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THE EVOLUTION OF WING COLOR: MALE MATE CHOICE OPPOSES ADAPTIVE WING COLOR DIVERGENCE IN *COLIAS* BUTTERFLIES

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Abstract.—Correlated evolution of mate signals and mate preference may be constrained if selection pressures acting on mate preference differ from those acting on mate signals. In particular, opposing selection pressures may act on mate preference and signals when traits have sexual as well as nonsexual functions. In the butterfly *Colias philodice eriphyle,* divergent selection on wing color across an elevational gradient in response to the thermal environment has led to increasing wing melanization at higher elevations. Wing color is also a long-range signal used by males in mate searching. We conducted experiments to test whether sexual selection on wing melanization via male mate choice acts in the same direction as natural selection on mate signals due to the thermal environment. We performed controlled mate choice experiments in the field over an elevational range of 1500 meters using decoy butterflies with different melanization levels. Also, we obtained a more direct estimate of the relation between wing color and sexual selection by measuring mating success in wild-caught females. Both our experiments showed that wing melanization is an important determinant of female mating success in *C. p. eriphyle*. However, a lack of elevational variation in male mate preference prevents coevolution of mate signals and mate preference, as males at all elevations prefer less-melanized females. We suggest that this apparently maladaptive mate choice may be maintained by differences in detectability between the morphs or by preservation of species recognition.

Key words.—Ecological speciation, elevational gradient, mate preference, mate signal, Pieridae, wing melanization.

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Correlated evolution of mate signals and mate preference requires that intraspecific variation in mate signals be matched by intraspecific variation in mate preference. The coevolution of mate signals and mate preferences is well studied for the evolution of sexual ornaments (Lande 1981; Kirkpatrick 1982; Bakker 1993; Andersson 1994). In this case, mate preference causes directional selection on signal evolution, and mate signals coevolve with mate preferences until resultant costs imposed by natural selection make further evolution unlikely. An alternative scenario for correlated evolution between mate signals and mate preferences occurs when divergent natural selection shapes mate signals, and sexual selection leads mate preferences to coevolve with mate signals (Jiggins et al. 2001). This scenario forms one of the key ingredients of ecological speciation theory, in which divergent natural selection results in ecotypes that differ in mate signals, followed by a corresponding divergence of mate preferences: for example, through genetic correlation between mate signals and mate preferences (Schluter 2001; Turelli et al. 2001). However, correlated evolution of mate preferences may be constrained if selection pressures acting on mate preferences are different from those acting on mate signals.

Particularly when traits have sexual as well as nonsexual functions, various factors could cause the sexually preferred ecotype to differ from the one favored by natural selection. For example, mechanisms underlying preference, such as detectability, may prevent the divergence of mate preference: even though mating with one phenotype may yield higher fitness once a mate is found, if mates of that type are more difficult to find, the overall fitness gains may be less (Endler 1992; Schluter and Price 1993). Also, intraspecific sexual selection often involves the same traits as those used in species recognition (West-Eberhard 1983; Ryan and Rand 1993), and therefore divergence of mate preferences along an ecological gradient may be constrained by the fact that species recognition leads to contraction of variance in mate preference.

Here, we use a system in which divergent natural selection results in population divergence in wing color (a mate signal) to study the corresponding effect on the evolution of mate preferences. In many butterflies, wing color is essential in thermoregulation, due to effects of wing color on body temperature and flight ability (Watt 1968; Kingsolver 1983a, 1988; Van Dyck et al. 1997). A higher degree of wing melanization results in darker wings. Darker wings absorb more sunlight and enable lateral basking butterflies to raise their body temperature sufficiently to allow flight and hence fitness-related activities such as oviposition and nectaring in females, and patrolling, mating, and nectaring in males. However, darker wings may also cause overheating in warm climates (Watt 1968; Kingsolver and Watt 1983; Kingsolver 1988, 1995; Van Dyck et al. 1997). The thermoregulatory function of wing melanin is under natural selection (Kingsolver 1995). At the same time, sexual selection plays an important role in the evolution of wing color in butterflies, as shown by color manipulation experiments that change attractiveness of potential mates (Cook et al. 1994; Wiernasz 1995).

We conducted experiments to test how sexual selection interacts with natural selection on wing color in the butterfly

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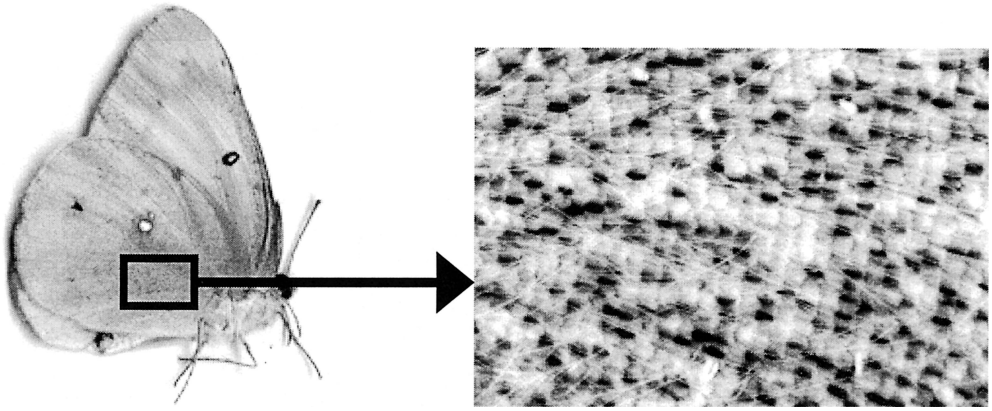

FIG. 1. The ventral side of the hindwing of *Colias philodice eriphyle*. Melanization of the hind wing was measured in an area of fixed size just below the discal cell (inside the black square). The magnified image clearly shows the individual scales that can either be yellow or black in this species. The percentage of this area covered by the black (melanized) scales is the degree of melanization.

Colias philodice eriphyle. In *C. p. eriphyle*, elevational variation in wing melanization is genetically based and heritable (Ellers and Boggs 2002). Earlier experiments showed divergent selection for wing color in *C. p. eriphyle* along an elevational gradient in the Rocky Mountains, leading to darker ecotypes in populations at higher elevations (Kingsolver 1983a; Ellers and Boggs 2002). If mate preference is evolutionarily tuned to favor ecotypes with the highest fitness, we expect to see different mate preferences at different elevations. However, if sexual selection opposes natural selection because of species recognition or detectability, mate preference is expected to be identical for all elevations. To test these predictions, we performed controlled mate choice experiments in the field over an elevational range of 1500 meters using decoy butterflies with different melanization levels to assess how female coloration affects males. Also, we obtained a more direct estimate of the relation between wing color and sexual selection by measuring mating success in wild-caught females.

MATERIALS AND METHODS

Study Sites and Populations

The butterfly *Colias philodice eriphyle* Edwards (Lepidoptera: Pieridae) is found over a large elevational range in the Colorado Rocky Mountains (1500–3000m). Located in Gunnison and Delta counties, our study sites were native meadow habitat in Paonia (Pa; 1840 m), lower Gold Basin (Gb; 2350 m), Elk Meadows (Em; 2420 m), Brush Creek (Bc; 2810 m), and Willow Creek (Wc; 2920 m). We also sampled populations in alfalfa fields at Delta, Utah (De; 1415 m) and Honey Lake, California (Hl; 1225 m) for studies of female mating success.

Measurement of Melanization Level

Colias wings consist of a large number of tiny scales that can either be yellow or black (melanized). Increasing darkness of the wings is caused by a greater number of scales being melanized. Melanization of the hind wing was measured in an area of fixed size and fixed location on the ventral side of the wing (Fig. 1). The wing was photographed on a standard gray background using a black and white camera mounted on a microscope and connected to a computer with MorphoSys software (Meacham and Duncon 1991). In Adobe Photoshop the image was standardized for contrast through a percentage saturation stretch of the tonal histogram of the image (Wilkie and Finn 1996). This commonly used remote sensing technique ensures that the full range of black tones for each image is used by setting the bottom and top first percentile of the black tonal range to pure black and white. Subsequently, the percentage of the standardized image that was melanized was measured using a threshold value of 70 (on a scale of 0–255 tones). Individuals with a higher level of melanization were referred to as ''darker,'' and individuals with a lower level of melanization were referred to as ''yellower.''

Male Mate Preference Experiment

The *Colias* mating system is nonterritorial, with males visually searching overlapping, large areas for females (Silberglied and Taylor 1978; Rutowski 1991). When a sitting female is seen, the male approaches her and initiates courtship. The number of matings a male can achieve is limited not only by the availability of females, but also by the male's ability to donate resources to the female in addition to sperm (Boggs and Watt 1981; Rutowski and Gilchrist 1986; Rutowski et al. 1987). This may be an important reason for males to discriminate among mates (Rutowski 1984; Forsberg 1987). Females also exhibit mate preference (Watt et al. 1986); however, it is based on male courtship persistence (Rutowski 1979). Females do not discriminate directly based on within-species differences in wing color (Silberglied and Taylor 1978). Therefore, only male mate choice is expected to be affected by wing color, so we did not investigate the female component of mating behavior here.

We used decoy butterflies to investigate differences in male mate preference among elevations. Decoy females were produced by scanning a newly dead *C. p. eriphyle* female with the wings closed. The coloration of the decoys was manipulated by changing the darkness of the decoy through adjusting the tonal histogram of the image. This darkens or lightens the overall color of the wing surface and thus results

TABLE 1. The number of *Colias philiodice eriphyle* males that passed at one meter or dipped toward at least one of the decoy females in the mate choice experiments. The three levels of wing melanization of decoy females were: yellow (Y), intermediate (I), and dark (M).

Morph:	Y:M			Y:I			I:M			Total		
Site	1 m	Dip	%	1 m	Dip	%	1 m	Dip	%	1 m	Dip	%
Pa	56	25	44.6	86	35	40.7	59	25	42.4	201	85	42.3
Gb	78	50	64.1	81	49	60.5	66	19	28.8	225	118	52.4
Em	20	8	40.0	17	5	29.4	23	8	34.8	60	21	35.0
Bc	45	20	44.4	44	30	68.2	43	16	37.2	132	66	50.0
Wc	57	32	56.1	96	38	39.6	27	8	29.6	180	78	43.3

in an increase or decrease in the number of black scales. The initial female scanned was of intermediate melanization level. The procedure thus resulted in decoys with three different levels of melanization that span the range from melanization levels of low elevation populations to high elevation populations: yellow, intermediate, and dark. Using the same method to evaluate degree of darkness as was used to determine melanization in real butterflies (see above, *Measurement of Melanization Level*), dark decoys were 15% darker than the average female from our high elevation sites, and yellow decoys were 15% yellower than the average female from our low elevation sites. Nonetheless, both decoys were well within the natural range of melanization levels that we found at these sites. After the images were printed out, a left and right side were glued together with a wire strip in between. This design assures that the three morphs were completely standardized for confounding factors such as scale wear, size, and other wing characteristics, and differed only in wing color. *Colias philodice eriphyle* wings do not reflect ultraviolet (Silberglied and Taylor 1978, Grula and Taylor 1980); this was reproduced in our decoys.

In the experiments, two decoy types were staked in the soil one meter apart with the decoy butterflies just above the top of the vegetation (about 15 cm from the soil). The vegetation consisted of open meadow, dominated by grasses and forbs. Three replicates of such pairs were placed three meters from each other. The behavior of each male flying within one meter of one of the decoys was recorded. Males were judged to be attracted to the decoy when they changed the direction of their flight path to approach within 20 cm of the decoy. Multiple approaches of one male toward decoys of the same phenotype were scored as a single approach to avoid pseudoreplication.

All experiments were carried out between 0930 h and 14 00 h in July and August 2000, solely under sunny conditions. Experiments lasted one to two hours and were performed three times at each site to test all possible combinations of melanization levels: yellow versus intermediate, yellow versus dark, and intermediate versus dark. Sites used were Pa, Gb, Em, Bc, and Wc (see above).

Female Mating Success

In a second test, we obtained a more direct estimate of the relation between wing color and sexual selection by measuring mating success in wild-caught females. While mating, male *Colias* transfer spermatophores that contain both sperm and nutrients, and remain detectable in the bursa copulatrix of the female (Boggs and Watt 1981). These spermatophores are incompletely digested, and the number of fragments in the bursa can be used to determine the number of matings a female has received (Burns 1968).

We collected females from the highland population of Bc and the two lowland populations of Hl and De by hand netting during September 1999 and September 2000. Females were frozen after capture. In the laboratory, the bursa copulatrix was dissected out of the abdomen of the females, and the number of spermatophores was counted. We discarded any females that were of the alba morph (a morph missing the yellow pigment in the wings [Gerould 1911; Watt 1973] and whose female mating rates are known to be different from the yellow morph [Graham et al. 1980]), or that showed any sign of introgression with the close sister species *C. eurytheme* (orange pigment in the wings; Taylor 1972; Grula and Taylor 1980). The age of the female was estimated based on wing wear using a scale from one (no scale loss) to five (more than 50% of the scales lost). Age was included as a factor in the analyses since the number of matings increases with age.

RESULTS

Male Mate Preference

We observed 798 male *C. p. eriphyle* flying within one meter of our paper decoys (Table 1). On average, among all populations, 44.6% of these males dipped to one or more of the decoy females. Although the number of males observed flying differed among populations ($\chi^2 = 107.1$, df = 4, $P < 0.001$), the percentage of males reacting to the decoys did not differ significantly among populations ($\chi^2 = 4.24$, df = 4, $P = 0.376$). Also, we did not observe any other species of butterfly approaching our models, indicating that the models sent out a species-specific signal and were not attractive because of their resemblance to more general stimuli such as flower color.

The results of the mate choice experiments were uniform: in all five populations, males dipped more often to the yellower decoy in any paired comparison (Fig. 2). This preference was significant in all but two cases (Pa, low elevation, and Em, intermediate elevation). Even at high elevations, where resident females resemble the darkest decoy phenotype, males significantly preferred the yellow and intermediate decoys over the darkest ones. The strength of male preference for each morph was relative rather than absolute: the number of approaches to intermediate phenotypes de-

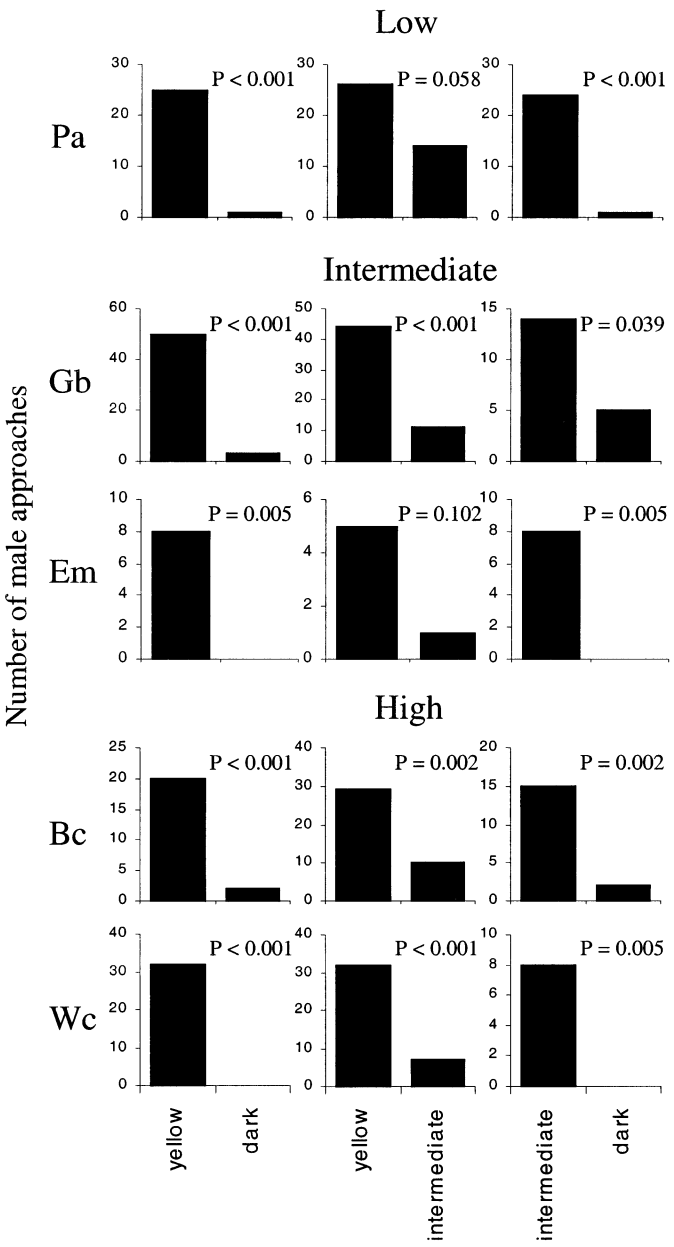

FIG. 2. The number of male approaches toward pairs of decoy females with three different wing melanization levels: yellow, intermediate, and dark. The experiments were performed at low (Pa: 1840 m), intermediate (Gb: 2350 m, Em: 2420 m), and high (Bc: 2810 m, Wc: 2920 m) elevation sites. See text for explanation of site codes.

pended on the melanization level of the paired phenotype. In a paired experiment with the yellow decoy the intermediate decoy received significantly fewer approaches than when paired with the dark decoy (Wilcoxon signed rank test: $n = 5$, $Z = -2.02$, $P = 0.043$). These results predict that throughout their elevational range, yellow females have a higher mating success than their darker conspecifics.

Female Mating Success

The relationship between wing melanization and number of matings by females was examined in two lowland and one highland populations of *C. p. eriphyle*. In total, we examined 149 females for the number of spermatophores and level of wing melanization. Earlier studies showed that in *Colias* the number of matings increases with age (Graham et al. 1980; Rutowski and Gilchrist 1986), and our results are consistent with that (Spearman rank correlation for all three populations: $R_S = 0.412$, $P < 0.001$). To avoid any confounding effects of age on the relationship between wing melanization and mating success, both age and wing melanization were included in the analysis.

For the lowland populations we used an analysis of covariance that included age as a factor and wing melanization as a covariate. The highland population data deviated from normality; hence we controlled for age using a Kendall partial rank order correlation. Again, there was a uniform result for all populations: mating success of females increased with decreased melanization of the hind wing (Fig. 3; De: $F = 4.05$, $P = 0.049$; Hl: $F = 5.48$, $P = 0.025$; Bc: Kendall's tau $= -0.31$, $P < 0.05$). These results are consistent with the behavioral experiments and strongly suggest that the lower attraction of males to darker females is a major part of the cause of the reduction of mating success of such females.

Evolution of Male and Female Wing Coloration

If sexual selection indeed favors pale females, there should be differential selection pressures on male and female wing coloration, since sexual selection would affect the wing color of females only, whereas natural selection for thermal characteristics should affect both sexes. However, the predicted evolutionary response of wing melanization does not depend only on the selection pressures on wing melanization but also on the underlying genetic structure. The genes involved in wing melanization in *C. p. eriphyle* are sex-linked (Ellers and Boggs 2002). Given that in Lepidoptera females are the heterogametic sex, yellow females will pass on their genes for yellow wings only to their sons, not to their daughters. If male preference for yellow females leads to a greater fitness for yellower females, then males in the next generation will be lighter than expected by natural selection alone, although this effect will be moderated by their paternal set of genes that have not been subject to sexual selection. On the other hand, the females in the next generation will receive their X-linked genes solely from their father, not their mother, and as a consequence they will exhibit the degree of melanization of their father. The net result is that male melanization reflects the balance of sexual and natural selection in the previous generation, whereas female melanization reflects the effects of natural selection alone in the previous generation, although ghosts of sexual selection past will certainly have some effect on female melanization. Given that natural selection favors increasing melanization with increasing elevation, the prediction therefore is that males should show a weaker increase in wing melanization with elevation than females.

Data for wing melanization in Ellers and Boggs (2002) allow us to test such a prediction. The data in Figure 1 in Ellers and Boggs (2002) indeed show a shallower slope for males than females, but the interaction between sex and elevation is not significant (regression analysis: $t = -0.71$, $P < 0.49$). Therefore, we should conclude that in these pop-

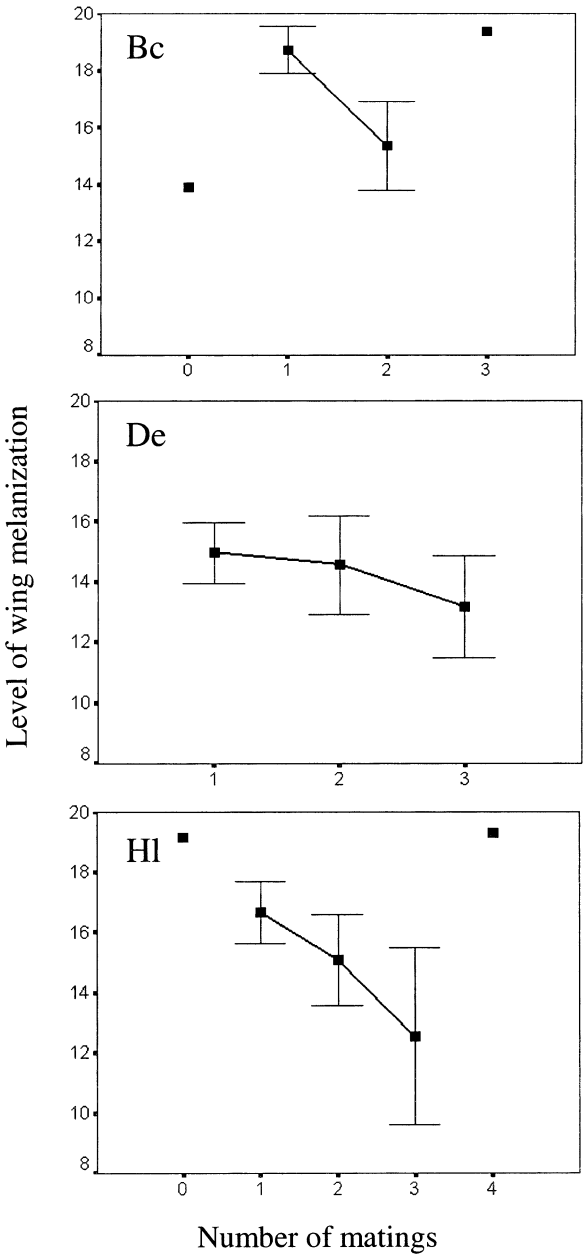

FIG. 3. The relationship between the level of hind wing melanization (means ± SE) and number of matings in *Colias philodice eriphyle* from a highland (Bc: 2810 m), and lowland populations (De: 1415 m and Hl: 1225 m). See text for explanation of site codes. Single datapoints are not connected by lines.

ulations at this point in time the strength of natural selection exceeds the strength of sexual selection, although both remain important.

DISCUSSION

Colias philodice eriphyle exhibit strong phenotypic divergence in wing melanization across an elevation gradient (Kingsolver 1983a; Ellers and Boggs 2002). Both males and females have a higher level of wing melanization at high elevations (Ellers and Boggs 2002), creating an opportunity for correlated evolution of mate preference and signal among elevations. Although our results show that wing melanization is an important determinant of female mating success in *C. p. eriphyle*, males at all elevations prefer less melanized (i.e., yellower) females; thus the lack of elevational variation in male mate preference constrains adaptive wing color divergence. Because increased wing melanization is essential to reach adequate body temperatures for flight at high elevations (Watt 1968; Kingsolver 1983b), but not at low elevations due to the risk of overheating (Kingsolver and Watt 1983), females face a trade-off between attractiveness and flight performance that increases with increasing elevation.

The use of simultaneous choice experiments to test the response of free-ranging males to different female morphs has been criticized by Silberglied (1984) as unrealistic because males rarely encounter more than one female at a time. However, a comparison between simultaneous, sequential choice tests and natural mate choice in *Papilio dardanus* showed that all three methods yielded similar results, thus validating the use of simultaneous tests (Cook et al. 1994). Furthermore, at least in some of the populations we examined, female densities were such that males may well encounter more than one female at a time. Another drawback of the use of paper decoys is that it only provides information about the very first stages of courtship, and may not reflect mating pattern beyond the first approach. Visual long-range signals only serve to bring potential mates together, whereas at close range the female may discriminate against males based on activity or pheromones (Rutowski 1979; Sappington and Taylor 1990). We addressed this problem by also looking at the relationship between wing color and mating success directly through counting the number of spermatophores in females. Since both approaches gave similar results, we can assume that the number of approaches by males is correlated to the actual number of matings achieved.

Despite the qualitative consistency between the two experiments, the relationship with wing color was stronger in the male preference experiments than inferred by differences in female mating success. Even among the more melanized females we caught in the field, only a very small proportion was unmated (J. Ellers and C. L. Boggs, unpubl. data), despite the fact that the dark decoy females were rarely courted in our male preference experiment. This suggests that female behavior can partly influence the number of matings that she receives. There are at least two possible ways by which this could happen. First, earlier work on *Colias* courtship behavior showed that females may actively solicit matings from males (Rutowski et al. 1981). Second, female melanization influences flight activity throughout the day, which may affect detectability by males. Such female behavior could act to ameliorate the negative effects of lower detectability of melanistic females. Also, there may be an advantage to low detectability because dark females may avoid time wasting as a result of harassment by males (e.g., for alba vs. yellow females, Nielsen and Watt 2000).

By contrast, few females received more than one spermatophore, especially at higher elevations. Given the fitness benefits of multiple matings it is highly likely that females would gain, rather than lose, from extra matings, and that a substantial proportion of females may be limited by matings.

In *Colias*, the causal relationship between spermatophore transfer and nutrient uptake by the female has been shown by a radiotracer study (Boggs and Watt 1981). Male-derived components were used in egg production and were distributed throughout the female's body, apparently aiding in somatic maintenance. Also, the amount of male-donated nutrients per mating has an effect on female reproductive output and longevity. A doubling of the male-ejaculate size results in a significant increase in female longevity of 25%, and significantly increases total egg production by 50% (Rutowski et al. 1987). A second benefit of a larger amount of male-donated nutrients is an increase in the rate of egg production. In the field, we found up to fourfold differences in mating success between the color morphs. Translating the effects of different sized contributions from one mating into effects of multiple matings, preferred color morphs may gain substantially in fecundity and reproductive output.

Male mate choice of yellow females at high elevations seems to be maladaptive, given the fitness differences associated with melanization levels (Kingsolver 1983b, 1995). This maladaptive mate choice can only persist if its fitness costs are counterbalanced by gene flow, constraints, or other selection pressures. A well-known reason for persistence of maladaptive characters is gene flow from populations under different selection pressures (Dias 1996). In *C. p. eriphyle*, gene flow from lower to higher elevations may exist as a result of the delayed phenology at higher elevations, as is known for other butterflies (Peterson 1995, 1997). Such predominantly upward dispersal patterns could lead to an influx of males with a mate preference for yellow females. However, two types of evidence invalidate this hypothesis: First, dispersal decreases with distance and thus we would expect to see a cline in the proportion of males preferring yellow females with increasing elevation, which is not supported by our data. Second, those migrant males themselves would experience a severe reduction in flight time, and consequently in mating success (Kingsolver 1983b).

Another hypothesis as to why males prefer yellower females at all elevations is detectability. Detectability is a function of the environment in which the courtship takes place, and the male's sensory system (Endler 1992; Schluter and Price 1993). For *Colias*, there is relatively little variation in the environmental background. *Colias philodice eriphyle* is found in similar open meadow habitat over its whole elevation range, which may explain the uniform preference of males. Also, a bias in the sensory system of males could favor yellow color patterns as more effective stimuli, and thus increase the perception of yellow wing color, as is known for specific colors in other butterfly species (Bernard and Remington 1991; Briscoe 2003).

Alternatively, the presence of another yellow *Colias* species, *C. alexandra*, may affect the evolution of wing color in *C. p. eriphyle*. Wing color signals may not only operate intraspecifically, but also interspecifically in species recognition. *Colias philodice eriphyle* and *C. alexandra* are sympatric at the higher elevations, and their adult flight periods partially overlap, which increases the likelihood of mating between the species. However, one distinction between these two species is that wing melanization is consistently higher in female *C. alexandra* compared to female *C. p. eriphyle* (J. Ellers unpubl. data). A tentative explanation for the lack of intraspecific divergence in mate preference in *C. p. eriphyle* is thus preservation of species recognition.

Several studies have addressed the interaction between sexual and natural selection within species. Previous studies focused on the evolution of male ornaments with a primarily sexual function (Lande 1981; Kirkpatrick 1982; Bakker 1993; Andersson 1994). However, in traits with multiple functions, trait evolution may be constrained if selection pressures work in opposing directions for each of the trait functions. More recent studies have considered traits under both natural and sexual selection pressures, resulting in trade-offs between attractiveness to mates and, for example, conspicuousness to predators (Endler and Houde 1995; Lederhouse and Scriber 1996; Gray and Cade 1999). In *C. p. eriphyle*, however, the divergence in mate signals results from divergent natural selection across a steep ecological gradient. Schluter and Price (1993) provided theoretical evidence that across an environmental gradient mate signals are expected to evolve far more readily than mate preferences. This finding may help explain why correlated evolution in mate preference has not evolved from divergence in mate signals in the *Colias* system.

Our results show a case of how natural and sexual selection interact in nature. We demonstrated that mate preference need not evolve as a correlated response to diverging mating signals. If our results have a more general applicability, they may be relevant to the study of ecological speciation. The key ingredient for the evolution of reproductive isolation in most models of ecological speciation is correlated evolution of mate signals and preferences (Schluter 2001; Turelli et al. 2001). Despite the fact that the *Colias* system follows the assumptions of the ecological speciation models (wing melanization is under divergent natural selection, is genetically based, and involved in mate choice), our results showed no evidence of correlated evolution of mate signals and mate preferences. Thus, at present, reproductive isolation is unlikely to develop in this system.

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