



Title	Local adaptation and ecological fitting in host use of the <i>Drosophila</i> parasitoid <i>Leptopilina japonica</i>
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1 **Masahito T. Kimura • Biljana Novković**

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3 **Local adaptation and ecological fitting in host use of the *Drosophila* parasitoid**

4 ***Leptopilina japonica***

5

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13

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

32

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

35

36 **Introduction**

37

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

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

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

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

84

85 **Materials and methods**

86

87 Study species and populations

88

89 The parasitoid study species *L. japonica* consists of two subspecies: *L. j. japonica*,
90 occurring in central and northern Japan, and *L. j. formosana*, present in Taiwan
91 (Novković et al. 2011). In this study, laboratory populations of *L. j. japonica* were
92 collected from Sapporo (SP: 43.0 °N in Japan; collected in July 2006) and Tokyo (TK:
93 35.7 °N in Japan; June 2007), while a population of *L. j. formosana* was collected from
94 Taipei (TP: 25.2 °N in Taiwan; March 2009). These populations were maintained using
95 *D. simulans* as the host. For use in “host acceptance” and “host suitability” experiments,
96 parasitoid females were also reared with *D. simulans*, and after eclosion they were
97 maintained for 2–6 days in on *Drosophila* medium with *D. simulans* larvae and allowed
98 to mate.

99 Populations of the major *Drosophila* species in the three sampling localities
100 were also collected along with the parasitoid populations. In addition, a population of *D.*
101 *sulphurigaster* was collected from Kota Kinabalu (KK: 5.3 °N in Malaysia) in June 2008.
102 The *Drosophila* laboratory populations were reared on medium containing cornmeal,
103 wheat germ, yeast and sugar. Table 1 shows their taxonomic positions, distribution and
104 feeding habits (Kimura et al. 1977; Hirai et al. 2000; Kimura 2004; Mitsui et al. 2010;
105 Kimura and Suwito 2012; Kasuya et al. 2013a). Maintenance of the parasitoid and
106 *Drosophila* populations was carried out and experiments were performed under a
107 15-h:9-h light:dark photoperiod at 23 °C.

108 Experiments using parasitoid and *Drosophila* populations from the same
109 localities were conducted within several months of collection. In contrast, experiments
110 using parasitoid and *Drosophila* populations from different localities were conducted in
111 2009–2010; this time period corresponds to several months to a year after collection of
112 populations from TP and 2 to 3 years after collection of SP and TK populations. The
113 results of experiments that used laboratory populations from different localities must
114 therefore be interpreted with caution, as populations from SP and TK may have changed
115 during the 2 to 4 years of laboratory rearing.

116 To investigate the influence of host abundance on parasitoid host use, the
117 abundance of frugivorous drosophilid species in the three localities was determined
118 based on our collection data and that of Beppu (2000). Collections were carried out
119 using banana-baited traps in wooded areas as follows: 6 times from May to October in
120 1971 in SP (our data), 14 times from July 1998 to July 1999 in TK (Beppu 2000), and 3
121 times from June 2010 to February 2011 in TP (our data). In SP and TP, drosophilid flies
122 attracted to traps were collected by nets or bags from morning to evening (13–16 times
123 daily in SP and 3 times in TP) for 3 or 2 successive days in SP and TP, respectively. In
124 TK, retainer-type traps were set for a week, with drosophilid flies retained in the traps
125 and then collected (Beppu 2000).

126

127 Host acceptance

128

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

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

135

136 Host suitability

137

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

150

151 Statistics

152

153 To compare oviposition rates in the acceptance experiment and frequencies of
154 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

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

190

191 Survival of parasitoids in *Drosophila* species of sympatric origin

192

193 All of the parasitoid populations successfully parasitized at least one of the dominant or
194 common frugivorous *Drosophila* species from their original localities. In particular, the
195 SP population was successful in *D. bauraria*, the TK population in *D. bauraria*, *D.*
196 *rufa* and *D. sukikii*, and the TP population in *D. albomicans* and *D. bocki* (Fig. 2). The
197 SP strain additionally showed limited success in *D. orientacea*, a mycophagous species.
198 Although all of the parasitoid populations generally oviposited well in members of the
199 *melanogaster* species group (Fig. 1), the SP and TK populations scarcely survived in *D.*
200 *auraria*, and the TP strain did not survive in *D. bipunctata* or *D. parabipunctata* (Fig.
201 2).

202

203 Survival of parasitoids in *Drosophila* species of allopatric origin

204

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

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

218

219 **Discussion**

220

221 Host association

222

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

251

252 Local adaptation and ecological fitting

253

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

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

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

292

293 Host acceptance for oviposition

294

295 From an adaptive point of view, parasitoids should not oviposit in sympatrically
296 occurring unsuitable hosts. Nevertheless, such maladaptive oviposition has often been
297 observed (Mitsui and Kimura 2010; Novković et al. 2012; Kimura and Suwito 2014). In
298 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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320

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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
<i>D. bifasciata</i> Pomini (bf)	<i>Sophophora</i>	<i>obscura</i>	<i>obscura</i>	cool-temperate	T
<i>D. bipectinata</i> Duda (bp)	<i>Sophophora</i>	<i>melanogaster</i>	<i>ananassae</i>	tropical	F
<i>D. parabipectinata</i> Bock (pr)	<i>Sophophora</i>	<i>melanogaster</i>	<i>ananassae</i>	tropical	F
<i>D. auraria</i> Peng (au)	<i>Sophophora</i>	<i>melanogaster</i>	<i>montium</i>	cool-temperate	F
<i>D. bauraria</i> Bock & Wheeler (ba)	<i>Sophophora</i>	<i>melanogaster</i>	<i>montium</i>	cool-temperate	F
<i>D. rufa</i> Kikkawa & Peng (rf)	<i>Sophophora</i>	<i>melanogaster</i>	<i>montium</i>	warm-temperate	F
<i>D. sp. aff. bicornuta</i> (bn)	<i>Sophophora</i>	<i>melanogaster</i>	<i>montium</i>	subtropical	F
<i>D. bocki</i> Baimai (bk)	<i>Sophophora</i>	<i>melanogaster</i>	<i>montium</i>	subtropical	F
<i>D. takahashii</i> Sturtevant (tk)	<i>Sophophora</i>	<i>melanogaster</i>	<i>takahashii</i>	subtropical	F
<i>D. lutescens</i> Okada (lt)	<i>Sophophora</i>	<i>melanogaster</i>	<i>takahashii</i>	warm-temperate	F
<i>D. suzukii</i> (Matsumura) (sz)	<i>Sophophora</i>	<i>melanogaster</i>	<i>suzukii</i>	warm-temperate	F
<i>D. immigrans</i> Sturtevant (im)	<i>Drosophila</i>	<i>immigrans</i>	<i>immigrans</i>	world-wide	F
<i>D. albomicans</i> Duda (al)	<i>Drosophila</i>	<i>immigrans</i>	<i>nasuta</i>	subtropical	F
<i>D. sulfurigaster</i> Duda (sl)	<i>Drosophila</i>	<i>immigrans</i>	<i>nasuta</i>	tropical	F
<i>D. sternopleuralis</i> Okada & Kurokawa (st)	<i>Drosophila</i>	<i>histrion</i>	-	warm-temperate	G
<i>D. nigromaculata</i> Kikkawa & Peng (ni)	<i>Drosophila</i>	<i>quinaria</i>	-	cool-temperate	G
<i>D. orientacea</i> Grimaldi, James & Jaenike (or)	<i>Drosophila</i>	<i>testacea</i>	-	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		
<i>Drosophila orientacea</i>	24.3	M
<i>Scaptodrosophila coracina</i> (Kikkawa & Peng)	21.0	G
<i>D. immigrans</i>	14.0	F
<i>Hirtodrosophila histrioides</i> (Okada & Kurokawa)	11.8	M
<i>D. biauraria</i>	6.3	F
<i>D. lacertosa</i> Okada	4.6	T
<i>D. nigromaculata</i>	4.4	G
<i>D. bifasciata</i>	3.7	T
Others	9.9	
Total number of flies	1,150	
Tokyo ^a		
<i>D. lutescens</i>	28.4	F
<i>D. rufa</i>	19.3	F
<i>D. bizonata</i> Kikkawa & Peng	15.0	M
<i>D. suzukii</i>	13.6	F
<i>D. immigrans</i>	10.9	F
<i>D. simulans</i>	4.1	F
<i>D. curviceps</i> Okada & Kurokawa	2.9	G
Others	5.8	
Total number of flies	39,519	
Taipei		
<i>D. albomicans</i>	67.7	F
<i>D. bocki</i>	10.4	F
<i>D. takahashii</i>	6.3	F
<i>D. ruberrima</i> Meijere	5.8	F
<i>D. bipectinata</i> ^b	4.5	F
<i>D. immigrans</i>	1.4	F
Others	3.9	
Total number of flies	1,479	

^a Data from Beppu (2000).

^b A few individuals of *D. parabiptinata* 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

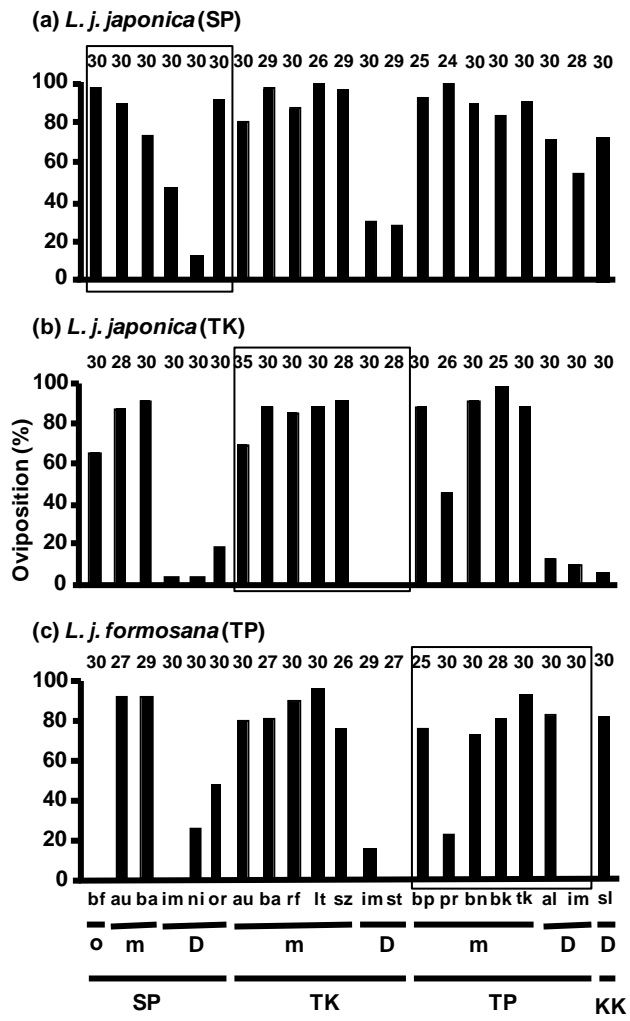


Fig. 1

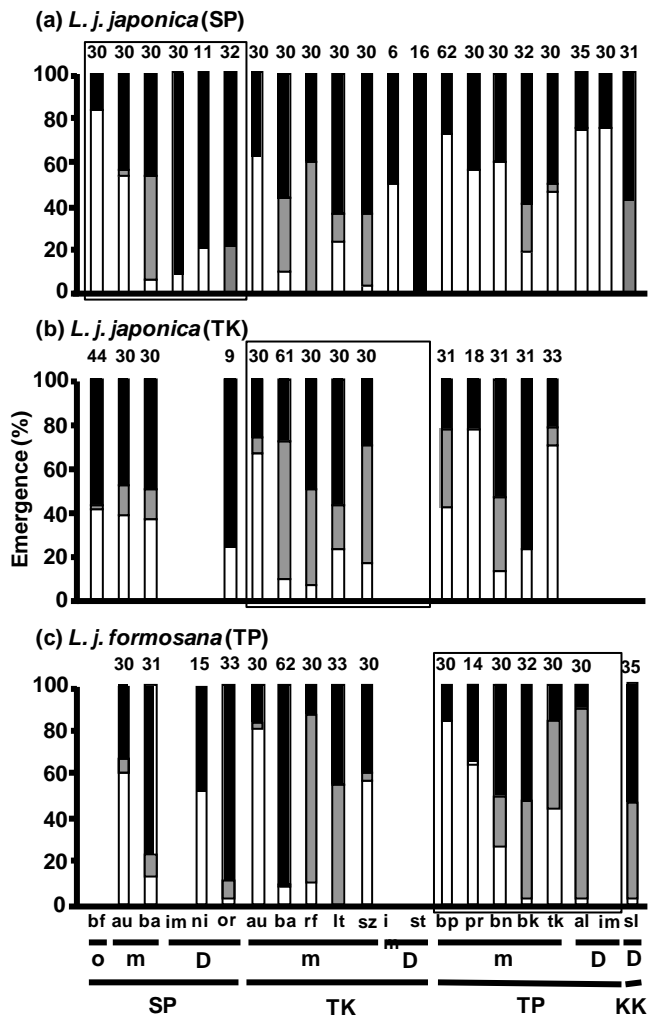


Fig.2