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Thermal Plasticity in a Cross-Sexual Transfer Trait: Geographic Variation and Phenotypic Integration of Blue Wing Colour in Female Butterflies

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ABSTRACT

Within-sex phenotypic variation can arise through co-option of sexual differentiation mechanisms. Recently, several such cross-sexual-transfer traits have been identified, but we lack a mechanistic understanding of their geographic variation, environmental influences, and phenotypic integration with other traits. Male *Polyommatus icarus* butterflies are blue, whereas female wing coloration varies from brown to blue. Here, we show that female wing colour varies in a geographic mosaic, with the spring generation being bluer than the summer generation. Laboratory experiments revealed that females developed both bluer wings and increased phenotypic integration between the amount of blue and total wing area at low temperature, qualitatively matching differences between spring and summer generations. Scanning electron microscopy revealed that female and male colour develop through similar mechanisms, supporting the cross-sexual-transfer hypothesis. Our study establishes a promising study system on cross-sexual-transfer and a solid foundation for research on the fitness consequences and evolutionary history of this trait.

1 | Introduction

Sexual dimorphism is ubiquitous and has fascinated biologists for more than 150 years (Andersson 1994; Darwin 1871). A major evolutionary route to sexual dimorphism is through sex-specific selection operating differently on males and females (Connallon and Clark 2010; Lande 1980). For example, sexual selection is expected to favour extravagant signalling in males due to female choice of ornamented males (van der Bijl et al. 2020; Fisher 1930; Kirkpatrick 1982; Lande 1981). By contrast, in females, natural selection should favour traits like camouflage, crypsis, or mimicry to avoid predation (Kunte 2008), as forcefully argued by Darwin's contemporary Alfred Russel Wallace (Cronin 1991).

Under the traditional view, sexual dimorphism emerges by males evolving exaggerated phenotypic traits by sexual selection, with females initially being dragged along the male trajectory as a correlated response (Lande 1980). Most phenotypic traits are autosomally inherited, and sex-limited phenotypic expression (sexual dimorphism) is under this traditional view assumed to be a derived trait (Connallon and Clark 2010). Subsequently, females are assumed to reduce the exaggerated male traits as an adaptive response after an initial displacement from their phenotypic optimum (Lande 1980). However, a shared genetic architecture of the two sexes may slow down the evolution of such complete sex-limited phenotypic expression (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; Rice and Chippindale 2001). Strong intersexual genetic correlation between phenotypic traits means that populations and species may go through extended periods of maladaptation before each sex has reached its adaptive peak (Connallon et al. 2010; Matthews et al. 2019). Vestigial features, such as the male-like traits of female Indian Peafowl (*Pavo cristatus*), are usually interpreted as a transitional stage towards sexual dimorphism (Darwin 1871; Harano et al. 2010).

A large body of empirical evidence supports the models above for the evolution of sexual dimorphism, in either Darwin's or Wallace's versions. However, there is now increasing empirical evidence that female-like phenotypes in males and male-like phenotypes in females are not always at a fitness disadvantage and may not simply reflect correlated responses to selection on the other sex. On the contrary, many such phenotypes resembling the other sex are adaptively maintained as phenotypic polymorphisms by balancing selection (Mank 2023; Willink et al. 2024). For example, some male phenotypes are similar to females, which can have fitness advantages due to intersexual mimicry (Dodge et al. 2024). Such intersexual mimicry could arise from reduced aggression from other males, which increases the mating success of female-like males under some circumstances (Jukema and Piersma 2006; Kupper et al. 2016; Lamichhaney et al. 2016; Shuster and Sassaman 1997; Sinervo and Lively 1996; Sternalski et al. 2011). Conversely, male-like female morphs coexist with other female phenotypes in several taxa, including birds (Diamant et al. 2021; Falk et al. 2021; Lee et al. 2019), lizards (Moon and Kamath 2019), and insects (Reinhardt et al. 2007; Cook et al. 1994; Kunte 2009). Polymorphisms with intersexual mimics are especially common in damselflies (Odonata: Zygoptera) (Blow et al. 2021; Cordero et al. 1998; Fincke 2004; Gering 2017; Robertson 1985; Svensson et al. 2005; Takahashi et al. 2010; Waller et al. 2019; Willink et al. 2019). Phylogenetic comparative studies (Blow et al. 2021), genomic evidence (Willink et al. 2024), experimental manipulations (Takahashi et al. 2014), population genetic modelling (Svensson et al. 2005) and longitudinal field studies (Le Rouzic et al. 2015) collectively suggest that such female phenotypic polymorphisms in damselflies are maintained by negative frequency-dependent selection, arising from sexual conflict. More generally, theory predicts that sexual conflict through male mating harassment is a powerful mechanism to promote female phenotypic and genetic diversity, whether in the form of discrete genetic polymorphisms or in quantitative traits (Gavrilets and Waxman 2002).

The proximate origin and developmental basis of female-like males and male-like females is unknown in many systems (but see Mank 2023; Willink et al. 2024). In 2003, Mary Jane West-Eberhard hypothesized that cross-sexual transfer of phenotypic traits between males and females could be both common and evolutionarily important (West-Eberhard 2003). She defined cross-sexual transfer as '...discrete traits that are expressed exclusively in one sex in an ancestral species that appear in the opposite sex of descendants' (West-Eberhard 2003). Under the cross-sexual transfer hypothesis, developmental plasticity of ancestral sex differentiating pathways can give rise to novel, potentially adaptive, traits in another sex than where it originated (Anderson and Falk 2023). The cross-sexual transfer hypothesis has rarely been tested empirically (Anderson and Falk 2023), although a growing body of studies have identified candidate cross-sexual transfer traits (Diamant et al. 2021; Enbody et al. 2022; Falk et al. 2021; Reinhardt et al. 2007; Willink et al. 2019). A key prediction of the cross-sexual transfer hypothesis is a shared developmental basis of the trait that is expressed in both sexes. Specifically, phenotypes resembling the other sex should have evolved through convergence, and not through other mechanisms (Anderson and Falk 2023). Cross-sexual transfer traits should ideally fit well within their new sex environment, and we would therefore expect such traits to become phenotypically integrated (*sensu* Pigliucci 2003) with other traits to serve new adaptive functions, although very few studies have addressed this question.

Here, we tested the cross-sexual transfer hypothesis in a promising study system: female wing colour variation in the common blue butterfly (*Polyommatus icarus*). Females in this species vary in dorsal wing coloration, ranging from entirely brown to almost completely blue, the latter phenotype being similar to males (Figure 1). Early work (Ford 1945) described blue-winged females as being increasingly common towards the north-western parts of the British Islands (Dennis and Shreeve 1989; Ford 1945). Also in Sweden, the proportion of blue females has been suggested to increase with latitude (Eliasson et al. 2005), indicating that blue females might be favoured in colder climates (Dennis and Shreeve 1989). However, the dorsal wing colour of female *P. icarus* also varies at small spatial scales, for example, between nearby island populations (Dowdeswell et al. 1940), and other wing pattern elements are highly variable in *P. icarus* (Artem'eva 2007; Artemyeva 2005). Thus far, no quantitative evidence has either confirmed or refuted any role for latitude or temperature in *P. icarus* female colour variation. Experimental manipulations are clearly needed to evaluate any role for developmental plasticity in female wing colour due to temperature exposure during larval development. Similarly, we do not know the mechanistic basis of female blue colour, although it could emerge through the same mechanism that generates blue colour in males (wing scale nanostructures). A small and unreplicated pilot experiment exposed pupae to experimental cooling and suggested that females eclosing from cooled pupae were more likely to produce at least some blue wing colour (Kertész et al. 2017). An important goal would be to disentangle and quantify the relative importance of phenotypic plasticity and genetic variation behind female colour variation. Female blue wing colour could potentially also vary between generations within years, as this species has multiple generations in most of its Eurasian range (Tolman 2001). Finally, if female blue wing coloration is a cross-sexual transfer trait that has a signalling function, it would be expected to become phenotypically integrated with for example, the total wing area to maximise signalling efficiency. Here, we combine data from museum collections, Citizen Science data, and experimental manipulations of temperature during larval development to fill these knowledge gaps.

We show (i) that female blue wing coloration varies geographically, but in a mosaic rather than in a clinal pattern and (ii) that thermal plasticity may contribute to generating geographic variation, because females develop bluer wings when exposed to a low-temperature treatment during larval development.

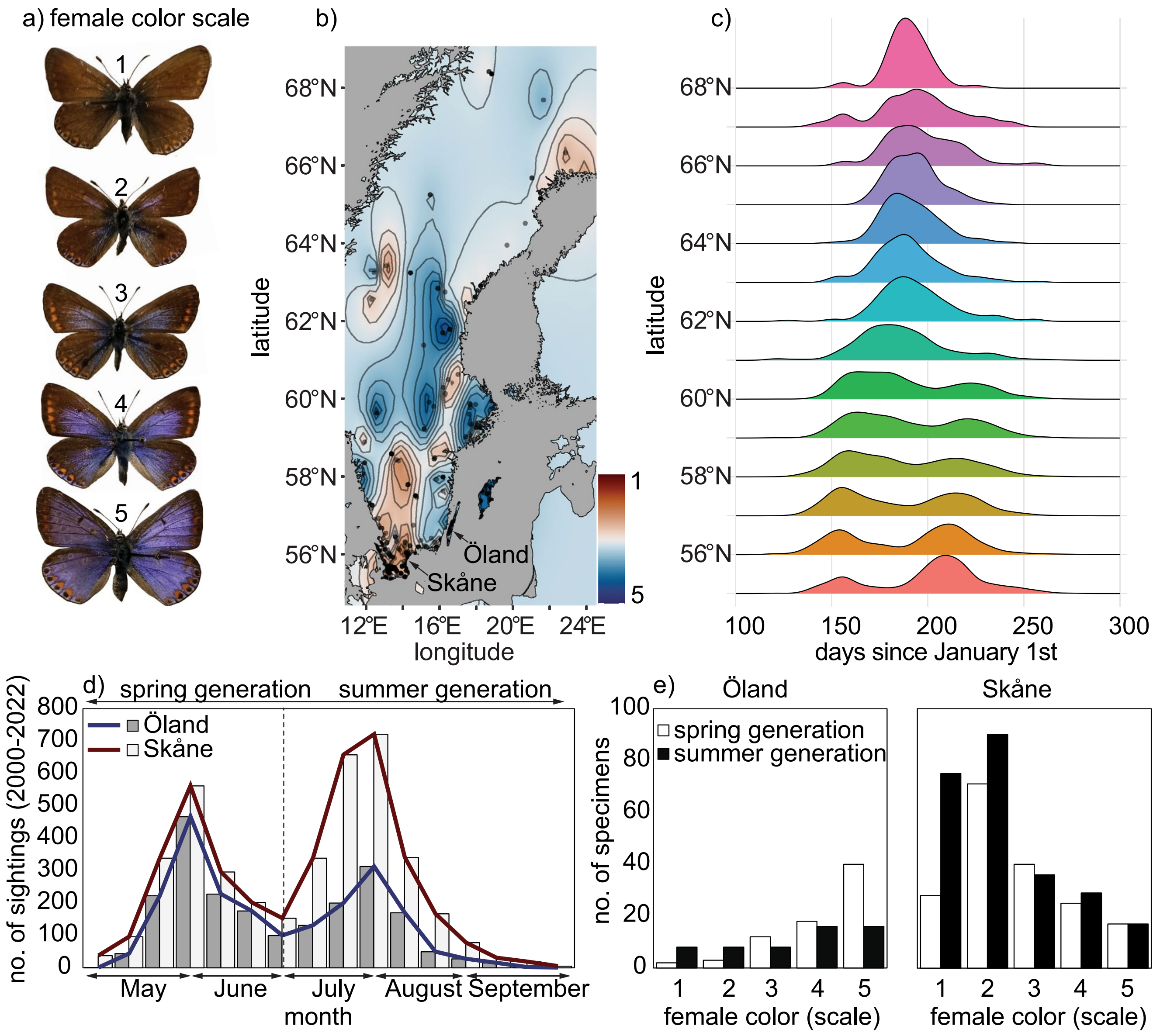

FIGURE 1 | Spatial and temporal variation in *Polyommatus icarus* female dorsal wing coloration. (a) Museum specimens were scored based on a 5-digit scale in terms of blue wing coloration, where (1) shows no or faded blue colour closest to the body; (2) shows distinct blue closest to the body; (3) has blue stretching out on the wings, not reaching the lunules; (4) has blue reaching the lunules in at least one location; and (5) shows blue all the way from the body out to the lunules near the wing edge. (b) There is a geographic mosaic pattern of female dorsal wing colour across Sweden with higher proportion of blue females in southeast Sweden in the Stockholm region and on the two islands in the Baltic Sea, Öland and Gotland. (c) South of latitude 60° N *P. icarus* flies in two major generations per year, and north thereof the species is univoltine. In the two focal areas of this study, Öland and Skåne (b), *P. icarus* is bivoltine (d), appearing in two clear flight peaks per year. Öland females were bluer than females from Skåne (b, e), and in both regions (e) museum specimens were bluer during the spring than the summer generation.

Furthermore, (iii) the phenotypic correlation between the amount of blue and total wing area increases when larvae are exposed to low temperatures (high phenotypic integration). Next, (iv) we show that wild-caught females of the spring generation are bluer and have higher phenotypic integration compared to the summer generation, qualitatively matching the results in our temperature experiment. Finally, (v) our results confirm that female blue wing colour arises by the same mechanism as male blue wing colour, revealed by scanning electron microscopy (SEM) of wing scale nanostructure. This finding provides mechanistic support for blue wing colour being a cross-sexual transfer trait. Collectively, our results establish a highly promising study system on female blue wing colour as a cross-sexual transfer trait that is influenced by both genetic factors and by temperature-mediated plasticity.

2 | Material and Methods

2.1 | Study Species

The common blue (*Polyommatus icarus*) is a small lycaenid butterfly with a wingspan of 21–33 mm. The dorsal side of male wings are blue with a thin black marginal line, whereas females are brown with a variable amount of blue colour, with orange lunules (Figure 1A). This species is found in various habitats across Eurasia, and its distribution includes all of Sweden, with little population structure at least in southern Sweden (Nolen et al. 2024). *Polyommatus icarus* appears in two to three, quite discrete, generations per year in the south, and is largely univoltine in the north of Sweden (Figure 1C). It overwinters as diapausing late-instar larvae and uses several host plants in the Fabaceae family (Eliasson et al. 2005). *Polyommatus icarus* is highly variable in both wing coloration and patterning (Artem'eva 2007; Artemyeva 2005; Kertész et al. 2017, 2019). Surprisingly, most attention has been focused on male coloration, which varies both in intensity and hue (Kertész et al. 2017, 2019), indicating that the blue variation arises mechanistically from variation in wing scale nanopatterns (Kertész et al. 2019).

2.2 | Museum and Citizen-Science Data Collection

We used material from the Biological Museum collections at Lund University. We included female specimens, where labels included the date and location of collection (parish), and obtained the coordinates of the centroid of each parish from Google Earth. These geolocations served as good estimates of sampling locations for the purpose and geographical scale of this study. In total, we could analyse 960 individual females that had been collected from 267 different locations across all of Sweden's 25 provinces. Southern Sweden, which is more densely populated, was more intensively sampled.

To be able to rapidly quantify the amount of wing colour, we developed an ordinal colour scale with five steps (Figure 1A). This scale was used to obtain a general picture of the distribution of female wing coloration across Sweden (for definitions, see Supporting Information). For a subset of our museum dataset ($n = 204$), we quantified the amount of blue on the wings (in mm^2) to obtain a fine-grained measure of the amount of blue (see Supporting Information).

To assign each museum individual into either belonging to the spring or summer generation, we used data from the Species Portal, which is a Swedish citizen science database (www.artportalen.se) where naturalists can upload their sightings to a public repository. We downloaded all reported sightings of adult *P. icarus* from 2000 to 2022. By focusing on two well-sampled regions, the island of Öland in the Baltic Sea and Skåne in southernmost Sweden (Figure 1), we identified two distinct flight peaks with a clear breakpoint near July 1st. Thus, museum specimens collected from these regions before June 30th were assigned to the spring generation, and specimens collected after July 1st were assigned to the summer generation.

2.3 | Field Collection and Animal Husbandry

Adult *P. icarus* females were collected from our two focal regions. On Öland, we collected from two populations: Grönhögen (56°16′10″ N 16°24′32″ E; 50 females) and Södra Sandby (56°33′12″ N 16°38′24″ E; 58 females). In Skåne, we collected from Lund (55°43′44″ N 13°11′08″ E; 52 females) and from Tvedöra (55°41′49″ N 13°25′49″ E; 71 females). Field-captured females were brought to our experimental greenhouses in Lund in coolers (~8°C). After egg-laying, females were euthanised by freezing (for animal husbandry details see Supporting Information).

2.4 | Common Garden Experiments and Temperature Treatments

Sixteen females from Skåne and 13 females from Öland laid enough eggs to be included in the experiment. Twenty newly hatched larvae from each female were distributed into four 1 L containers (5/jar) filled with cuttings of *Medicago sativa*. Two jars with offspring from each female were distributed into environmentally controlled rooms keeping a constant temperature of either 18°C (cold treatment) or 26°C (warm treatment) in a 22-h day length. Jars were kept on shelves and lit from above (Civilight LED 800 lm, Wernhout, The Netherlands). The cuttings of *M. sativa* host plants were standing in water to maintain freshness and were replaced by new cuttings every 2–3 days. We included the female offspring of mothers from all four field populations from Öland (Södra Sandby, 5 females; Grönhögen, 47 females) and Skåne(Lund, 39 females; Tvedöra, 40 females). Pupae were moved to individual plastic cups lined with paper towels to allow space for wings to unfold and kept in the same constant room until adult eclosion. The experiment resulted in 131 adult females.

2.5 | Wing and Colour Measurements

All field-collected butterfly females, the females produced in the temperature experiment, and a subset of the butterflies in the museum collection were photographed *postmortem* in a window-less room, under controlled light conditions. Photos were taken in raw format and both blue wing area and total wing area were measured using the software ImageJ. For details on photographic setup and ImageJ analysis, see Supporting Information.

2.6 | Scanning Electron Microscopy

We used a scanning electron microscope (SEM, Hitachi SU3500) to investigate wing structure at a level of individual scales of laboratory reared butterflies. A total of 24 (8 males, 7 brown females and 9 blue females) laboratory reared individuals from both temperature treatments, originating from both Öland and Skåne, were scanned. For details, see Supporting Information.

2.7 | Statistical Analyses

All analyses were performed using R Statistical Software version 4.2.2 (R Development Core Team 2022). First, we generated a heatmap to visualise the geographic distribution of female wing colour across Sweden using the R-package *spaMM* (version 4.4.0; Rousset and Ferdy 2014). We used georeferenced information from all 960 female specimens that we phenotyped in the large museum dataset. We visualised how female brownness (ordinal five step scale; see above and Figure 1) varied geographically, based on a random effects model only (latitude and longitude included as a random factor using the *matern*-function) and using the *filled.mapMM*-function for visualisation. To test if museum samples from Öland and Skåne varied in the frequency of our five major wing colour phenotypes between the spring and the summer generation, we performed separate χ^2-tests for each region. Finally, we analysed the blue wing colour of the newly field-caught females from Öland and Skåne using a two-factor ANOVA with region (Skåne and Öland) and population (nested in region) as factors to verify if the findings from historical museum samples were consistent with colour distributions in modern times.

To test direct effects of phenotypic plasticity on female wing coloration driven by temperature during development, we analysed the experimental dataset using a linear mixed model with blue wing area as the response variable and with total wing area, region, and temperature treatments as fixed effects. We included maternal identity as a random factor to account for statistical non-independence of siblings. We tested for all potential two- and three-way interactions between the three main fixed effects above, but we only present a final model with the lowest Akaike Information Criterion (AIC), which we consider as the 'best' model.

Using the subset of museum specimens for which blue wing area was measured, we applied the *spaMM* package (version 4.4.0; (Rousset and Ferdy 2014)) to carry out generalised mixed models (Figure 1B). We accounted for spatial autocorrelation in these biogeographic analyses, utilising georeferenced specimens from museum collections and by incorporating latitudinal and longitudinal position as random factors using the *matern*-function. We incorporated various fixed variables of biological interest in these mixed models, depending on the analysis. These fixed variables include total wing area, which is expected to be correlated with the total amount of blue, because a larger wing area has more space for blue colour. The other variables were butterfly generation (spring vs. summer) and climatic variables during the larval period (mean temperature and mean precipitation) that were downloaded from the *WorldClim* dataset (Fick and Hijmans 2017) (https://www.worldclim.org/data/bioclim.html).

We counted the number of scales on standardised areas (500 × 500 pixels) from the SEM images and used a Kruskal–Wallis test to statistically compare the proportion of membranous tissue belonging to the four scale types: female brown scales from brown ('spiky scales') and blue ('mixed scales' wing areas), female blue scales ('round') and male blue scales ('round') (see Section 3).

3 | Results

3.1 | Geographic Variation in Female Wing Colour

Spatial prediction analyses of all 960 females scored in the museum samples showed no strong evidence for females becoming bluer in northern Sweden, compared to southern Sweden (Figure 1B). Instead, the female wing colour was distributed across Sweden in a mosaic pattern (Figure 1B). For example, in the southernmost region, Skåne, the typical female was brown or had only small patches of blue close to the wing margin (phenotype classes 1–2; Figure 1B), whereas the dorsal wing coloration of females from the Baltic Islands Öland and Gotland was dominated by blue (phenotype classes 4–5; Figure 1A,B).

Analyses of Citizen Science data from the Swedish Species Portal (www.artportalen.se) further demonstrated the shift from bivoltinism in the south to univoltinism in the northern part of Sweden, with a discrete change north of 60° N (Figure 1C). In the subset of museum specimens for which we measured the dorsal blue wing area ($n = 204$ females) we found significant positive effects of longitude on the amount of blue (Table 1). This effect, with more blue females in the east, was largely driven by a high frequency of blue females on the Baltic Islands and the area around Stockholm. Similarly, the high frequency of blue females on the Baltic Islands likely contributed to a weak negative effect of latitude on blue wing area, with fewer blue females in the north (Table 1), despite brown females dominating in southernmost Sweden (Figure 1B). In this smaller dataset, including both uni- and bivoltine populations, we could not detect any significant effect of generation on female blue wing area (Table 1).

The Citizen Science data revealed two distinct flight peaks in both focal regions, Öland and Skåne (Figure 1D). In both regions, museum-collected females of the spring generation were significantly bluer compared to females of the summer generation (Öland $\chi^2_4 = 14.6$, $p = 0.0055$; Skåne $\chi^2_4 = 14.4$, $p = 0.0062$; Figure 1E).

3.2 | Genetic Differentiation Between Regions and Thermal Plasticity

Field collected female *P. icarus* of the summer generation from two populations within each of our two target regions confirmed the findings in the museum data that female butterflies from Öland had six times larger blue wing areas than females from Skåne, controlling for total wing area (Figure 2A). We did not detect any significant differences between populations within regions (linear model: total wing area $F_{1,185} = 5.29$, $p = 0.023$; Region $F_{1,185} = 96.8$, $p < 0.001$; Population within Region $F_{2,185} = 0.059$, $p = 0.94$).

TABLE 1 | Statistical output from a fixed-effects only general linear model (Anova type III) on the effects of Total wing area, Generation (factor: summer or spring), Latitude and Longitude one female blue wing area.

	df	F	p
Total wing area	1	102	< 0.001
Generation	1	0.59	0.44
Latitude	1	4.18	0.042
Longitude	1	8.31	0.0044
Residuals	199		

Note: Data come from the subset of the museum dataset where we quantified the amount of blue wing area (in mm^2). Total sample size: 204 females.

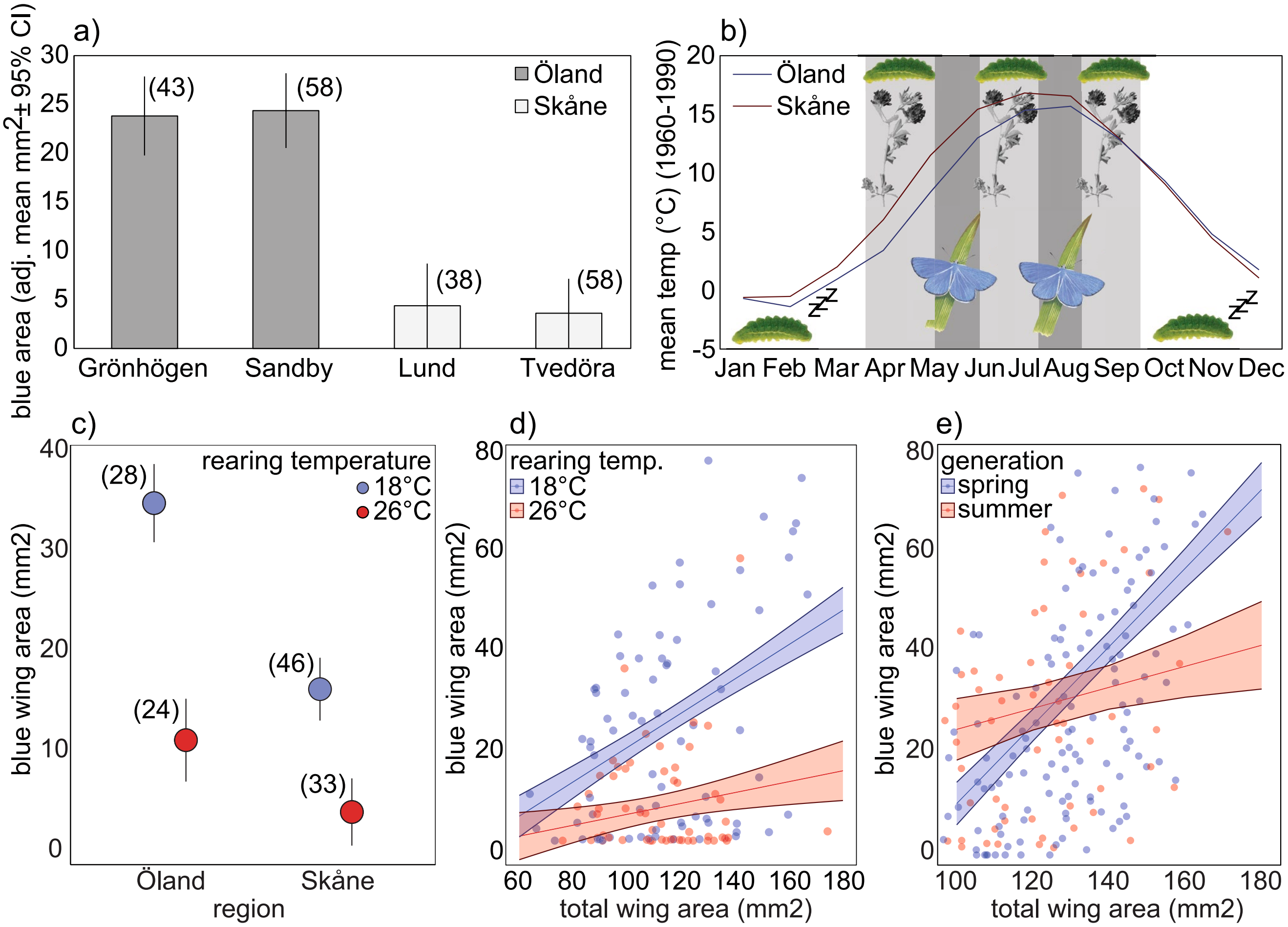

FIGURE 2 | Variation in female *Polyommatus icarus* wing coloration between the Öland and Skåne regions. (a) Wild-caught Öland females had bluer wings than Skåne females. (b) Putative environmental effects include temperature, where monthly average temperatures are 1°C–3°C colder in Öland than in Skåne. (c) Temperature during development affect female wing coloration, but Öland females developed bluer wings than Skåne females, both at 18°C and at 26°C. There are significant effects of both temperature region ($p < 001$) and the temperature × region interaction ($p = 0.01$). Thus, warmer temperature treatment reduced the amount of blue more strongly in Öland females than in Skåne females (Table 2). (d): The relationship between total wing area and blue wing area differed significantly between the temperature treatments (Wing area × temperature treatment: $p = 0.013$; Table 3). (e) Similarly, analysis of museum samples showed that the relationship between total wing area and blue wing area was significantly stronger in the spring generation than in the summer generation. Number in parentheses in (a, c) denote samples sizes in each group.

One environmental factor that varies among these regions is temperature. The monthly average temperature is 1°C–3°C higher in Skåne than on Öland between February and August (SMHI; 1960–1990), that is, during periods of larval development (Figure 2B). Our rearing experiment, that exposed larvae from Skåne and Öland either to a low-temperature treatment (18°C) or to a high-temperature treatment (26°C) throughout development, showed a significant negative effect of temperature on female blue wing coloration (Figure 2C). Females from both regions developed bluer wings in the cold treatment, but females from Öland developed bluer wings than females from Skåne across both rearing temperatures (Table 2; Figure 2C).

The positive relationship between blue wing area and total wing area became significantly stronger in the cold than in the warm temperature treatment (Table 2; Figure 2D). A similar pattern emerged when comparing the relationship between blue wing area and total wing area in the large museum sample of

TABLE 2 | Statistical output from a linear mixed model (analysis of deviance) testing for the effects of total wing area (TWA: continuous covariate), rearing temperature (RT: factor) and region (R: factor) on female blue wing area from the laboratory rearing experiment.

	df	χ^2	p
Total wing area (TWA)	1	31.8	<0.001
Rearing temperature (RT)	1	0.099	0.75
Region (R)	1	13.71	0.00021
TWA × RT	1	6.14	0.013
RT × R	1	6.62	0.010

Note: Maternal family was incorporated as a random factor, whereas TWA, RT, R and the two two-way interacts (TWA × RT and RT × R) were treated as fixed variables. The three-way interaction (TWA × RT × R) was non-significant and was removed as the model below had a lower Akaike Information Criterion (AIC) score than a full model with the three-way interaction included.

butterflies belonging to the spring and summer generations, respectively (Table 3; Figure 2E). Thus, the relationship between the amount of blue and total wing area was significantly stronger in spring than in summer (Table 3; Figure 2E).

3.3 | Cross-Sexual Transfer

The SEM-images revealed several structural differences in the wing scales of brown females, blue females, and males (Figure 3A). The single scale type of brown females was elongated with a spiky edge, whereas male scales were more square-like and had a rounded edge. The males also had androconia scales (Figure 3A). In brown wing areas, blue females displayed the same scale type as brown females, whereas in the blue areas, there were two different types of scales. In addition to the rounded scales carried also by males, the blue female wing areas included a unique scale type that could be described as a mixture of the scales of the brown area and the male scales (Figure 3A). These scales were short and compact like male scales but had spiky edges like the brown female scales. Additionally, these three different scale types showed variation in nanoscale architecture. The scales carried by both males and blue females showed a so-called 'Pepper-Pot' pattern (Tilley and Eliot 2002), which looks like a membranous surface inside the scale cavities. In contrast, the scale cavities of brown female scales and the intermediate scales of blue females largely lacked such surfaces (Figure 3B).

TABLE 3 | Statistical output from a general mixed model testing for the fixed effects of total wing area (TWA), Generation (G), standardised larval temperature (SLT), precipitation (P) and the three two-way interactions between the climatic variables and TWA on female blue wing area.

	df	*F*	*p*
Total wing area (TWA)	1, 202.86	36.3	< 0.001
Generation (G)	1, 200.94	7.50	0.0067
Standardised larval temperature (SLT)	1, 203.96	1.29	0.26
Standardised larval precipitation (SLP)	1, 186.94	0.17	0.68
TWA × G	1, 199.89	8.57	0.0038
TWA × SLP	1, 203.97	1.72	0.19
TWA × STP	1, 182.98	0.32	0.57

Note: Data come from the sub-sample of the museum dataset where we measured both female wing area and the blue area (both in mm^2). To control for statistical non-independence among these field-collected museum specimens and spatial autocorrelation, latitude and longitude were included as a random effect using the *matern*-function in the R-package *spaMM* (version 4.4.0; Rousset and Ferdy 2014). All the variables below are fixed effects. The significant interaction between total wing area and generation (TWA × G) reflects the changing strength of the phenotypic correlation between the blue wing area and total wing area between the spring and summer generations, and it is illustrated in Figure 2E.

4 | Discussion

Here, we have shown that the extent of blue wing coloration in female *P. icarus* has a genetic basis, revealed by significant regional differences that persist when butterflies are reared in a common environment (Figure 2A,C). In addition, we demonstrate a role for developmental plasticity, reflecting temperature conditions during larval growth (Figure 2C). Furthermore, the extent of phenotypic integration between the amount of blue wing colour and total wing area is temperature-dependent, with the correlation becoming stronger when larvae are raised under low-temperature conditions (Figure 2C). These experimental results are qualitatively similar and consistent with generational differences in the field, where female butterflies emerging in the colder spring are bluer than butterflies emerging in the warmer summer (Figure 2E). Thus, blue wing colour is thermally plastic, and so is the phenotypic correlation between blue wing colour and total wing area. Phenotypic integration and covariation are

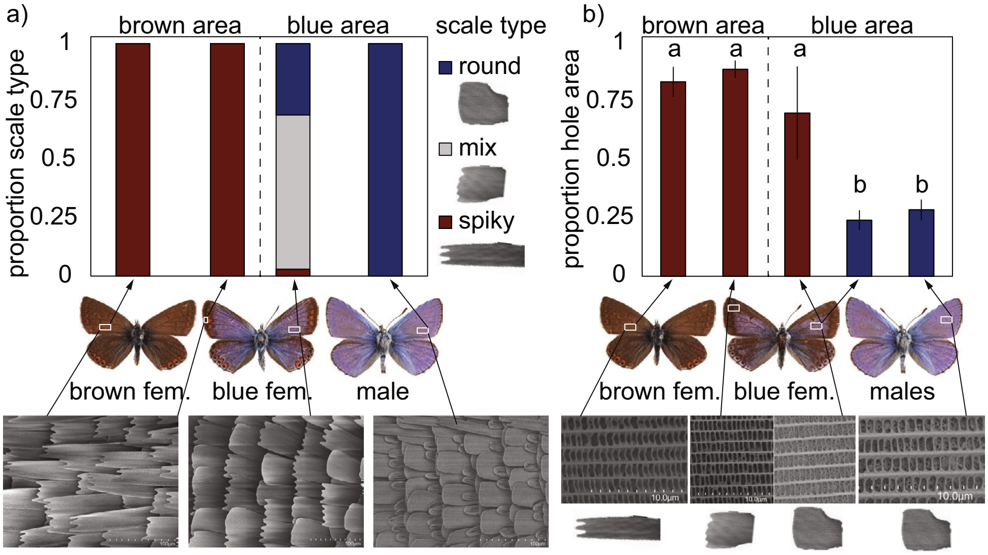

FIGURE 3 | Results of the scanning electron microscopy. (a) The three different scale types vary in proportion between brown females (left), blue females (middle) and males (right), as well as between the blue and brown areas of the wing in blue females. (b) The male scales (and male-like scales of blue females) showed significantly different nanoarchitecture than the other scale types (Kruskal–Wallis test $n = 43$, $\mathrm{df} = 4$, $\chi^2 = 25.3$, $p < 0.001$).

of central interest in evolutionary biology (Pigliucci 2003). Such phenotypic integration can reflect underlying genetic covariation (Steppan et al. 2002), emerge as a result of correlational selection (Svensson et al. 2021) or reflect developmental plasticity during ontogeny (Morel-Journel et al. 2020). In *P. icarus*, there is an obvious physical constraint, because wings cannot be bluer than the total wing area, and future functional studies are needed to determine to what extent wing colour affects for example, signalling efficiency or thermoregulation.

In contrast to previous suggestions (Dennis and Shreeve 1989; Eliasson et al. 2005; Ford 1945), we found no clear latitudinal gradient in the extent of female blue wing colour in Sweden, but rather a mosaic-like pattern (Figure 1B). For example, females from the two Baltic Sea islands (Öland and Gotland) were bluer than females in Skåne (Figure 1B). These regional differences were confirmed in our laboratory experiments, where laboratory-raised females from Öland remained significantly bluer than females from Skåne in shared thermal environments (Figure 2C). Thus, temperature is clearly not the only factor behind the development of blue wing coloration, although it explains a considerable amount of phenotypic variation.

Our scanning electron images of the nanostructure of the wing scales clearly revealed that blue females produce their colour through a similar mechanism as the males (Figure 3). These results suggest that blue colour is indeed a cross-sexual transfer trait, rather than female colour resulting from convergence through some other mechanism. This finding supports a central prediction of the cross-sexual transfer hypothesis, namely that a trait expressed in the alternate sex should have been derived from the same ancestral developmental mechanism in the other sex (Anderson and Falk 2023; West-Eberhard 2003). Full support for the cross-sexual transfer hypothesis would require phylogenetic evidence in the form of reconstructed ancestral states of males and females (Anderson and Falk 2023). Specifically, the cross-sexual transfer hypothesis predicts that the ancestor of *P. icarus* was sexually dimorphic, having only brown females, and blue females would subsequently have acquired their male-like traits secondarily, by co-opting the developmental pathway that produces blue wings in males. Preliminary evidence, using phenotypic data and phylogenetic comparative methods, from 57 species of the tribe Polyommatini supports this scenario and suggests that the ancestor of *P. icarus* was indeed sexually dimorphic and had only brown females (M. Friberg, Z. Aliwi, S. Halali, N. Wahlberg, E.I. Svensson, unpublished data). However, further analyses of an expanded dataset are needed to test the hypothesis that the blue female phenotype of *P. icarus* evolved *de novo* from a non-plastic female monomorphic ancestor, in line with the cross-sexual transfer hypothesis (Anderson and Falk 2023).

In addition to colour, the nanostructure of butterfly wing scales could also affect performance in relation to climatic factors like temperature and precipitation, for example, the ability to repel water and absorb heat (Kim et al. 2020; Krishna et al. 2020). Brown and blue females could have differential tolerance to heat and cold, based on mechanistic studies on wing scales in other butterfly species (Kim et al. 2020; Krishna et al. 2020). In other animals, like African sunbirds, the structural coloration that gives rise to iridescent feathers also increases thermal absorption and risk of overheating (Rogalla et al. 2021). If similar physical principles apply also to structural colour in blue butterflies, we expect blue females and males to heat up faster than brown females, which could be a fitness advantage in cooler environments. Conversely, under warmer conditions, such as in the summer, blue wing coloration may carry a cost of overheating, and hence brown females might have an advantage. If so, thermal plasticity of blue wing colour could be adaptive and selectively favoured (Figure 2C–E). Specifically, if temperature experienced during the larval period provides a reliable cue to future temperatures during the adult developmental stage, developing blue wing colour under colder conditions could be beneficial to fitness. This hypothesis remains to be tested, and whether the thermal plasticity is adaptive, maladaptive or even nonadaptive is an open question for future research.

Apart from its potential thermal consequences, colour could also affect the nature and outcome of male–female mating interactions, including antagonistic interactions and sexual conflict over mating. Male-like female phenotypes in several taxa, including butterflies and damselflies, have been shown or suggested to suffer from less male mating harassment due to the benefits of intersexual mimicry (Cook et al. 1994; Cordero et al. 1998; Gosden and Svensson 2009; Takahashi and Watanabe 2009; Turlure et al. 2016; Willink et al. 2019). Alternatively, but not mutually exclusive, brown females could benefit from crypsis and thereby avoid male mating harassment through other means. Regardless of the mechanism, the maintenance of genetic and phenotypic variation in female phenotypes usually requires a feedback mechanism, such as negative frequency-dependent selection, where the net fitness of each phenotype changes depending on the selective environment (e.g., rare-morph advantage) (Kunte 2009; Le Rouzic et al. 2015; Svensson et al. 2005). Such frequency-dependent advantages could arise from elevated male mating harassment as a given female morph increases in frequency (Gosden and Svensson 2009; Svensson et al. 2005; Takahashi et al. 2014; Van Gossum et al. 2001) or through Batesian mimicry, when predators selectively target common morphs (Kunte 2009). Other mechanisms, like static trade-offs between natural and sexual selection, are not expected to maintain polymorphism, because they are unlikely to be perfectly balanced in the long run (Kunte 2009).

Abiotic and biotic factors could also interact and differentially affect the relative fitness of the different female forms in *P. icarus*. For example, if heat absorption rates vary between female phenotypes, some females can have an advantage under cold environmental conditions (i.e., blue females, which are common in the spring generation) in terms of escaping male mating harassment, but such blue females might then have a disadvantage under warm environmental conditions (i.e., in summer). However, a previous study indicated little to no variation in warming rate between *P. icarus* of different sexes (and thus coloration) (Keyser et al. 2015). Other potentially important phenotypic effects of wing scale structures include hydrophobia (Potyrailo et al. 2007), which could be advantageous under high precipitation conditions. Thus, future studies should experimentally test to what extent brown and blue wing scales provide differential tolerance to temperature, humidity and other environmental factors.

Interactions between abiotic factors like temperature and sexual selection, sexual conflict and frequency-dependent selection are gaining increased attention and merit further investigation (Chevin et al. 2022; García-Roa et al. 2019, 2020; Parrett and Knell 2018; Svensson et al. 2020; Svensson and Connallon 2019). Female blue wing colour in *P. icarus* is (semi-)continuous and is not only genetically determined but also partly phenotypically plastic and affected by temperature (Figure 2C–E), which makes this butterfly system differ from other polymorphic systems with a few quite discrete, highly heritable morphs (Iversen et al. 2019; Kunte 2009; Kunte et al. 2014; Willink et al. 2024). Nevertheless, the challenge remains of explaining the maintenance of genetic phenotypic variation. Based on our electron microscopy results (Figure 3) we suggest that blue females are partly masculinised, since they have a scale nanostructure similar to males. It remains to be investigated if blue *P. icarus* females are also masculinised in other traits, such as wing shape, behaviour, or physiology. Recent empirical research is consistent with cross-sexual transfer and includes molecular studies focusing on Dmrt genes, including the transcription factor doublesex (Dsx). Dmrt genes affect sexual dimorphism (Kopp 2012) and play causal roles in the development of intrasexual phenotypic variation in several female colour polymorphic systems (Kunte et al. 2014; Willink et al. 2020). One future goal would be to test to what extent this gene family is mechanistically involved also in generating female colour variation in *P. icarus*.

In conclusion, our study reveals that the striking variation in the amount of blue on female *P. icarus* wings arises through the same mechanism that produces the entirely blue wings of males, strongly suggesting that this trait emerged through cross-sexual transfer and through co-option of an already existing developmental mechanism. The genomic architecture and the adaptive significance of this extensive phenotypic variation remain to be investigated, including how ecological factors like predation and sexual conflict interact with environmental factors like temperature and precipitation.

Author Contributions

Magne Friberg and Erik I. Svensson designed the research. Kristoffer Mjörnman, Karolina Pehrson and Magne Friberg collected data. Erik I. Svensson; Magne Friberg, Kristoffer Mjörnman and Karolina Pehrson analysed the data. Magne Friberg and Erik I. Svensson wrote the manuscript, with contributions from Kristoffer Mjörnman and Karolina Pehrson.

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Data Availability Statement

The data that support the findings of this study and the R-scripts are openly available in Zenodo. DOI: https://doi.org/10.5281/zenodo.15936583.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70190-sup-0001-Supinfo.docx.