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On the origins of sexual dimorphism in butterflies

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The processes governing the evolution of sexual dimorphism provided a foundation for sexual selection theory. Two alternative processes, originally proposed by Darwin and Wallace, differ primarily in the timing of events creating the dimorphism. In the process advocated by Darwin, a novel ornament arises in a single sex, with no temporal separation in the origin and sex-limitation of the novel trait. By contrast, Wallace proposed a process where novel ornaments appear simultaneously in both sexes, but are then converted into sex-limited expression by natural selection acting against showy coloration in one sex. Here, we investigate these alternative modes of sexual dimorphism evolution in a phylogenetic framework and demonstrate that both processes contribute to dimorphic wing patterns in the butterfly genera *Bicyclus* and *Junonia*. In some lineages, eyespots and bands arise in a single sex, whereas in other lineages they appear in both sexes but are then lost in one of the sexes. In addition, lineages displaying sexual dimorphism were more likely to become sexually monomorphic than they were to remain dimorphic. This derived monomorphism was either owing to a loss of the ornament ('drab monomorphism') or owing to a gain of the same ornament by the opposite sex ('mutual ornamentation'). Our results demonstrate the necessity of a plurality in theories explaining the evolution of sexual dimorphism within and across taxa. The origins and evolutionary fate of sexual dimorphism are probably influenced by underlying genetic architecture responsible for sex-limited expression and the degree of intralocus sexual conflict. Future comparative and developmental work on sexual dimorphism within and among taxa will provide a better understanding of the biases and constraints governing the evolution of animal sexual dimorphism.

Keywords: *Bicyclus*; *Junonia*; phylogeny; Nymphalidae; stochastic character mapping

1. INTRODUCTION

Animal sexual dimorphism played a large role in the development of sexual selection theory [1–3]. The importance of sexual dimorphism in sexual selection theory began with an unresolved debate between Charles Darwin and Alfred Wallace on the timing of sex-limited inheritance of sexually dimorphic traits. Specifically, Darwin asserted that a novel trait preferred by the opposite sex would arise simultaneously with sex-limited inheritance, and that sexual selection maintained and exaggerated the dimorphism [1]. By contrast, Wallace hypothesized that traits arose without sex-limited inheritance (i.e. were expressed in both sexes), and natural selection acted against conspicuous traits in the sex that suffered greater risk of predation [3]. By Wallace's reasoning, natural selection, not sexual selection, subsequently produced the dimorphism by 'converting' equal inheritance of the trait to sex-limited inheritance [2]. Although sexual selection theory has significantly matured since the debate between Darwin and Wallace, both hypotheses remain plausible explanations for the origin of sexual dimorphism and deserve re-examination in a phylogenetic context [4,5].

Primary in discussions of sexual dimorphism are the ornamentation patterns in butterflies and birds [1,3].

Plumage evolution in birds has received considerable phylogenetic treatment, and multiple modes of dimorphism evolution are evident [6]. In some taxa, dimorphism evolves by a single sex becoming more conspicuous [7], while others support the model of Wallace, where both sexes are ancestrally conspicuous, but one sex, most often female, becomes less conspicuous [8]. By contrast, although both Darwin's and Wallace's models of sexual dimorphism evolution are evident in avian taxa, no study, to our knowledge, has tested the applicability of each model to sexual dimorphism in butterflies.

To assess the relative support for alternative models of sexual dimorphism evolution, a comparative approach is necessary. This approach must account for potentially independent trait evolution in males and females because sexual dimorphism may originate in two ways: (i) a trait may arise in one sex alone, corresponding to Darwin's model of simultaneous origin and sex-limited expression of a trait (single sex gain, SSG) or (ii) a trait arises in both sexes but is subsequently lost in one sex, as predicted by Wallace's model (single sex loss, SSL) [4]. The applicability of these two models, SSG and SSL, can then be assessed by measuring the frequency of each process in ancestral state estimates of sexual dimorphism.

Also critical to our understanding of sexual dimorphism are the events following the evolution of dimorphic characters. Sexually dimorphic characters may follow one of three fates: stasis, where the lineage remains sexually dimorphic; loss of the dimorphic character, where the lineage becomes monomorphic and neither sex

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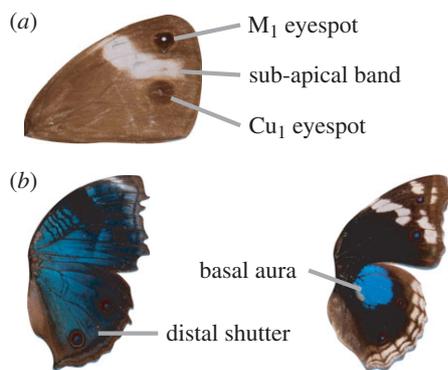


Figure 1. Schematic of dorsal wing characters of (a) *Bicyclus* and (b) *Junonia* included in this study.

possesses the conspicuous ornament; or gain of the dimorphic character by the non-ornamented sex, where the lineage becomes monomorphic and both sexes possess the conspicuous ornament [5]. In the latter case, sex-limited expression of a trait is converted to dual-sex expression; the possibility of such occurrences is a relatively unexplored mechanism for explaining the evolution of mutual ornamentation.

Here we present a phylogenetic investigation of sexual dimorphism evolution using the butterfly genera *Bicyclus* Kirby (Nymphalidae: Satyrinae) and *Junonia* Hübner (Nymphalidae: Nymphalinae). In *Bicyclus*, eyespots and bands present on the dorsal surface of the forewings are probably under sexual selection [9–11], and phylogenetic data for this genus are available [12], making it a model system to test hypotheses of sexual dimorphism. Although little is known about the selective pressures on *Junonia* dorsal characters (but see [13]), the presence of sexual dimorphism in some species, coupled with the available genetic data [14] provide another opportunity for investigations of sexual dimorphism evolution. We analysed wing pattern evolution in *Bicyclus* and *Junonia*, focusing on conspicuous dorsal wing characters which exhibit sexual dimorphism in at least one species (figure 1). We addressed three questions critical to our understanding of the evolution of sexual dimorphism: (i) by what mode does sexual dimorphism arise? (ii) how often do lineages switch between monomorphism and dimorphism? and (iii) what is the evolutionary fate of sexually dimorphic lineages?

2. MATERIAL AND METHODS

(a) Ancestral state estimates of wing characters

We used available genetic data for *Bicyclus* [12] and *Junonia* [14] to generate Bayesian posterior distributions of tree estimates for ancestral state reconstructions. For each of the two datasets, we performed two Bayesian Markov Chain Monte Carlo (MCMC) runs of four chains each [15], using a separate model of evolution for each of the loci. The two *Bicyclus* loci each fit a unique HKY + G + I model (partition 1: mitochondrial cytochrome oxidase subunits I and II; partition 2: nuclear elongation factor 1- α ; [9]), while the three *Junonia* loci were each allowed a unique GTR + I model (partition 1: mitochondrial cytochrome oxidase subunit I; partition 2: nuclear elongation factor 1- α ; partition 3: nuclear wingless). Trees sampled before likelihood values converged and the standard deviation of the split frequencies of the two runs

decreased below 0.01 were discarded. For the *Bicyclus* data, we ran a total of 20 million MCMC generations, retaining only trees sampled from the latter 10 million generations. The two Bayesian runs on the *Junonia* data converged in fewer generations, so we only ran 10 million MCMC generations, sampling trees from the latter 5 million generations. Bayesian consensus trees were congruent with those of previous published studies [9,12,14].

We scored dorsal wing characters in *Bicyclus* and *Junonia*, and for ancestral state reconstructions focused on those characters displaying sexual dimorphism (figure 1; see the electronic supplementary material, table S1). We analysed three dorsal forewing characters in *Bicyclus*: the eyespot in cell M_1 (also known as the ‘anterior’ eyespot), the Cu_1 (‘posterior’) eyespot, and the sub-apical band. The sub-apical band is a clearly defined band of colour, usually white or violet, distinct from the brown wing ground colour in the anterior-distal portion of the forewing. For *Junonia*, we analysed two dorsal hindwing characters, the basal aura and the distal shutter. The basal aura is an elliptical patch of colour, usually blue or purple, located on or proximal to the discal cell. The distal shutter is characterized by blue scaling which extends from the wing margin inward to at least the discal cell. All characters were scored as ‘present’ or ‘absent’ based on museum specimens housed at the Harvard Museum of Comparative Zoology, the Yale Peabody Museum or the American Museum of Natural History. In cases where museum specimens were unavailable or ambiguous in character state, we referred to species diagnoses in published works [16–18]. For species with sub-specific variation in character states, we used the character state observed in the subspecies from which genetic material was obtained. Digital images of all museum specimens used for character scoring are available at <http://www.lepdata.org/monteiro/lepdata.html> or by request from the authors.

We first performed likelihood ratio tests to determine whether a one-rate (gains and losses happen at the same rate) or a two-rate (gains and losses occur at significantly different rates) model of evolution better fits each character [19]; a distribution of the test statistic (difference in likelihood scores using a one-rate versus two-rate model) was generated on a sample of 1000 trees from the post-burn-in posterior distribution of trees produced in MCMC searches. A two-rate model was assigned to those characters in which the critical value ($\Delta \ln L = 2$) fell below the 95 per cent upper tail of the distribution; when the critical value was above the lower 95 per cent of the distribution, a one-rate model was applied (see the electronic supplementary material, table S3). Using stochastic character mapping [20] in MESQUITE [21], we simultaneously reconstructed male and female ancestral states of each character on a tree drawn randomly from the post-burn-in posterior distribution of trees generated in MCMC searches, using the best-fit model from likelihood ratio tests for each character. We repeated the ancestral state estimation for 10 000 post-burn-in trees to generate a distribution of 10 000 estimates of ancestral states for each character; MESQUITE modules for generating ancestral state distributions are available in the AUGIST package for MESQUITE [22]. These ancestral state distributions were used in all subsequent analyses of sexual dimorphism evolution.

(b) Origins of sexual dimorphism

We assessed the applicability of the two models of sexual dimorphism origin (SSG and SSL) by comparing the

number of times each process was responsible for the evolution of sexual dimorphism. For each tree, we counted the number of dimorphisms originating via SSG and the number originating via SSL. To evaluate if one process (SSG versus SSL) occurred more often than the other, we calculated the difference in the estimated number of SSGs and SSLs for a given tree drawn from the Bayesian posterior distribution. We concluded that the two processes occurred at different rates when zero (equal number of SSGs and SSLs) fell outside the 95 per cent distribution. This approach is more conservative than a paired *t*-test, but provides a rigorous assessment of relative importance of each process in generating sexual dimorphism. An alternative to this approach would use likelihood ratio tests (or similar parametric assessments), but current models do not allow for simultaneous changes in multiple characters [21,23]; this condition almost certainly occurs at a non-trivial frequency within the taxa investigated here.

(c) *Relative rate of dimorphism evolution*

We estimated the relative likelihood of gains and losses of sexual dimorphism by comparing the frequency at which dimorphism evolves from monomorphism and vice versa. Although there are two qualitatively different ways dimorphism may shift to monomorphism (the dimorphic trait could be lost, or the dimorphic trait could be gained by the opposite sex), we first consider both types of monomorphism (both sexes lack the trait or both sexes possess the trait) together. For each tree sampled from the posterior distribution, we calculated the difference in the number of origins of sexual dimorphism and origins of monomorphism (loss of sexual dimorphism). Significant differences in rates were indicated by frequency distributions in which zero (equal number of gains and losses of sexual dimorphism) was in the lower 5 per cent of the observed distribution. We provide estimated frequencies at which gains and losses occurred for each character for qualitative comparisons.

(d) *Fate of sexual dimorphism*

To investigate the evolutionary fate of sexually dimorphic lineages, we estimated: (i) the frequency at which sexual dimorphism was lost, relative to how often lineages remained sexually dimorphic (stasis); (ii) the relative frequencies at which the two types of monomorphism (neither sex possesses the ornament versus both sexes possess the ornament) arise from sexual dimorphism; and (iii) the frequency that sex-limited expression of a character was converted to a dual-sex expression. In these three comparisons, we restricted our analyses to those trees in which at least one ancestral node in the tree was estimated to be sexually dimorphic. That is, we excluded histories in which the fate of sexually dimorphic characters could not be assessed owing to the absence of any ancestral (non-contemporary) sexually dimorphic lineages. This resulted in fewer than 10 000 trees being included in final results; see the electronic supplementary material, table S4 for a full list of the number of trees included in specific analyses.

For (i), we calculated the difference in the number of static lineages and the number of lineages in which sexual dimorphism shifted to monomorphism. This differs from the preceding analysis in that we are not considering only those branches in the tree where a change occurs (e.g. gains and losses), but rather we are considering all branches in the tree where an ancestral node was reconstructed as

sexually dimorphic for the character in question, and assessing whether the lineage remained sexually dimorphic (i.e. no changes along the branch leading to the immediate descendant) or the lineage became sexually monomorphic (i.e. a loss of sexual dimorphism). Positive values of this difference indicate that dimorphic lineages were more likely to convert to monomorphism than remain dimorphic, while negative values indicate a greater likelihood of stasis, relative to shifts to monomorphism. We again applied a 95 per cent cut-off to measure significance: a difference in stasis versus shifts to monomorphism was only inferred if zero fell beyond the 95 per cent frequency distribution.

We compared the relative frequencies of the two types of transitions from dimorphism with monomorphism (ii) by counting the number of times each occurred in a sampled history. In those lineages that shift from sexual dimorphism to sexual monomorphism, two types of monomorphism are possible: 'drab monomorphism' occurs when the ornament is lost and 'mutual ornamentation' occurs when the opposite sex gains the ornament. To assess if the two types of monomorphism evolved from dimorphism at different rates, we calculated the difference in the number of each transition type for each sampled tree. We concluded rates were significantly different when a difference of zero occurred in fewer than 5 per cent of the sampled trees.

In addition to comparing the rates of evolution of mutual ornamentation and drab monomorphism, we measured the frequency of changes from sex-limited expression to dual-sex expression (iii). We estimated the absolute number of times mutual ornamentation evolved from sexual dimorphism for each character, and we tested if this occurred at least once for each character. We concluded conversion to dual-sex expression for a character occurred at least once if fewer than 5 per cent of the reconstructions returned estimates of zero conversions to monomorphism for that character. In addition to this conservative assessment of whether this conversion in expression is possible, we also report the average number of times such events were estimated to occur for each character.

3. RESULTS

(a) *Origins of sexual dimorphism*

Both modes of evolution, single-sex gain (figure 2*a,c*) and single-sex loss (figure 2*b*), are responsible for the evolution of sexual dimorphism in the taxa studied here, although there is a variation between sexes and among characters in the frequencies of each process (figure 3). In female *Bicyclus* and both sexes of *Junonia*, SSGs were more common than SSLs, significantly so for the sub-apical band in *Bicyclus* ($p = 0.001$); the band originated with female-limited expression more often than it was converted from dual-sex expression to male-limited expression. The two processes, however, did not occur at significantly different rates for the M_1 eyespot ($p = 0.255$) and Cu_1 eyespot ($p = 0.125$) in *Bicyclus* females. The two processes did not occur at significantly different rates in either *Junonia* character, although SSGs may occur at higher rates than SSLs in males (basal aura: females $p = 0.852$, males $p = 0.069$; distal shutter: females $p = 0.534$, males $p = 0.058$). By contrast, SSLs were more common than SSGs in *Bicyclus* males, i.e. dimorphism was owing more often to a loss of the ornament in males, rather than a gain by males alone; however, no character displayed significant differences

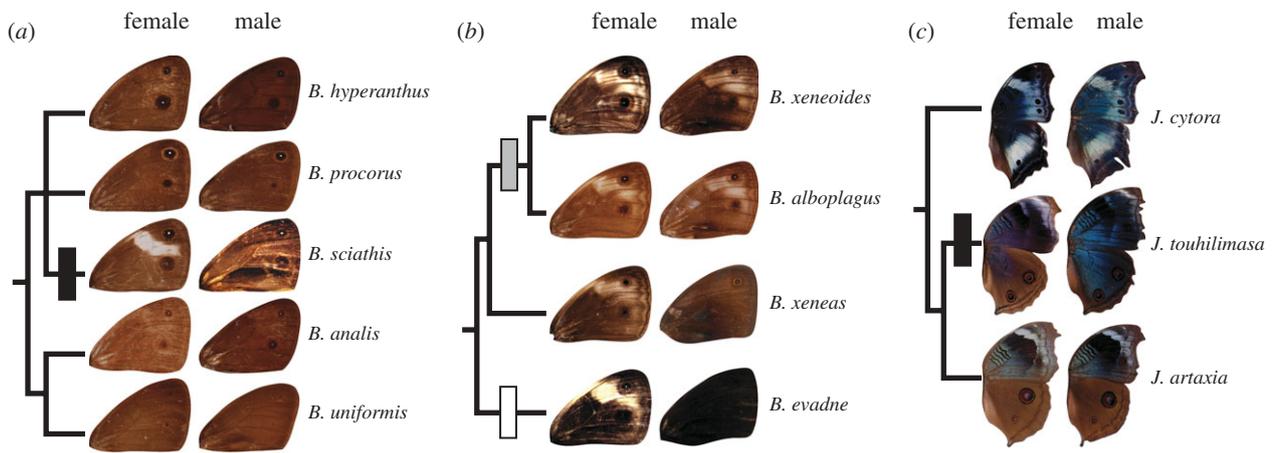


Figure 2. Examples of sexual dimorphism evolution in *Bicyclus* and *Junonia*. (a) Single sex gain (SSG): the sub-apical band was gained by females alone in the lineage leading to *B. sciathis*. (b) Single sex loss (SSL): male expression of the M_1 eyespot was lost in the lineage leading to *B. evadne* (white bar). (c) SSG: the distal shutter was gained by males alone in the lineage leading to *Junonia touhilimasa*. The grey bar in (b) highlights conversion of female-limited expression of the sub-apical band to dual-sex expression in the lineage ancestral to *B. alboplagus* and *B. xeneoides*.

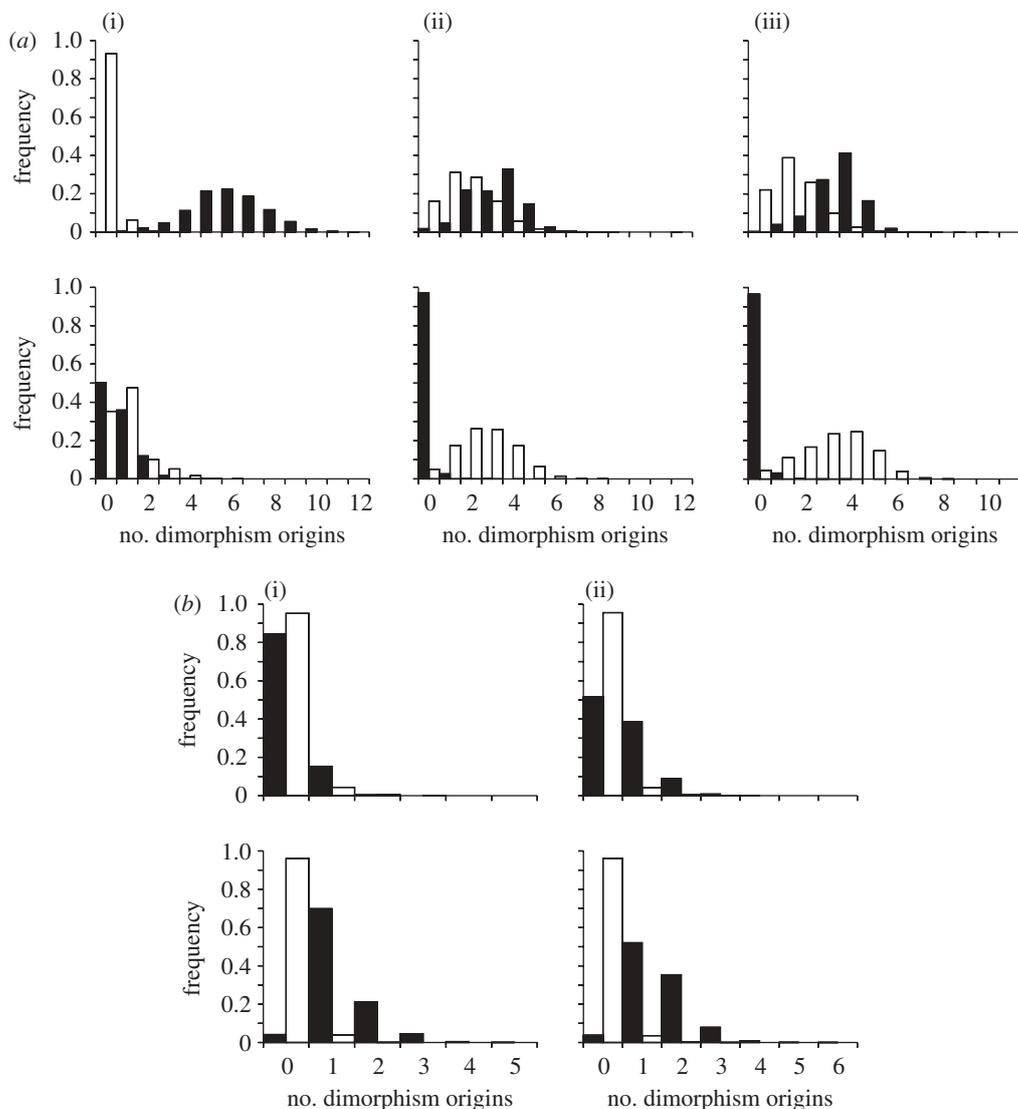


Figure 3. Frequency of each mode of sexual dimorphism evolution in (a) *Bicyclus* and (b) *Junonia*. The y-axis depicts frequency in the Bayesian tree distribution of estimated number of origins of sexual dimorphism owing to SSGs (black) and SSLs (white). Changes that occur in female characters are shown in the top row of graphs, while the bottom row of graphs reflects changes in male characters. (a) (i) Sub-apical band; (ii) M_1 , eyespot and (iii) Cu_1 , eyespot. (b) (i) Basal aura and (ii) distal shutter.

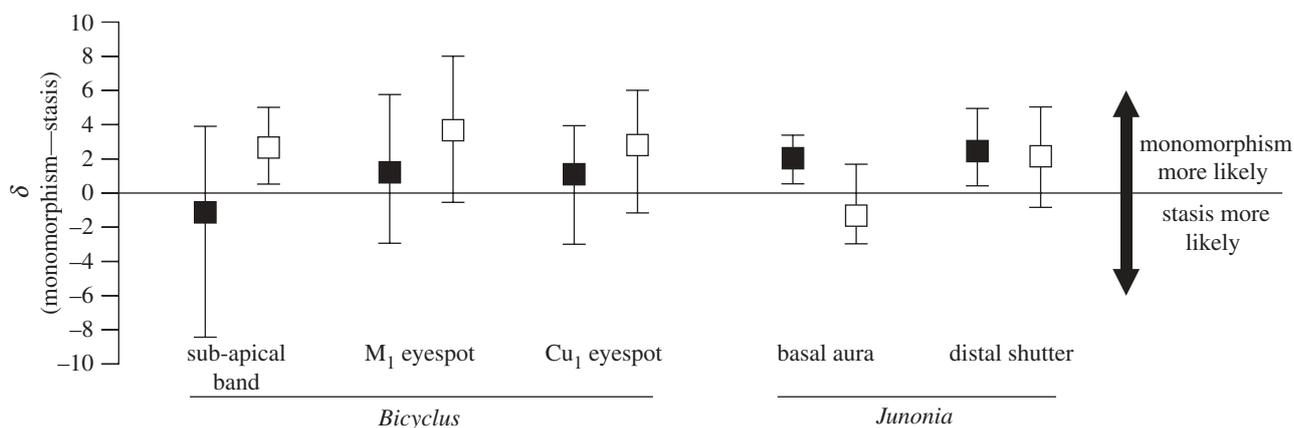


Figure 4. Comparisons between the number of lineages shifting from dimorphism to monomorphism and lineages maintaining sexual dimorphism (stasis) in (a) *Bicyclus* and (b) *Junonia*. Estimated number of differences (δ) are based on stochastic character mapping on post-burn-in Bayesian trees. Filled squares represent lineages where females were the ornamented sex, open squares represent lineages in which males were the ornamented sex. Positive values indicate more occurrences of shifts to monomorphism than stasis; negative values indicate stasis occurred more often than shifts to monomorphism. Bracketed values show upper and lower bounds of 95% distribution.

in the relative frequencies of each process in males (sub-apical band, $p = 0.614$; M₁ eyespot, $p = 0.059$; Cu₁ eyespot, $p = 0.053$).

(b) Relative rate of dimorphism evolution

On average, shifts from dimorphism to monomorphism occurred at higher frequencies than shifts from monomorphism to dimorphism for all characters and sexes in both *Bicyclus* and *Junonia* (see the electronic supplementary material, figure S1). Although mean estimates of losses of sexual dimorphism were consistently higher than gains, our conservative approach failed to detect significant differences between gains and losses.

(c) Fate of sexual dimorphism

The majority of dimorphic characters, on average, were more likely to become monomorphic than remain dimorphic (figure 4). Three characters displayed significant differences between the two processes: *Bicyclus* lineages with sub-apical band expression restricted to males were more likely to become sexually monomorphic than remain sexually dimorphic ($p = 0.005$); both *Junonia* characters, when only present in females, were more likely to become sexually monomorphic than remain sexually dimorphic (basal aura, $p = 0.001$; distal shutter, $p = 0.001$).

Both types of sexual monomorphism (drab monomorphism and mutual ornamentation) have evolved from sexually dimorphic lineages in *Bicyclus*. The evolution of drab monomorphism occurred at a significantly higher frequency than the evolution of mutual ornamentation for two *Bicyclus* characters, the M₁ and Cu₁ eyespots (see the electronic supplementary material, figure S2a). In sexually dimorphic lineages where females alone were ornamented with either the M₁ eyespot or the Cu₁ eyespot, these characters were more likely to be lost by females (resulting in drab monomorphism) than gained by males (resulting in mutual ornamentation) (M₁: $p = 0.007$; Cu₁: $p = 0.036$). In *Junonia*, the evolution of drab monomorphism occurred, on average, more often than the evolution of mutual ornamentation, although we did not detect any significant

differences between the two processes (see the electronic supplementary material, figure S2b).

The evolution of mutual ornamentation from sexual dimorphism, via a gain of the dimorphic trait by the opposite sex, occurred in at least two characters in *Bicyclus*, the sub-apical band and the M₁ eyespot (see the electronic supplementary material, table S2). This mode of evolution is not only probable but in some cases necessary to explain the current patterns of character diversity in *Bicyclus* (see the electronic supplementary material, table S2). The recipient sex (the unornamented sex that subsequently gained the character in question) varied by character: both males and females gained the sub-apical band from the opposite sex at least once (males: mean number of gains, $g = 3.95$, probability of zero conversions to dual-sex expression, $p = 0.030$; females: $g = 2.74$; $p = 0.033$), whereas *Bicyclus* females gained the M₁ eyespot from sexually dimorphic males at least once ($g = 6.83$; $p = 0.034$). Although the evolution of mutual ornamentation from sexual dimorphism is possible in the history of *Junonia*, we could not reject the possibility of zero conversions to dual-sex expression in any *Junonia* characters investigated here (see the electronic supplementary material, table S2).

4. DISCUSSION

Our analyses support both hypotheses advocated by Darwin [1] and Wallace [3] for the origin of sexual dimorphism: some sexually dimorphic ornaments arise concomitantly with sex-limited expression (figure 2a,c), while others arise in both sexes but are subsequently lost in one sex (figure 2b). Thus both modes of evolution are applicable to the evolution of sexual dimorphism in butterflies. There were notable differences between sexes, however, in the frequency of each mode of evolution in *Bicyclus*: SSGs were always more frequent in females than SSLs, while the opposite, SSLs more frequent than SSGs, was true for males (figure 3a). That is, when dimorphism arose owing to a change in female ornamentation, it was most often owing to the simultaneous origin of the trait and female-limited

expression of that trait rather than by the temporal separation of these two processes advocated by Wallace. However, when dimorphism arose via a change in male ornaments, it was most often owing to a loss of that ornament in males alone, while females retained the ornament. This two-step process, the origin of a trait in both sexes, followed by its subsequent loss in one sex, presumably owing to the cost of bearing that trait, has generally been applied to ornaments limited to males, not females [3].

Our results show notable differences and similarities with previous phylogenetic analyses of the evolution of sexual dimorphism. Origins of sexual dimorphism in birds are commonly owing to losses of ornamentation or bright coloration in females, corresponding to the SSL model of Wallace [3,8,24]. Although two characters had relatively higher rates of SSLs than SSGs (the M_1 and Cu_1 eyespots of male *Bicyclus*), the majority of our estimates suggest SSGs are more common than SSLs in explaining the evolution of sexual dimorphism in *Bicyclus* and *Junonia* (figure 3). The simultaneous gain and sex-limited expression of dimorphic traits is relatively uncommon in birds ([8,24]; but see [7,25] for possible examples), but it contributes significantly to sexual dimorphism in the butterflies studied here. In the special case of female-limited mimicry, the butterfly genus *Papilio* demonstrates sexual dimorphism originating as an amalgamation of the theories of Darwin and Wallace: female-limited expression evolves with the novel aposematic wing pattern, as hypothesized by Darwin, yet the novel phenotype is advantageous owing to natural selection, not sexual selection, via increased protection from predators gained by mimicking an unpalatable model species [26,27]. The diversity of mechanisms underlying the evolution of sexual dimorphism demonstrates the use of both models [1,3] and highlights the necessity of considering both male and female trait evolutions separately in the study of sexual dimorphism [4,24].

In another striking departure from avian systems, the females of most *Bicyclus* species are more ornamented on the dorsal surface than males. There are multiple, although not mutually exclusive, explanations for this phenomenon. First, female ornamentation could be owing to direct selection on females [4]. The high frequency of SSGs relative to SSLs in females (figure 3a) is predicted under a model where males select mates on the basis of female dorsal wing patterns. Recent behavioural work on *Bicyclus anynana* corroborates the possibility of sexual selection acting on female *Bicyclus* dorsal wing patterns [10]. Female ornamentation in *Bicyclus* may also be a byproduct of selection against dorsal ornaments in males, evidenced by the repeated losses of the two dorsal forewing eyespots in males (figure 3a, bottom row). *Bicyclus* wing evolution fits a signal partitioning model, where ornaments presumed to be under sexual selection are hidden on the concealable, dorsal surfaces of the wings [9]. Despite this strategy, it is possible that during flight the dorsal wing ornaments are still conspicuous to predators. If male *Bicyclus* do most of the mate searching, as observed in *B. anynana*, then males could be at greater risk of predation than females, and conspicuous ornaments in males are selected against by natural enemies. Dorsal wing patterns may serve

different functions in the two sexes, and thus be subject to different selective regimes, especially if there are significant differences in behaviour or habitat use. The relative costs and benefits of ornamentation in butterflies should be further assessed in order to determine the importance of natural and sexual selection in determining butterfly coloration across taxa.

An alternative explanation for the variation in dorsal surface ornamentation between the sexes could involve differences between the sexes in selection on ventral patterns, coupled with genetic correlations between dorsal and ventral wing patterns [28,29]. If selection favouring ventral eyespots is stronger in females than in males, this could lead to more ornamented female dorsal patterns if correlations between eyespots on different surfaces are strong enough. However, the ubiquitous presence of ventral hindwing eyespots in both sexes and near absence of dorsal hindwing eyespots in the genus *Bicyclus* [9], coupled with selection experiments demonstrating the potential for developmental independence among eyespots in *B. anynana* [30,31], argues against selection on ventral wing patterns being a major driver of dorsal pattern evolution.

Differences in the modes of sexual dimorphism evolution between butterflies and birds, e.g., SSGs being more common in butterflies, whereas SSLs more common in birds [8,24], may be owing to different proximate mechanisms used to control sex-limited expression of traits in insects versus vertebrates. For instance, in *Drosophila* the only cells and tissues that express either the male or the female splice versions of transcription factors at the end of the sex-determination pathway (*double-sex* and/or *fruitless*) are those involved in building sexually dimorphic traits, whereas most other cells in the body are not sex-aware [32]. By contrast, in birds and other vertebrates, sex-determination transcription factors determine the identity of the gonads, which, in turn, secrete different ratios of male and female hormones into the bloodstream [33]. Every cell in the vertebrate body is thus potentially aware of its sex. How these distinct mechanisms of informing cells about their male and female identities influence the likelihood of traits being gained or lost in a sex-specific way requires additional investigation.

Despite the differences in mode of character evolution between the sexes, male and female characters showed similar patterns in the tempo of sexual dimorphism evolution: losses of sexual dimorphism were, on average, more common than gains (see the electronic supplementary material, figure S1). This trend away from sexual dimorphism was also evident when we measured the relative occurrence of stasis in sexually dimorphic lineages, and found that it generally occurs less frequently than a conversion to sexual monomorphism (figure 4). Shifts in habitat use (e.g. between open and closed habitats) have the potential to influence sexual dimorphism evolution [34,35], and may explain patterns observed in *Bicyclus* and *Junonia*. Both genera have experienced repeated shifts from dense equatorial forest habitats to more open habits [12,13,16], a process which may influence the evolutionary dynamics of sexual dimorphism.

The conversion of sex-limited expression to dual-sex expression (figure 2b, see the electronic supplementary material, table S2; [24,36]), illustrates the potential role

of sexual dimorphism in adaptive evolution of phenotypes shared by both sexes. Novel signals may arise as sexually dimorphic traits and evolve via sexual selection, but subsequently become co-opted for a similar signalling function in the opposite sex or for alternative functions. If the selective benefit, either owing to reciprocal sexual signalling or natural selection, becomes great enough, dual-sex expression may become favoured over sexual dimorphism, resulting in the evolution of mutual ornamentation [37]. Sexual dimorphism may be a relatively ephemeral condition, a midpoint crossing an adaptive valley leading to mutual ornamentation. This transition could occur in the following series of steps: (i) a novel trait evolves in both sexes, but is beneficial to one sex and detrimental to the other, leading to 'intra-locus sexual conflict' [37]; (ii) sexual dimorphism in the trait is favoured (either evolving with the origin of the trait or arising subsequently by selection against the presence of the trait in the sex to which it is detrimental); (iii) the trait becomes beneficial to both sexes, owing to changes in the trait or changes in the fitness of bearing the trait; and (iv) mutual ornamentation evolves, either owing to a loss in sex-specific expression, or a gain of sex-specific expression in the sex which formerly did not express the trait. This potential for sexual dimorphism to drive adaptive evolution requires additional attention to determine its relative importance in butterfly wing pattern evolution.

5. CONCLUSION

Considerable attention has been paid to the evolution of sexual dimorphism, and our results support a pluralistic view of sexual dimorphism origins [1,3]. The diversity of processes giving rise to sexual dimorphism in butterflies illustrates the complex mechanisms probably underlying wing pattern evolution. SSGs (figure 2*a,c*) may occur via co-option of pre-existing genetic architecture underlying differences in trait expression between the sexes [38], while SSLs (figure 2*b*) suggest that sexual dimorphism may arise to alleviate intra-locus sexual conflict [37]. Pursuing the developmental mechanisms underlying sex-limited expression of colour patterns in butterflies, as well as shifts to mutual ornamentation, will allow a more detailed mechanistic understanding of the diversity of evolutionary patterns, and the potential biases and constraints underlying those processes. Finally, additional studies of butterfly sexual dimorphism will allow comparisons with other taxa, most notably birds, to assess how different sex-limited gene expression mechanisms influence modes of sexual dimorphism evolution.

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