Convergence in wing coloration between orange underwing moths (*Archiearis* spp.) and tortoiseshell butterflies (*Aglais* spp.)

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We analysed the wing coloration of the orange underwing moth *Archiearis parthenias* (Geometridae, Archiearinae) in comparison with the small tortoiseshell butterfly *Aglais urticae* (Nymphalidae). Both species fly in early spring and occur sympatrically in the northern Palaearctic. *Aglais*, the more common species, has a longer flight period and uses a broader range of habitats. Both species show a camouflaged colour pattern on surfaces exposed at rest but a bright orange signal in flight. Although the evolution of its coloration is constrained by its geometrid morphology, *Archiearis* is functionally similar to *Aglais* both while resting and in flight. *Archiearis* has presumably evolved from nocturnal geometrid ancestors. Its shift to diurnality has included a change in the predator defence system from one based on ultrasonic hearing, functional against bats, to one presumably functional against birds. Preliminary palatability tests showed that *Aglais* is distasteful to birds (chicken), while *Archiearis* seems to be palatable. The function of the convergent coloration is unknown, but several possibilities are discussed.

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1. Introduction

An adequate predator defence system is essential for the survival of any animal population. Insect defences against birds include visual concealment or crypsis (Cott 1940, Kettlewell 1955, 1959, Edmunds 1990), aposematic or mimetic signals (Bates 1862, Poulton 1890, Cott 1940, Wickler

1968, Rettenmeyer 1970, Benson 1972, Rothschild 1985, Waldbauer 1988, Guilford 1990) and probably startle signals (Sargent 1990). Crypsis and aposematism or mimicry are often complementary, frequently occurring on the same animal although usually on different parts of it ("integrated defence systems"; Edmunds 1974). For example, many Lepidoptera such as the small tortoiseshell butterfly *Aglais urticae* (L.) are camouflaged when the wings are folded but show bright coloration when alert and in flight. Furthermore, the same colour pattern may serve two or more functions depending on the situation ("dual signals"; Rothschild 1975, Brown 1988). For example, a signal may be aposematic or mimetic at close range but cryptic at a distance (Papageorgis 1975, Endler 1978, 1981).

The Archiearinae is a small (12 species) and exclusively diurnal subfamily among the Geometridae, which otherwise consists mostly of nocturnal moths (Scoble 1992). The subfamily is believed to have originated in the southern hemisphere (McQuillan *in* Common 1990), and the present distribution includes the mountains of Tasmania, Patagonia, North America and the northern Palaearctic including Japan. Characteristically, the Archiearinae have camouflaged forewings but hindwings show a high-contrast pattern in black and either white, yellow or orange (Prout 1932, Common 1990, E. Schmidt-Nielsen pers. comm.). The hindwing colours of the two northern Palaearctic species *Archiearis parthenias* and *A. notha* as well as that of the Nearctic *A.*

infans are bright orange and black (Skou 1984, Covell 1984). This coloration is otherwise rare among holarctic geometrids but shows limited similarity to those of some common, sympatric nymphalid butterflies including e.g. the tortoiseshell *Aglais urticae* of the Palaearctic (Stoltze 1996) and Milbert's tortoiseshell *Nymphalis milberti* of the Nearctic (Scott 1986). We suggest that through the shift to diurnality (Surlykke *et al.* 1997) and range expansion to the northern Holarctic, the archiearines have adopted a coloration that functionally resembles the tortoiseshell butterflies and some other similarly coloured nymphalid butterflies.

2. Wing colour and its distribution

The dorsal and ventral surfaces of ten dried and spread individuals of each of the two species, obtained from the Natural History Museum in Göteborg, were photographed against a white background, and the pictures were then scanned (resolution 150 DPI) using Hewlett-Packard ScanJet 6100C and edited using Adobe Photoshop. Only the right wing pair of each specimen (all males) was analysed. Forewings and hindwings were treated separately. For each wing, we determined the total area (in cm^2) and for the upper and lower wing surfaces also the area covered by (a) black and dark grey colours, (b) brown, (c) white and yellow and (d) orange.

On five specimens of each species, we meas-

Table 1. Total wing areas (cm^2) and the area of each of four colour categories on dorsal and ventral sides of the right wings of *Archiearis parthenias* and *Aglais urticae* (*n* = 10 for each species). "Total" implies the sum of the areas of the dorsal and ventral wing surfaces.

	A. parthenias		*A. urticae*			
	mean	S.D.	mean	S.D.	*t*	*p*
Total area	3.65	0.33	9.06	0.57	8.25	<0.001
Black, total	0.50	0.10	3.69	0.28	10.77	<0.001
Brown, total	1.90	0.25	3.59	0.33	4.09	<0.001
White/yellow, total	0.15	0.04	0.71	0.06	8.16	<0.001
Orange, total	1.11	0.11	1.12	0.13	0.06	n.s.
dorsal forewing	0.00	–	0.68	0.09	7.75	<0.001
dorsal hindwing	0.33	0.05	0.44	0.07	1.30	n.s.
ventral forewing	0.49	0.06	0.00	–	8.50	<0.001
ventral hindwing	0.29	0.04	0.00	–	6.62	<0.001

Fig. 1. Average spectral reflectance (mean ± S.D.) of the orange wing coloration in *Archiearis parthenias* (solid line; $n = 5$) *and Aglais urticae* (dashed line; $n = 5$). To illustrate the close resemblance in spectral shape (i.e. colour), spectra were set to the same overall brightness (total reflectance 300–700 nm).
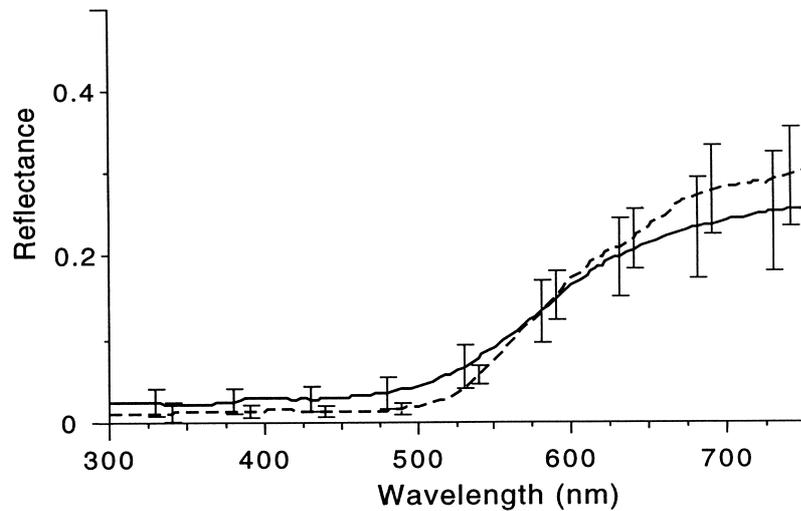
ured the reflected radiance from the orange parts of the wings, using a PS 1000 UV/VIS diode-array spectrometry equipment (Ocean Optics Inc., Dunedin, USA) described by Andersson (1996). The reflectance probe, consisting of one reading fiber surrounded by six illuminating fibers, was mounted perpendicularly to the wing surface and at a distance giving a measuring spot approximately 1.5 mm in diameter. Reflectance was calculated in relation to a Spectralon™ white standard. The average of three scans from each specimen was used. To facilitate comparisons of colour properties (spectral shape), the average reflectance spectra from the two species were set to the same brightness ($R_{300-700}$). We also computed coefficients for hue (h_{ab}) and chroma (C_{ab}) in the human CIELAB colour space (D65 daylight, 10-degree observer; C.I.E. 1971).

Both *Archiearis parthenias* and *Aglais urticae* show a mixture of camouflage (black, brown and white/yellow) and bright orange. The camouflage pattern of *Archiearis* is on the dorsal side of the forewings in a typical geometrid manner, while the camouflage of *Aglais* is on the entire ventral surface of the wings, typical of butterflies, in both cases covering the wing surfaces exposed at rest. Although *Archiearis* is less than half the size of *Aglais*, the total area of orange on the wings is the same for both species (Table 1). In *Archiearis*, the orange "signal" colour is on the upper side of the hindwings and on the ventral side of both wings, while in *Aglais* the orange is entirely on the upper side.

To the human eye, the orange colour of *Archiearis* appears very similar to that of *Aglais*. The reflectance curves, controlled for brightness, show that spectral shape (colour) is very similar across the entire 300–700 nm spectral range (Fig. 1). *Archiearis* was somewhat brighter than *Aglais* (14 units in CIE L*, corresponding to about one step on a 10-step grey scale), but brightness is of little importance in prey recognition compared to colour variables. Coefficients in the CIELAB colour space (computed on the original spectra) were also similar. Hue angle (h_{ab}) differed by only 0.8 degrees (there is a 90 degree difference between a pure red and pure yellow) and chroma by 4.4 units (on a 0–100 scale; *Aglais* being slightly more chromatic). Both these differences are below the least detectable differences to the human eye (Wyszecki & Stiles 1982), and most likely to birds as well.

3. Palatability tests

Archiearis and *Aglais* used for palatability tests were caught in daytime by hand netting in birch woodlands near Göteborg, southern Sweden (57°N) in April 1997 and 1998 or near Stockholm (60°N) in April 1997. They were kept alive in a refrigerator at 6 °C until the experiment, which took place at most 5 days after capture. Two to four week old domestic chicks, which had no pre-

vious experience with Lepidoptera, were used as predators. They arrived from the hatchery when < 20 hours old, were fed with chick starter crumbs and live mealworms and housed in a $100 \times 55 \times 20$-cm cage and heated with a 60-W carbon light bulb. The cage had wooden sides, steel-net floor made partly of wood and chicken wire and a floor covered with sawdust.

The palatability tests took place in the same kind of cage, covered with a fine net and partly screened off, leaving a 30×55-cm testing arena. The insects, which were released in the testing cage one at a time, could be reached everywhere in the cage. As controls, we used the speckled wood butterfly *Pararge aegeria* (Satyrinae), which is palatable to birds (Tullberg & Gamberale Stille unpubl.), and these were given to each chick before and after the test insects. Thirteen chicks were presented with four *Aglais* and four chicks were presented with two *Archiearis* each.

The chicks usually started to hunt the control butterfly (*Pararge aegeria*) a few seconds after it was released in the test cage. In two cases it failed to catch the butterfly, but all that were caught were eaten. Each chick attacked at least one *Aglais urticae*, but several did not attack more than one. The proportion that were attacked differed significantly between *Pararge aegeria* (the control; mean 0.94) and *Aglais urticae* (the test insects; mean 0.67) (Wilcoxon's Matched Pairs test: $n = 13, Z = 2.55, p = 0.011$), indicating that *Aglais* was sometimes avoided upon sight. Seven of the 13 chicks left all *Aglais* uneaten whereas six consumed at least one. The proportion eaten was significantly higher for *Pararge* (mean 1.0) than for *Aglais* (mean 0.39) (Wilcoxon's Matched Pairs test: $n = 13, Z = 2.80, p = 0.005$). Thus, *Aglais urticae* was unpalatable compared to the control.

All of the four chicks that were presented with *Archiearis parthenias* and ate *Pararge aegeria*, also attacked both moths. There was thus no indication that they were avoided upon sight. Moreover, three of the chicks ate both *Archiearis* individuals and one chick ate one but not the other. The proportion eaten of those that were attacked does not differ significantly between *Pararge* and *Archiearis* (Paired t-test: $t = 1.00$, d.f. = 3, $p = 0.39$), but this could be due to small sample size. A comparison of the proportion of chicks that did not eat any of the test insects (*Aglais*, 7/13

and *Archiearis*, 0/4) suggests that *Aglais* may be more distasteful than *Archiearis*. However, the sample size was small and the difference not quite significant (Fisher's Exact Test; $p = 0.088$).

4. Discussion

Archiearis parthenias, its congener *A. notha* and *Aglais urticae* occur sympatrically over much of the northern Palaearctic (Skou 1984, Stoltze 1996). Both *Aglais* and *Archiearis* are active only during the day and fly in sunshine. In southern Scandinavia, *Archiearis* usually emerges in April. Adult *Aglais urticae* emerge in August, fly throughout the autumn, overwinter and then fly again from March to May (Svensson 1993). *Archiearis parthenias* lives in birch forest and *A. notha* on aspen (Skou 1984), but *Aglais urticae* uses a much broader range of habitats than the archiearines (Thomas & Lewington 1991, Stoltze 1996). Hence, the distribution and flight period of the butterfly encompass those of the Archiearines.

The orange underwing moths (Archiearinae) presumably evolved from a nocturnal geometrid ancestor but are entirely diurnal. They are equipped with tympanic organs, which in other geometrids are used for defence against echolocating bats (Surlykke & Filskov 1997), but that no longer function for this purpose (Surlykke *et al.* 1997). At the same time, they have evolved wing coloration that differs drastically from that of most other geometrids but closely resembles that of sympatric and distasteful butterflies.

Archiearis and *Aglais* are very different in appearance with outspread wings. This relates to differences in size and in the distribution of colour on the wings. In the field, however, the two insects show very similar signals. The orange parts of the wings are virtually identical in coloration and size and are displayed only in flight. At rest, butterflies and moths fold their wings differently, and the distribution of camouflaged coloration reflects the portions of the wings that are visible. That the camouflaged parts are different in size and location on the wings may be irrelevant, since camouflage is a "non-signal" (Wickler 1968). Hence the apparent difference in coloration between *Archiearis* and *Aglais* may be illusory.

Because of morphological constraints imposed by its ancestry, *Archiearis* have adopted a novel distribution of colour patterns and achieved a functional similarity in appearance to *Aglais* both in flight and at rest.

What is the function of the orange signal shown in flight? Earlier work has indicated that *Aglais* is distasteful to birds (Pocock 1911, Blest 1957) and mammals (Møhl & Miller 1976), and our results support this conclusion. Our limited experiment did not provide any evidence that *Archiearis* is distasteful to birds (chicks in the present study). Hence, it seems possible that a flying *Archiearis* could be a Batesian mimic of a flying *Aglais*, which probably is aposematic. To test this hypothesis conclusively, it would be necessary to investigate whether predators (birds) generalize between flying *Archiearis* and *Aglais*.

The presence of both camouflage and bright wing surfaces in *Aglais* and *Archiearis* (and in many other butterflies and moths) suggests that the situation is often more complex than this and that movement is also involved in the insect's signalling strategy. Many predators detect prey by movement, and animals therefore increase the risk of being detected when they move. At the same time they become more difficult to catch. Therefore, many animals including *Aglais* and *Archiearis* forego crypsis as a defence when they take flight (Wiklund & Sillén-Tullberg 1985) and shift to a bright signal. The fact that *Aglais* shifts from camouflage to orange signalling when it is ready to move suggests that its distastefulness is not strong enough to provide efficient protection from predation, unless it is also alert and able to move rapidly and erratically. A flying *Aglais* is presumably difficult to catch; therefore its expected value for a predator is lower than that of a resting individual. Hypothetically, the orange signal may thus carry the message that the insect is unprofitable, and the underlying defence may then consist of two components: distastefulness and rapid movement.

It could also be argued that the orange signal shown by *Archiearis* in flight could be a startle signal analogous to that shown by some larger moths (i.e. *Catocala* spp.; Sargent 1990), or a signal that serves to confuse the predator by suddenly appearing when the insect takes flight and then disappearing again when the insect settles.

Although these explanations cannot be excluded with the data at hand, they seem unlikely in our case. They do not explain the observed convergence in the signal of *Archiearis* towards that of *Aglais*.

Although the colour vision of birds differs from that of humans in several respects, such as UV vision and tetrachromacy (Varela *et al*. 1993), we believe that it is a reasonable assumption that birds cannot tell apart the *Archiearis* and *Aglais* wing colours. Firstly, the UV waveband contained no additional difference in reflectance shape (colour). Secondly, the subtle difference is located in the orange-red spectral region, where human colour resolution peaks and outperforms other known visual systems (Neumeyer 1991), including recent models of avian colour space (Vorobyev *et al*. 1998). The barely perceivable difference in terms of human CIE coefficients strongly suggests that the two orange colours are indistinguishable for birds.

Even if the colour convergence seems convincing, however, predators might distinguish prey based on other visual cues. For example, the rufous-tailed jacamar *Galbula ruficauda*, a neotropical butterfly specialist, recognizes palatable mimics of *Heliconius* spp. and other butterflies by subtle differences in flight characteristics (Chai & Srygley 1990). Likewise, Müllerian mimics among *Lygaeus* bugs must be almost identical to achieve full mutual protection from predation by great tits *Parus major* (Wiklund & Järvi 1982). On the other hand, a predator may have little chance to notice details of a prey that is moving rapidly and erratically, as in the case of *Archiearis*, particularly if the predator is a non-specialist like a migratory bird. Hence, according to Fisher (1958), "conspicuously different insects may enjoy the advantage of Müllerian selection provided they display in common any one conspicuous feature". This applies well to the combined signalling behaviour of *Aglais* and *Archiearis*, in which the most conspicuous visual feature, the orange wing coloration, seems to have converged to a spectacular degree.

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