

# FACULTATIVE MIMICRY? THE EVOLUTIONARY SIGNIFICANCE OF SEASONAL FORMS IN SEVERAL INDO-AUSTRALIAN BUTTERFLIES IN THE FAMILY PIERIDAE

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**Abstract-** Several Asian pierid butterflies exhibit a pattern of phenotypic plasticity whereby the wing surfaces are more melanized in the wet season than in the dry season. The wet season in the Indo-Australian regions where these species occur is warmer, so this pattern cannot be explained as an adaptation for thermoregulation. We propose an alternative hypothesis of facultative mimicry to explain this pattern. Species in the aposematic pierid genus *Delias* are widespread through Indo-Australia, and feed on host plants that are assumed to be toxic. The wet season forms of pierid species such as *Appias lyncida*, *Prioneris thestylis* and *Cepora nerissa* have darkened wing patterns that make them likely mimics of *Delias* species. Other species such as *Ixias pyrene* also have a wet season pattern that may benefit from its resemblance to *Delias* species. This hypothesis could be tested with experiments on the differential success of the seasonal forms under varying conditions. Facultative mimicry may represent a previously undocumented means by which insects can adjust their participation in mimetic relationships by using cues from their environment.

**Key words:** phenotypic plasticity, polyphenism, Pieridae, dry season, wet season, mimicry, crypsis, visual selection, adaptation

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## INTRODUCTION

Seasonality has had important consequences in the evolution of Lepidoptera. Across seasons, sequential generations experience many fluctuations in both abiotic aspects of the environment such as temperature and humidity, and biotic ones in terms of predation and parasitism. These changes can alter the phenotypic requirements for success under particular conditions. The adult stage of lepidopterans rarely spans multiple seasons, and different characters may be optimal under different seasonal conditions.

Phenotypic plasticity (or simply “plasticity”) refers to how the phenotype of an organism changes in response to environmental cues. In the case of adult Lepidoptera, a variety of characters including overall size and the presence or absence of wings are phenotypically plastic (e.g. Kimura and Masaki, 1977; Boppré and Schneider, 1985). However, the majority of plasticity is expressed in wing coloration in groups such as Geometridae (Ferguson, 1985), Sphingidae (Pittaway, 1993), Saturniidae (Janzen, 1984), and all families of skippers and butterflies (Talbot, 1939; Shapiro, 1976; Bascombe *et al.*, 1999; Braby, 2000). The underlying mechanisms and environmental cues that control phenotypic plasticity in wing patterns are documented in several model species such as *Araschnia levana* (Koch and Buckmann, 1987; Windig and Lammar, 1999) and *Bicyclus anynana* (Monteiro *et al.*, 1994; Brakefield *et al.*, 1998), and studies of the evolutionary significance of this variation have focused on nymphalids and pierids.

The adaptive value of seasonal plasticity was explored in the nymphalid subfamily Satyrinae by Brakefield and Larsen (1984). Building on a model developed to account for the differences between eyespots in males and females of *Maniola jurtina* (Brakefield, 1984), Brakefield and Larsen suggest that the seasonal fluctuation in eyespots of some tropical nymphalids is the result of a balance between selection for cryptic and anti-predator phenotypes. In tropical and subtropical regions, seasons are subject to less extreme fluctuations in temperature than temperate zones, but many areas experience pronounced wet and dry seasons. Butterflies in these regions exhibit phenotypic

plasticity where wet season conditions cause the development of pronounced ocelli on the ventral hind wing (VHW), and dry season conditions create a cryptic pattern with reduced or absent ocelli on the VHW (Brakefield and Larsen, 1984). These authors argue that this seasonal variation reflects a balance between anti-predator patterns in the wet season when adults are active and vulnerable to a host of visually searching predators, and cryptic patterns in the dry season when adults are much less active and susceptible to predators that are more likely to be browsers (Brakefield and Larsen, 1984). A similar phenomenon exists in *Bicyclus anynana*, and recent experiments using bird predators showed that the cryptic forms of this species are attacked less in dry season conditions than in wet, and that the form with eyespots on the VHW are attacked less by naïve birds (Lyytinen *et al.*, 2004). Research on sexual selection and eyespot characteristics in *B. anynana* has further shown that mate choice can play an important additional role in shaping seasonal forms (Costanzo and Monteiro, 2007). The theory that butterfly eyespots provide protection from visually searching predators has recently gained more rigorous empirical support (Vallin *et al.*, 2005).

The adaptive value of phenotypic plasticity in wing color has also been tested in the Pieridae. Extensive experimental work suggests that *Colias* and *Pieris* species use seasonal differences in wing coloration as a mechanism for thermoregulation (discussion in Kingsolver, 1987). In order to fly in cool conditions, many Lepidoptera need to raise their body temperature above ambient temperatures, and many diurnal species do this by basking in the sun. The wing surface that absorbs solar radiation varies among taxa, and documented strategies include absorbance on the ventral hindwing (VHW) (lateral absorbance), absorbance on the dorsal wing (DW) (dorsal absorbance) and absorbance of radiation reflected off of the wings onto the wing bases (dorsal reflectance) (Dennis, 1993). Many of the *Colias* species in North America have populations that differ in the pigmentation of the ventral hindwing (VHW) across geographic locations (Watt, 1968), and some species, such as *C. eurytheme*, vary seasonally (Watt, 1969). Species in the genus *Colias* bask with their wings closed above their thorax and use lateral absorbance to raise

the temperature of their body; the VHW is therefore the area in which wing pigmentation has a major effect on thermoregulation (Watt, 1969; Hoffmann, 1973; Hoffman, 1978; Kingsolver and Watt, 1983). At low temperatures, individuals orient themselves perpendicular to the sun, whereas at high temperatures they rest parallel to the sun's rays to minimize absorbance and avoid overheating (Watt, 1968). In *Pieris*, individuals bask with their wings partially open, and absorb energy by reflectance basking, where the sun's rays are reflected from the outer parts of the wing to the area near the body (Kingsolver, 1987). In *Pontia occidentalis*, the amount of melanin varies in basal areas on the dorsal forewing (DFW) and dorsal hindwing (DHW) and is typically determined by environmental cues (Kingsolver, 1995b; Kingsolver and Wiernasz, 1991).

Melanin in the VHW of pierines is also affected by seasons (Shapiro, 1976). Field experiments provide strong evidence that the seasonal differences in *P. occidentalis* pigmentation have fitness consequences (Kingsolver, 1995a; Kingsolver, 1996). These studies suggest that thermoregulation is an important factor driving the evolution of pierid wing patterns and coloration. Thus under cooler conditions, adaptations for thermoregulation include: (1) increased melanin on the VHW in coliadines and pierines, (2) increased melanin on the basal regions of the DFW and DHW of pierines, and (3) decreased melanin on the medial DFW and DHW in pierines (to facilitate reflectance basking).

#### EXCEPTIONS TO THE HYPOTHESIS OF THERMOREGULATION

Although thermoregulation provides an explanation of the adaptive value of the seasonal wing plasticity seen in temperate pierids, it is unlikely to account for all of the pierid wing plasticity observed in tropical and subtropical taxa. Tropical and subtropical pierids exhibit a variety of phenotypic responses to seasons on different areas of the wings (Table 1). In some taxa, phenotypic variation is consistent with a hypothesis of thermoregulation. For example, the Australasian coliadines *Eurema laeta* and *Eurema smilax* have darker VHW markings in the dry season (when it is cooler) that may make them both more cryptic and aid in thermoregulation (Jones *et al.*, 1985; Jones, 1992), and a similar pattern is found in several *Eurema* species in the southeastern United States and Neotropics (Daniels, 1995).

However, many other taxa, such as *Appias lyncida*, *Prioneris thestylis* and *Cepora nerissa* have markings that are more melanized on the dorsal and ventral surfaces of the wings in the wet season form (WSF), when the temperatures are warmer, and are less melanized on these surfaces in the dry season when it is cooler (Fig. 1). If this plasticity were adaptive for thermoregulation, the opposite pattern of melanization would be predicted. Other species, such as the coliadine *Catopsilia pyranthe*, has a WSF with more extensive melanization on the dorsal wing margins and bases in the wet season when compared with the dry season form (DSF), and this is also inconsistent with a thermoregulatory explanation because coliadines bask with their wings closed. Many tropical pierids exhibit plasticity inconsistent with a thermoregulatory function and thus alternative explanations for their phenotypic plasticity must exist.

#### PROPOSAL OF A NEW HYPOTHESIS: FACULTATIVE MIMICRY

We propose that facultative participation in mimetic relationships provides a likely alternative explanation for the adaptive value of certain examples of phenotypic plasticity. The wing patterns of lepidopterans encode signals that are perceived by potential predators. The way in which species exploit these systems with dishonest and/or honest signals has been of constant interest to biologists since they were first described by Bates (1862) and Müller (1878). Exploitation of the communication between distasteful prey and predators has become a model for the study of natural selection, and many theoretical and experimental aspects of mimicry are still being developed (Mallet and Joron, 1999). Batesian mimicry occurs when a relatively palatable species evolves a resemblance to an unpalatable species; this relationship between mimic and model is negatively frequency dependent. In Müllerian mimicry, unpalatable species may converge on a common pattern, thereby sharing the cost of educating predators. Two of the best studied examples of mimicry in butterflies are the sex-limited mimicry in *Papilio dardanus* (Clarke and Sheppard, 1960; Nijhout, 1991) and the coevolved races of *Heliconius erato* and *H. melpomene* (Turner, 1981; Mallet and Gilbert, 1995). In these systems, species exhibit several genetically determined forms favored by selection to resemble models present in various geographic locations (Wallace, 1865, 1889; Kunte, 2008). For example, the sex-limited mimicry in *Papilio dardanus* exhibits female forms that mimic different distasteful models across its African range (Nijhout, 1991). In these systems, each individual is genetically determined to resemble (with greater or lesser accuracy) a particular model, and selective forces from the environment have honed these phenotypes.

The Indo-Australian genus *Delias* (Hübner) is a widespread group of approximately 200 species distributed from China and India through southeast Asia and Indonesia to Australia (Braby and Pierce, 2007; Braby *et al.*, 2007). These species are generally brightly colored (see Fig. 1), feed as larvae on mistletoe species (Loranthaceae) as well as plants in the Viscaceae and Santalaceae (Braby, 2006), and are thought to sequester toxic compounds that make them distasteful to predators (Brower, 1984; Orr, 1999). Although this toxicity has not been established experimentally (Braby and Trueman, 2006), we assume that many *Delias* species are in fact toxic models. Other species of pierids have a striking resemblance to *Delias* species, and have often been considered likely candidates for Batesian mimicry (see Table 2), although some have called these relationships into question (Corbet and Pendlebury, 1992). However, the black wing coloration, marginal spots, and the heavily darkened veins (especially on the VHW) characteristic of *Delias* species are also displayed by other sympatric pierid species. Even if mimics are not perfect, studies of other taxa such as syrphid flies have indicated that imperfect mimics can benefit from resembling an aposematic model (Edmunds, 2000; Holloway *et al.*, 2002). Given the striking similarities, it seems likely that *Delias* serves as a model for a number of other pierid species.

Assuming that palatable butterflies sometimes mimic distasteful *Delias* models, we argue that facultative participation in mimetic relationships can account for some of the seasonal plasticity observed in pierids in the northern part of the Indo-Australian

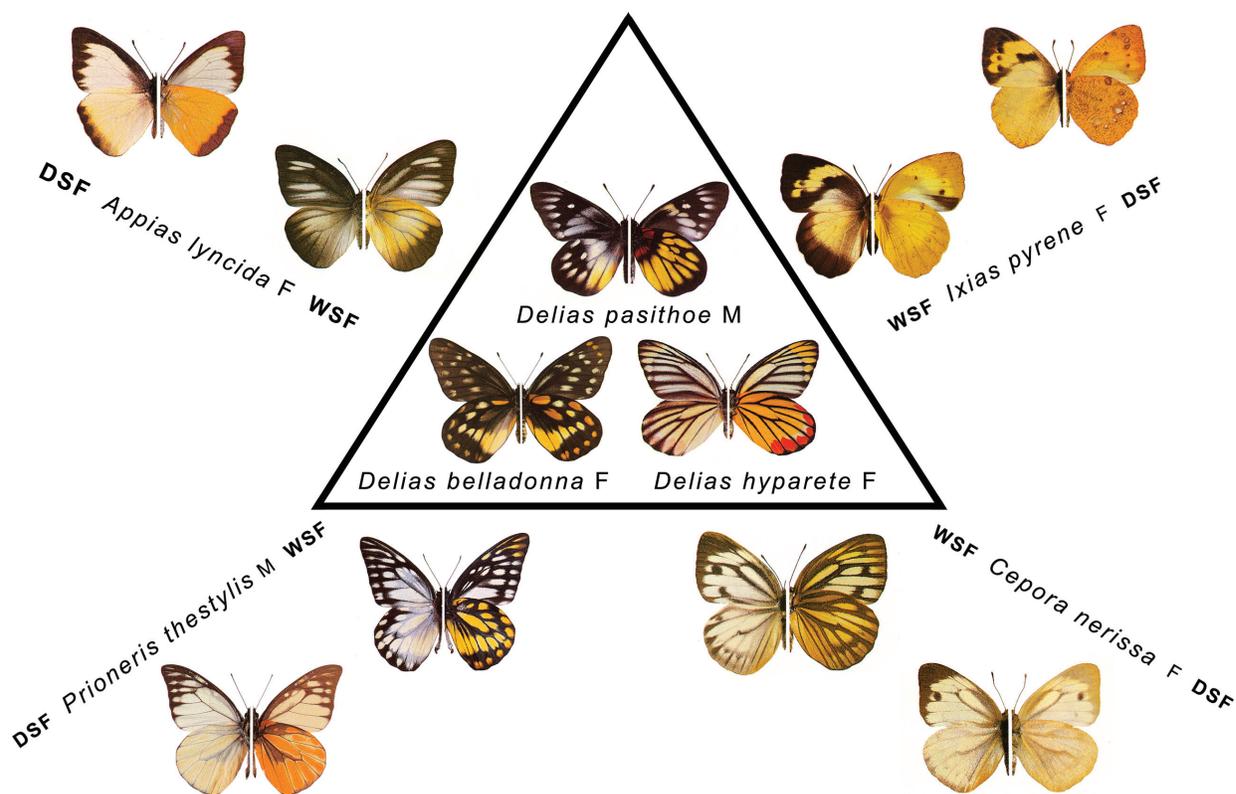


Fig. 1. Several *Delias* species, with the wet and dry season forms of four possible *Delias* mimics. M = male; F = female. Butterfly images reprinted from *The Butterflies of Hong Kong*, © Bascombe, M. J., Johnston, G. and F. S. Bascombe 1999, with permission of Elsevier.

region. This argument extends Brakefield and Larsen's (1984) cryptic balance hypothesis by proposing that significantly different selection pressures in the wet and dry seasons have selected for seasonal production of warning coloration. In the case of the north Indo-Australian pierids, the start of the wet season brings greater lepidopteran activity, higher temperatures and the start of the breeding season of resident birds (Kai and Corlett, 2002). Higher levels of temperature and activity, along with more active foraging of resident birds, leads to concomitant changes in selection pressures on butterflies. In the dry season, resident birds are not breeding and have lower nutrient needs. The dry season also brings lower temperatures, lower levels of activity for butterflies, and different suites of visually searching predators. In Hong Kong, for example, the influx of migratory birds in the dry season (McClure, 1998; Carey *et al.*, 2001) alters the predatory landscape.

Multiple species often participate in Müllerian mimicry rings, and common elements of the *Delias* wing pattern may provide some level of protection for mimics. Although the species we discuss below are all sympatric with *Delias* species, a particular mimetic interaction may involve one or more model species. We have created range maps (Figs. 2-5) for each potential mimic species and its likely model from distribution data in the literature (Yata, 1985; Corbet and Pendlebury, 1992; Bascombe *et al.*, 1999; Ek-Amnuay, 2006). We will discuss these candidates for this novel plastic mimetic strategy individually (refer to Fig. 1 for color images).

#### CANDIDATES FOR FACULTATIVE MIMICRY

We have identified four species from Table 1 as good candidates for facultative mimicry. These species are *Appias lyncida*, *Prioneris thestylis*, *Cepora nerissa* and *Ixias pyrene*. The first three of these species exhibit darker coloration on all three wing areas in the wet season; *Ixias pyrene* has darker coloration on the dorsal surface in the wet season, but does not show similar darkening on the VHW. Although wet and dry season temperatures vary across geographic locations, the temperatures across the northern range of these species are generally cooler in the dry season and warmer in the wet season (*e.g.* Hong Kong).

##### *Appias lyncida*

*Appias lyncida* is widespread throughout Sri Lanka, southern India, Indo-China, Taiwan, through the Malay Peninsula to Sumatra, Java and Borneo. In the dry season, both males and females have a blackish-brown marginal border on both the dorsal and ventral wing surfaces. In the wet season, however, there is marked sexual dimorphism, with the female being heavily marked with brownish-black throughout the dorsal surface. The ventral surface has extended marginal borders and thickened veins. The male WSF has slightly thickened black borders, but is not nearly as darkened as the female. The brownish-black dorsal surface and the DHW with a wide blackish marginal border and thickened veins against a yellow ground color of the *A. lyncida* female bear a significant resemblance to species of *Delias* such as *D. pasithoe* (see Fig. 1) and the ranges have significant overlap

(Fig. 2). The DSF female is very similar to the male (Bascombe *et al.*, 1999) with its narrow blackish marginal borders and extended white and yellow areas, and resemble a common pierid pattern of yellow or white wings with a black border. Several other species of *Appias* (*A. libythea*, *A. albina*, and *A. indra*) also exhibit darker wing coloration in the wet season in the northern parts of their ranges (Yato, 1985; Corbet and Pendlebury, 1992).

#### *Prioneris thestylis*

The resemblance between *Prioneris* and *Delias* species was noted by Wallace in 1867, and numerous authors have since remarked on the similarity between *P. thestylis* and *Delias* species, especially *D. belladonna* (Talbot, 1939; Yato, 1985; Corbet and Pendlebury, 1992; Bascombe *et al.*, 1999). The ranges of these two species show significant overlap (Fig. 3). The dorsal surface of the WSF is white with black margins that contain white post-cellular spots. The ventral surface is darker, with more extensive black regions, and the VHW ground color is yellow. In the DSF of both sexes, the black markings are much reduced (Talbot 1939; Bascombe *et al.*, 1999). This reduction in markings in the DSF changes the appearance of the wing, especially the VHW, to the point where cells are no longer ringed with black, and instead the wings appear much more like the VHW of the DSF *A. lycinda*. The overall effect of this seasonal change causes the DSF to be an unlikely mimic of *Delias* species, whereas the WSF shows striking similarity (Fig. 1).

#### *Cepora nerissa*

The genus *Cepora* has approximately 20 species throughout the Indo-Australian region, and these species are generally highly variable with a large number of subspecies and races described with different color patterns (D'Abrera, 1982). Throughout North Vietnam, northern Laos and southern China, *C. nerissa* individuals on the wing in the wet season have darkened veins and a blackish apex on the dorsal surface, with the veins more heavily darkened on the ventral surface, and more extensive in females than males. In the DSF, the wings are much paler with the black markings reduced on the dorsal surface and virtually absent on the ventral surface left with a creamy ground color (Talbot, 1939; D'Abrera, 1982; Yato, 1985; Bascombe *et al.*, 1999). Although the WSF and DSF of *C. nerissa* show significant overlap in appearance, the difference in pattern, especially of the VHW is marked. The pattern of darkened veins of the WSF matches the general pattern on the VHW of many *Delias* species, and it is sympatric through most of its range with the very similar *Delias hyparete* (Fig. 4). Alternatively, the VHW of the DSF has a homogeneous appearance that is likely to be cryptic against the leaves and foliage of the dry season, and it does not exhibit a similar wing pattern to *D. hyparete*.

#### *Ixias pyrene*

*Ixias pyrene* is distributed across India and southern China south to the Malay Peninsula. In this species, the VHW pattern is pale yellow in the wet season, and is darker with brown-bordered white spots in the dry season. The VHW of the DSF is similar to the pattern of many other pierid species that are considered cryptic, but the VHW of the WSF does not have a pattern that is clearly cryptic or mimetic. The DHW, however, displays the same pattern of plasticity that exists in the other pierids with the increased black coloration in the WSF. The WSF has a broad marginal black band on the DHW, whereas the DHW of the DSF

does not have a band and is pale yellow. This pattern on the dorsal surface of wider marginal bands may also be selected for in the context of mimicry. *Ixias pyrene* individuals may not be mimetic while at rest, but may get some benefit from the *Delias*-like coloration while on the wing with sympatric species (Fig. 5) such as *D. pasithoe* (see Fig. 1).

## DISCUSSION

A clear pattern of phenotypic plasticity in some pierid butterflies has not been explained in terms of its evolutionary significance. The increased wing melanization of the wings for wet season forms cannot be explained as a thermoregulatory adaptation to the warmer season in tropical and subtropical regions, and here we suggest that this pattern may be explained at least partly by facultative participation in mimicry rings. An alternative hypothesis is that the sexual dimorphism observed in seasonal forms of *A. lycinda* and *C. nerissa* is caused by sexual selection operating differently in the wet and dry seasons, but we think this unlikely since the VHW has broadly darkened veins in the wet season, and the patterns have a striking resemblance to the VHW pattern of *Delias* species. In the dry season, these species have greatly reduced darkening of the VHW, and we suggest that they bow out of the mimetic relationship in the dry season. Cool temperatures and dry conditions reduce the activity of a variety of butterflies (Brakefield and Larsen, 1984, and references therein). The dry season heralds a different set of avian predators that consist of a large number of migratory species that descend into subtropical Asia during the dry season, and then head to more northern regions for breeding during the wet season. Resident bird species begin their breeding season at the start of the wet season and therefore have higher nutritional requirements than they do in the dry season. We propose that selection for mimicry may be stronger in the wet season due to changes in visually searching predators during this time.

In the dry season, selection may favor either crypsis or forms that resemble a common pierid pattern. The stress of the dry season may also select for conservation of energy and reduce the production of melanin, a process that can be energetically expensive to lepidopterans (Talloen *et al.*, 2004). It is possible that selection on the intensity of the aposematic pattern exhibited by *Delias* species is stronger in the wet season due to the increased activity of models and mimics, and also a different guild of visually searching predators. Some candidate model species, such as *Delias hyparete*, also show darkened pigmentation in the wet season (Bascombe *et al.*, 1999), through a process that may also be the result of selection for a stronger aposematic pattern in the wet season.

This striking pattern of phenotypic plasticity in wing coloration is highly suggestive of a situation where participation in a mimicry ring is adaptive in one season but not in another. Genetically different populations of species are known to participate in geographically diverse mimetic relationships. Some insects also have aposematic coloration that is facultative (Sword, 2002). However, to our knowledge, this is the first time that facultative participation in mimicry rings has been suggested. Other variation in Lepidoptera also presents possible examples of facultative mimicry. For example, many lepidopteran larvae such as *Acrionicta oblinita* (Noctuidae) and *Hyles gallii* (Sphingidae) and *Lycia ypsilon* (Geometridae) (see images in Wagner, 2005) exhibit several color forms, only some

Table 1. Relative amounts of wing melanization on Nearctic and Indo-Australian pierids when entering the warm season (the wet season or summer). A “+” indicates that a wing region is darker in the warmer season, where a “-“ means the wing surface is lighter in the warm season.

Taxon	Subfamily	sex	DW dis	DW prox	VHW
<b>Nearctic</b>					
<i>Pontia occidentalis</i>	Pierinae	M/F	-/-	-/-	-/-
<i>Colias eurytheme</i>	Coliadinae	M/F	+/+	-/-	-/-
<b>Indo-Australian</b>					
<i>Catopsilia pyranthe</i>	Coliadinae	M/F	+/+	0/+	-/-
<i>Eurema brigitta</i>	Coliadinae	M/F	0/0	0/0	-/-
<i>Eurema laeta</i>	Coliadinae	M/F	0/0	0/0	-/-
<i>Pieris rapae</i>	Pierinae	M/F	-/-	-/-	-/-
<i>Appias lycida</i>	Pierinae	F	+	+	+
<i>Delias hyparete</i>	Pierinae	F	+	+	0
<i>Appias albina</i>	Pierinae	M/F	+/+	+/+	+/+
<i>Cepora nerissa</i>	Pierinae	M/F	+/+	+/+	+/+
<i>Ixias pyrene</i>	Pierinae	M/F	+/+	+/+	-/-
<i>Prioneris thestylis</i>	Pierinae	M/F	+/+	+/+	+/+
<i>Hebomoia glaucippe</i>	Pierinae	M/F	0/+	0/0	-/-

Table 2. Proposed mimetic relationships involving the pierid genus *Delias*.

Model	Possible Mimics	Type	Region	Refs.
<i>Delias belladonna</i>	<i>Prioneris thestylis</i>	Batesian	N. India, N. Burma, China	Dixey 1920; Talbot, 1928-37
<i>Delias belisama</i>	<i>Prioneris autothisbe</i>	Batesian	Indonesia	Morinaka and Yata, 1994
<i>Delias singapura</i>	<i>Prioneris cornelia</i>	Batesian	Borneo	Talbot, 1928-37
<i>Delias blanca</i>	<i>Ixias pyrene</i> <i>Appias cardena</i>	Batesian	Borneo	Talbot, 1928-37; Yato 1985
<i>Delias nigrina</i>	<i>Mynes geoffroyi</i>	Batesian	Eastern Australia	Orr 1999
<i>Delias</i> sp.	<i>Cepora</i> sp.	Batesian or weak Müllerian	New Guinea, Indonesia, Malaysia	Yato, 1985; Orr 1999
<i>Delias nigrina</i> ; <i>D. argenthona</i> ; <i>D. harpalyce</i> ; <i>D. mysis</i> ; <i>D. aganippe</i> ; <i>D. aruna</i> ; <i>Mynes geoffroyi</i>		Müllerian	Australia	Kitching, 1981 (but see Orr, 1999 and Braby, 2000 for alternative hypothesis)

of which are likely to act as warning coloration. If this variation is the result of environmental cues (such as host plant cues) it is possible that these larvae could facultatively exhibit mimetic forms. Although the nature of this larval variation has not been studied, it warrants consideration in the context of facultative mimicry.

Thorough tests of this hypothesis of facultative mimicry in pierids are needed. Given the possibility of rearing the two different forms simultaneously under artificial conditions, survivorship of two seasonal forms could be compared and predator damage assessed by mark-release-recapture experiments. Reciprocal experiments examining mate preferences of dry and wet season forms could also be conducted. These types of experiments could be done in locations with and without the presence of *Delias* models. If these experiments support the hypothesis of facultative mimicry, this will demonstrate a new way in which phenotypic plasticity has evolved in butterflies to evade predation and enhance survival.

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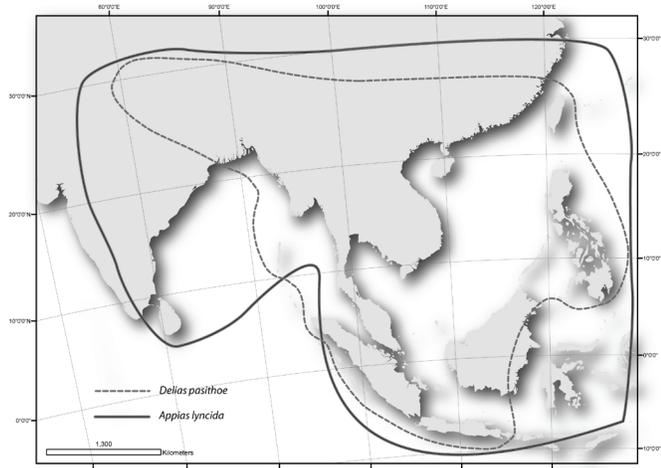


Fig. 2. Overlapping ranges of *Delias pasithoe* and *Appias lycinda*.

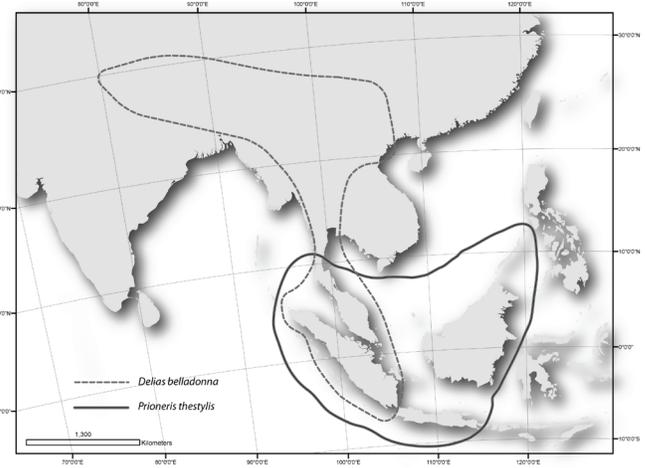


Fig. 3. Overlapping ranges of *Delias belladonna* and *Prioneris thestylis*.

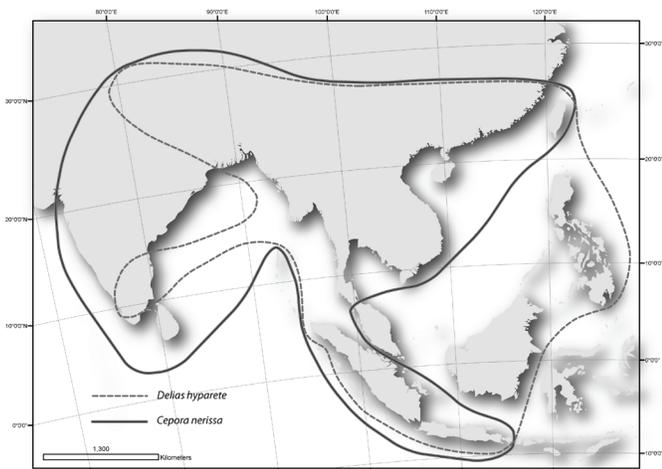


Fig. 4. Overlapping ranges of *Delias hyparete* and *Cepora nerissa*.

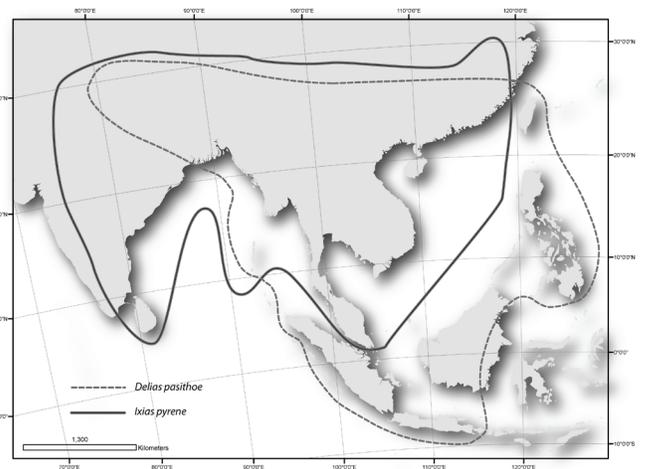


Fig. 5. Overlapping ranges of *Delias pasithoe* and *Ixias pyrene*.

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