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**Masahito T. Kimura • Biljana Novković**

# Local adaptation and ecological fitting in host use of the *Drosophila* parasitoid *Leptopilina japonica*

Masahito T. Kimura (Correspondence)

Biljana Novković

Graduate School of Environmental Earth Science, Hokkaido University, Sapporo, Hokkaido 060-0810, Japan

mtk@ees.hokudai.ac.jp

**Abstract** Local adaptation and ecological fitting are the major processes by which organisms colonize and persist in novel environments and form novel associations with unfamiliar species. In this study, we assessed the role of these two processes in the formation of associations between the parasitoid *Leptopilina japonica* and various host *Drosophila* species using laboratory populations from three different localities. Each *L. japonica* population was highly virulent to some *Drosophila* species from its original locality, meaning they used these *Drosophila* species as major hosts. However, major host species at a given locality were usually less successfully parasitized by parasitoid populations from different localities. These results indicate that the investigated parasitoid populations showed local adaptation in host use. We also observed cases in which unfamiliar *Drosophila* species were successfully parasitized or allopatric *Drosophila* populations were more successfully parasitized. These findings suggest that *L. japonica* can form novel associations with some *Drosophila* species in novel environments without undergoing adaptive changes, a phenomenon called ecological fitting. In this study, *L. japonica* also usually appeared to have oviposited well in *D. melanogaster* species group members irrespective of their suitability as hosts. This result suggests that the parasitoid makes oviposition decisions based on characteristics common to the drosophilids in this species group.

**Keywords** Allopatric · Host acceptance · Host suitability · Sympatric · Taxonomic effect

## Introduction

How organisms colonize novel environments, use novel resources, and form novel associations with other species is one of the central issues in evolutionary ecology. The most important and well-documented evolutionary process is adaptation to novel situations (Schulter 2000; Thompson 2005; Futuyma 2013). Another major phenomenon is “ecological fitting”, in which organisms cope with new situations using the suite of traits carried at the time of the encounter (Janzen 1985; Wilkinson 2004; Agosta 2006; Agosta and Klemens 2008; Harvey et al. 2012). If an introduced population has low fitness in its newly colonized environment, ecological fitting may provide sufficient time for the population to evolve novel adaptive traits and thereby avoid extinction (Agosta 2006; Agosta and Klemens 2008). In spite of its major evolutionary role, however, ecological fitting still receives relatively little attention and its importance is underappreciated.

To assess the roles of local adaptation and ecological fitting in the formation of novel parasitoid-host associations, we compared the responses of different populations of a *Drosophila* parasitoid, *Leptopilina japonica* Novković & Kimura (Hymenoptera: Figitidae), to potential host species having sympatric or allopatric origins. When parasitoids colonize a novel environment, they encounter potential new host species. Coevolutionary theory suggests that encounters of parasitoids and hosts may lead these organisms to respectively develop virulence or resistance against antagonists if the cost of such evolution is lower than the benefits (Hawkins 1994; Sheehan 1994; Sasaki and Godfray 1999; Thompson 2005). In *Drosophila*-parasitoid systems, however, interaction occurs between multiple hosts and parasitoid species. Under such a situation,

both parasitoids and hosts are expected to gain benefits from specialization toward the most frequent antagonists, at least when the frequency of encounter with the antagonist species is constant (Lapchin 2002). How often parasitoids and hosts encounter each other in the field is not generally known. The parasitoid species in this study, *L. japonica*, has not been the most abundant parasitoid of frugivorous *Drosophila* species in previously surveyed localities (Mitsui and Kimura 2010; Novković et al. 2011; Kasuya et al. 2013b; Kimura, unpublished data), suggesting that host *Drosophila* species rarely encounter this parasitoid. As a consequence, *Drosophila* species may not evolve (high) resistance against *L. japonica*, whereas the parasitoid is expected to evolve high virulence against abundant *Drosophila* species. The parasitoid populations evaluated in this study are therefore expected to become more virulent to sympatric populations of major host species than to allopatric ones. Here, we examined this expectation.

Although the evolution of novel virulence mechanisms (i.e., adaptation) is the major process enabling parasitoids to use novel hosts, a number of parasitoids are known to parasitize unfamiliar host species, both in the laboratory and in the field (Cameron et al. 2006; Kaufman and Wright 2010; Harvey et al. 2012). In our previous studies, for example, we observed that some *Leptopilina* species from the Ryukyu Islands or Taiwan parasitize *D. simulans* Sturtevant, an exotic species seldom found in those regions (Novković et al. 2011, 2012). Thus, novel associations with unfamiliar host species can be formed using virulence mechanisms already possessed by the parasitoids—in other words, through ecological fitting. In this study, we therefore examined whether the investigated parasitoid populations can parasitize *Drosophila* species with which they have had no previous contact.

## Materials and methods

### Study species and populations

The parasitoid study species *L. japonica* consists of two subspecies: *L. j. japonica*, occurring in central and northern Japan, and *L. j. formosana*, present in Taiwan (Novković et al. 2011). In this study, laboratory populations of *L. j. japonica* were collected from Sapporo (SP: 43.0 °N in Japan; collected in July 2006) and Tokyo (TK: 35.7 °N in Japan; June 2007), while a population of *L. j. formosana* was collected from Taipei (TP: 25.2 °N in Taiwan; March 2009). These populations were maintained using *D. simulans* as the host. For use in "host acceptance" and "host suitability" experiments, parasitoid females were also reared with *D. simulans*, and after eclosion they were maintained for 2–6 days in on Drosophila medium with *D. simulans* larvae and allowed to mate.

Populations of the major *Drosophila* species in the three sampling localities were also collected along with the parasitoid populations. In addition, a population of *D. sulfurigaster* was collected from Kota Kinabalu (KK: 5.3 °N in Malaysia) in June 2008. The *Drosophila* laboratory populations were reared on medium containing cornmeal, wheat germ, yeast and sugar. Table 1 shows their taxonomic positions, distribution and feeding habits (Kimura et al. 1977; Hirai et al. 2000; Kimura 2004; Mitsui et al. 2010; Kimura and Suwito 2012; Kasuya et al. 2013a). Maintenance of the parasitoid and *Drosophila* populations was carried out and experiments were performed under a 15-h:9-h light:dark photoperiod at 23 °C.

Experiments using parasitoid and *Drosophila* populations from the same localities were conducted within several months of collection. In contrast, experiments using parasitoid and *Drosophila* populations from different localities were conducted in 2009–2010; this time period corresponds to several months to a year after collection of populations from TP and 2 to 3 years after collection of SP and TK populations. The results of experiments that used laboratory populations from different localities must therefore be interpreted with caution, as populations from SP and TK may have changed during the 2 to 4 years of laboratory rearing.

To investigate the influence of host abundance on parasitoid host use, the abundance of frugivorous drosophilid species in the three localities was determined based on our collection data and that of Beppu (2000). Collections were carried out using banana-baited traps in wooded areas as follows: 6 times from May to October in 1971 in SP (our data), 14 times from July 1998 to July 1999 in TK (Beppu 2000), and 3 times from June 2010 to February 2011 in TP (our data). In SP and TP, drosophilid flies attracted to traps were collected by nets or bags from morning to evening (13–16 times daily in SP and 3 times in TP) for 3 or 2 successive days in SP and TP, respectively. In TK, retainer-type traps were set for a week, with drosophilid flies retained in the traps and then collected (Beppu 2000).

Host acceptance

To determine host acceptance, 30 to 40 2-day-old (second instar) drosophilid larvae and five parasitoid females were placed in a Petri dish (3-cm diameter) containing a small amount of Drosophila medium for 4 h. After removal of parasitoids, fly larvae were

dissected under a stereoscopic microscope and checked for the presence/absence of parasitoid eggs. Oviposition rate was calculated as the number of parasitized larvae per total number of checked larvae.

Host suitability

To determine host suitability for development, approximately 50 2-day-old larvae and several (two to five) parasitoid females were placed in a Petri dish containing a small amount of Drosophila medium, and the parasitoid females were monitored for oviposition under a stereoscopic microscope. Characteristic oviposition behaviors, such as full extension of the ovipositor after contact with the host and prolonged (>10 s) insertions of the ovipositor into the larvae, were used as indicators of successful oviposition (Vet and Bakker 1985; Dubuffet et al. 2006). When oviposition was confirmed, the parasitized fly larvae were transferred into vials containing Drosophila medium. The vials were later checked for the emergence of flies and/or parasitoids. Approximately 30 parasitized larvae were prepared for each combination of parasitoid and host populations or species. In some cases, few or no parasitized larvae were obtained because of the absence or low rate of oviposition.

Statistics

To compare oviposition rates in the acceptance experiment and frequencies of parasitized larvae from which fly, parasitoid or neither of them emerged in the

155 suitability experiment, we performed Fisher's exact test with Bonferroni corrections
156 using R software version 2.15.1 (R Development Core Team 2012).
157
158 **Results**
159
160 Abundance of drosophilid species
161
162 The major drosophilid species collected by banana-baited traps in SP, TK and TP along
163 with their frequencies in the collection samples and feeding habits are shown in Table 2.
164 With increasing latitude, the diversity and relative abundance of frugivorous species
165 decreased, while those of mycophagous and generalist species increased. All of the
166 major frugivorous species belonged to the *melanogaster* and *immigrans* species groups;
167 most were used in subsequent laboratory experiments (Table 1).
168
169 Host acceptance
170
171 No clear difference in host acceptance was observed between sympatric and allopatric
172 laboratory populations in the experiments. Except for *D. parabipectinata*, species from
173 the *melanogaster* group were frequently (>71 %) oviposited by parasitoid populations
174 from both the same and different localities (Fig. 1), with no significant ($P > 0.05$)
175 difference in oviposition rate observed among parasitoid populations. The TP
176 population of *D. parabipectinata* was significantly more frequently oviposited by the SP
177 population of *L. japonica* compared with the TP or TK parasitoid populations ($P < 0.01$).
178 In contrast to members of the *melanogaster* species group, species of the subgenus

*Drosophila* were usually less frequently oviposited by the studied parasitoid populations, except that *D. sulfurigaster*, *D. albomicans* and *D. orientacea* were oviposited by SP and/or TP populations at high frequencies. The difference in oviposition rate among the three parasitoid populations was significant in species from the subgenus *Drosophila* except for *D. nigromaculata* ($P < 0.01$). Generally, the SP population of *L. japonica* oviposited more frequently in species of the subgenus *Drosophila* than did the TP and TK populations, regardless of the original localities of the drosophilids. The exceptions were *D. albomicans* and *D. sulfurigaster*, which were frequently oviposited by the TP population of *L. japonica* in addition to the SP population. *Drosophila bifasciata* was significantly more frequently oviposited by the SP and TK populations of *L. japonica* compared with the TP population (Fisher's exact test, Bonferroni-corrected $P < 0.01$).

Survival of parasitoids in *Drosophila* species of sympatric origin

All of the parasitoid populations successfully parasitized at least one of the dominant or common frugivorous *Drosophila* species from their original localities. In particular, the SP population was successful in *D. biauraria*, the TK population in *D. biauraria*, *D. rufa* and *D. suzukii*, and the TP population in *D. albomicans* and *D. bocki* (Fig. 2). The SP strain additionally showed limited success in *D. orientacea*, a mycophagous species. Although all of the parasitoid populations generally oviposited well in members of the *melanogaster* species group (Fig. 1), the SP and TK populations scarcely survived in *D. auraria*, and the TP strain did not survive in *D. bipectinata* or *D. parabipectinata* (Fig. 2).

Survival of parasitoids in *Drosophila* species of allopatric origin

In parasitism experiments involving the *melanogaster* species group, the survival of one or both of the parasitoid populations of allopatric origin differed from that of parasitoid populations of sympatric origin in nine cases ($P > 0.05$). In particular, the sympatric parasitoid population showed a higher survival rate than did at least one allopatric population in six cases (*D. biauraria* from SP and TK, *D. suzukii* from TK, and *D*. sp. aff. *bicornuta*, *D. bocki* and *D. takahashii* from TP), whereas the sympatric parasitoid population showed a lower survival rate than did at least one allopatric population in three cases (*D. rufa*, *D. lutescens* and *D. bipectinata*). In *D. rufa*, however, a difference was observed in the frequency of parasitized larvae from which no flies or parasitoids emerged ($P<0.05$).

Among species of the subgenus *Drosophila*, *D. sulfurigaster* from KK was successfully parasitized by the SP and TP populations of *L. japonica*. In addition, *D. orientacea* from SP was parasitized to some extent by the TP population (Fig. 2).

## Discussion

Host association

The *L. japonica* laboratory populations in this study each successfully parasitized at least one abundant or common forest-inhabiting frugivorous *Drosophila* species collected from the original locality of the corresponding parasitoid. In particular, the SP population showed high survival in *D. biauraria* from SP, as did the TK population in *D.*

227 *rufa* and *D. suzukii* from TK and the TP population in *D. albomicans* and *D. bocki* from
228 TP. *Leptopilina japonica* has indeed been observed to parasitize *D. biauraria*, *D. rufa*,
229 *D. suzukii* and *D. albomicans* larvae in banana baits and cherry fruits in wooded areas
230 (Mitsui and Kimura 2010; Novković et al. 2011; Kasuya et al. 2013b). For unknown
231 reasons, however, the parasitoid population from TK is only moderately virulent to *D.*
232 *lutescens*, the most abundant frugivorous species (see also Beppu 2000 and Mitsui et al.
233 2010 concerning its abundance). One possible explanation is that competition with the
234 abundant parasitoid species *Ganaspis xanthopoda* (Ashmead) (Mitsui et al. 2007;
235 Mitsui and Kimura 2010) may have led *L. japonica* to avoid exploitation of *D.*
236 *lutescens*; alternatively, *D. lutescens* may have evolved some resistance against this
237 parasitoid.
238 Even though the rate of successful parasitism was not high, it is noteworthy
239 that *L. j. japonica* from SP parasitized *D. orientacea*. In SP, *D. biauraria* is the only
240 native frugivorous host species of *L. j. japonica*. This parasitoid may have evolved to
241 exploit the abundant mycophagous species *D. orientacea* as a subsidiary host to survive
242 situations in which *D. biauraria* is scarce or unavailable.
243 In most cases, the parasitoid species in this study did not successfully parasitize
244 the *Drosophila* species abundant in domestic areas, such as *D. auraria*, *D. bipectinata*,
245 *D. parabipectinata* and *D. immigrans* (Kurokawa 1967; Kimura 1987; Hirai et al. 2000;
246 Kondo and Kimura 2008; Kimura and Suwito 2012, 2014). Evolution of virulence (or
247 counter-resistance) against these domestic *Drosophila* species may not be beneficial to
248 *L. japonica*, as it would seldom encounter them because of differences in habitats. An
249 exception to this situation is *D. simulans* (Novković et al. 2011); as discussed later, its
250 successful parasitism of domestic species may be due to ecological fitting.

## Local adaptation and ecological fitting

The major host species from SP, TK and TP were often more successfully parasitized by sympatric *L. japonica* populations than by allopatric ones. One noteworthy example is *D. albomicans* from TP, which was a very suitable host for *L. j. formosana* from TP but an unsuitable host for *L. j. japonica* from SP and TK. These results suggest that the investigated parasitoid populations are adapted to local populations of these *Drosophila* species. Local host adaptation has also been observed in some other *Drosophila* parasitoids, namely *L. heterotoma* (Thomson) and *Asobara tabida* Nees (Kraaijeveld and Godfray 2001; Gilbert et al. 2010). In the present case, however, the differential responses of sympatric and allopatric parasitoid populations could also be due to unintentional selection in the laboratory, as the parasitoid and *Drosophila* populations from SP and TK were maintained for 2 to 4 years in the laboratory.

In contrast to the above cases, *D. bipectinata* from TP was somewhat exploitable as a host by *L. j. japonica* from TK, where this fly species rarely occurs, but was not suitable as a host of *L. j. formosana* from TP. In addition, *D. lutescens* from TK was more suitable as a host of *L. j. formosana* from TP than of *L. j. japonica* from TK. Furthermore, *D. sulfurigaster* from KK was successfully parasitized by *L. j. formosana* from TP and *L. j. japonica* from SP, while *D. orientacea* from SP was parasitized by *L. j. formosana* from TP. This successful parasitization of unfamiliar host species or populations allows the parasitoid to colonize new environments where the unfamiliar host species are abundant or common—in other words, successful colonization through ecological fitting.

Agosta (2006) has listed three mechanisms for ecological fitting: 1) phenotypic plasticity, 2) phylogenetic conservatism, and 3) correlated evolution of some traits that provide preadaptations to novel environments. Phenotypic plasticity does not apply in the present cases. Phylogenetic conservatism also does not explain the survival of the SP and TK populations in *D. sulfurigaster* or *D. bipectinata*, because these two parasitoid populations do not successfully parasitize the related species *D. albomicans* or *D. parabipectinata*. Likewise, the two sibling species *D. auraria* and *D. biauraria* differed in suitability as hosts for the investigated *L. japonica* populations. A difference in host suitability of closely related *Drosophila* species has also been observed in our previous studies (Mitsui and Kimura 2010; Kimura and Suwito 2014). Consequently, preadaptation by correlated evolution of other traits may be responsible for the successful parasitism of unfamiliar host species or populations by *L. japonica*. Alternatively, the successful parasitism may be due not to the intrinsic parasitoid virulence, but instead to the absence of resistance against unfamiliar parasitoids in the host species. Distinguishing between these two possibilities is difficult, but identification of virulence and resistance genes and analysis of their interactions may provide some insights into this issue.

Host acceptance for oviposition

From an adaptive point of view, parasitoids should not oviposit in sympatrically occurring unsuitable hosts. Nevertheless, such maladaptive oviposition has often been observed (Mitsui and Kimura 2010; Novković et al. 2012; Kimura and Suwito 2014). In these cases, host taxonomy (i.e., phylogenetic conservatism) seems to play an important

299 role. For example, *L. victoriae* Nordlander oviposits in species from the *melanogaster*
300 species group, irrespective of suitability, but rarely in those from the *immigrans* species
301 group. In addition, *L. pacifica* Novković & Kimura oviposits only in species of the
302 subgenus *Drosophila*, including the *immigrans* species group (Novković et al. 2012;
303 Kimura and Suwito 2014). In our study, with some exceptions, the parasitoid *L.*
304 *japonica* likewise oviposited in individuals of the *melanogaster* species group
305 regardless of their suitability. In addition, the SP population of *L. japonica* more or less
306 oviposited in species of the subgenus *Drosophila*; the TP population did likewise in *D.*
307 *albomicans* and *D. sulfurigaster* of the *nasuta* species subgroup, while the TK
308 population scarcely oviposited in these species. The ability to distinguish related species
309 may evolve less readily than that needed to discriminate between species of different
310 lineages, because fewer distinguishing traits are available in related species.
311 Nonetheless, *L. j. formosana* from TP can discriminate between the two sibling species
312 *D. bipectinata* and *D. parabipectinata*, suggesting that taxonomic proximity is not the
313 only factor affecting this discrimination.
314
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**Table 1** Taxonomy, distribution and feeding habits of *Drosophila* species used in experiments

| Species[a] | Subgenus | Species group | Species subgroup | Distribution | Feeding habit[b] |
|---|---|---|---|---|---|
| *D. bifasciata* Pomini (bf) | *Sophophora* | *obscura* | *obscura* | cool-temperate | T |
| *D. bipectinata* Duda (bp) | *Sophophora* | *melanogaster* | *ananassae* | tropical | F |
| *D. parabipectinata* Bock (pr) | *Sophophora* | *melanogaster* | *ananassae* | tropical | F |
| *D. auraria* Peng (au) | *Sophophora* | *melanogaster* | *montium* | cool-temperate | F |
| *D. biauraria* Bock & Wheeler (ba) | *Sophophora* | *melanogaster* | *montium* | cool-temperate | F |
| *D. rufa* Kikkawa & Peng (rf) | *Sophophora* | *melanogaster* | *montium* | warm-temperate | F |
| *D.* sp. aff. *bicornuta* (bn) | *Sophophora* | *melanogaster* | *montium* | subtropical | F |
| *D. bocki* Baimai (bk) | *Sophophora* | *melanogaster* | *montium* | subtropical | F |
| *D. takahashii* Sturtevant (tk) | *Sophophora* | *melanogaster* | *takahashii* | subtropical | F |
| *D. lutescens* Okada (lt) | *Sophophora* | *melanogaster* | *takahashii* | warm-temperate | F |
| *D. suzukii* (Matsumura) (sz) | *Sophophora* | *melanogaster* | *suzukii* | warm-temperate | F |
| *D. immigrans* Sturtevant (im) | *Drosophila* | *immigrans* | *immigrans* | world-wide | F |
| *D. albomicans* Duda (al) | *Drosophila* | *immigrans* | *nasuta* | subtropical | F |
| *D. sulfurigaster* Duda (sl) | *Drosophila* | *immigrans* | *nasuta* | tropical | F |
| *D. sternopleuralis* Okada & Kurokawa (st) | *Drosophila* | *histrio* | - | warm-temperate | G |
| *D. nigromaculata* Kikkawa & Peng (ni) | *Drosophila* | *quinaria* | - | cool-temperate | G |
| *D. orientacea* Grimaldi, James & Jaenike (or) | *Drosophila* | *testacea* | - | cool-temperate | M |

[a] Abbreviations for species names are given in parentheses.

[b] Feeding habits: T = tree-sap feeding; F = frugivorous; G = generalist; M = mycophagous

**Table 2** Relative frequencies (%) of major drosophilid flies in collection samples

| | Relative frequency | Feeding habit[c] |
|---|---|---|
| Sapporo | | |
| *Drosophila orientacea* | 24.3 | M |
| *Scaptodrosophila coracina* (Kikkawa & Peng) | 21.0 | G |
| *D. immigrans* | 14.0 | F |
| *Hirtodrosophila histrioides* (Okada & Kurokawa) | 11.8 | M |
| *D. biauraria* | 6.3 | F |
| *D. lacertosa* Okada | 4.6 | T |
| *D. nigromaculata* | 4.4 | G |
| *D. bifasciata* | 3.7 | T |
| Others | 9.9 | |
| Total number of flies | 1,150 | |
| Tokyo[a] | | |
| *D. lutescens* | 28.4 | F |
| *D. rufa* | 19.3 | F |
| *D. bizonata* Kikkawa & Peng | 15.0 | M |
| *D. suzukii* | 13.6 | F |
| *D. immigrans* | 10.9 | F |
| *D. simulans* | 4.1 | F |
| *D. curviceps* Okada & Kurokawa | 2.9 | G |
| Others | 5.8 | |
| Total number of flies | 39,519 | |
| Taipei | | |
| *D. albomicans* | 67.7 | F |
| *D. bocki* | 10.4 | F |
| *D. takahashii* | 6.3 | F |
| *D. ruberrima* Meijere | 5.8 | F |
| *D. bipectinata*[b] | 4.5 | F |
| *D. immigrans* | 1.4 | F |
| Others | 3.9 | |
| Total number of flies | 1,479 | |

[a] Data from Beppu (2000).
[b] A few individuals of *D. parabipectinata* were included.
[c] Feeding habits: F = frugivorous; G = generalist; M = mycophagous; T = tree-sap feeding

**Figure legends**

**Fig. 1** Oviposition rates of *L. japonica* from (a) Sapporo (SP), (b) Tokyo (TK) and (c) Taipei (TP) in *Drosophila* species from these three localities and Kota Kinabalu (KK). The number of individuals used in each experiment is given above bars. Abbreviations for drosophilid species are given in Table 1. Abbreviations for taxonomic groups are as follows: o, *obscura* species group; m, *melanogaster* species group; D, subgenus *Drosophila*. Results of experiments using parasitoid and *Drosophila* populations of sympatric origin are framed by rectangles

**Fig. 2** Frequency of fly larvae from which flies (white), parasitoids (grey) or neither organism (black) emerged in parasitism experiments using *Leptopilina japonica* from (a) Sapporo (SP), (b) Tokyo (TK) and (c) Taipei (TP) and *Drosophila* species from these three localities and Kota Kinabalu (KK). The number of individuals used in each experiment is given above bars. Abbreviations for drosophilid species are given in Table 1. Abbreviations for taxonomic groups are as follows: o, *obscura* species group; m, *melanogaster* species group; D, subgenus *Drosophila*. Results of experiments using parasitoid and *Drosophila* populations of sympatric origin are framed by rectangles

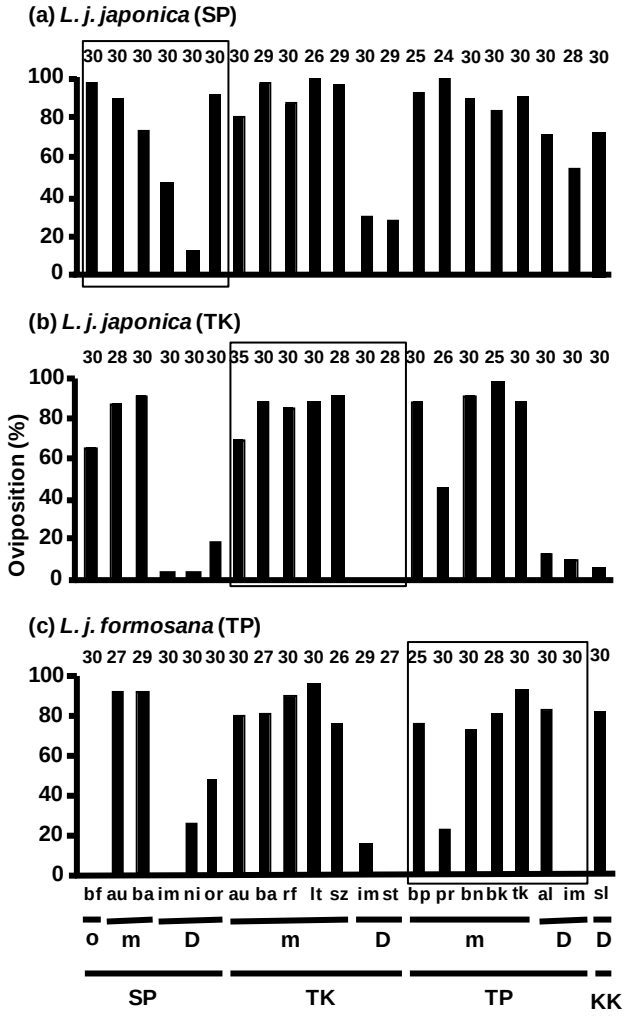

(a) L. j. japonica (SP)
30 30 30 30 30 30 30 29 30 26 29 30 29 25 24 30 30 30 30 28 30
100
80
60
40
20
0
(b) L. j. japonica (TK)
30 28 30 30 30 30 35 30 30 30 28 30 28 30 26 30 25 30 30 30 30
Oviposition (%)
100
80
60
40
20
0
(c) L. j. formosana (TP)
30 27 29 30 30 30 30 27 30 30 26 29 27 25 30 30 28 30 30 30 30
100
80
60
40
20
0
bf au ba im ni or au ba rf lt sz im st bp pr bn bk tk al im sl
o m D m D m D D
SP TK TP KK

Fig. 1

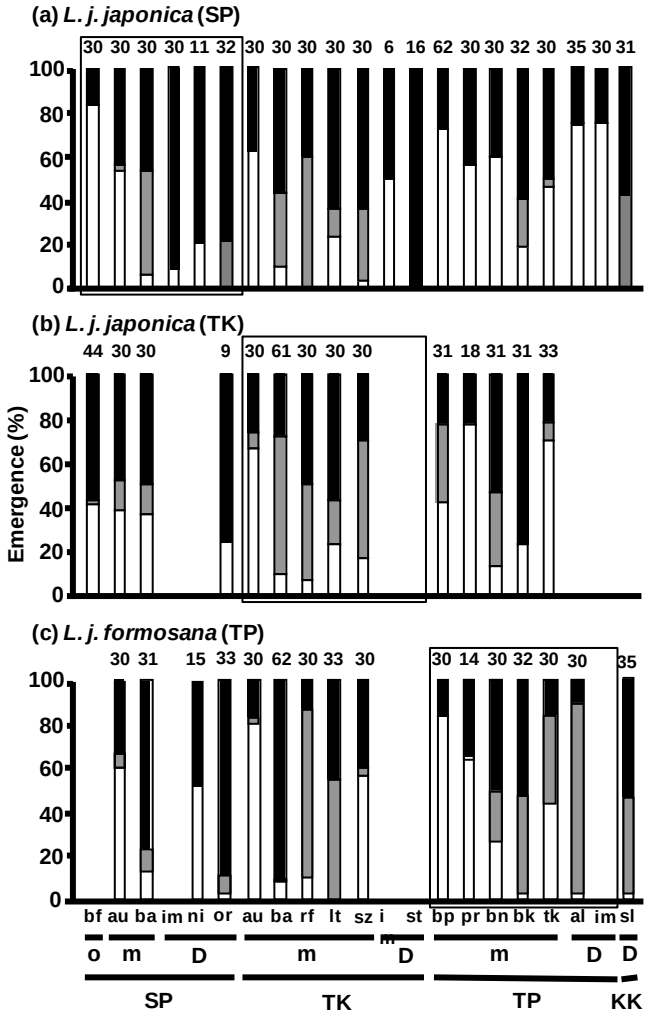

(a) L. j. japonica (SP)
30 30 30 30 11 32 30 30 30 30 30 6 16 62 30 30 32 30 35 30 31
(b) L. j. japonica (TK)
44 30 30 9 30 61 30 30 30 31 18 31 31 33
Emergence (%)
(c) L. j. formosana (TP)
30 31 15 33 30 62 30 33 30 30 14 30 32 30 30 35
bf au ba im ni or au ba rf lt sz i st bp pr bn bk tk al im sl
o m D m D m D D
SP TK TP KK

Fig.2