). Therefore, arthropods seek to avoid dropping to the ground (Brackenbury 1996; Sugiura and Yamazaki 2006; Yanoviak et al. 2005, 2009, 2015).

Host plant architecture (e.g., leaf shape) may modulate the ground-dropping frequency of phytophagous insects. Large oval leaves serve as safety nets for insects dropping from overlying leaves; insects on host plants that have oval leaves drop to the ground less frequently than do insects on plants with small or cleft leaves. Therefore, it is likely that the costs of dropping behaviour vary among host plant species. However, this hypothesis has not been tested. Such work would allow us to understand the evolution of escape behaviour in, and host selection by, phytophagous insects.

To explore the influence of host plant architecture on the costs of dropping in phytophagous insects, we investigated the escape and defensive behaviours of the daikon leaf beetle *Phaedon brassicae* (Baly) (Coleoptera: Chrysomelidae) living on three host plants differing in terms of leaf shape.

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*Phaedon brassicae* is a well-recognised pest of cruciferous crops (Funaki 1958; Kimoto and Takizawa 1994; Miura and Shigeta 1967; Okada 2003). The insect feeds on many species and varieties of cruciferous crops that differ in terms of leaf shape (Kimoto and Takizawa 1994). Both larvae and adults of *P. brassicae* drop from host plants when they are disturbed (Okada 2003). Thus, *P. brassicae* is a suitable model to clarify the effects of leaf shape on post-dropping behaviour. The ground mortality risk may be higher for larvae than adults because adults are more mobile than larvae. Thus, the effects of host plant architecture on post-dropping behaviour may differ between larvae and adults. To compare the effects of leaf shape on the dropping behaviour costs of larvae and adults, we performed the following field observations and experiments. First, we observed dropping and other defensive behaviours of *P. brassicae* larvae and adults living on three host plants. Second, we explored whether larvae and adults dropped to the ground or to host plant leaves. If larvae and adults dropped to the ground, we explored whether they returned to the host plants. If return was successful, the time required for return was recorded. In addition, we investigated the abundance and distributions of *P. brassicae* larvae and adults on three host plants to explore the relationship between dropping behaviour and host plant use. Finally, we discuss the effects of host plant architecture on the costs of dropping behaviour in *P. brassicae*.

## Materials and methods

### Study site and species

Field observations and experiments were conducted at a farm located in Sannan-cho, Tamba, Hyogo Prefecture, Japan (35°05'N, 135°05'E; 128 m above sea level; Matsubara and Sugiura 2017). Various crops (cruciferous, leguminous, and solanaceous plants) are cultivated on the farm. Many pests, including *P. brassicae* and its natural enemies, live on the farm; neither pesticides nor herbicides are used.

We studied larvae and adults of the leaf beetle species *P. brassicae* to explore defensive behaviours and associated costs; the beetle serves as a model phytophagous insect. *Phaedon brassicae* growth proceeds through three larval instars before pupation; each instar is identifiable by body colour and the number of body hairs (Funaki 1958). When larvae and adults were disturbed, they folded their legs and antennae (a tonic immobilising behaviour) and consequently dropped to the ground (Fig. 1a), underlying leaves (Fig. 1b), or the same leaves (Fig. 1c). Both larvae and adults were abundant at our field site from October to November. Third-instar larvae and adults were used in the following experiments because first- and second-instar larvae were too small to allow investigations to be made under field conditions.

#### (a) Dropping to the ground



#### (b) Dropping to an underlying leaf



#### (c) Dropping to the same leaf



**Fig. 1** Hypothetical dropping patterns of *Phaedon brassicae*. An adult drops to **a** the ground through a leaf cleft, **b** an underlying leaf of the same plant, and **c** the same leaf. The illustrations were modified from Matsubara and Sugiura (2018)

The body length of third instars was 3.4–5.9 mm and that of adults 3.3–4.9 mm. To explore the effects of host plant architecture on the costs of dropping behaviour, we used three host plants (two species but of three varieties: Brassicales: Brassicaceae): daikon (Japanese white radish; *Raphanus sativus* L. var. *longipinnatus*); bok choy (*Brassica rapa* var. *chinensis*); and Chinese cabbage (*Brassica rapa* var. *pekinensis* L.). During our experimental period, 66 daikon, 51 bok choy, and 62 Chinese cabbage plants

were under cultivation at the study site. Daikon plants have cleft leaves, whereas bok choy and Chinese cabbage plants have oval leaves (Fig. 2). The leaf widths and lengths were respectively 58–84 and 97–297 mm for daikon, 82–138 and 75–187 mm for bok choy, and 122–228 and 53–231 mm for Chinese cabbage. Because of their leaf shapes, bok choy and Chinese cabbage leaves are more likely to overlap than are daikon leaves (Fig. 2). We hypothesised that the difference in leaf shape would predict the ground-dropping frequency of *P. brassicae* (Fig. 1).

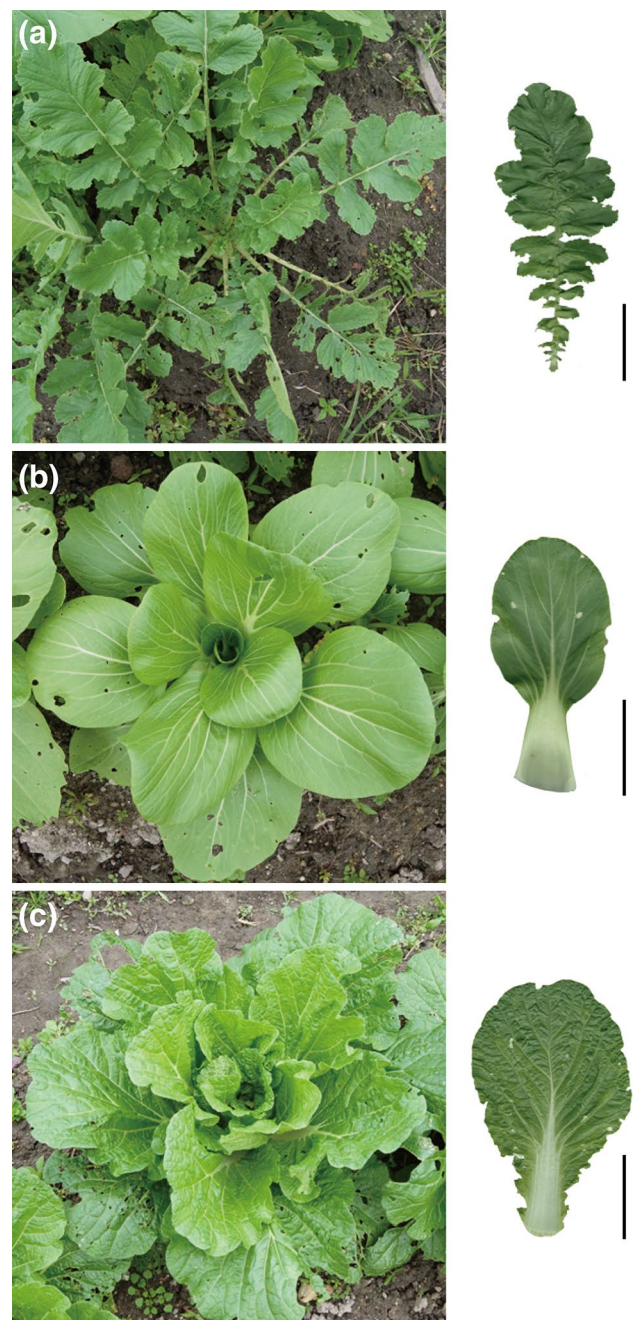
### Dropping and other defensive behaviours

To explore the influence of host plant type on the defensive behaviours of *P. brassicae* larvae and adults, we observed the responses of third-instar larvae and adults to simulated attacks. We poked larval abdomens and adult elytrons with forceps to simulate attacks by predacious insects, such as ants. Twenty larvae and 20 adults randomly selected from leaves of each host plant (i.e., 60 larvae and 60 adults in all) were used for the experiments. In control experiments, we held the forceps 100 mm away from larvae and adults. Similarly, 20 larvae and 20 adults randomly selected from leaves of each host plant were used for the control experiments (i.e., 60 larvae and 60 adults in all).

The leaf positions [dorsal (adaxial) or ventral (abaxial)] of all larvae and adults were recorded. In a preliminary experiment, we found that both larvae and adults exhibited escape or defensive behaviour in response to poking, but not to other stimuli (e.g., air blowing). After poking with forceps, we observed whether larvae or adults exhibited dropping behaviour, and whether they dropped to the ground or to the same or other leaves (Fig. 1). If such behaviour was lacking, any alternative behaviour was observed. Larvae mobilise chemical defences as alternatives to dropping (Kimoto and Takizawa 1994; Sugawara et al. 1979). When the larvae secreted liquids from their bodies, we considered that a chemical defence was in play. We performed our experiments from early October to early November 2016 (09:30–18:00; temperature 17.3–23.2 °C at the Kaibara Meteorological Station, 35°08'N, 135°04'E, 98 m above sea level).

### Post-dropping behaviours

To explore the influence of plant architecture on the post-dropping behaviour of *P. brassicae*, we performed the following experiment. Insects were more likely to drop from outer leaves to the ground, but more likely to drop from inner leaves to other leaves of the same host plant. Therefore, we did not use insects found on either the outermost or innermost leaves. To evoke dropping behaviour, we poked randomly selected larvae and adults on each host plant. When



**Fig. 2** The three host plants used in this study. **a** Daikon, *Raphanus sativus* L. var. *longipinnatus*. **b** Bok choy, *Brassica rapa* var. *chinensis*. **c** Chinese cabbage, *Brassica rapa* var. *pekinensis* L. Daikon plants have cleft leaves, whereas bok choy and Chinese cabbage plants have oval leaves, rendering leaf overlap more likely in the latter two plants. Scale bar: 50 mm. The images of host plants were modified from Matsubara and Sugiura (2018)

they exhibited dropping behaviour, we determined whether they dropped to the ground or to leaves of the host plant. Individuals that did not exhibit dropping behaviour were removed from the experiments. Therefore, we investigated the sites to which 11 larvae and 11 adults dropped from



the dorsal leaf surfaces of each host plant type. Similarly, we investigated the sites to which 11 larvae and 11 adults dropped from the ventral leaf surfaces of each host plant type. When larvae and adults dropped to the ground, we explored whether they returned to host plants, and recorded the return times to the nearest second using a stopwatch. When larvae and adults became inactive in the soil, we considered that they had failed to return to the host plants. Experiments were conducted from early October to early November 2016 (09:30–17:00; temperature 10.6–25.5 °C).

### Abundance and distribution on host plants

To explore the host plant use of *P. brassicae*, we investigated the abundance and distribution. Ten daikon plants, 10 bok choy plants, and 10 Chinese cabbage plants were randomly selected on 24 October 2016. The numbers of third-instar larvae and adults were counted on each plant (08:30–12:30; temperature 15.0–18.1 °C). Their positions (dorsal or ventral leaf side) were also recorded. The plant heights of daikon, bok choy, and Chinese cabbage were 285–439, 199–277, and 172–291 mm, respectively.

### Data analyses

Generalised linear mixed models (GLMMs) with binomial error distributions and logit links were used to determine (1) factors affecting defensive behaviours of *P. brassicae*; (2) factors determining the places to which *P. brassicae* dropped; and (3) factors affecting the return rates of *P. brassicae* to host plants. (1) Whether *P. brassicae* exhibited dropping or other behaviour (1/0) served as the response variable; host plant types (daikon, bok choy, or Chinese cabbage), the developmental stage of *P. brassicae* (larva or adult), and the position of *P. brassicae* (the ventral or dorsal leaf side) were fixed factors; and individual host plants were treated as random factors. (2) Whether *P. brassicae* dropped to the ground or onto leaves of the same host plant (1/0) served as the response variable; host plant types, the developmental stage of *P. brassicae*, and the position of *P. brassicae* were fixed factors; and individual host plants were treated as random factors. (3) Whether *P. brassicae* could successfully return to the host plant or not (1/0) served as the response variable; host plant types and *P. brassicae* stages as fixed factors; and host plant individuals as random effects. In addition, a GLMM with a Gaussian error distribution and an identity link was used to define factors affecting the time required for insects to return to host plants from the ground. This time was the response variable; the host plant types and *P. brassicae* stages were fixed factors, and host plant individuals were treated as random effects. To define factors affecting the abundance of *P. brassicae* larvae or adults, we also ran

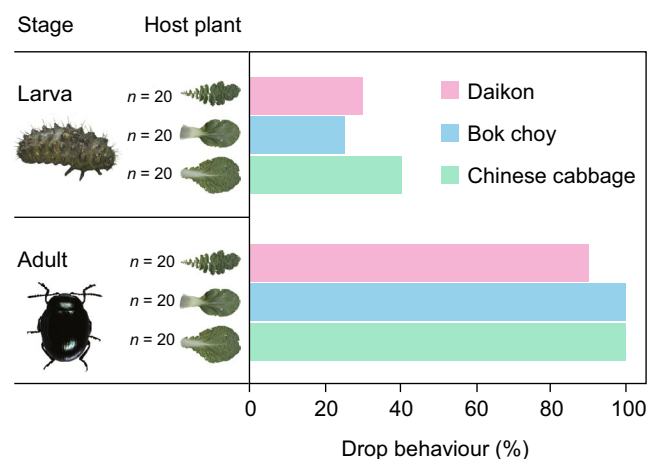
GLMMs with Poisson error distributions and log links. The numbers of *P. brassicae* larvae or adults per plant served as the response variables, host plant types were fixed factors, and host plant individuals were treated as random effects. Furthermore, GLMMs with binomial error distributions and logit links were used to clarify the effects of host plant type on the distribution of *P. brassicae* larvae or adults on leaves on each plant. The presence of *P. brassicae* on the dorsal or ventral side of leaves (1/0) was the response variable, the host plant types were fixed factors, and host plant individuals were considered random effects.

All analyses were performed using R software version 3.4.1 (R Development Core Team 2015). GLMMs were run using the lme4 package 1.1.13 (Bates et al. 2017) and the lmerTest package 2.2.33 (Kuznetsova et al. 2016).

## Results

### Dropping behaviour

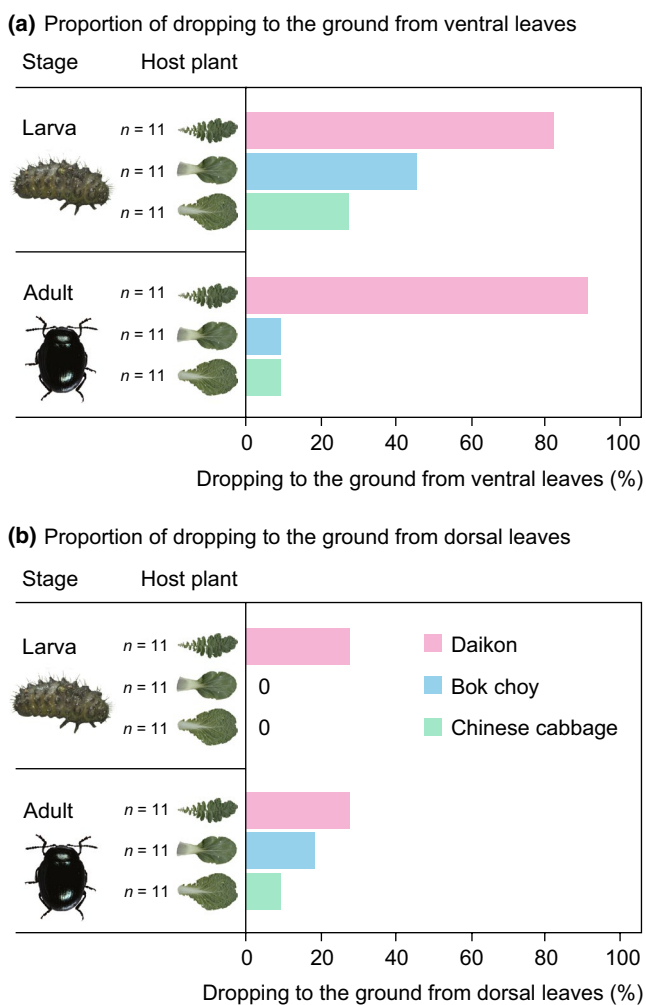
When poked by forceps, *P. brassicae* adults dropped more frequently than did larvae (Fig. 3). Almost all adults dropped on all three host plants (Fig. 3). Less than half of all larvae dropped (Fig. 3). Therefore, the rates differed significantly between adults and larvae, but not among host plants (Table S1 in the electronic supplementary material). Two adults that did not drop walked for 5–20 mm and sat still. All larvae that did not drop mounted a chemical defence, secreting liquid from their bodies. No larva or adult responded to control stimuli.



**Fig. 3** Frequencies of *Phaeton brassicae* exhibiting dropping behaviour. The dropping behaviour included all three patterns (see Fig. 1). Pink, blue, and green bars indicate daikon, bok choy, and Chinese cabbage, respectively. The images of leaf beetles and host plants were modified from Matsubara and Sugiura (2018) (colour figure online)

### Post-dropping behaviour

Larvae and adults dropped to the ground or to the same host plant (Fig. 1). Both larvae and adults more frequently dropped to the ground from the ventral leaf surfaces of daikon plants than from the ventral leaf surfaces of bok choy and Chinese cabbage plants (Fig. 4a; Table S2 in the electronic supplementary material). Larvae and adults on the ventral leaf surfaces of bok choy and Chinese cabbage plants frequently dropped to underlying leaves of the same host plants (Fig. 4a; Table S2). Therefore, the frequency of dropping to the ground differed significantly among host plants, but not between *P. brassicae* larvae and adults (Table S2). In addition, an effect of feeding position (i.e., on the ventral



**Fig. 4** Frequencies of *Phaedon brassicae* dropping to the ground. **a** Dropping from the ventral sides of leaves. **b** Dropping from the dorsal sides of leaves. Pink, blue, and green bars indicate daikon, bok choy, and Chinese cabbage, respectively. Individuals that did not exhibit dropping behaviour were removed from the experiments. The images of leaf beetles and host plants were modified from Matsubara and Sugiura (2018) (colour figure online)

or dorsal leaf side) was evident (Fig. 4a, b; Table S2). Therefore, *P. brassicae* more frequently dropped to the ground from ventral than dorsal leaf surfaces (Table S2).

When larvae and adults dropped to the ground, the sites to which they dropped were 0.1–0.2 m from the bases of the host plants. Dropping larvae and adults folded their legs and antennae (a tonic immobilising behaviour). Larvae and adults revived in  $133.3 \pm 74.8$  s [mean  $\pm$  standard error (SE),  $n = 16$ ] and  $52.4 \pm 33.4$  s ( $n = 17$ ), respectively, after dropping to the ground. In total, 67–80% and 92–100% of larvae and adults successfully returned to host plants (Table 1). Of 16 larvae, one was observed to repel an ant of a *Formica* species (Hymenoptera: Formicidae) by secreting a chemical. The return rate did not differ significantly among *P. brassicae* stages or host plants (Table S3 in the electronic supplementary material). However, the time required to return to host plants differed significantly between larvae and adults (Fig. 5; Table S4 in the electronic supplementary material). Therefore, the larvae required more time than adults to return.

### Abundance and distribution on host plants

The numbers of *P. brassicae* larvae per plant differed significantly between daikon and bok choy, but not daikon and Chinese cabbage (Table 2; Table S5 in the electronic supplementary material). The numbers of *P. brassicae* adults per plant differed between daikon and bok choy and daikon and Chinese cabbage (Table 2; Table S6 in the electronic supplementary material). Both larvae and adults were more frequent on ventral than the dorsal leaf surfaces (Table 2); the proportions did not differ significantly among host plants (Tables S7 and S8 in the electronic supplementary material).

### Discussion

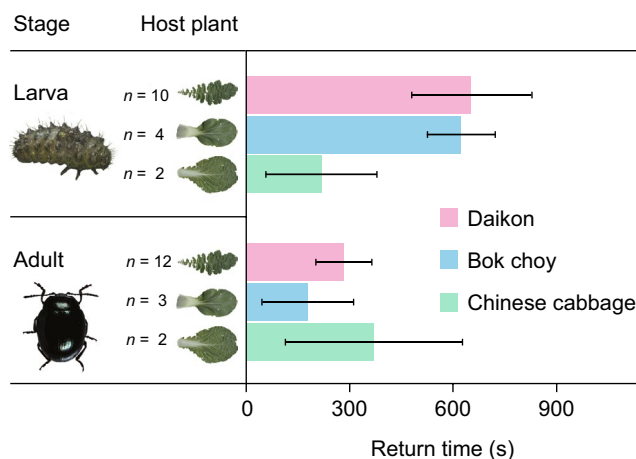
Some phytophagous insects escape predators by dropping from host plants (Castellanos et al. 2011; Losey and Denno 1998a; Sato et al. 2005), but few studies have focused on

**Table 1** Post-dropping behaviours of *Phaedon brassicae* larvae and adults living on three host plants

Host plants	Percentages of <i>P. brassicae</i> returning to host plants ( $n$ ) <sup>a</sup>	
	Larvae	Adults
Daikon	83.3 (12)	92.3 (13)
Bok choy	66.7 (3)	100.0 (2)
Chinese cabbage	80.0 (5)	100.0 (3)
Total	80.0 (20)	94.4 (18)

<sup>a</sup>Values in parentheses indicate the total numbers of larvae or adults

**Fig. 5** Times required for third-instar larvae and adults of *Phaedon brassicae* to return to host plants. The bars indicate mean  $\pm$  standard errors. Pink, blue, and green bars indicate daikon, bok choy, and Chinese cabbage, respectively. The images of leaf beetles and host plants were modified from Matsubara and Sugiura (2018) (colour figure online)



**Table 2** The abundance and distributions of *Phaedon brassicae* larvae and adults on each of three host plants

Host plants	Larvae		Adults			
	Numbers $\pm$ SE <sup>a</sup>	Distribution (%) <sup>b</sup>		Numbers $\pm$ SE <sup>a</sup>	Distribution (%) <sup>b</sup>	
		Ventral	Dorsal		Ventral	Dorsal
Daikon	2.1 $\pm$ 0.7	76.2	23.8	8.0 $\pm$ 0.9	58.8	41.3
Bok choy	3.7 $\pm$ 0.4	73.0	27.0	4.8 $\pm$ 0.9	64.6	35.4
Chinese cabbage	2.3 $\pm$ 0.5	95.7	4.3	1.0 $\pm$ 1.4	60.0	40.0

<sup>a</sup>Numbers of *Phaedon brassicae* per plant

<sup>b</sup>Percentages of individuals on the ventral or dorsal side of leaves

the sites to which phytophagous insects drop (Castellanos and Barbosa 2011). We found that the leaf shapes of the host plants affected the sites to which *P. brassicae* dropped (Fig. 4) and that the host plant effects differed between larvae and adults (Fig. 5). However, the findings reflect limited aspects of *P. brassicae* dropping behaviour because factors other than leaf shape (e.g., leaf hairs, hardness, and chemicals) may influence the behaviour. Ideally, *P. brassicae* behaviour should be compared among different leaf shapes (i.e., cleft vs. oval) of the same plant species to investigate the effects of leaf shape. Considering this limitation, we examined the dropping behaviour of *P. brassicae* in terms of defensive strategies and energy costs.

### Defensive strategies

Some insects change defensive strategies during development (e.g., Cornell et al. 1987; Grant 2007; Watanabe and Yano 2010). However, few studies have explored whether the relative significance of dropping and other defensive behaviours changes during the development of phytophagous insects (Lucas et al. 1997). The differences in dropping behaviour between adults and larvae (Fig. 3) indicate that *P. brassicae* changes its defensive strategy during development from the larval stages to adulthood.

The time required to return to the host plants was longer for larvae than adults (Fig. 5; Table 1); thus, the costs associated with dropping to the ground were higher for larvae than adults. Therefore, larvae exhibited dropping behaviour in response to simulated attacks less frequently than did adults (Fig. 3). The relative significance of dropping behaviour was lower for larvae than adults.

*Phaedon brassicae* larvae mainly mounted a chemical defence to simulated attacks. This can repel predators such as ants (Sugawara et al. 1979). Indeed, one larva that dropped to the ground was observed to repel an ant using chemical defence. However, some larvae exhibited dropping behaviour (Fig. 3), which suggests that such behaviour is more effective against some predators than chemical defence. For example, crab spiders and frogs feed on *P. brassicae* larvae on crop leaves (Matsubara 2017).

*Phaedon brassicae* adults mainly exhibited dropping behaviour in response to simulated attacks (Fig. 3). As adults cannot fly, they walk on the ground to move among host plants. Therefore, the costs of dropping behaviour are not considered high for adults. Although adults do not secrete defensive chemicals, the hard exoskeleton (i.e., the elytra) of adults may function as a physical defence against predators. Indeed, we observed that ground-dwelling wolf

spiders failed to kill adults (Matsubara and Sugiura personal observations).

### Effects of host plant architecture

Previous studies explored the roles played by host plants on insect development, behaviour, and host selection (Awmack and Leather 2002; Müller and Müller 2017), but not the costs of dropping behaviour in phytophagous insects. In this study, we found that the costs of dropping behaviour differed among host plant types in the leaf beetle *P. brassicae*. The beetles frequently dropped to the same leaves from the dorsal sides of leaves (Fig. 1c), while they were physically unable to drop from the ventral side of leaves to the same leaves. Accordingly, *P. brassicae* dropped more frequently to the ground from ventral than dorsal leaf surfaces on the three host plant types (Table S2). In addition, we found that *P. brassicae* more frequently dropped to the ground from the ventral leaf surfaces of daikon than from those of other host plants (Fig. 4), which suggests that the costs of dropping from the ventral sides of daikon leaves were higher than those associated with dropping from bok choy and Chinese cabbage leaves. Therefore, different costs of dropping behaviour from distinct host plants might induce the following responses: *P. brassicae* changes its behaviour from dropping to other defences when on daikon, and avoids the ventral leaf surfaces of daikon. However, such responses were not observed in this study (Fig. 3, Tables 2 and S5–S8).

Some phytophagous insect species feed on several plant species that differ in terms of architecture (Strong et al. 1984). Predation pressures imposed by natural enemies differ among host plants (Barbosa et al. 2001; Lill et al. 2002; Sugiura 2007), which suggests that both enemies and host plant architecture impose selective evolutionary pressures on defensive behaviour and host plant selection. Further studies are needed to clarify the effects of host plants on the success of various defences mounted by phytophagous insects.

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**Author contribution** SM and SS conceived and designed experiments. SM conducted field observations and experiments. SM analyzed the data. SM and SS wrote the manuscript.

### Compliance with ethical standards

The experiments complied with the current laws of Japan.

**Conflict of interest** The authors declare that they have no competing interests.

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