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ORIGINAL ARTICLE

Müllerian mimetic radiation of *Delias* butterflies (Lepidoptera: Pieridae) in Bali and Timor

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Abstract

Mimicry rings are present among *Delias* butterflies, and those butterflies are also considered to be mimetic models of other lepidopteran insects; however, experimental evidence for their unpalatability to predators is limited. In Bali and Timor, a total of three mimicry rings of *Delias* species are present; particularly, male and female *D. lemoulti* join different rings in Timor. The present study examined the unpalatability of *Delias* in Bali and Timor to the caged avian predator *Pycnonotus aurigaster*. The birds ate eight *Delias* species in similar numbers, and ate the palatable butterfly *Mycalesis horsfieldii* much more frequently than *Delias* butterflies. The result suggests that the three mimicry rings of *Delias* species in Bali and Timor are Müllerian rather than Batesian. Based on previous findings on their phylogenetic relationships, the Müllerian mimicry rings of *Delias* in Bali and Timor are suggested to have emerged through the convergent evolution and phylogenetic constraints of wing color patterns. In the *D. hyparete* species group, mimetic radiation may have occurred between Bali and Timor.

Key words: Greater Sunda Islands, Indo-Pacific archipelago, learning, Lesser Sunda Islands, palatability, toxicity.

INTRODUCTION

Mimicry is both an old and new subject of evolutionary biology. When a prey animal with a warning (i.e. aposematic) color pattern is distasteful or toxic (i.e. unpalatable) to predators, they learn to avoid the aposematic prey based on their initial experience of its distastefulness or another adverse effect (Mallet & Joron 1999). When sympatric animal species share a warning color pattern, the animal community is referred to as a mimicry ring (Mallet & Gilbert 1995; Sherratt 2008). When members of a mimicry ring are unpalatable to predators, they share a mutualistic benefit by reducing the cost of being eaten for educating naive predators: these mimetic species are referred to as Müllerian co-mimics (Müllerian mimicry; Müller 1879; Wickler 1968; Mallet 1999; Ruxton *et al.* 2004; Sherratt 2008). However, when a member of a mimicry ring is palatable to predators, this member might have the parasitic benefit of reducing the predation risk at the expense of unpalatable members: this mimetic species is referred to as a Batesian mimic (Batesian mimicry; Bates 1862; Wickler 1968; but see also Honma *et al.* 2008 and Rowland *et al.* 2007 for an alternative view).

Butterflies show a diverse of mimicry, and thus, have been used as a model group in mimicry studies. The unpalatability of butterflies has been demonstrated or suggested in various taxa such as Nymphalidae, Papilionidae and Pieridae, in terms of the behavioral responses of predators to prey in the field or in cages (Brower 1957, 1958a,b,c; Platt *et al.* 1971; Pough & Brower 1977; Bowers 1980; Brower & Fink 1985; Chai 1986; Kingsolver 1987; Brower 1989; Ritland & Brower 1991; Pinheiro 1996, 2003; Lyytinen *et al.* 1999; Arias *et al.* 2016). Some butterflies have also been shown to possess toxic compounds in their body/

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wings (Rothschild *et al.* 1970; Bae *et al.* 2012). However, many apparently aposematic and supposedly mimetic model butterflies are still considered to be unpalatable without experimental evidence. Furthermore, empirical studies on Müllerian mimicry have so far been biased to Neotropical butterflies (Sherratt 2008).

The genus *Delias* Hübner, [1819] is widely distributed in the Australian and Oriental regions and has the most species in Pieridae (Talbot 1928; Yata 1981; Yagishita *et al.* 1993; Parsons 1998; Braby & Pierce 2007). The butterflies of most *Delias* species have brightly colored markings on the underside of their wings. This is reasonable because *Delias* butterflies rest on flowers, the ground and leaves with the wings folded together dorsally (personal observation by S. Morinaka). Some lepidopteran species outside of *Delias* have bright wing markings that resemble those of *Delias* (Wallace 1867a; Finn 1896; Fruhstorfer 1909; Dixey 1920; Yata 1981; Morinaka & Yata 1994; Yen *et al.* 2005). *Delias* butterflies mostly fly slowly in the field (Wallace 1867a; Yata 1981). Larvae of *Delias* species are gregarious (Braby & Lyonns 2003; Braby & Nishida 2010; and references therein). Based on these findings, butterfly researchers have speculated that *Delias* butterflies are unpalatable to predators and that bright wing markings are aposematic to predators (Wallace 1867a; Dixey 1920; Talbot 1928; Yata 1981; Parsons 1998; Orr 1999; Braby & Trueman 2006; Canfield & Pierce 2010; Joshi *et al.* 2017; Wee & Monteiro 2017). Canfield and Pierce (2010) proposed a hypothesis that some *Delias* species are a model of facultative mimicry in other pierid species. Furthermore, mimicry associations have been reported among some *Delias* species (Dixey 1920; Talbot 1928; Yata 1981; Müller *et al.* 2012).

Thus, *Delias* butterflies are potentially good model species for the study of aposematic signals and mimicry. Experimental evidence for the aposematic function of wing markings was recently obtained for *D. hyparete* (Linnaeus, 1758) in Singapore (Wee & Monteiro 2017). However, the palatability of *Delias* butterflies to predators currently remains unclear (Braby & Trueman 2006). Finn (1896) reported that the common babbler does not like to eat *D. eucharis* (Drury, 1773) in India, based on experiments using caged birds. Orr (1999) suggested that *D. argenthona* Fabricius, 1793 and *D. nigrina* (Fabricius, 1775) are distasteful to birds, based on field observations in Australia. Direct experimental evidence has not yet been obtained for the unpalatability of *Delias* butterflies. Previous studies presumed that mimetic associations among *Delias* species are Müllerian (Yata 1981); however, the nature of these mimetic associations has not been investigated in terms of Batesian or Müllerian mimicry.

Mimicry rings might have emerged through the convergent evolution of color patterns among distantly related species or evolutionary constraints on color patterns among closely related species (Brower 1994, 1996; Savage & Mullen 2009; Oliver & Prudic 2010; Ebel *et al.* 2015; Joshi *et al.* 2017; Moraes *et al.* 2017). As mimicry rings among *Delias* species often include closely related butterflies, it has not yet been clarified, based on phylogenetic relationships, whether mimetic associations emerged through phylogenetic constraint or convergent evolution.

The present study focused on *Delias* species in Bali and Timor. These two islands are located in the Indo-Australian archipelago, but in different zoogeographical regions: Bali is an island in the Greater Sunda Islands, the Oriental region, whereas Timor is an island in the Lesser Sunda Islands, Wallacea (Wallace 1867b; Michaux 2010; Lohman *et al.* 2011). In Bali and Timor, one and two mimicry rings of *Delias* butterflies occur: *D. oraia* Doherty, 1891/*D. sambawana* Rothschild, 1894/*D. belisama* Cramer, 1779 in Bali; *D. eileenae* Joicey and Talbot, 1926/*D. splendida* Rothschild, 1894/male *D. lemoulti* and *D. timorensis* Boisduval, 1836/female *D. lemoulti* in Timor (see Materials and Methods for details) (Dixey 1920; Talbot 1928; Turlin 1989). The mimicry rings of *Delias* in Bali and Timor are potentially good models for the study of the evolution of mimicry in butterflies.

The present study examined the palatability of *Delias* species in Bali and Timor to a captive bird, with the primary aim of assessing whether the *Delias* mimicry rings in Bali and Timor are Müllerian or Batesian. With the aid of previous phylogenetic findings on *Delias* (Müller *et al.* 2012; Morinaka *et al.* 2017), the authors also discuss the evolution of *Delias* mimicry in Bali and Timor.

MATERIALS AND METHODS

Mimicry rings in Bali and Timor

Dixey (1920) proposed that *D. oraia* and *D. sambawana* belong to a mimicry complex in Lombok, another island in the Indo-Australian archipelago. These two species co-occur in Bali, and comprise a mimicry complex together with another *Delias*, *D. belisama* (hereafter, Bali mimicry ring; Fig. 1). These three species co-occur in mountains in Bali; *D. oraia* is found at higher altitudes than *D. belisama* with an overlap (Morinaka 1988, 1996). Furthermore, *D. belisama* and *D. oraia* are considered to be unpalatable models of another pierid *Prioneris autothisbe* (Hübner, 1826) in Bali and Java (Morinaka & Yata 1994; Canfield & Pierce 2010).

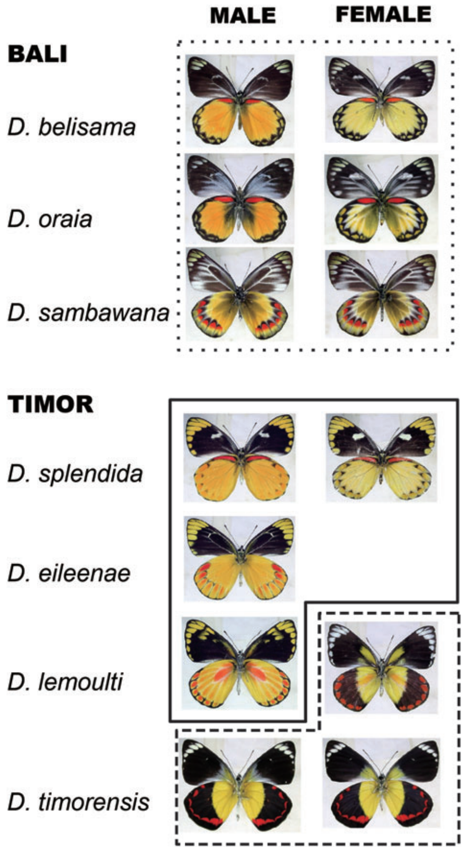

Figure 1 Mimicry rings of *Delias* butterflies in Bali and Timor. The underside of the wings is shown. Different types of line surround mimicry rings. Photographs were taken by S. Morinaka. No female *Delias eileenae* specimens are shown because S. Morinaka's collection includes only male specimens; however, the wing markings of females are similar to those of males.

In Timor, two mimicry rings of *Delias* are present. *Delias eileenae*, *D. splendida* and the males of *D. lemoulti* have very similar wing markings (Dixey 1920; Talbot 1928) (Timor mimicry triplet; Fig. 1). Furthermore, another pierid species in Timor, *Cepora laeta* (Hewitson, [1862]), is considered to be a mimic of the Timor mimicry triplet (Dixey 1920). However, the wing markings of *D. timorensis* and the females of *D. lemoulti* closely resemble each other (Turlin 1989) (Timor mimicry doublet; Fig. 1). *Delias lemoulti* is noteworthy in that the males and females mimic different *Delias* species. The *Delias* species in Timor are endemic except for *D. timorensis*; the two mimicry rings are unique to Timor.

Palatability assays

Palatability was examined in two series of assays. Fresh specimens of *D. belisama*, *D. oraia*, *D. sambawana*, *D. periboea* (Godart, 1819) and *Mycalesis horsfieldii* (Moore, [1892]) were used in palatability assay A. *Mycalesis horsfieldii* belongs to Satyrinae (Nymphalidae) and was used as a presumably palatable species. These butterflies were collected in Bali by local catchers, except for one butterfly of *D. periboea* in Lombok, and kept alive or nearly alive in folded paper at room temperature for 1–2 days.

Dried specimens of *D. lemoulti*, *D. eileenae*, *D. timorensis* and *D. splendida* in Timor and *D. periboea* and *D. belisama* in Bali were used in palatability assay B. *Delias periboea* and *D. belisama* were used in assays A and B, but as fresh and dried specimens, respectively; if the condition of butterfly (i.e. fresh/dried) affects the result of unpalatability assays in general, such an effect would be found for *D. periboea* and/or *D. belisama*. Butterflies were collected in Timor and Bali by local catchers and kept dried under room temperature with insect repellents for a few months to a few years. Before the assay, dried butterflies were exposed to air at room temperature for several days to reduce the residual amount of insect repellents.

The sooty-headed bulbul *Pycnonotus aurigaster* was obtained in Bali. Bulbuls generally consume various types of food, including insects, in the field. Experiments were undertaken in a shed in Bali. The birds were kept individually in cages made of wood and bamboo for approximately 2 months in order to acclimatize them to the captive environment (Fig. 2a). Every bird was fed commercially available mash meal for birds ad libitum, a piece of banana every 2 days and two crickets once a week. Fresh water was provided ad libitum and replaced every evening. Regarding bathing, birds were soused every morning using a sprinkling can. In the 2 weeks before palatability assays, each bird was trained every day to eat food that was stabbed at the tip of a bamboo piece. Specifically, a living cricket was stabbed at the tip of a bamboo stick and held near the beak of a bird, and then the bird was allowed to eat it. Crickets were given to birds repeatedly until they ceased eating.

On the days of the palatability assay, birds for assays were not fed until 14:00, at which time the assays were started. The birds used in the present study may have learned that some *Delias* butterflies are distasteful in the wild before being captured. Therefore, in order to eliminate the possible effects of wing markings on palatability assays, the wings of butterflies were removed with scissors just before the assay. The antennae were also removed. A butterfly body was stabbed at the tip of a bamboo piece and presented to a bird, as carried out in the training phase (Fig. 2b). When the bird

Figure 2 (a) Experimental cages housing *Pycnonotus aurigaster* hung in a shed. (b) *Pycnonotus aurigaster* fed a butterfly body stabbed at the tip of a bamboo stick in an experimental cage.

pecked and swallowed at least a part of the butterfly body, we recorded that the sample was eaten. This was iterated with single butterfly species until the bird did not eat an additional butterfly body within 5 min. The total number of butterflies of the species eaten by a single bird was used in analyses. Different assays used different individual birds; two to eight birds were used per single species of butterfly. After the assay, the life of some birds was observed for a maximum of 1 month. Living birds were released to the field after experiments.

Statistical analysis

Data were analyzed using R 3.2.1 (R Core Team 2015). For each of palatability assays, A and B, a generalized linear model was used in order to test for the palatability differences among butterfly species. A Poisson distribution was used as the error distribution. The log function was used as the link function. The dependent variable used in the models was the number of butterflies of the species eaten by a single bird. The butterfly species was used as the nominal independent variable. *P*-values were corrected for multiple comparisons by Tukey's method using the R package "multcomp" (Hothorn *et al.* 2008).

RESULTS

In palatability assay A, individual birds learned to reject any *Delias* species after experiencing 1–3 fresh bodies (Table 1). In contrast, single birds ate 14–34 bodies of *M. horsfieldii*, possibly up to satiation. Significant differences were observed in the number of butterflies eaten between *M. horsfieldii* and any *Delias* species, but not among *Delias* species (Table 2). Seven out of ten birds that ate *Delias* butterflies died within 1 month, whereas all the four birds that ate *M. horsfieldii* did not.

In assay B, 1–4 dried butterfly bodies were eaten for any *Delias* species (Table 3). The number of butterflies eaten was not significantly different among *Delias* species (Table 4). Two out of four birds that ate *D. lemoulti* died within 1 month, whereas the other two birds that ate *D. periboea* remained alive for 1 month after the assays.

Table 1 Number of fresh butterflies eaten by *Pycnonotus aurigaster* and the life of *P. aurigaster* for 1 month after feeding on butterflies (palatability assay A)

Species (locality)	Trial†	No. of butterflies eaten	Life of birds for 1 month
D. belisama (Bali)	1	1 Male	Not examined
	2	1 Male	Not examined
	3	1 Female	Not examined
	4	1 Male	Not examined
D. oraia (Bali)	1	2 Males	Died on day 10
	2	2 Males	Died on day 11
	3	2 Males	Alive
	4	3 Males	Alive
D. sambawana (Bali)	1	2 Males	Died on day 8
	2	3 Males	Died on day 11
	3	1 Males	Alive
	4	3 Males	Died on day 28
D. periboea (Bali)	1	1 Males	Died on day 10
(Lombok)	2	2 Males	Died on day 10
M. horsfieldii‡ (Bali)	1	14	Alive
	2	21	Alive
	3	27	Alive
	4	34	Alive

†Different individuals of *P. aurigaster* were used in different trials. ‡The sex of *Mycalesis horsfieldii* was not examined: this species has sexually monomorphic wing markings.

Table 2 Pairwise comparisons of palatability among butterfly species in palatability assay A

Species 1	Species 2	Estimate (SE)	z-value	Significance
D. belisama	*M. horsfieldii*	−3.18 (0.510)	−6.228	*
D. oraia	*M. horsfieldii*	−2.37 (0.349)	−6.790	*
D. periboea	*M. horsfieldii*	−2.77 (0.586)	−4.729	*
D. sambawana	*M. horsfieldii*	−2.37 (0.349)	−6.790	*
D. oraia	*D. belisama*	0.811 (0.601)	1.349	n. s.
D. periboea	*D. belisama*	0.406 (0.764)	0.531	n. s.
D. sambawana	*D. belisama*	0.811 (0.601)	1.349	n. s.
D. periboea	*D. oraia*	−0.406 (0.667)	−0.608	n. s.
D. sambawana	*D. oraia*	<0.001 (0.471)	0.000	n. s.
D. sambawana	*D. periboea*	0.406 (0.667)	0.608	n. s.

*P < 0.001. n. s., not significant; SE, standard error.

Table 3 Number of dried butterflies eaten by *Pycnonotus aurigaster* and the life of *P. aurigaster* for 1 month after feeding on butterflies (palatability assay B)

Species (locality)	Trial†	No. of butterflies eaten	Life of birds for 1 month
D. lemoulti (Timor)	1	1 Male	Not examined
	2	1 Male	Not examined
	3	1 Female	Not examined
	4	1 Female	Not examined
	5	2 Males	Alive
	6	2 Males	Died on day 9
	7	2 Males	Died on day 9
	8	2 Males	Alive
D. splendida (Timor)	1	1 Male	Not examined
	2	1 Male	Not examined
	3	2 Male	Not examined
	4	4 Male	Not examined
D. eileenae (Timor)	1	1 Male	Not examined
	2	1 Male	Not examined
	3	1 Male	Not examined
	4	1 Male	Not examined
D. timorensis (Timor)	1	1 Male	Not examined
	2	1 Male	Not examined
	3	1 Male	Not examined
	4	2 Males	Not examined
D. belisama (Bali)	1	1 Male	Not examined
	2	2 Males	Not examined
	3	1 Female	Not examined
	4	2 Males	Not examined
D. periboea (Bali)	1	3 Males	Alive
	2	3 Males	Alive

†Different individuals of *P. aurigaster* were used in different trials.

DISCUSSION

Most studies on butterfly mimicry have been focusing on the assumption that after a bird eats particular distasteful/toxic butterflies then becomes ill and/or vomits, the bird learns to avoid capturing the unpalatable butterfly using visual cues, such as the wing markings (e.g. Dell'aglio *et al.* 2016 and references therein). However, such a bird with the unpleasant experience presumably learns to also distinguish the unpalatable butterfly by the taste when seizing the prey in its beak (Brower & Fink 1985; Garcia *et al.* 1985). These are two types of the conditioned taste aversion (Garcia *et al.* 1985; Shimura *et al.* 1994). The present study relied on the latter type of conditioned taste aversion in order to behaviorally examine the unpalatability of *Delias* butterflies with the wings removed, as in previous studies (e.g. Ritland & Brower 1991; Arias *et al.* 2016); it was presumed that as the degree of unpalatability (i.e. distastefulness and/or toxicity) of the prey species is higher, the taste aversion learning is developed with fewer experiences (cf. Yamamoto *et al.* 1996).

In palatability assay A, *P. aurigaster* learned to reject the four *Delias* species in Bali after less experience than the supposedly palatable butterfly *M. horsfieldii*. This result suggests that the four *Delias* species in Bali are distasteful to avian predators, supporting the Bali mimicry ring (i.e. *D. oraia*/*D. belisama*/*D. sambawana*) functioning as Müllerian rather than Batesian mimicry.

Palatability assay B showed that *P. aurigaster* learned to reject *Delias* butterflies in Timor after only several samples. Assay B differed from assay A: assay B did not include *M. horsfieldii* and used dried, not fresh butterflies. We assume these differences did not strongly affect the experimental results obtained. This assumption is supported by the number of *Delias* butterflies eaten in assay B being similar to that in assay A: fresh and dried butterflies were similarly eaten in assays A and B, respectively, for *D. belisama* and *D. periboea*. Thus, assay B suggested that the *Delias* species in Timor are distasteful to avian predators at a similar level to those in Bali. This result supports the two mimicry rings in Timor being Müllerian rather than Batesian.

Table 4 Pairwise comparisons of palatability among butterfly species in palatability assay B

Species 1	Species 2	Estimate (SE)	z-value	Significance
D. eileenae	*D. belisama*	−0.406 (0.646)	−0.628	n. s.
D. lemoulti	*D. belisama*	<0.001 (0.500)	0.000	n. s.
D. periboea	*D. belisama*	0.693 (0.577)	1.201	n. s.
D. splendida	*D. belisama*	0.288 (0.540)	0.533	n. s.
D. timorensis	*D. belisama*	−0.182 (0.606)	−0.301	n. s.
D. lemoulti	*D. eileenae*	0.406 (0.577)	0.702	n. s.
D. periboea	*D. eileenae*	1.10 (0.646)	1.702	n. s.
D. splendida	*D. eileenae*	0.693 (0.612)	1.132	n. s.
D. timorensis	*D. eileenae*	0.223 (0.671)	0.333	n. s.
D. periboea	*D. lemoulti*	0.693 (0.500)	1.386	n. s.
D. splendida	*D. lemoulti*	0.288 (0.456)	0.630	n. s.
D. timorensis	*D. lemoulti*	−0.182 (0.532)	−0.343	n. s.
D. splendida	*D. periboea*	−0.406 (0.540)	−0.751	n. s.
D. timorensis	*D. periboea*	−0.876 (0.606)	−1.446	n. s.
D. timorensis	*D. splendida*	−0.470 (0.570)	−0.824	n. s.

n. s., not significant; SE, standard error.

Toxicity of *Delias*

Host plants of *Delias* butterflies include plants of families including toxic plants, such as mistletoe; however, the toxicity of *Delias* butterflies has remained unclear to date (Braby 2006; Braby & Nishida 2010; also see Braby 2012). In the present study, some *P. aurigaster* died 8–28 days after eating several bodies of *Delias*, and even one body in one bird. This result suggests the body, at least, of a *Delias* butterfly includes some toxic chemical(s) that slowly act against avian predators. The authors speculate that predatory birds that forage in a group may learn the unpalatability of or avoiding *Delias* by observing a member of the foraging group becoming sick after eating a *Delias* butterfly due to the toxin; the social learning of preferring/avoiding unpalatable prey has been experimentally shown, sometimes in relation to the warning color, in several bird species (Mason & Reidinger 1982; Fryday & Greig-Smith 1994; Johnston *et al.* 1998; Landová *et al.* 2017; Thorogood *et al.* 2017).

Orr (1999) found that some *Delias* butterflies in the Australian field had beak marks on their wings at a time of the year that many insectivorous young birds fledge in, suggesting that young predatory birds might learn the distastefulness of *Delias* in the field by eating even a small part of wings. This implies that *Delias* species are generally toxic and that a small part of the *Delias* wing includes a markedly smaller amount of the supposed toxin(s) than the whole body.

Bali mimicry rings

The Bali mimicry ring consists of *D. sambawana*, which phylogenetically belongs to the *D. hyparete* species group, and the other two species that phylogenetically belong to the *D. belisama* species group (Morinaka *et al.* 2017). Therefore, the convergent evolution of wing markings most likely contributed to the involvement of *D. sambawana* in the mimicry ring. However, *D. belisama* and *D. oraia* are closely related in the *D. belisama* species group (Yagishita *et al.* 1993; Müller *et al.* 2012). Therefore, it is reasonable that *D. oraia* and *D. belisama* have similar wing markings due to phylogenetic constraints. However, the wing color patterns of the Bali subspecies of the two species (i.e. *D. oraia bratana* and *D. belisama balina*) resemble each other so closely that Morinaka (1988, 1990) examined their distinctions in the morphology; however, they less resemble each other outside of Bali (personal observation by S. Morinaka). Therefore, convergent evolution may have made the Bali populations of the two species resemble each other more closely after they colonized Bali.

Timor mimicry rings

The Timor mimicry triplet is composed of members of different species groups (Yagishita *et al.* 1993; Müller *et al.* 2012; Morinaka *et al.* 2017). In the Timor mimicry doublet, *D. timorensis* and *D. lemoulti* belong to the *D. hyparete* and *D. nysa* (Fabricius, 1775) species groups, respectively (Yagishita *et al.* 1993; Müller *et al.* 2012; Morinaka *et al.* 2017). Therefore, both mimicry rings in Timor most likely involved the convergent evolution of wing color pattern.

Delias lemoulti is interesting in that males and females join different mimicry rings, demonstrating sexually dimorphic mimicry (Kunte 2009; dual sex-limited mimicry, Vane-Wright 1971; dual mimicry with simple sexual dimorphism, Vane-Wright 1975). Sexually dimorphic mimicry in butterflies has not been reported in Pieridae, but has been suggested in *Mydosama drusillodes* (Oberthür, 1894) (Nymphalidae: Satyrinae; Vane-Wright 1971, 1975) (formerly placed under the genus *Mycalesis*, Aduse-Poku *et al.* 2015), several species of genus *Elymnias* Hübner, 1818 (Nymphalidae: Stayrinae; Vane-Wright 1975; Wei *et al.* 2017) and *Papilio erostratus* Westwood, 1847 (Papilionidae; Kunte 2009). In addition, *P. troilus* Linnaeus, 1758 shows sexual dimorphism in its wing color pattern and mimics another swallowtail *Battus philenor* (Linnaeus, 1771), which is sexually dimorphic (Kunte 2009). Although *D. lemoulti* joins sexually dimorphic Müllerian mimicry, the others are considered to join sexually dimorphic Batesian mimicry. The evolutionary trajectory among sexually dimorphic and other forms of mimicry in butterflies currently remains unclear (Kunte 2009).

Mimicry evolution in the *D. hyparete* group

As all mimicry rings in Bali and Timor include single members of the *D. hyparete* species group (*D. eileenae* in the Timor triplet, *D. timorensis* in the Timor doublet and *D. sambawana* in the Bali triplet), how mimicry evolved in this group in Bali and Timor attracts interest. The authors previously reported phylogenetic relationships between and within species of this group (Morinaka *et al.* 2017).

Delias eileenae in the Timor triplet and *D. sambawana* in the Bali mimicry ring are sister species. *Delias eileenae* is endemic to Timor, whereas *D. sambawana* occurs in Bali and the western part of the Lesser Sunda Islands, but not in Timor. Therefore, the ancestral species of this pair colonized either Timor or Bali from the other island across Wallace's Line, and descendants of the colonizer appear to have transferred from the original to another mimicry ring in the new habitat. This historical dispersal was previously estimated to have occurred <1 million years ago (Ma) (see fig. 4 in Morinaka *et al.* 2017), after the emergence of Timor ca. 2 Ma (Hall 2002; Lohman *et al.* 2011). This may reflect mimetic radiation (otherwise, mimetic diversification), in which a species diverges/radiates to mimic different model species in different geographical areas (Mallet & Joron 1999; Symula *et al.* 2001; Sanders *et al.* 2006; Hines *et al.* 2011). *Delias timorensis* in Timor is phylogenetically distant from *D. eileenae* and *D. sambawana* in the species group (Morinaka *et al.* 2017). This species is distributed not only in Timor but also in the other islands in the eastern part of Lesser Sunda, whereas *D. lemoulti* is endemic to Timor. Therefore, *D. timorensis* most likely did not transfer mimicry rings in Timor; it appears to have gained its wing color pattern without adaptive evolution, namely, *D. lemoulti* females evolved to mimic *D. timorensis*.

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