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Hidden in taxonomy: Batesian mimicry by a syrphid fly towards a Patagonian bumblebee

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Abstract. 1. Batesian mimicry has been repeatedly reported in syrphid flies (Diptera: Syrphidae), with noxious Hymenoptera identified as the models, including bumblebees (Hymenoptera: Aculeata). Despite the number of detailed studies of bumblebee mimics from the Holarctic, only minimal biological and ecological information is available for the same phenomenon in most other biogeographical regions.

2. Here, we analyse in detail a case of Batesian mimicry by the syrphid fly *Aneriophora aureorufa* Philippi towards the bumblebee *Bombus dahlbomii* Guérin from Patagonia, a relationship only briefly noted previously in taxonomic studies. *A. aureorufa* possesses strikingly similar red tawny colouration to the highly hairy body of its model, and somewhat resembles it also in size. Cluster analysis suggests that the mimicry is more pronounced towards larger rather than smaller bumblebee workers.

3. The mimicry is visually very good, but there was no evidence of a behavioural component. Foraging activity of both species seems to be largely restricted to the endemic plant *Eucryphia cordifolia*. The time spent on flowers was much higher in syrphid flies than in *B. dahlbomii* and other pollinators, and the time spent between flower visits largely overlapped between all the tested species.

4. The endemic distribution, the apparent plant specialisation, and the invasion of alien bumblebees, make *B. dahlbomii* and *A. aureorufa* potentially threatened in some parts of the austral American forests, a priority conservation area.

Key words. *Aneriophora*, *Bombus*, Chile, foraging behaviour, mimicry, morphology.

Introduction

The resemblance of a palatable species to an unpalatable (or armoured/defended) species is referred to as Batesian mimicry (Bates, 1862; Edmunds, 1974), and is generally believed to help to deter predation (e.g. Green *et al*., 1999; Kauppinen & Mappes, 2003; Rashed *et al*., 2005). Batesian mimicry is widespread in insects, but is especially commonly recorded in the syrphid flies (flower flies, also called hover flies in Europe) (Diptera: Syrphidae). This large and diverse family of Diptera, with more than 5600 species described (Gilbert, 1986; Rotheray & Gilbert, 1999), includes nearly 280 species that mimic Hymenoptera (bees and wasps) in the Holarctic (Gilbert, 2005). Mimetic syrphid flies are palatable to their potential predators (Mostler, 1935) and thus it is believed that by mimicking noxious Hymenoptera they limit the attacks by birds, which learn to avoid stinging Hymenoptera (Gilbert, 2005).

Batesian mimicry of syrphid flies towards hymenopteran models is essentially morphological, with the flies having similar (but often not very close) colour patterns, body size, and perhaps body shape, to their models (Heal, 1982; Holloway, 1993); but recent studies showed that the mimicry has also a behavioural component:

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syrphid fly daily activity correlates in many cases with that of their models (Howarth *et al.*, 2004), and mimics spend similar times visiting and flying between flowers (Golding & Edmunds, 2000).

Among the hymenopteran models of syrphid flies are many species of the social bee genus *Bombus* (bumblebees) (reviewed in Gilbert, 2005). Bumblebees comprise ≈240 species which occur mostly in the Holarctic region, largely in boreal or high-altitude habitats (Goulson, 2010). These bees are certainly noxious or unprofitable to their predators, as shown experimentally with a variety of bird species, which, once experienced, almost invariably did not attempt to attack them again (Mostler, 1935). The source of this aversion is still debated, though it probably mainly derives from the great difficulty of handling bumblebees compared to other insect prey (Mostler, 1935), rather than merely the possession of a sting (Evans & Waldbauer, 1982).

Among the syrphid fly mimics of bumblebees, the quality of the mimicry is generally very high (Gilbert, 2005), as further suggested by the distributional correspondence of fly-bee patterns: many Palaearctic mimics are, like their Palaearctic models, either black with red metasomal tips, or all tawny-coloured, or black-and-yellow-banded with a white metasomal tip. In contrast, Nearctic syrphid flies that mimic bumblebees have a pattern of a yellow anterior and black posterior, as do the common Nearctic bumblebee models (Gilbert, 2005). Almost nothing is known about the quality and patterns of syrphid-bumblebee mimetic associations in other biogeographical regions, such as the Neotropics, despite the importance that this information could have in building a global picture of the evolution of mimicry. In fact, currently there is only circumstantial information, largely derived from taxonomic studies, to suggest a number of cases of mimicry in Neotropical Syrphidae. For example, Shannon (1925, 1926, 1927a,b), Steyskal (1953) and Shannon and Aubertin (1933) made statements about the mimetic resemblance to hymenopterans in different genera of syrphid flies, often naming them after their putative models. Cases include bee-mimics [*Halictomyia* to *Halictus* (Halictidae), *Microdon* to *Trigona* (Apidae)], wasp mimics [*Odyneromyia* to *Odynerus*, *Pelecinobaccha* to *Pelecinus*, *Polybiomyia* to *Polybia*, *Tatuomyia* to *Tatua* wasps (Vespidae)], and sawfly-mimics [*Tenthredomyia* to *Tenthredo* sawflies (Symphyta)]. Hull (1949) reported that *Ocyptamus*, *Odyneromyia*, *Salpingogaster* and *Senogaster* mimic wasps, and even suggested cases in which the models are represented by mutillid wasps (*Sterphus*) and chrysidid wasps (*Nausigaster*). As with the many similar and often mutually incompatible statements from the Old World (see Gilbert, 2005), as far as we know there is no ecological or behavioural evidence for these suggestions. Very few other observations on possible Neotropical mimetic associations are available from more recent years (but see Olesen, 1991; Rotheray *et al.* 1998; Thomson & Zumbado, 2000).

In this study, we contribute to filling this gap by reporting the first detailed study of Batesian mimicry by syrphid flies towards bumblebees from South America, and in particular from Patagonia. The mimetic system includes the syrphid fly *Aneriophora aureorufa* Philippi, a Chilean endemic (Thompson *et al.*, 1976), and its model, the bumblebee *Bombus* (*Fervidobombus*) *dahlbomii* Guérin, endemic to Chile and Argentina and distributed from the central to the southern areas of these countries (Abrahamovich *et al.*, 2004). The resemblance of *Aneriophora* to *Bombus* was noted 80 years ago by Shannon and Aubertin (1933) in their revision of the Syrphidae of Patagonia: no one has studied the syrphid fly fauna since then.

Materials and methods

Study area and sample collection

All the individuals of *A. aureorufa* and *B. dahlbomii* were collected between the 20th and 27th January, 2012, around the Huinay Scientific Field Station, in Southern Chile. The station (42°22′S, 72°24′W) is located in the Commune of Hualaihué, in the 10^{th} Region of Chile, between the Comau fjord in the Province of Palena and the border with the Republic of Argentina. The study site is thus in northern Patagonia, thus included in the Neotropical zoogeographical region (Holt *et al.*, 2013). In particular, the site is located in a coastal area covered mainly by temperate forests known to be particularly rich in endemic animals and plants, and for this reason is considered a priority conservation area (Heywood, 1995).

Insects were collected from 9.00 to 12.00 (solar time) at the most-visited plants. Individuals were netted while visiting flowers and preserved in 96% ethanol in individual test tubes for morphological analysis (see below). Only females of *A. aureorufa* were collected. From the key provided by Abrahamovich *et al.* (2005), it was clear that only workers of *B. dahlbomii* were collected. In particular, mesosoma width, metasoma width, head width and forewing length reported for queens are about 1.5–4.5 mm above the maximum values reported for these variables in our sample (see Results). Murúa *et al.* (2011) reported queens with forewings of up to 25 mm, much greater than the maximum value reported here (17 mm) and Peat *et al.* (2005) reported mesosoma width for foraging workers (mean: 6.01 mm, up to 7.5 mm) similar to our sample (see Results). In addition, queen/worker ratio for mesosoma width (0.5) and head with (0.6) reported in a recent study (Cueva del Castillo & Fairbairn, 2012) were larger than the ratio between the largest and the smallest individual in our sample (0.8 for both variables). Finally, in other areas of Chile (Tregualemu, about 600 km north to our study site), queens were generally recorded early in the season (spring) and workers found later in the season (summer, i.e. the same period of our collection) (Murúa *et al.*, 2011).

Morphological data

In the laboratory, all the collected individuals (12 females of *A. aureorufa* and 14 workers of *B. dahlbomii*) were measured to compare size and shape between the mimic and the model. A total of six size variables that were considered were as follows: head width, thorax (more properly mesosoma for bees) width and length, abdomen (more properly metasoma for bees) width and length, and forewing length. These measurements were taken with a calliper to the nearest 0.1 mm.

Morphological data appeared to be normally distributed (Jarque–Bera test: $0.1 < JB < 2.9$, $0.2 < P < 0.9$); we thus used non-transformed data in the statistical analyses. To test for differences in morphological variables between syrphid flies and bumblebees we first performed a Principal Component Analysis (PCA) on the six measurements taken on the 26 individuals, and then tested for differences along the first two PC axes with two-tailed Student's *t*-test. If homogeneity of variance was not present (i.e. a significant *F*-test), the Aspin–Welch test was used. The hypothesis is that mimicry promotes similarity in body size between the two species, evident as non-significant differences along the two axes. For a medium effect size of 0.5, a test with good power (0.80) would need sample sizes of 65 for each group, far greater than was possible here. Nevertheless, the results suggested that our low sample sizes were not problematic (see below). We do not report meaningless post hoc power tests (following Steidl *et al*., 1997; Hoenig & Heisey, 2001), but instead [as suggested by Steidl *et al*., 1997) where necessary we report the 95% confidence limits of the effect size, calculated following Howell (2011)].

We then conducted a cluster analysis (through the Ward method) to explore the morphological relationships between the two species in a multivariate environment, using the scores of the first two PCA factors as variables. The hypothesis is that, due to mimicry, syrphid fly individuals do not form a clear cluster separated from bumblebees, but are mixed among the bumblebee individuals.

Behavioural field data

The bumblebee models and syrphid fly mimics regularly fed together on flowering trees of the native *Eucryphia cordifolia* Cavanilles (Eucryphiaceae) (known as 'ulmo' in Chile), particularly between 10.00 and 12.00 (hours). We performed the behavioural observations on a single large plant of this species. Because of the abundance of individuals and because flower-visiting parameters can be involved in the behavioural component of mimicry (Golding & Edmunds, 2000), we recorded data on the time spent on flowers during visits and the time between consecutive visits for *A. aureorufa*, *B. dahlbomii* and two other common bee species visiting *E. cordifolia*, both foreign invaders: the European bumblebee *Bombus ruderatus* (Fabr.) and the honeybee *Apis mellifera* L. The hypothesis is that the time syrphid flies spend foraging on flowers and the time they spend flying between flowers will be more similar to the times recorded for *B. dahlbomii* than to the times recorded for the other bee species.

A focal-watch technique was used to record the behaviour of individual insects. The times (to the nearest second) were recorded using a tape recorder. A total of 86 bouts (sequences of visits by the same individual) were recorded (73 with both variables and 13 where only the time spent on flowers was recorded), for a total of 253 visit times (2.9 ± 1.8, range 1–8 per bout) and 135 between-visit times (2.5 ± 1.8, range 1–8 per bout). The data were ln-transformed to achieve normality, because the distributions were not normal (Jarque-Bera test: $8.1 < JB < 678$, $0.0001 < P < 0.02$) and then one-way ANOVAS were performed; in case of significant ANOVA, the following contrasts were then performed: mimic vs. model, mimic vs. (*B. ruderatus* + *A. mellifera*), and model vs. (*B. ruderatus* + *A. mellifera*). We applied a Dunn-Sidak correction ($\alpha' = 1 - (1 - \alpha)^{1/k}$, where $\alpha = 0.05$ and k is the number of tests) to adjust the error rate to account for multiple comparisons (Quinn & Keough, 2002). To limit problems of pseudo replication, the ANOVAS were performed using the mean values per bout, rather than the raw data per visit.

All the statistics were performed with the software XLSTAT 2011 (Addinsoft®, New York, NY, USA). In the text and tables, means are expressed ±SE.

Results

Morphology

Females of *A. aureorufa* are large flies with a robust body largely covered by reddish/tawny hair, clearly resembling workers of *B. dahlbomii*, especially while foraging on flowers (Fig. 1). The syrphid flies and bumblebees seem to differ more in some of the size variables, such as abdomen/metasoma length (greater in the model) and head width (greater in the mimics), and less in others, such as thorax/mesosoma width and forewing length (Fig. 2).

The PCA carried out on the six morphological variables showed that the two main factors accounting for size (together explaining 81.7% of the variance; eigenvalues: F1 = 3.43, F2 = 1.46) were forewing length (highest contributor to the F1 with 21.4%) [in close combination with thorax/mesosoma width, as its contribution (21%) was almost identical to that of forewing length] and abdomen/metasoma length (highest contributor to the F2 with 43.1%). The tests performed along these two axes (i.e. using the PCA scores) revealed significant differences between mimics and models (F1: Student's *t*-test: $t = 2.34$, d.f. = 24, $P = 0.028$; F2: Aspin–Welch test: $t = -7.93$, d.f. = 19.1, $P < 0.0001$). Thus, overall size differed between the two species, though notably more weakly

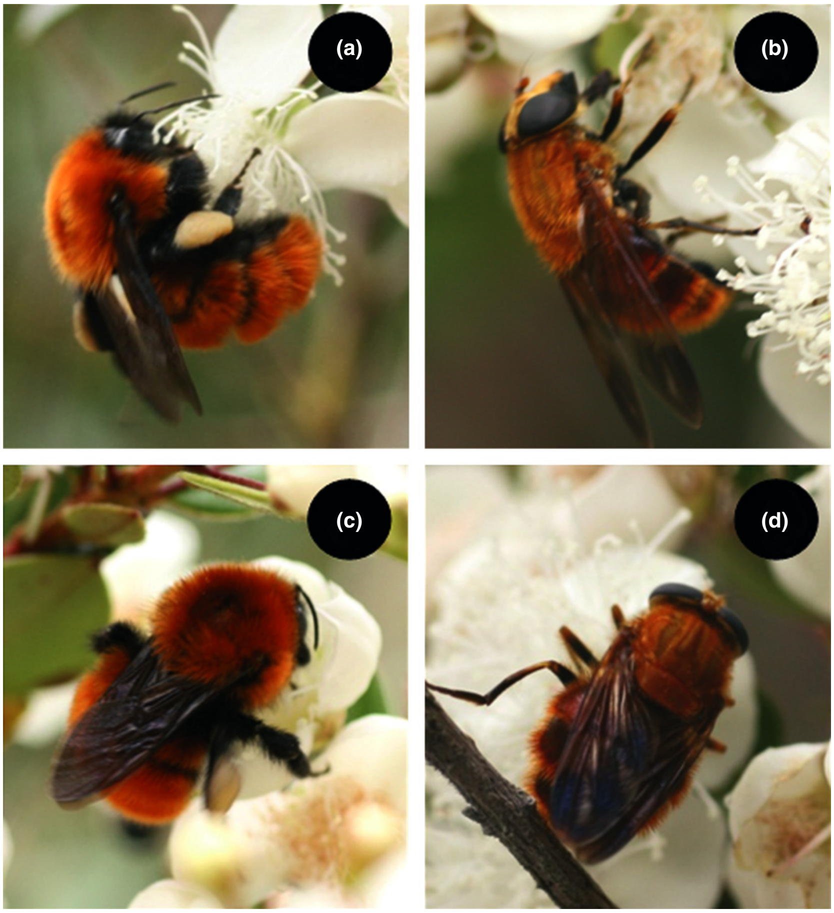

Fig. 1. Bumblebee worker *Bombus dahlbomii* (a and c) and syrphid fly female *Aneriophora aureorufa* (b and d) while foraging on flowers of *Eucryphia cordifolia* at Huinay Scientific Field Station, Southern Chile.

along the main size axis (for forewing length + thorax/mesosoma width) (Fig. 3a).

The cluster analysis based on the PCA factor scores grouped the 14 measured individuals in three clusters (truncation value: 22.90) (Fig. 3b). The two more closely associated groups (distances between the group centroids: 2.78) included all the syrphid flies bar one, plus seven bumblebee workers, while the other, more distant cluster (distances to the other two group centroids: 3.62–3.72) included the remaining bumblebee workers and a single syrphid fly (Fig. 3b). These seven bumblebee individuals more closely related to the syrphid flies were also the larger ones along the F1 (Fig. 3a). For example, all of them had forewings longer than 14.5 mm (in the other group forewing length was always <14.5 mm), and almost all had mesosoma widths greater than 6.7 mm. When the Student *t*-test was repeated considering only these seven bees, the size difference with flies along the first factor axis (F1) disappeared ($t = 0.15$, d.f. = 17, $P = 0.88$), although the power of this test is low, given the small sample sizes (effect size = 0.804, 95% confidence limits −0.013 and 0.939: calculated according to Howell, 2011).

Behaviour

Both *A. aureorufa* and *B. dahlbomii* were found foraging mostly on flowering trees of the native *E. cordifolia*, compared to other flowering plants in the study area. In particular, the syrphid fly was only observed on this plant, while the bumblebee was extremely common on it and only occasionally seen on flowers of the native ‘chilco’, *Fuchsia magallanica* (Onagraceae), and also on the introduced European species *Digitalis purpurea* (Scrophulariaceae), *Hypochoeris radicata* and *Taraxacum officinale* (Asteraceae).

The general behaviour of *A. aureorufa* while visiting *E. cordifolia* flowers approximated that of bumblebees, particularly in the speed of flight and position of the body while feeding (Fig. 1). But, this resemblance was more apparent than real. In fact, our hypothesis that the times spent by the syrphid fly on flowers and between flowers are more similar to those of the models than to those of other pollinators is rejected with the present data. Syrphid flies spent much more time feeding or resting on flowers [20.9 ± 5.1 (6–98) s, $n = 23$] than all the other tested bees

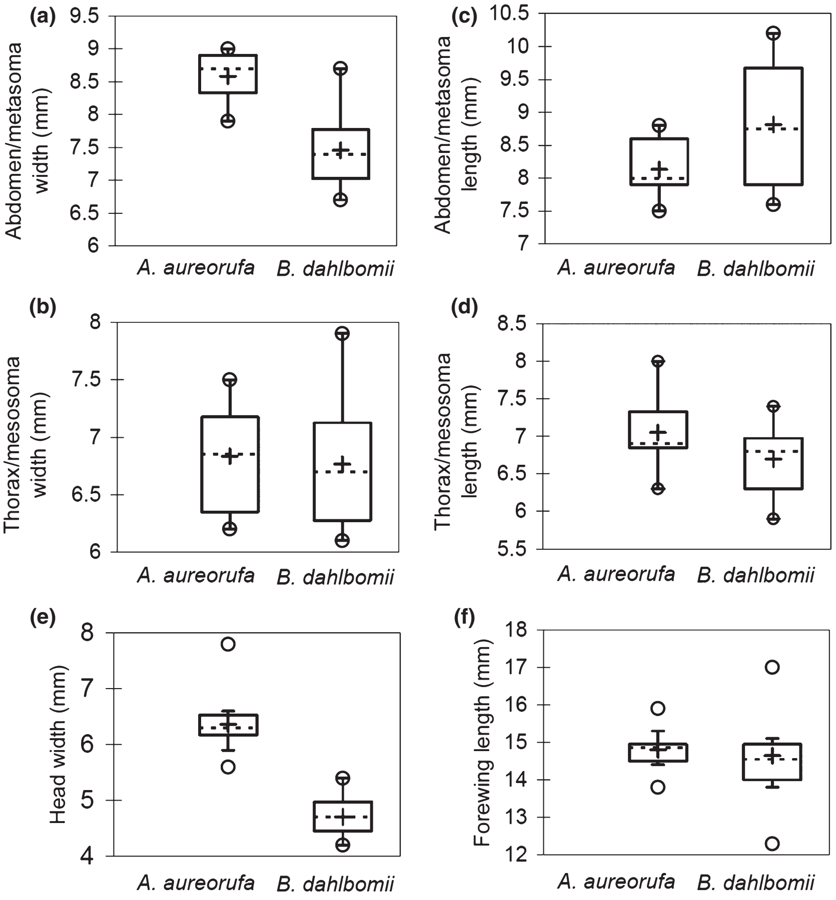

Fig. 2. Box-and-whisker diagrams showing medians (horizontal dashed lines), means (+), 1° and 3° quartile (horizontal continuous lines), and maximum and minimum values (○) for the six measured morphological variables in *Bombus dahlbomii* and *Aneriophora aureorufa*. Ends of the whiskers represent the lowest datum still within 1.5 × interquartile range of the lower quartile, and the highest datum still within 1.5 × interquartile range of the upper quartile. (a) abdomen/metasoma width; (b) abdomen/metasoma length; (c) thorax/mesosoma width; (d) thorax/mesosoma length; (e) head width; (f) forewing length.

[*B. dahlbomii*: 4.3 ± 0.4 (1.8–14.2) s, $n = 37$; *B. ruderatus*: 3.4 ± 0.5 (2–6) s, $n = 10$; *A. mellifera*: 6.5 ± 1 (2–15.5) s, $n = 23$] (Table 1). Statistical contrasts (Dunn-Sidak's modified significance threshold: $P = 0.017$) show significant differences between *A. aureorufa* and *B. dahlbomii* ($P < 0.0001$) and between *A. aureorufa* and *B. ruderatus* + *A. mellifera* (P < 0.0001), while *B. dahlbomii* and *B. ruderatus* + *A. mellifera* did not differ ($P = 0.59$) (Fig. 4).

There were only almost significant differences in the time spent flying between consecutive flowers among the four tested species [*A. aureorufa*: 3.0 ± 0.4 (2–8) s, $n = 14$; *B. dahlbomii*: 2.7 ± 0.2 (1–7) s, $n = 34$; *B. ruderatus*: 1.7 ± 0.2 (1–2) s, $n = 10$; *A. mellifera*: 2.4 ± 0.2 (1–4) s, $n = 15$] (Table 1 and Fig. 4).

Discussion

This is the first detailed study, as far as we know, of a syrphid fly mimicking a bumblebee species from the Neotropics. It is also the first study of Batesian mimicry for a syrphid fly in the genus *Aneriophora*, increasing the number from five (*Criorhina*, *Pocota*, *Blera*, *Lycastris*, *Hadromyia*) to six genera involved in bumblebee mimicry within the syrphid tribe Xylotini (=Milesiini) (subfamily Eristalinae) (Gabritschevsky, 1924). Thompson (1972) suggested that *Aneriophora* might be related to *Temnostoma* (a Holarctic group of hornet/wasp mimics), but currently *Aneriophora* is considered to be related to *Criorhina* (a genus of mainly bumblebee mimics, discussed in Katzourakis *et al.*, 2001). Relatively little information is available on the mimicry relationships within Xylotini. Among the putative models of xylotine syrphids, the only previously identified orange/brownish species is *B. muscorum* (L.), mimicked by the yellow/brownish *Criorhina* spp. (Gabritschevsky, 1924). Taxonomically, the species of *Bombus* which are models for xylotine syrphid flies span five different subgenera (*Bombus s. str.*, *Thoracobombus*, *Alpigenobombus*, *Melanobombus* and *Pyrobombus*) (Gabritschevsky, 1924;

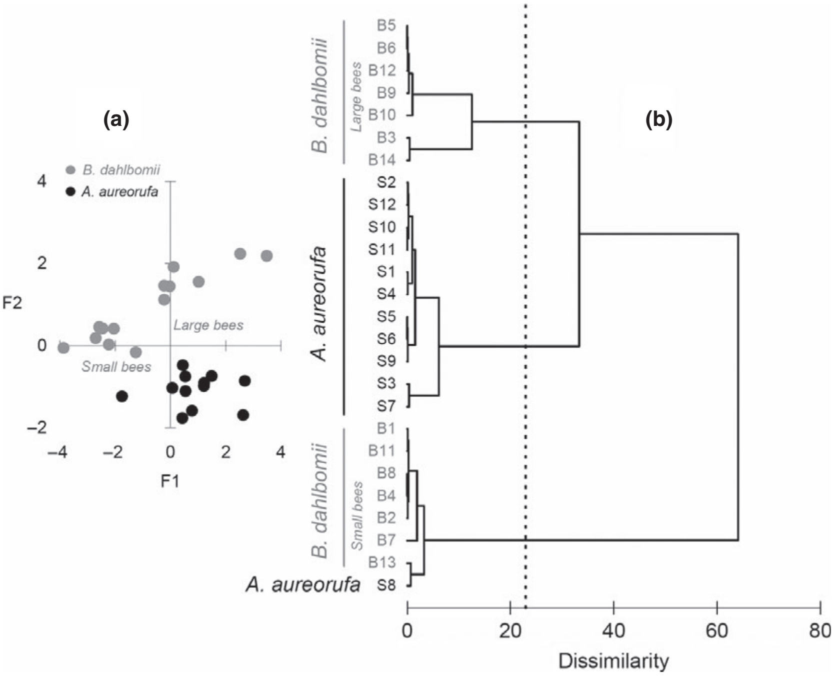

Fig. 3. (a) Scores along the first PC axis (F1, horizontal) plotted against those of the second PC axis (F2, vertical) from a Principal Component Analysis of six size-related morphological variables; notice how there is very little obvious separation along the first axis, but clear separation along the second; (b) dendrogram obtained with the cluster analysis based on F1 and F2 scores, showing the morphological relationships between individuals of *Bombus dahlbomii* and *Aneriophora aureorufa*; the dashed line in (b) is our chosen truncation that segregates three different clusters; notice how the syrphid flies segregate with some but not all of the bumblebees.

Table 1. Comparisons of flower-visiting times and between-visit times among taxa (*Aneriophora aureorufa*, *Bombus dahlbomii*, *B. ruderatus* and *Apis mellifera*) using ANOVA.

	Source	d.f.	Sum of squares	Mean squares	*F*	*P*
Time on flowers	Model	3	26.100	8.700	19.298	<0.0001
	Error	82	36.969	0.451		
	Corrected total	85	63.069			
Time between flowers	Model	3	1.297	0.432	2.587	0.060
	Error	69	11.530	0.167		
	Corrected total	72	12.827			

Howarth *et al.*, 2004); *Fervidobombus*, close to *Thoracobombus* (Williams *et al.*, 2008), is here reported for the first time as a xylotine model. South American bumblebee models have various colour patterns (see fig. 5 in Williams, 2007), and the all-orange pattern of *B. dahlbomii* appears to be relatively unusual even for bumblebees within Chile.

According to the morphological analysis, *A. aureorufa* is a very good visual mimic. First, colour patterns are very similar to those of the model. Second, a size similarity occurs, as revealed by the relatively weak difference in forewing length and mesosoma width. Such results agree with the general view that bumblebee-like syrphid flies are normally very accurate mimics (Gilbert, 2005), while in other cases of Batesian mimicry in the syrphids where the models are honeybees or wasps, the resemblance is often poor (Gilbert, 2005). The resemblance in size between drone flies (*Eristalis* spp.) and honeybees has often been invoked (van Brower & Brower, 1962, 1965; Heal, 1979, 1982; Holloway, 1993), but not really quantified. Our results also agree with the theory that while mimics are under constant selection pressure to improve their mimetic resemblance, the strength of selection depends on model palatability (Duncan & Sheppard, 1965): if the model is very noxious (e.g. hornets), then protection can be extended to less faithful mimics, while if models are only moderately noxious or merely unprofitable (e.g. bumblebees), a better visual mimicry should be the expected outcome (Gilbert, 2005).

Interestingly, it is possible that the syrphid flies resemble the larger workers more closely than smaller ones, although a great deal more data would be needed to verify this. The cluster analysis showed a clear segregation of two groups of workers (basically small and large), with syrphid flies closer to the cluster of ‘large workers’. Even just in the Syrphidae there are many cases where the mimics are polymorphic, with each morph resembling a different species of model, but it is very rare to find a

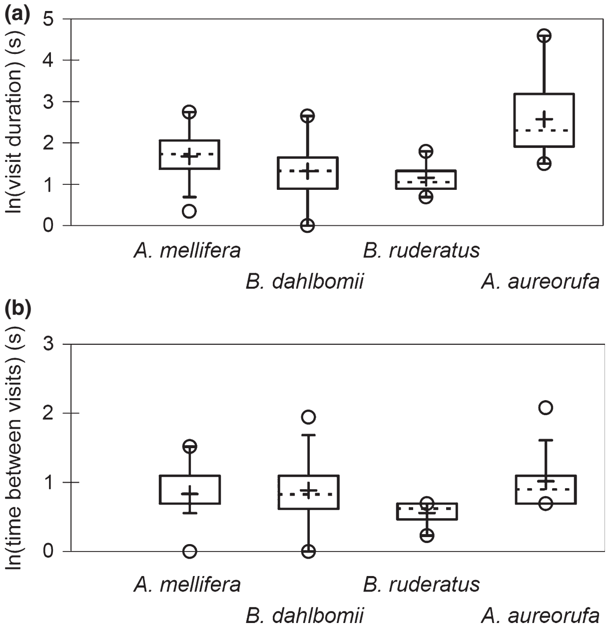

Fig. 4. Box-and-whisker diagrams showing medians (horizontal dashed lines), means (+), 1° and 3° quartile (horizontal continuous lines), and maximum and minimum values (○) for the time spent on flowers (a) and the time interval between subsequent flower visits (b) in *Bombus dahlbomii*, *Bombus ruderatus*, *Apis mellifera* and *Aneriophora aureorufa*. Ends of the whiskers represent the lowest datum still within 1.5 × interquartile range of the lower quartile, and the highest datum still within 1.5 × interquartile range of the upper quartile.

mimic that resembles only part of the population of the model species. In syrphids, only three examples are known to us: *Merodon velox* Loew is reported to have an all-black female morph *anathema* Paramonov (Sack, 1932: 331), which corresponds to the all-black bumblebee morphs of many species of bumblebee (Williams, 2007); *Criorhina quadriboscis* Lovett from the Pacific Northwest of the Nearctic very closely resembles the orange-metasomal tip morph of *B. flavifrons* Cresson (see plate 43 in Heinrich (1979)); and the large early-spring Palaearctic mimics such as *C. ranunculi* Panzer could reasonably be labelled as mimics of emerging queen bumblebees rather than workers. This phenomenon could be facilitated by the fact that, even within bumblebee colonies, workers in general differ greatly in size (Goulson, 2010). Because it is probable that the larger the model, the better the signal of noxiousness to predators, syrphid flies which evolve towards the large workers rather than the small ones will deter predators better. Alternatively, large mimics may evolve to resemble their models more closely simply because predator pressure is greater as they represent a better meal (Penney *et al.*, 2012).

The very good visual resemblance between *A. aureorufa* and *B. dahlbomii* is interesting also when considering that *Fervidobombus* would have arrived to New World (from the Old World Palaearctic, where *Bombus* probably originated about 25–47 mya) about 10–15 mya, with a subsequent south American speciation (including the origin of *B. dahlbomii*) estimated at about 7.5 mya (Hines, 2008). Thus, morphological resemblance of *A. aereorufa* towards *B. dahlbomii* in temperate South America may have evolved relatively rapidly compared to other syrphid-bumblebee systems in the temperate areas of the Northern hemisphere.

Contrary to morphology, we did not find any evidence for a behavioural component of mimicry, apart from the general model-like flight (as reported for other mimics: Wickler, 1968). Although the time spent flying between successive flower visits was similar among all the tested species, the time spent on flowers by *A. aureorufa* was clearly longer than that of any bee. This result contrasts with a previous study carried out on drone flies (Golding & Edmunds, 2000) where, on a range of plant species, the time drone flies spent on individual flowers and the time spent flying between them was more similar to honeybees than to other Hymenoptera and Diptera. It is possible that behavioural mimicry depends on the history of mimicry in the taxonomic group. Honeybee mimicry may be a very old phenomenon in syrphid flies, while mimicry of *Bombus* may have evolved only much later (see Howarth *et al.*, 2004). If this is the case, it is possible that behavioural resemblance has still not evolved in the more recent mimetic systems. Although the time spent on flowers was higher in syrphid flies than in all the other species, among the three bee species the honeybee spent the longest time on flowers. Thus, *A. aureorufa* seems to approach more the behaviour of the honeybee, an invasive alien, perhaps because of phylogenetic inertia.

We invoke this 'phylogenetic inertia' hypothesis because of the two other studies of behavioural mimicry in syrphid flies (Golding & Edmunds, 2000; Howarth *et al.*, 2004), both of which have found similarity to honeybee behaviour. Howarth *et al.* (2004) tested the prediction that the numerical abundance of syrphid mimics at each hour of the day is related to the numbers of their hymenopteran models flying at the same time in the same sites. Interestingly, apart from having found a positive correlation in many cases, they also reported that several eristaline flies showed correlations with honeybees even though some of them mimic wasps or bumblebees, and they suggested that perhaps this may be caused by phylogenetic inertia from a honeybee-mimicking ancestor. In support of this idea, Howarth *et al.* (2004) also found that in *C. berberina* (Fabr.) there was a similarity to the activity pattern of one of the two models, *B. pratorum* (L.), even though many of the flies belonged to the morph that actually mimicked a different species of bumblebee. It is possible that this hypothesis also applies to other components of behaviour, such as foraging behaviour on flowers. An alternative hypothesis is that behavioural mimicry is lacking in *A. aureorufa* because of the relatively recent arrival of *B. dahlbomii* in South America (Hines, 2008) (see also above). Further studies in other biogeographical regions, involving both morphological and behavioural analyses, together with a robust phylogeny, are necessary to understand more about the global evolution of Batesian mimicry in syrphid flies, and hence a proper assessment of the 'phylogenetic inertia' hypothesis.

Finally, the endemic distribution, the apparent plant specialisation, and the invasion of South America by alien bumblebees make it possible that *B. dahlbomii* and *A. aureorufa* are threatened species, at least in some parts of the austral American forests. For example, *B. dalbhomii* seems to prefer the cooler parts of Patagonia, and hence climate warming could negatively affect its populations; in addition, *B. dahlbomii* was observed to be less frequent in areas where the alien *B. ruderatus* was more abundant (Madjidian *et al*., 2008). As a consequence, exclusion of the model bee species from an area, either by climate warming or by competition, might in turn reduce the effectiveness of mimicry as a protection strategy for *A. aureorufa*.

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