

# Trabala Vishnou Gigantina Yang (Lepidoptera: Lasiocampidae) Larval Fitness on six Sympatric Plant Species in Sea-Buckthorn Forest

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**Abstract** *Trabala vishnou gigantina* Yang (Lepidoptera: Lasiocampidae) is a major pest that damages the sea-buckthorn, *Hippophae rhamnoides*. We observed and compared the feeding preferences of *T. vishnou gigantina* larvae on six sympatric plant species in a two-choice test. We also compared *T. vishnou gigantina* fitness, as measured by the following variables: larvae weight, developmental period, pupae versus adult weight, longevity, and fecundity rates. Between host and non-host plants, larvae showed a strong preference for their natural host (sea-buckthorn), followed by apricot, poplar, and willow. Caragana and locust were the least preferred plants when the natural host plant was not present. Larvae reared on sea-buckthorn possessed greater pre-pupal weight, had lower mortality, and developed more quickly into heavier pupae than either poplar-raised or willow-raised larvae. Fecundity was highest on sea-buckthorn, second highest on apricot, and lowest on poplar. Longevity (of both females and males) was not significantly different across plant species. These results clearly demonstrate that *T. vishnou gigantina* larvae are able to distinguish between host versus non-host plants, and that their preference translates to increased fitness. Possible, non-mutually exclusive explanations for observed preference and fitness differences include variation in required nutritional content across plant species or the presence of plant traits (morphological features or chemical metabolites) that negatively affect larval development. While the exact mechanisms are unknown, these data may be useful for

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the development of appropriate counter-measures to the damage caused by *T. vishnou gigantina* on sea-buckthorn.

**Keywords** Feeding preference · larval development · polyphagous insects · plant host selection

## Introduction

The ability to consume a broad range of plants is a common characteristic of many herbivorous insects. Polyphagous herbivores may increase their overall fitness by using various hosts (Uechi and Yukawa 2006). Larval diet is known to affect growth rates and is frequently the adult's primary source of nitrogen. Therefore a varied diet buffers the larvae from suboptimal host choices by the mother, thus increasing their chances of survival (Gamberale-Stille et al. 2014). Given the wider range of potentially suitable plants, polyphagous insects must be able to discriminate between appropriate versus inappropriate—even harmful—hosts. This host plant selection process can be divided into two aspects: (1) the ability of an adult female to find and recognize a suitable host for egg laying and (2) the ability of larvae to develop successfully on the plant (Thorsteinson 1953; Bernays and Chapman 1994). Thus, the presence of traits that facilitate oviposition success and larvae survival contribute to the suitability of a plant species as host. Understanding these host criteria is very important for predicting pest expansion (Henniges-Janssen et al. 2014). Further, studying host selection gives valuable insight into the co-evolution of herbivorous insects and their plant hosts (Silva et al. 2014).

While some polyphagous herbivores benefit from shared physical or chemical features by feeding on closely related hosts (Fahey et al. 2001), others are also able to use plants from different families (Tikkanen et al. 2000; Friberg and Wiklund 2009; Prager et al. 2014). For instance, *Trabala vishnou gigantina* Yang (Lepidoptera: Lasiocampidae) is a defoliator moth that is mainly distributed in the provinces of Shaanxi, Ningxia, Gansu, Qinghai, Hebei, Henan, and Shanxi, as well as the Inner Mongolia autonomous region. The moth has numerous host plants all belonging to different families, including Elaeagnaceae: *Elaeagnus pungens*, *Hippophae rhamnoides*; Rosaceae: *Malus spectabilis*, *Malus pumila*, *Rosa chinensis*; Fagaceae: *Quercus variabilis*, *Quercus aliena*; Salicaceae: *Salix matsudana*, *Populus davidiana*; Juglandaceae: *Juglans regia*; Ulmaceae: *Ulmus pumila*, and Aceraceae: *Acer* spp. (Wang et al. 1987; Liu and Wu 2006; Liu et al. 2013). The wide range of potential hosts available to *T. vishnou gigantina* has caused serious economic losses for all provinces in which the moth is primarily found. For example, Wuqi County of Shaanxi Province has recently seen a large increase *T. vishnou gigantina* populations feeding on sea-buckthorn (*Hippophae rhamnoides*). This plant is widely distributed in the Loess Plateau, where it is crucial for water and soil conservation (Luo et al. 2003). The damage to sea-buckthorn has severely impaired local eco-environmental construction and economic development (Liu et al. 2013). In addition to sea-buckthorn, caragana was widely planted in Wuqi country, which is well adapted to drought conditions, and is good forage (Liu et al. 2014). Apricot as an important economic forest tree species, have very strong resistant cold and drought tolerant characteristics (Bao 2015). The

field survey resulted that *T. vishnou gigantina* larvae was sometimes feeding on apricot, which is widely distribution on sea-buckthorn forests, however the present of investigation on this species does not imply that apricot is host. Previous studies we know that *T. vishnou gigantina* can utilize other species of poplar and willow as well (Liu and Wu 2006). So, in relatively dense population, some of switching will take place between trees of different species, finally selected the above six kinds of plants to carry out our study.

*Trabala vishnou gigantina* has one generation per year (Wang et al. 2012; Liu et al. 2013). Eggs overwinter for approximately eight to nine months and hatch in early May. The newly hatched larvae undergo seven instars. Larvae usually consume the leaves of their host plant, weakening plant growth and eventually causing its death. Two months post-hatching, pupation occurs in late July, and adults begin to emerge from late August to late September, mating near their pupation site. Eggs are frequently found on the old cocoon or the plant bark near the cocoon (Wang et al. 2012; Liu et al. 2013).

Although *T. vishnou gigantina* has numerous hosts, the moth appears to use sea-buckthorn exclusively in the sea-buckthorn forests of Shaanxi Province, despite the presence of other potential host plants (including apricot, poplar, willow, caragana, and locust). It is unclear why *T. vishnou gigantina* does not choose these sympatric plant species as hosts, and to date, no studies exist to investigate the mechanism or the host selection behavior of *T. vishnou gigantina* larvae.

Therefore, in this study, we studied the fitness of *T. vishnou gigantina* larvae on six sympatric plant species in a sea-buckthorn forest. Our objectives were (1) to determine *T. vishnou gigantina* larval preferences for six sympatric plant species in a two-choice behavior assay and (2) to investigate *T. vishnou gigantina* larval fitness on the six plant species, using a host of morphological and life history variables as proxies for fitness.

## Materials and Methods

### Insect and Plant Materials

For the fitness experiments, *T. vishnou gigantina* eggs were collected from a sea-buckthorn forest in Wuqi County, Yan'an City, Shaanxi Province, China (108°38' E, 35°38' N). Eggs were disinfected via a 2-min soak in sodium hypochlorite, rinsed with distilled water for 5 min, and dried. Eggs were kept in a 100-mL plastic vial (diameter: 8 cm, depth: 5 cm) until eclosion. Hatched larvae were reared in plastic vials as well (see below in "Measurement of larval fitness on six sympatric plant species").

Third-instar larvae were collected from the sea-buckthorn forest in mid-June of 2014 and kept in cages until molt. The newly molted, fourth-instar larvae were food deprived for approximately 24 h, and then used in the choice experiments.

Six plant species belonging to four different families were used as potential hosts, namely, sea-buckthorn (*Hippophae rhamnoides*) from Elaeagnaceae, poplar (*Populus davidiana*) and willow (*Salix matsudana*) from Salicaceae, apricot (*Armeniaca sibirica*) from Rosaceae, as well as caragana (*Caragana korshinskii*) and locust (*Robinia pseudoacacia*) from Leguminosae. These plant species are all sympatrically distributed in the same sea-buckthorn forest from which the insect samples were collected.

## Larval Choice of Six Sympatric Plant Species

A two-choice feeding preference assay was conducted following previously described methods (Berdegue and Trumble 1996). The experiment was carried out using a behavior test chamber, stored in the laboratory at L: D 14:10 and 60 % relative humidity. Day and night temperatures were 18 °C and 29 °C, respectively.

Each morning of the experiment, plant samples were newly cut from the field and then placed into a cage (50 × 50 × 50 cm) for the choice test. Each choice involved a plant pair of two different species, with one species on the right and another on the left. To maintain freshness, twig ends were kept in paper cups (250 mL) filled with water. The cups were covered with gauze nets to prevent larvae from falling in and drowning. Ten food-deprived, fourth-instar larvae were then released on the center of the cage bottom. Larval preference was evaluated by calculating the proportion of larvae on different plant twigs. Three replications were conducted per treatment. Individual larvae were used only once and none had previously experienced the test condition. The number of larvae on the plant samples was recorded 6 h, 12 h, 24 h, and 36 h post-release into the cage.

## Measurement of Larval Fitness on Six Sympatric Plant Species

Based on the outcome of the choice experiment, four plant species—sea-buckthorn, apricot, poplar, and willow—were selected for use in the larval fitness experiment. Preliminary tests also indicated that *T. vishnou gigantina* larvae did not pupate successfully on the caragana and locust.

The experiment was carried out using a behavior test chamber, located in the laboratory under the same environmental conditions as the choice experiments.

We used 120,100-mL plastic vials (diameter: 8 cm, depth: 5 cm) to rear larvae. The vials were disinfected with 90 % ethanol and were covered with gauze for aeration. Freshly detached leaves from different plant species were placed into the vials as feed. Newly hatched neonate larvae were also placed into the vials, with one larva per vial. At the third instar stage, all larvae fed on the same plant species were simultaneously transferred into a cage (50 × 50 × 50 cm) containing the same plant species. Plants were replaced every two days to ensure that the larvae were fed ad libitum. Twig set-up was the same as the choice test.

We checked for larvae mortality and molting daily. Total larval mortality was calculated as the proportion of all dead larvae during the full larval stage to the total number of larvae at the start of the fitness experiment. Every three days, we weighed the larvae individually. In addition, for each instar molting stage, we measured larval body length, body weight, and the time of molting to investigate the influence of different plants on larval development speed. Thirty replications were performed for each plant species.

Newly formed pupae were checked individually. All pupae were weighed two days post-pupation, when the cuticle had sufficiently hardened enough for handling. Male and female mean weights from each replication were calculated. In addition, pupal duration was recorded.

After adult emergence, both sexes were transferred to oviposition containers (50 × 50 × 50 cm). Each male and female pair was provided with fresh host plant

twigs until oviposition occurred. All deposited eggs found on host twigs and the inner walls of each container were counted daily for fecundity calculations. We checked for adult mortality daily, until all adults had died out. Adult lifespans on various host plants were then calculated.

An electronic scale (METTLER TOLEDO, AB204-S, Switzerland), accurate to 0.10 mg, was used to weigh the larvae, pupae, and adults. A caliper (Blue Light, China), accurate to 0.02 mm, was used to measure larvae body lengths.

## Statistical Analysis

Independent samples t-tests were used to analyze larvae host selection and female versus male weights. The effect of host plant species on larval development time, weights, body length per instar, larval stage duration, total larval mortality in the early and late instars, pupae weights, pupae duration, adult weights, adult lifespan, and adult fecundity were analyzed with individual one-way ANOVAs. Post-ANOVA, we tested the significance of variable means using least significant difference multiple range tests ( $P < 0.05$ ) (SPSS 16.0, SPSS Inc. Chicago, IL, USA).

## Results

### Larval Selection of Six Sympatric Plant Species

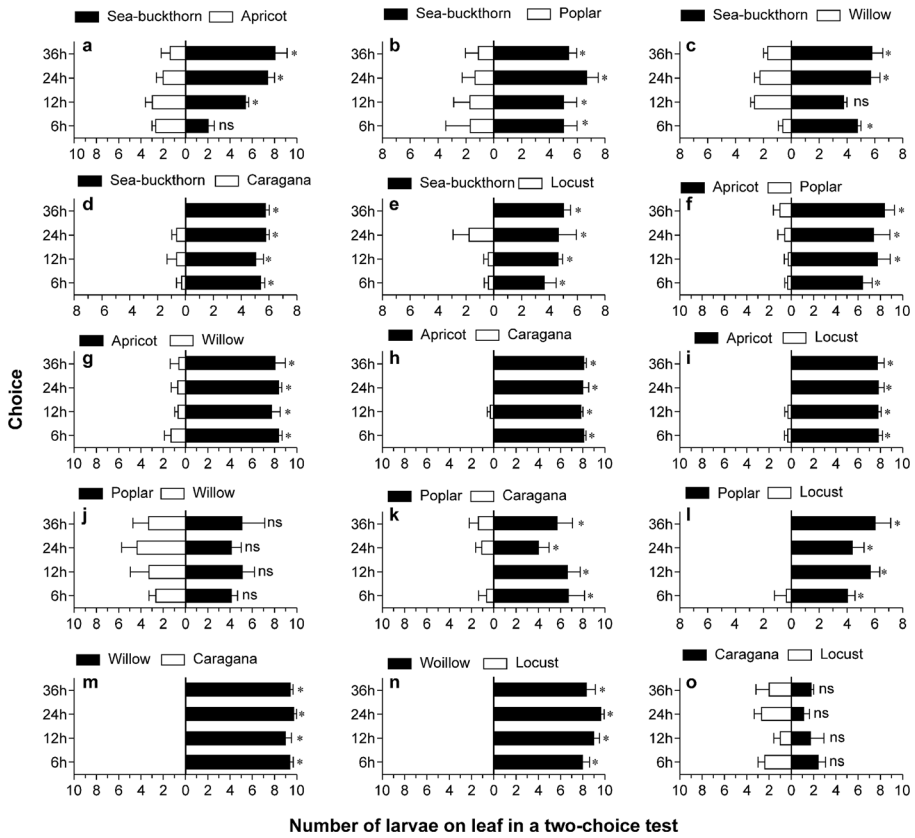
We found that *T. vishnou gigantina* larvae were able to distinguish between six sympatric plant species (Fig. 1). Overall, sea-buckthorn was preferred above the other plants during the entire observation period (Fig. 1b–e). For several plants, namely apricot and willow, the significant preference occurred only at certain periods post-release into the cages (sea-buckthorn preferred over apricot, 12, 24, and 36 h, Fig. 1a; preferred over willow, 6, 24, and 36 h, Fig. 1c).

Excluding sea-buckthorn and compared with apricot, significantly fewer larvae preferred poplar, willow, caragana, or locust throughout the full observation period (Fig. 1f–i). No significant preference was found between poplar and willow (Fig. 1j), but poplar was significantly more attractive than caragana or locust (Fig. 1k, l).

Compared with willow, no *T. vishnou gigantina* larvae chose caragana or locust at 6, 12, 24, or 36 post-release into the cages (Fig. 1m, n). No significant preference was found between caragana and locust (Fig. 1o).

### Means Weights of Larvae and Pupae

None of the larvae survived more than seven days on caragana and locust. However, larvae were able to complete their life cycle on sea-buckthorn, apricot, poplar, and willow, which all significantly affected the larval weight over time (Fig. 2). Larvae weights did not differ on the first day of the experiment, but significantly differed from the sixth day to the end of the experiment. Sea-buckthorn or apricot-reared larvae were significantly heavier than those reared on both poplar and willow throughout the experiment. Significant differences in larval weight were apparent between sea-buckthorn-reared and apricot-reared conditions at 36 days until the end of the



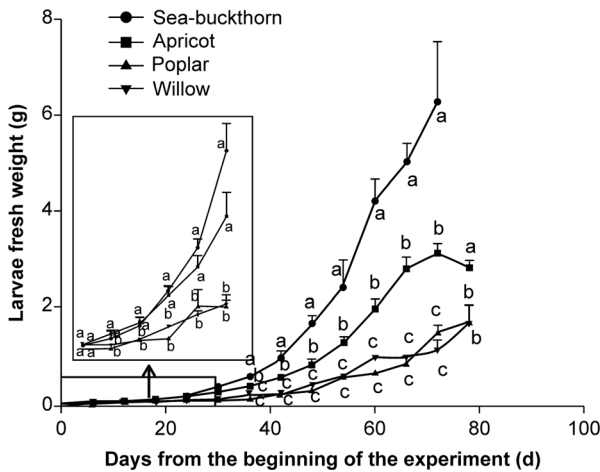
**Fig. 1** Mean number ( $\pm$  SE) of *Trabala vishnou gigantina* larvae that settled on different plants over time in a two-way choice test. \* indicates significant differences (t-test,  $P < 0.05$ ), ns = not significant ( $P \geq 0.05$ )

experiment. The weights of willow-reared versus poplar-reared larvae were not significantly different throughout the experiment.

Female pupae were heavier than male pupae regardless of the plant species on which they were reared. Sea-buckthorn- or apricot-reared female pupae were significantly heavier than those reared on poplar or willow, but no significant difference was found between female pupal weights on sea-buckthorn and apricot. Male pupae reared on sea-buckthorn were lighter than those reared on apricot, but heavier than those reared on poplar or willow (Fig. 3).

**Larval Weight, Length, and Duration of Instars**

When we examined mean larval development by instars, we found that durations were shortest on sea-buckthorn across all instars (Table 1). We also found that apricot-reared larvae grew faster than poplar- or willow-reared larvae during the first and second instar. No duration differences were found during the third and fourth instar across apricot-, poplar-, and willow-reared larvae. Larvae reared on these three plants also did not significantly differ in developmental duration in the fifth and sixth instar, although willow-reared larvae achieved the longest duration. Further, larvae underwent six



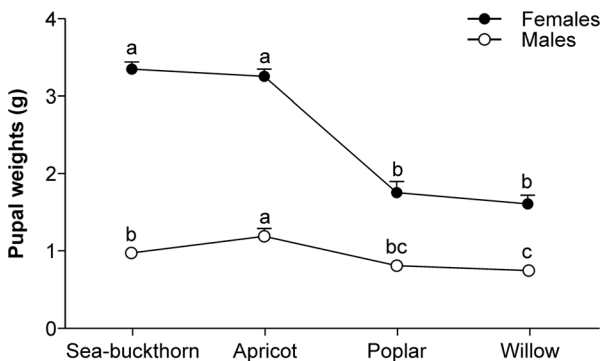
**Fig. 2** Growth within larval stages on different plant species. Different letters correspond to significantly different larval weights across three days (one-way ANOVA, least significant difference test,  $P < 0.05$ )

instars on poplar, but seven instars on sea-buckthorn, apricot, and willow (Table 1, Figs. 4, and 5). When comparing durations only at the seventh instar, sea-buckthorn-reared larvae developed significantly faster than willow- or apricot-reared larvae.

At all instars, neither larval weight nor length differed significantly across the plant species (Figs. 4, and 5).

### Larval Mortality

Mortality rates on the different plant species did not differ significantly in either the early instars ( $P = 0.781$ ) or in the later instars ( $P = 0.045$ ). In the early instars, the highest larval mortality rate was associated with poplar, whereas rates were very low on sea-buckthorn, apricot, and willow (Table 2). In later instars, larvae suffered significantly higher mortality compared to earlier instars, with the highest rates on poplar (Table 2). Overall, sea-buckthorn-reared larvae exhibited the lowest mortality rates, followed by apricot and willow.



**Fig. 3** Mean weights ( $\pm$  SE) of pupae males and females reared on four plant species. Different letters above the bars indicate statistically significant differences between plant species (one-way ANOVA, least significant difference test,  $P < 0.05$ )

**Table 1** The duration of larval stages in days (means  $\pm$  SE) during development of *Trabala vishnou gigantina* Yang reared on different plants

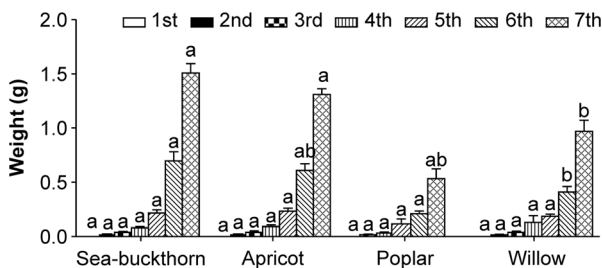
Stage (days)	Host plant species				Statistics	
	Sea-buckthorn	Apricot	Poplar	Willow	Test	P
1st instar	6.8 $\pm$ 0.2 d	9.0 $\pm$ 0.2 c	11.4 $\pm$ 0.4 a	9.8 $\pm$ 0.3 b	F = 56.08	P < 0.0001
2nd instar	8.6 $\pm$ 0.3 d	11.4 $\pm$ 0.3 c	14.3 $\pm$ 0.6 a	12.7 $\pm$ 0.5 b	F = 43.68	P < 0.0001
3rd instar	11.0 $\pm$ 0.4 b	14.2 $\pm$ 0.3 a	14.7 $\pm$ 0.6 a	13.6 $\pm$ 0.3 a	F = 18.62	P < 0.0001
4th instar	12.6 $\pm$ 0.4 b	14.9 $\pm$ 0.6 a	15.1 $\pm$ 0.7 a	15.1 $\pm$ 0.6 a	F = 5.80	P = 0.001
5th instar	12.9 $\pm$ 0.4 b	13.8 $\pm$ 0.6 b	14.9 $\pm$ 1.3 ab	16.7 $\pm$ 0.9 a	F = 5.59	P = 0.002
6th instar	13.6 $\pm$ 0.6 b	15.0 $\pm$ 1.2 b	17.5 $\pm$ 0.5 ab	18.9 $\pm$ 1.0 a	F = 4.22	P = 0.009
7th instar	13.8 $\pm$ 1.9 b	18.7 $\pm$ 1.2 a	—	19.1 $\pm$ 0.7 a	F = 4.90	P = 0.017
Total larval	74.5 $\pm$ 1.8 c	95.5 $\pm$ 1.5 b	89.5 $\pm$ 0.5 b	106.0 $\pm$ 1.5 a	F = 68.43	P < 0.0001
Pupae	39.6 $\pm$ 0.4 b	38.5 $\pm$ 0.9 b	44.0 $\pm$ 1.0 a	32.7 $\pm$ 1.0 c	F = 21.19	P < 0.0001
Development time	114.1 $\pm$ 1.9 b	134.25 $\pm$ 2.10 a	133.5 $\pm$ 1.5 a	138.1 $\pm$ 1.3 a	F = 34.92	P < 0.0001

Different letters within a row following the values indicate significant differences based on post-ANOVA LSD (least significant difference) multiple range tests ( $P < 0.05$ )

## Durations of Larval and Pupal Stages

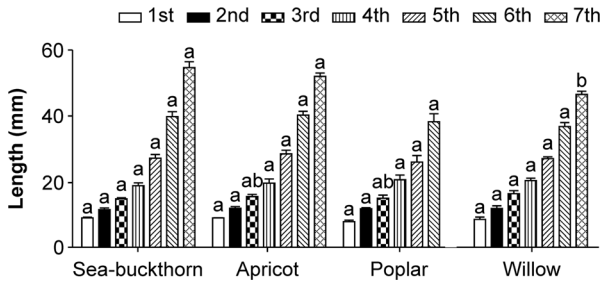
The plant species on which larvae were reared significantly affected larval development duration (ANOVA;  $F = 68.43$ ; d.f. = 3, 38;  $P < 0.0001$ ), pupal development duration ( $F = 21.19$ ; d.f. = 3, 38;  $P < 0.0001$ ), and overall development duration ( $F = 34.92$ ; d.f. = 3, 38;  $P < 0.0001$ ) (Table 1). Larvae developed fastest on sea-buckthorn (approximately 10 weeks), followed by apricot and poplar (approximately 13 weeks, no significant difference in development duration on these two plants). In contrast, larvae developed much slowly on willow (approximately 15 weeks).

For pupae, poplar-rearing resulted in the longest development duration (44.0 d), while willow-rearing resulted in the shortest duration (32.7 d). Combining both larval and pupal development durations revealed that the overall development period was shorter on sea-buckthorn than on apricot, poplar, or willow (Table 1).



**Fig. 4** Mean ( $\pm$  SE) body weight (mg) of each larval instar on different plant species. Different letters above the bars indicate statistically significant differences between plant species (one-way ANOVA, least significant difference test,  $P < 0.05$ )





**Fig. 5** Mean ( $\pm$  SE) body length (mm) of each larval instar on different plant species. Different letters above the bars indicate statistically significant differences between plant species (one-way ANOVA, least significant difference test,  $P < 0.05$ )

### Sex Differences in Weight and Longevity of Adults

Despite the weight differences noted during the pupae stage, no significant differences were detected in adult female ( $P = 0.646$ ) or male ( $P = 0.382$ ) longevity across plant species (Table 2). Regardless of the plants on which they were reared, adult females were heavier than adult males (t-test;  $t = 105.74$ ;  $P < 0.0001$ ). Sea-buckthorn-reared adult females were heavier than apricot-reared females, although the difference was not significant. Moreover, poplar- and willow-reared females did not differ significantly in weight. Male adults reared on different plants also did not vary significantly in weight, but in contrast to females, apricot-reared males were heaviest (Fig. 6).

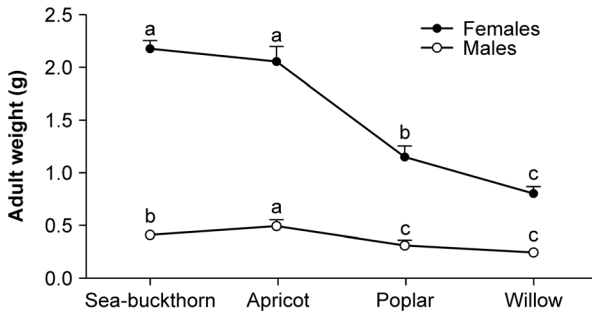
### Fecundity

Adult fecundity rates were significantly different depending on the plant species (ANOVA;  $F = 102.11$ ; d.f. = 3, 23;  $P < 0.0001$ ). When larvae were reared on poplar, fecundity rates were significantly lower than those reared on sea-buckthorn and apricot. However, fecundity rates between poplar- and willow-reared larvae did not significantly differ (Table 2).

**Table 2** Larval mortality, adult longevity, and adult fecundity of *Trabala vishnou gigantina* Yang (means  $\pm$  SE) reared on different plants

Plant species	Mortality (%)		Longevity (days)		Fecundity (eggs)
	1st–3rd instar	4th–7th instar	Female	Male	
Sea-buckthorn	6.67	46.67	8.1 $\pm$ 0.3 a	6.3 $\pm$ 0.2 a	319.8 $\pm$ 11.6 a
Apricot	3.33	56.67	8.1 $\pm$ 0.3 a	7.3 $\pm$ 0.4 a	255.5 $\pm$ 8.5 b
Poplar	13.33	80	8.4 $\pm$ 0.4 a	7.0 $\pm$ 0.5 a	126.4 $\pm$ 7.1 c
Willow	3.33	60	7.7 $\pm$ 0.4 a	6.4 $\pm$ 0.6 a	135.3 $\pm$ 5.9 c

Different letters within a column following the values indicate significant differences based on post-ANOVA LSD (least significant difference) multiple range tests ( $P < 0.05$ )



**Fig. 6** Mean weights ( $\pm$  SE) of adult males and females reared on four plant species. Different letters above the bars indicate statistically significant differences between plant species (one-way ANOVA, least significant difference test,  $P < 0.05$ )

## Discussion

In this study, we found that *T. vishnou gigantina* larvae differed in their preferences towards the six plants present in their habitat. In particular, larvae significantly preferred sea-buckthorn, a species classified as major hosts, to those classified as minor host. When the major host was not present, then larvae preferred apricot to all other plants, with caragana and locust as the least preferred. Given that the sea-buckthorn is a known host, these results are perhaps not too surprising, especially as the threat of starvation will drive many insects to feed on less desirable or completely unsuitable minor host (Dethier 1954). However, previous studies have demonstrated that larval preferences are not entirely innate (Schoonhoven et al. 1998; Silva et al. 2014). Furthermore, there should be considerable evolutionary advantage for larvae to be capable of surviving on a wider variety of plant species. Mistaken identification of host plants from egg-laying adult females, accidental larval dislodgement, or damage to the natural hosts are all occurrences likely to exert selective pressure on larvae in terms of plant preferences (Janz et al. 1994; Foster and Howard 1999; Shikano et al. 2010). Therefore, to survive in the absence of their major host plant, we would expect larvae to move to a different, slightly less preferred plant, which they did in the choice test.

We currently have no data to explain why *T. vishnou gigantina* larvae have these feeding preferences. However, we speculate that the plant leaves may contain levels of nutrients, water, secondary compounds, or a combination of the above, which are beneficial to the larvae (Otte 1975; Rank 1992; Fuentes and Yates 1994; Pappers et al. 2002; Rather and Azim 2009). Although we were unable to validate the specific mechanisms involved in eliciting larval feeding preference, it is possible that larvae use the different volatile compounds or defensive chemicals excreted from leaves as cues in their choice (Rodrigues and Moreira 1999).

Although some larvae appear fairly accepting apricot, poplar, and willow, we noted that most larvae strongly rejected feeding on caragana and locust (approximately 80 %; Fig. 1). Thus, even among non-host plants, larvae have strong preferences that are not simply dependent on the egg-laying position of females. Rejected plants may have higher levels of defensive compounds compared to accepted plants, exceeding the tolerance threshold of the larvae (Rodrigues and Freitas 2013). In general, our laboratory observations did not fully correspond to field observations: while larvae were able

to complete their development successfully on apricot, poplar, and willow under laboratory conditions as minor hosts, sea-buckthorn remains their major host plant in the field. We cannot explain this difference given our data, but we clearly showed that host suitability was consistent with the feeding preference.

In conjunction with other studies (Chapman 1998; Saeed et al. 2010), we found that fitness was strongly influenced by the plant species on which larvae were reared. Generally, shorter development times, greater pupal weight, and higher rates of reproduction on a plant are indicative of greater host suitability for the insect (Awmack and Leather 2002; Tikkanen and Lyytikäinen-Saarenmaa 2002). In the present study, all variables used as proxies for fitness indicated that sea-buckthorn is the best host for *T. vishnou gigantina* under laboratory conditions. Feeding on sea-buckthorn resulted in faster growth and development, as well as greater weight gain at all stages of life. As the energy required for successful growth and development is mainly accumulated during the larval stages, the ontogenetic changes we observed may be related to the variation in nutrition, chemistry, or mechanical barriers present in different plant species (Naseri et al. 2009; Razmjou et al. 2014). Our results confirm the importance of variation in plant species in relation to *T. vishnou gigantina* larval fitness.

In our study, we also found that the developmental duration of *T. vishnou gigantina* larvae varied greatly at the first and second instars on different plant species, while larval weight and length did not differ significantly at any instar. Regarding the significant effect on developmental duration, previous research has shown that physical traits of leaf tissues, such as pubescence and hardness, vary across plants (Roden et al. 1992; D'Costa et al. 2014). Such morphological traits in host plants can influence larval development (D'Costa et al. 2014). For example, a recent study (Niu et al. 2014) found that larvae fed on *Orychophragmus violaceus* (L.) exhibited a first-instar duration that was much longer than on other host plants. The difference occurred because the small larvae were trapped on the leaf pubescence. Due to the blockade resulting from plant morphology, larvae were only able to consume the small pieces of leaf tissue that they could reach and were unable to move elsewhere. Therefore, a longer development time was necessary for these larvae to consume an amount equivalent to those raised on a more suitable plant species (Itoyama et al. 1999; Niu et al. 2014). We suggest that the longer developmental duration on apricot, poplar, and willow may also be associated with morphological constraints on the *T. vishnou gigantina* larvae feeding apparatus. Specifically, early instars of Lepidoptera do not feed upon harder leaf tissues, because the mandibles are either not strong enough for effective chewing, or their gape is not wide enough to grasp thick tissues (Bernays et al. 1991). Future studies may focus on whether leaf tissue characteristics are, in fact, a major contributor to *T. vishnou gigantina* larval feeding preferences.

Total larval development time was the shortest on sea-buckthorn (74.5 days), compared with other plants. Generally, a shorter development time is important for larval survival in the field because it decreases the risk of exposure to predators, parasites, and unfavorable environmental conditions (Tikkanen et al. 2000; Cahenzli and Erhardt 2013; Uyi et al. 2014). Although this hypothesis has not been fully verified, some data exist to support it. For instance, Loader and Damman (1991) suggest that *Pieris rapae* caterpillars reared on high-nitrogen food developed faster and were less susceptible to predators than those reared on low-nitrogen food.

Food quality is considered a good determinant of the size and fecundity in herbivorous insects (Awmack and Leather 2002). As insects in Lepidoptera do not acquire nutrition as adults and must accumulate all their reserves during the larval stage, food quality is of particular importance (Mondy et al. 1998). In this study, females reared on sea-buckthorn and apricot laid significantly more eggs and weighed significantly more. Partridge and Fowler (1993) showed that these body size differences were caused by increased consumption. Nevertheless, adult longevity did not significantly vary across the four plant species, despite the large differences in developmental time and pupae mass. While this result is puzzling and warrants further examination, our results do corroborate a previous study demonstrating a lack of correlation between increased pupae mass and adult longevity (Hillesheim and Stearns 1992).

To conclude, larvae feeding preferences appear to correlate with larvae fitness. Our results clearly show that *T. vishnou giganteina* larvae are physiologically the most well-adapted to use sea-buckthorn as a major host plant. Larvae also grew well on apricot, but the longer larval developmental duration implies that apricot is not an ideal host. On two other minor hosts (poplar and willow), larvae successfully completed their development cycle, but demonstrated abnormalities in the pupae and adult mass. We suggest that the differences observed in larval preferences and fitness were mostly related to variation in constitutive defense mechanisms, as well as chemical and physical characteristics of the plants. Clearly, follow-up studies are necessary to address the exact mechanisms influencing *T. vishnou giganteina* feeding preferences and survival on potential hosts.

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#### Compliance with Ethical Standards

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

## References

- Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47:817–844. doi:10.1146/annurev.ento.47.091201.145300
- Bao H (2015) Response of growth characteristics of *Prunus ansu* from different provenances in seedling stage to drought stress. *Inn Mong For Sci Technol* 41:5–8
- Berdegue M, Trumble JT (1996) Effects of plant chemical extracts and physical characteristics of *Apium graveolens* and *Chenopodium murale* on host choice by *Spodoptera exigua* larvae. *Entomol Exp Appl* 78: 253–262. doi:10.1111/j.1570-7458.1996.tb00789.x
- Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Springer, New York
- Bernays EA, Jarzembowski EA, Malcolm SB (1991) Evolution of insect morphology in relation to plants [and discussion]. *Philos Trans R Soc B* 333:257–264. doi:10.1098/rstb.1991.0075
- Cahenzli F, Erhardt A (2013) Transgenerational acclimatization in an herbivore-host plant relationship. *Proc R Soc B* 280:20122856. doi:10.1098/rspb.2012.2856

- Chapman RF (1998) The insects: structure and function, 4th edn. Cambridge University Press, Cambridge ISBN: 0521578906
- D'Costa L, Simmonds MSJ, Straw N, Castagnyrol B, Koricheva J (2014) Leaf traits influencing oviposition preference and larval performance of *Cameraria ohridella* on native and novel host plants. *Entomol Exp Appl* 152:157–164. doi:10.1111/eea.12211
- Dethier VG (1954) Evolution of feeding preferences in phytophagous insects. *Evolution* 8:33–54
- Fahey JW, Zalcmann AT, Talalay P (2001) The chemical diversity and distribution of glucosinolates and isothiocyanates among plants. *Phytochemistry* 56:5–51. doi:10.1016/S0031-9422(00)00316-2
- Foster SP, Howard AJ (1999) Adult female and neonate larval plant preferences of the generalist herbivore, *Epiphyas postvittana*. *Entomol Exp Appl* 92:53–62. doi:10.1046/j.1570-7458.1999.00524.x
- Friberg M, Wiklund C (2009) Host plant preference and performance of the sibling species of butterflies *Leptidea sinapis* and *Leptidea reali*: a test of the trade-off hypothesis for food specialisation. *Oecologia* 159:127–137. doi:10.1007/s00442-008-1206-8
- Fuentes JE, Yates LR (1994) Host nutritional-value in larval feeding preference of *Ormiscodes socialis* (Feisthammel) (Lepidoptera, Saturniidae) in Chile. *Rev Chil Hist Nat* 67:27–33
- Gamberale-Stille G, Söderlind L, Janz N, Nylin S (2014) Host plant choice in the comma butterfly—larval choosiness may ameliorate effects of indiscriminate oviposition. *Insect Sci* 21:499–506. doi:10.1111/1744-7917.12059
- Henniges-Janssen K, Heckel DG, Groot AT (2014) Preference of diamondback moth larvae for novel and original host plant after host range expansion. *Insects* 5:793–804. doi:10.3390/insects5040793
- Hillesheim E, Stearns SC (1992) Correlated responses in life-history traits to artificial selection for body weight in *Drosophila melanogaster*. *Evolution* 46:745–752. doi:10.2307/2409642
- Itoyama K, Kawahira Y, Murata M, Tojo S (1999) Fluctuations of some characteristics in the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae) reared under different diets. *Appl Entomol Zool* 34: 315–321. doi:10.1303/aez.34.315
- Janz N, Nylin S, Wedell N (1994) Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. *Oecologia* 99:132–140. doi:10.1007/BF00317093
- Liu YJ, Wu CS (2006) Fauna sinica insecta, vol. 47, 1st edn. Science Press, Beijing ISBN: 7-03-016877-1
- Liu YH, Zhang YQ, Yan XF, Zong DL, Zong SX, Luo YQ (2013) Damage of *Trabala vishnou gigantina* (Lepidoptera: Lasiocampidae) to the sea-buckthorn forest and its biological characteristic. *Plant Prot* 39: 147–152. doi:10.3969/j.isn.0529.1542.2013.02.030
- Liu RT, Chai YQ, XU K, Yang MX, Zhu F (2014) Seasonal changes of ground vegetation characteristics under artificial *Caragana intermedia* plantations with age in desert steppe. *Acta Ecol Sin* 34:500–508. doi:10.5846/stxb201204040468
- Loader C, Damman H (1991) Nitrogen content of food plants and vulnerability of *Pieris rapae* to natural enemies. *Ecology* 72:1586–1590. doi:10.2307/1940958
- Luo YQ, Lu CK, Xu ZC (2003) Control strategies on a new serious forest pest insect—sea buckthorn carpenter worm, *Holcocerus hippophaecolus*. *For Pest Dis* 22:25–28. doi:10.3969/j.issn.1671-0886.2003.05.010
- Mondy N, Charrier B, Fermaud M, Pracros P, Corio-Costet M-F (1998). Mutualism between a phytopathogenic fungus (*Botrytis cinerea*) and a vineyard pest (*Lobesia botrana*). Positive effects on insect development and oviposition behaviour. *Cr. Acad. Sci. III-Vie* 321:665–671. doi:10.1016/S0764-4469(98)80006-1
- Naseri B, Fathipour Y, Moharrampour S, Hosseinaveh V (2009) Comparative life history and fecundity of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) on different soybean varieties. *Entomol Sci* 12: 147–154. doi:10.1111/j.1479-8298.2009.00310.x
- Niu YQ, Sun YX, Liu TX (2014) Development and reproductive potential of diamondback moth (Lepidoptera: Plutellidae) on selected wild crucifer species. *Environ Entomol* 43:69–74. doi:10.1603/EN13206
- Otte D (1975) Plant preference and plant succession. *Oecologia* 18:129–144. doi:10.1007/BF00348094
- Pappers SM, Van der Velde G, Ouborg JN (2002) Host preference and larval performance suggest host race formation in *Galerucella nymphaeae*. *Oecologia* 130:433–440. doi:10.1007/s00442-001-0822-3
- Partridge L, Fowler K (1993) Responses and correlated responses to artificial selection on thorax length in *Drosophila melanogaster*. *Evolution* 47:213–226. doi:10.2307/2410130
- Prager SM, Esquivel I, Trumble JT (2014) Factors influencing host plant choice and larval performance in *Bactericera cockerelli*. *PLOS One* 9:e94047. doi:10.1371/journal.pone.0094047
- Rank NE (1992) Host plant preference based on salicylate chemistry in a willow leaf beetle (*Chrysomela aeneicollis*). *Oecologia* 90:95–101. doi:10.1007/BF00317814
- Rather AH, Azim MN (2009) Feeding response in *Pieris brassicae* larvae to host/non-host plants. *World J Agric Sci* 5:143–145 [http://www.idosi.org/wjas/wjas5\(2\)2.pdf](http://www.idosi.org/wjas/wjas5(2)2.pdf)

- Razmjou J, Naseri B, Hemati S (2014) Comparative performance of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on various host plants. *J Pest Sci* 87:29–37. doi:10.1007/s10340-013-0515-9
- Roden DB, Miller JR, Simmons GA (1992) Visual stimuli influencing orientation by larval gypsy moth, *Lymantria dispar* (L. Can Entomol 124:287–304
- Rodrigues D, Freitas AV (2013) Contrasting egg and larval performances help explain polyphagy in a florivorous butterfly. *Arthropod Plant Interact* 7:159–167. doi:10.1007/s11829-012-9230-3
- Rodrigues D, Moreira GRP (1999) Feeding preference of *Heliconius erato* (Lep.: Nymphalidae) in relation to leaf age and consequences for larval performance. *J Lepid Soc* 53:108–113. doi:10.1590/S0101-81752005000100006
- Saeed R, Sayyed AH, Shad SA, Zaka SM (2010) Effect of different host plants on the fitness of diamond-back moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Crop Prot* 29:178–182. doi:10.1016/j.cropro.2009.09.012
- Scobonhoven LM, Jermy T, Van Loon JJA (1998) Insect-plant biology: From physiology to evolution, 1st edn. Chapman & Hall, London ISBN: 0412804808
- Shikano I, Akhtar Y, Isman MB (2010) Relationship between adult and larval host plant selection and larval performance in the generalist moth, *Trichoplusia ni*. *Arthropod Plant Interact* 4:197–205. doi:10.1007/s11829-010-9100-9
- Silva AK, Gonçalves GL, Moreira GRP (2014) Larval feeding choices in heliconians: induced preferences are not constrained by performance and host plant phylogeny. *Anim Behav* 89:155–162. doi:10.1016/j.anbehav.2013.12.027
- Thorsteinson AJ (1953) The role of host selection in the ecology of phytophagous insects. *Can Entomol* 85: 276–282. doi:10.4039/Ent85276-8
- Tikkanen OP, Lyytikäinen-Saarenmaa P (2002) Adaptation of a generalist moth, *Operophtera brumata*, to variable budburst phenology of host plants. *Entomol Exp Appl* 103:123–133. doi:10.1046/j.1570-7458.2002.00966.x
- Tikkanen OP, Niemelä P, Keränen J (2000) Growth and development of a generalist insect herbivore, *Operophtera brumata*, on original and alternative host plants. *Oecologia* 122:529–536. doi:10.1007/s004420050976
- Uechi N, Yukawa J (2006) Host range and life history of *Asphondylia sphaera* (Diptera: Cecidomyiidae): use of short-term alternate hosts. *Ann Entomol Soc Am* 99:1165–1171. doi:10.1603/0013-8746(2006)99[1165:HRALHO]2.0.CO;2
- Uyi OO, Hill MP, Zachariades C (2014) Variation in host plant has no effect on the performance and fitness-related traits of the specialist herbivore *Pareuchaetes insulata*. *Entomol Exp Appl* 153:64–75. doi:10.1111/eea.12229
- Wang GC, Wu Y, Gui SY (1987) Four nuclear polyhedrosis viruses of poplar and willow insect pests newly discovered in China. *Sci. Silvae Sinica* 22:90–93
- Wang SF, Zong SX, Zhang JT, Qi Z, Zhang YF (2012) Biological characteristics of the *Trabala vishnou gigantina* Yang (Lepidoptera: Lasiocampidae). *J Shanxi Agric U Nat Sci Ed* 32:235–239