Review

Phenotypic plasticity, sexual selection and the evolution of colour patterns

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Summary

When a population comes to occupy a new environment, phenotypically plastic responses alter the distribution of phenotypes, and hence affect both the direction and the intensity of selection. Rates of evolution can be accelerated or retarded compared to what would happen in the absence of plasticity. Plastic responses in one trait result in novel selection pressures on other traits, and this can lead to evolution in completely different directions than predicted in the absence of plasticity. In this paper I use the concept of the adaptive surface in order to identify conditions under which the various different outcomes are expected. I then discuss differences between sexually and naturally selected traits. Sexually selected traits are often expected to be plastic in their expression, with individuals in high condition developing greater elaboration. As examples of sexually selected traits I review the evolution of colour patterns in birds with a view to assessing the magnitude of plastic responses in their development, and to ask how such responses may have influenced genetic evolution. The common colour pigments in birds are carotenoids and melanins. Both are used in social signaling, and consequently are expected to evolve to be phenotypically plastic indicators of an individual's quality. Perhaps partly because they are condition indicators, the quantity of carotenoids in the plumage can be strongly influenced by diet. Examples are described where alterations of carotenoids in the diet are thought to have altered the phenotype, driving genetic evolution in novel directions. Melanin patterns seem to be less affected by diet, but the intensity of melanization after moult is affected by social interactions during the moult and by raising birds in humid conditions. Hormonal manipulations can have dramatic effects on both the kinds of melanin produced (eumelanin or phaeomelanin) as well as the patterns they form. Differences between species in melanin patterns resemble differences produced by environmental manipulations, as well as those produced by simple modulations of parameters in computer simulations of pattern formation. While phenotypic plasticity is one way that genetic change in plumage patterns (and other traits) could be driven, there are others, including the appearance of major mutations and selection on standing variation whose distribution is not altered in the new environment. I consider some evidence for the different alternatives, and ask when they might lead to qualitatively different evolutionary outcomes.

Introduction

Phenotypic plasticity is defined as an organism's ability to express different phenotypes depending on its environment (Agrawal, 2001; Garland, Jr and Kelly, 2006). It may take the form of a flexible behaviour that changes over a few seconds or a developmental switch that permanently affects the adult form. Phenotypic plasticity has two potential roles to play in driving genetic changes. First, once a population becomes established in a new environment, plasticity may be essential for that population to survive and persist (Baldwin, 1896; Morgan, 1896; Robinson and Dukas, 1999). Second, the plastic response itself also sets the context whereby selection pressures drive evolution (Pigliucci and Murren, 2003; Price et al., 2003; West-Eberhard, 2003). For example, a population of sharp-beaked ground finches *Geospiza difficilis* in the Galápagos feed extensively on blood from boobies, and this population has a particularly sharp bill (Schluter and Grant, 1984). The interpretation is that behavioural change – blood feeding – has precipitated novel selection pressures favoring increased efficiency on this resource, resulting in evolution of beak shape.

Sexually selected traits are theoretically expected to be phenotypically plastic indicators of an individual's condition or quality (e.g. Nur and Hasson, 1984; Grafen, 1990;

Qvarnström and Price, 2001). This is because advertising at high levels reaps higher benefits in terms of high mating success, but only those individuals in good condition are able to bear the costs of carrying an exaggerated version of the trait. Similar principles apply to traits used in other social contexts, for example in threat displays (Hurd and Enquist, 2001) or mate stimulation after pair formation (Wachtmeister, 2001). The way by which such plasticity might influence evolution of socially selected traits does not seem to have been widely discussed (West-Eberhard, 2003). In this paper I investigate the role of phenotypic plasticity in affecting the expression of colour patterns in birds, and consider examples where plastic responses may have been evolved in affecting directions of genetic evolution. The paper is in two parts. (1) I review the general mechanism whereby plasticity influences genetic evolution. (2) I ask how plasticity and novel selection pressures interact to drive the evolution of colour patterns in birds.

Genetic differentiation

Probably the most important way by which plastic traits become genetically based lies in the process known as genetic assimilation (Waddington, 1953; Waddington, 1959; Waddington, 1961; Waddington, 1965; Pigliucci and Murren, 2003; Price et al., 2003). In this case the plastic response to the new environment is incomplete. There is therefore directional selection favouring extreme phenotypes in the novel environment and hence some genetic evolution of the trait (e.g. Waddington, 1959). Plasticity may be reduced as part of the selection regime, but this is not part of genetic assimilation as it was originally defined [e.g. (Waddington, 1961), p. 289]. For example, in one experiment (Waddington, 1959), Waddington investigated the magnitude of a phenotypically plastic response to altered salt conditions in larvae of *Drosophila melanogaster* (described in Price et al., 2003). When Waddington raised a population in high salt he found that the area between the anal papillae increased. After maintaining the population in high salt for ~20 generations, he found the area between the anal papillae in normal salt was similar to the phenotypic response to high salt at the beginning of the experiment. The trait had been genetically assimilated, but plasticity was not reduced, because when the pupae were raised in high salt conditions the area was reduced still further.

Genetic assimilation is one of a number of ways whereby evolution in response to selection is precipitated by phenotypically plastic changes (West-Eberhard, 2003). These alternatives have been extensively reviewed by West-Eberhard, who classes them all in the term 'genetic accommodation' (West-Eberhard, 2003). A particularly important additional class is when plastic responses in one trait, e.g. a foraging behavior, lead to genetic changes in other traits, e.g. morphology. A second way arises if phenotypically plastic changes produce maladaptive responses, resulting in genetic evolution that restores the mean phenotype (Grether, 2005). Grether labels this process 'genetic compensation' (Grether, 2005), and in this case geographic uniformity in

phenotype masks underlying geographical variation in genotype.

A simple way to model genetic accommodation is *via* the adaptive surface (Price et al., 2003). The concept of the adaptive surface was introduced by Sewall Wright to model changes in gene frequencies (e.g. Wright, 1959). It was extended to phenotypic evolution in a verbal model (Simpson, 1953), and this model was subsequently mathematically addressed using quantitative genetic theory (Lande, 1976). Suppose each individual in a population is measured for a trait of interest, e.g. its colour, and each individual is also assigned a fitness value (e.g. the number of young it produces over its lifetime). The adaptive surface is a plot of how the average fitness of all the individuals in the population would change as a function of the average value of the trait, provided the variability in the population is held constant (Lande, 1976; Fear and Price, 1998) (an example is in Fig. 1). In theoretical work, the main purpose of the adaptive surface is to model directions and rates of evolution. Given several critical assumptions (Wright, 1959; Lande, 1976; Fear and Price, 1998), the average value of a trait evolves to a position determined by a peak in the adaptive surface, and then remains there. Because the population may become stuck at a low peak, a central question in evolutionary theory has been how valleys in the adaptive surface are crossed (Wright, 1959; Coyne et al., 1997; Fear and Price, 1998). Phenotypic plasticity is one method of crossing valleys.
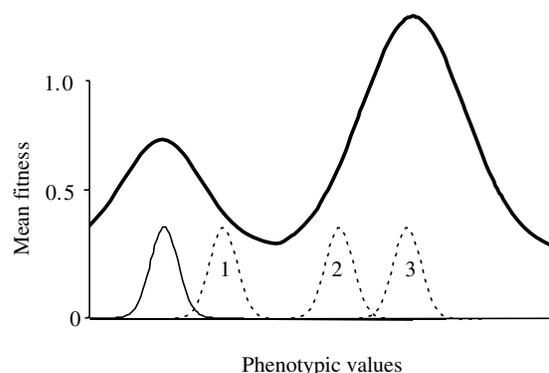

Fig. 1. The adaptive surface model of the contribution of phenotypic plasticity to successful colonization of a new environment. In this example the bold line is the adaptive surface (i.e. mean fitness curve). The solid thin line is the phenotypic distribution. For illustration, an environmental change is assumed to affect phenotypic plasticity without affecting the mean fitness curve, and to cause a shift in the mean of the phenotypic distribution without changing the variance. Broken lines indicate three levels of plasticity, from small (1) to moderate (2) to large (3). In (1), plasticity is insufficient to bring the population into the realm of attraction of the higher peak. This then leads to genetic evolution back towards the first peak, a process termed genetic compensation (Grether, 2005). In (2), plasticity brings the population into the realm of attraction of the higher peak, and there is then directional selection resulting in genetic change. In (3), plasticity is large, and the population is immediately centered under the higher peak; in this case there is no genetic change. A moderate amount of plasticity (2) is thus optimal for genetic assimilation.

The adaptive surface model can be used to illustrate when alternative outcomes such as genetic assimilation and genetic compensation are to be expected (Fig. 1). If in a new environment plasticity is small, a population remains stuck near the original peak. In this case selection results in evolution back towards the original peak (genetic compensation). The ancestral and derived populations have similar phenotypes, but the derived population evolves a different mean genotype to compensate for the plastic response, and differences should be revealed if populations are raised in a common environment. If plasticity is very large the population may move to the other peak, but here there will be no genetic change, because the population is already close to the optimal value. The absence of genetic response in the presence of much plasticity has been labeled the 'Bogart effect' and is discussed further elsewhere (Huey et al., 2003). An intermediate level of plasticity places a population on the other side of the valley, and results in selection for increased efficiency, hence genetic assimilation.

Price et al. studied these alternative outcomes using computer simulations (Price et al., 2003). If environments fluctuate randomly through time there is a threshold value of plasticity that is optimal for the maximal amount of genetic change. A run of extreme environments results in the population being held just across the valley for a series of generations. Each generation there is selection and evolution towards the higher peak. Then, even if there is a run in more mild environments, a reduction in the plastic response is insufficient for the population to come back into the realm of the lower peak, and evolution towards the higher peak continues.

There are several other ways by which populations can traverse adaptive surfaces (Wright, 1959; Coyne et al., 1997; Fear and Price, 1998). Two of the most common are likely to be environmental variation in both space and time that changes the form of the surface itself, and major mutations that bring a population into the realm of attraction of another peak (Fear and Price, 1998). Often the adaptive surface is likely to be complex, with many peaks and valleys. In this case phenotypic plasticity may result in exploration of the adaptive surface that results in adaptive change not realized through these alternative ways, such as when new behaviors result in genetic evolution of other traits. One example might be the way by which the woodpecker-niche in birds has been occupied. Although woodpeckers (family Picidae) themselves occupy this niche in most places of the world they have not colonized remote areas, and in their absence other species have evolved mechanisms to exploit grubs in trees. In the Galápagos islands, the woodpecker finch, *Camarhynchus pallidus*, uses a twig to extract grubs from crevices, whereas in the extinct New Zealand Huai, *Heteralocha acutirostris*, males and females had very different beaks, one for probing and one for mandibulating prey [on Madagascar and New Guinea, mammals, the aye aye *Daubentonia madagascariensis* and a marsupial *Dactylopsila palapator*, respectively, have elongated digits used for extracting grubs (Soligo, 2005)]. Such unusual mechanisms are most likely to have been driven, at least in part, by behavioural changes, and it seems less likely that major mutation or different selection regimes driven by unusual environments were the primary factors behind these unusual solutions to extracting grubs.

Sexually selected traits

The peak shift model is most suited to model the evolution of naturally selected traits. This is for at least two reasons. First, sexually selected traits are subject to frequency dependent selection. The absolute level of advertising is likely to be less important than the level relative to other individuals displaying in the population. For example, under sexual selection, provided all females mate, the average mating success (i.e. mean fitness) of a male never changes. This means that the adaptive surface describing the relationship between average mating success and the mean value of the male trait is flat, with no peaks and valleys. Thus, with frequency dependence, formal models of peak shifts become imprecise or cannot be used at all. Nevertheless the adaptive surface is still a useful heuristic concept: when there is frequency dependence, Wright described a surface depicting different optimal values and sketches of evolutionary trajectories towards these optima as a 'selective surface' (Wright, 1959). A second reason why sexual selection may be less well modeled by the adaptive surface than natural selection is because many examples of sexual selection indicate that extreme values are often the most attractive (bigger, brighter, louder) (Ryan and Keddy-Hector, 1992; Price, 1998). At first sight this implies that there are no true peaks in the surface, and all optima lie at infinity. However, when naturally selected costs are included there should be intermediate optima (e.g. being bigger, brighter or louder attracts predators) and there may well be a great diversity of different optima. Different environments impose different costs and as well as benefits (Endler, 1992; Schluter and Price, 1993; Slabbekoorn and Smith, 2002), and even in the same environment there are likely to be multiple solutions to the same problem. For example, two closely related species of warbler occupying very similar habitats sing songs of similar length and complexity, but different structure (Irwin, 2000).

It appears that the concept of the adaptive surface can be applied, at least for hueristic purposes, to the evolution of sexually selected traits. Few studies have explicitly investigated the importance of plasticity in driving the evolution of sexually selected traits from one peak to another on such a surface, but there are many studies that can be used to assess the plausibility of the process. Here I review studies on the evolution and plasticity of colour patterns, primarily of birds.

Diet, social behaviours and pigmentation

Many experimental and correlative studies have demonstrated the importance in social interactions of plumage

patterns in birds (Rohwer, 1982; Andersson, 1994; Jawor and Breitwisch, 2003). Unlike the other main socially selected trait in birds, vocalizations, colour patterns have clearly identifiable environmental and genetic bases. The size and brightness of a colour patch is often correlated with the condition and/or social status of the individual (Rohwer, 1982; Andersson, 1994; Johnstone, 1995; Pryke et al., 2002; Alonso-Alvarez et al., 2004). I focus on two major classes of pigment in birds, carotenoids and melanins, and consider some examples where these effects have contributed to population divergence.

Carotenoids

Different kinds of carotenoids are responsible for most of the red, orange and yellow colours in birds (Brush, 1990). They may also cause the occasional blue and violet (Völker, 1953), but this needs to be confirmed with modern analyses.

Carotenoid coloration is phenotypically plastic. Carotenoid-free diets result in very little colour in normally pigmented species, such as the house finch, *Carpodacus mexicanus* (reviewed by Hill, 1994a; Hill, 2002; Hudon, 1994) and great tit *Parus major* (see Figs 2, 3). Canaries are fed cayenne pepper and other additives to improve their feather colouration (Vriends, 1992). Manipulation of carotenoids also affects the colour of pigmented bare parts, such as the beak of the zebra finch, *Taeniopygia guttata* (McGraw and Ardia, 2003; Alonso-Alvarez et al., 2004). In natural populations, quantitative differences in carotenoid concentrations in different localities have been related to the presence of specific food plants (Ryan et al., 1994; Slagsvold and Lifjeld, 1985). In the great tit the carotenoid-based yellow in the breast plumage has been demonstrated to be a result of phenotypic plasticity *via* a cross-fostering experiment, and related to the quantity of caterpillars in the diet (Fig. 3) (Slagsvold and Lifjeld, 1985). In this species, nestling coloration is strongly affected by food

Fig. 2. Effects of an absence of carotenoids in the diet on the plumage colouration of male house finches from Michigan. The orange male was fed a carotenoid restricted diet (Hill, 1994b). Photo courtesy of Geoffrey E. Hill and David Bay.
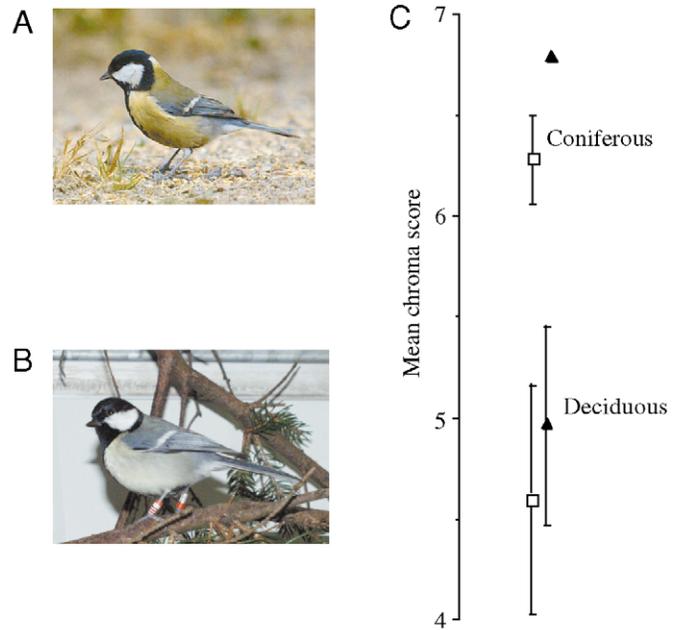

Fig. 3. (A) Great tit *Parus major*, from Holland. (B) Great tit raised in captivity. This individual resembles closely the phenotype of the subspecies of great tit that breeds in India (see Gompertz, 1968). Photographs courtesy of the Archives Netherlands Institute of Ecology, provided by A. J. van Noordwijk. (C) Chroma score (mean ± s.e.m.) (i.e. colour saturation) of whole great tit *Parus major* broods raised in deciduous and coniferous woodland near Trondheim, Norway (after Slagsvold and Lifjeld, 1985). Colour was measured on the yellow breast of young chicks at age 10–15 days. Chroma score is in arbitrary units, estimated by comparison to a colour guide. Triangles, broods transferred as eggs from one habitat to the other; squares, broods not transferred. Sample sizes are from top: 1 (hence no standard error on this point), 7, 3 and 6 broods. In a two-way ANOVA comparing locality of origin with locality of rearing, there is a significant effect of rearing environment ($F_{1,13}$=7.5, P=0.02) but none of laying environment ($F_{1,13}$=0.01, P=0.9).

provisioning in the first few days of nestling development (Fitze et al., 2003; Tschirren et al., 2003). In the related blue tit *Parus caeruleus*, provisioning of mothers with extra carotenoids resulted in brighter yellow plumage of their offspring (Biard et al., 2005).

The presence of carotenoids in the diet and their deposition in the plumage has led to genetic evolution. Thus, in many species carotenoids are modified biochemically after ingestion, including modifications that change yellow pigments to red (Brush, 1990; McGraw et al., 2004). Breeding experiments and analysis of hybrids have demonstrated genetic differences among species and populations in the quantity, colour and location of carotenoids deposited in the plumage (reviewed by Brush, 1990). For example, two closely related species of tanagers differ in having red or yellow rumps, and the hybrid is intermediate. In this case colour differences result from differences in the quantity (not type) of a single carotenoid, lutein, deposited in the feathers (Brush, 1990). In many species, genetically determined colour in the plumage may

have originally resulted from ingestion of carotenoids, followed by genetic evolution. In doves, the only species containing carotenoid pigments in their plumage are those that are frugivorous: carotenoid pigmentation has independently evolved three times in association with frugivory, but never appears in granivores (Mahler et al., 2003). This result is general: across species, availability of carotenoids in the diet is associated with the presence of carotenoids in the plumage; however, such an association has not been detected with respect to coloured bare parts (e.g. beaks, wattles, etc) (Olson and Owens, 2005).

Three examples of sexually selected carotenoid coloration have been reviewed (Grether, 2005), where some aspects of the colour (e.g. the brightness) are geographically rather invariant, even though the quantity or type of carotenoid available is geographically variable. Two are from different fish species, salmon *Oncorhynchus nerka* and guppy *Poecilia reticulata*, and one from a bird, the western tanager *Piranga ludoviciana*. The invariance is attributed to genetic compensation, and in the two fish examples, fish from geographically different locations were raised on common diets, clearly revealing underlying genetic differences despite phenotypic similarity.

A final example of genetic evolution comes from Hill's work on the size of the red breast patch of the male house finch (Hill, 1993; Hill, 1994b; Hill, 2002). Subspecies from Mexico and Michigan have similar patch colours, but the Mexican subspecies has a smaller patch (Fig. 4). Using morphological and biogeographical evidence, Hill estimated phylogenetic relationships among the subspecies (Hill, 1994b; Hill, 2002), and concluded that the Mexican subspecies was the derived one (however, the direction of evolution is not critical for the argument). Hill found that carotenoid manipulated diets prior to moult affected patch colour of both subspecies, but the size of the patches was not affected (Fig. 2) (Hill, 1993; Hill, 1994b). A hybrid between the two had an intermediate patch size, suggesting that size is genetically determined. Colour is a sexually selected trait and females from both populations prefer small red patches over large drab ones (Hill, 1994b). In the Mexican population Hill argues that a carotenoid deficient diet would have initially led to large drab patches (Hill, 1994b). Subsequently there was sexual selection favoring the sequestering of carotenoids over a smaller area of feathers, thereby increasing its brightness. In this way the patch evolves to a smaller size as a consequence of a direct environmental influence on the development of patch colour. The adaptive surface is illustrated in Fig. 5.

The major missing component to this study is the demonstration that carotenoid availability does differ between locations, as was shown in the salmon and guppy examples described by Grether (Grether, 2005). Hill brings several lines of circumstantial evidence that this is indeed the case [(Hill, 2002), chapter 11], including the finding of lower carotenoid concentrations in the diet of the Mexican population, as determined from gut contents.

Fig. 4. Geographical variation in colour patch size of house finches, *Carpodacus mexicanus.* The male on the left with the large patch is from Michigan (as in Fig. 2), that on the right with the smaller patch from Guerrero in Mexico (see Hill, 1993). Photo courtesy of Geoffrey E. Hill and David Bay.

Melanins

Melanins are the other major pigment in bird plumage, and are responsible for blacks, browns, many reds and occasional greens and yellows (Brush, 1978; Jawor and Breitwisch, 2003). Melanin pigments are formed very differently from carotenoids, being synthesized from the amino acid tyrosine as precursor. Dietary differences can affect the amount of melanin deposited (Sage, 1962), but the effects are not as striking as they are with respect to carotenoids.

Many species show geographical variation in melanin pigmentation. According to 'Gloger's rule', darker birds live in more humid environments; e.g. darker birds live in the Pacific north-west, and lighter ones in the Arizona deserts (Zink and Remsen, 1986). The rule is extremely strongly
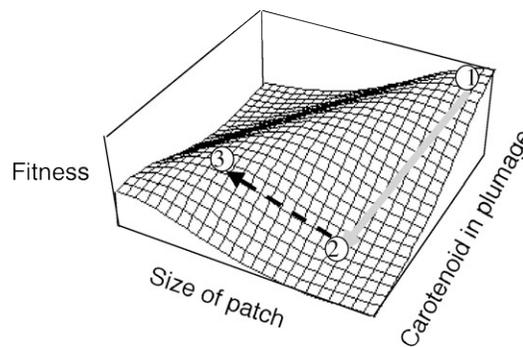

Fig. 5. Peak shift model for the evolution of the colour patch in male house finches, following published descriptions (Hill, 1993; Hill, 1994b). The Michigan population (1) is inferred to be ancestral, with a large red patch (see Fig. 4). Establishment in Mexico is thought to have resulted in fewer carotenoids in the diet, resulting in a large pale patch as a phenotypically plastic response (2; see Fig. 2). Subsequent selection to increase patch brightness resulted in genetic evolution of small patch size (3) as in the Mexican population (Fig. 4).

supported: in a survey of North American birds the association was found in 50/52 cases (Zink and Remsen, 1986). Underlying causes are poorly understood, but camouflage is the usual explanation (Zink and Remsen, 1986). Although the general intensity of pigmentation may be driven by naturally selected pressures, melanin patterns are widely used in social interactions. For example, painting experiments manipulating the size of many melanin-based patches have affected male dominance (Rohwer, 1982; Senar and Camerino, 1998; Jawor and Breitwisch, 2003).

Wood thrushes *Catharus mustelinus,* white-throated sparrows *Zonotrichia albicollis* and Inca doves *Columbina inca* were raised in extremely humid conditions indoors (Beebe, 1907), and after moult they all became much darker. In the white-throated sparrow the increase in melanin was associated with the appearance of a dark breast spot; such a spot is present in juveniles of this species, as well as in adults of the closely related American tree sparrow, *Spizella arborea.* After six moults, one Inca dove had become almost entirely black. Of particular interest was the development of a metallic sheen on the upperparts of this bird: such a sheen is present in the closely related scaled dove, *Columbina squammata.* Beebe also demonstrated changes in the size of pigmented patches in the tail and wing feathers of the Inca doves that matched and in later moults exceeded geographical variation.

Melanins are synthesized in specialized cells, melanocytes, and then transferred to growing feather cells. The interaction between the melanocyte and growing feather can result in a rich variety of alternative patterns, as has been demonstrated by introducing melanocytes from different breeds of chickens into the feather ectoderm of other breeds (Rawles, 1948). Such patterns can be easily altered experimentally. Particularly striking examples are shown in Fig. 6. In these examples injection of thyroxin (Lillie, 1932) or removal of the thyroid gland (Voitkevich, 1966) resulted in novel patterns. The modulations may result from effects on either the melanocyte or the feather, including growth rates, and can be mimicked by altering these parameters in computer simulations (Prum and Williamson, 2002) (see Fig. 6).

Besides thyroxin, several other hormones are known to influence the intensity and pattern of melanin pigmentation (Ralph, 1969). The male house sparrow *Passer domesticus* has a large melanin-based breast patch. Individuals injected with testosterone develop larger patches after moult (Evans et al., 2000). McGraw et al. maintained 14 triads of three male house sparrows each in captivity through the Autumn moult, and recorded the number of aggressive interactions the sparrows engaged in (McGraw et al., 2003). They found that triads engaging in more interactions amongst themselves on average grew larger black patches, and suggested a direct causal link between aggressive interactions, which lead to elevated testosterone levels, and the subsequent increased patch size (McGraw et al., 2003). There are many other examples where an individual's condition and/or dominance status is correlated with the size of melanin patches (Jawor and Breitwisch, 2003).

Thus, it seems possible that the establishment of genetically

based geographical variation and species differences in melanin patterns could be aided through environmental effects on both melanin intensity and pattern. However, genetic accommodation requires that plasticity affects many individuals, across several generations, so that selection can sort among them (Price et al., 2003). Many environmental variants in melanin patterns of large effect in nature seem to be confined to a single individual and disappear with that individual. Often, they are haphazard, asymmetrically placed patches of pigmented or unpigmented plumage that do not resemble differences seen between species (Sage, 1962). There are examples of more symmetrical patches as well as completely melanistic and albinistic individuals, but these often seem to be a result of genetic mutations of large effect, some of which may occasionally rise to high frequency (Sage, 1962).

In several carefully studied examples of melanism a single mutation of large effect has clearly driven divergence between populations (Mundy, 2005). Among bananaquit *Coereba flaveola* populations on the West Indies, an all-black form inhabits the humid highlands of two islands (Grenada and St Vincent). In the lowlands on each island the melanic type is replaced by the typical form. The gene responsible for the melanism has been identified and sequenced (Theron et al., 2001). The difference between the two forms appears to be due to a mutation at a single base position, so in this case differentiation is best attributed to a major mutation, and plasticity is unlikely to have played much of a role. It is worth noting, however, that in other cases of melanism invoking the MC1R gene, multiple base substitutions do seem to be involved (Mundy, 2005). This points to more continuous variation, and environmental effects could presumably have greater influence on this variation.

Discussion

Sexually selected traits are theoretically expected to be phenotypically plastic indicators of condition. Given that sexually selected traits are phenotypically plastic, this plasticity must affect rates and directions of evolution. In this discussion I ask whether such plasticity causes evolution in directions that would not otherwise be reached by other modes of evolution (specifically, selection in response to changing environments, or in response to the appearance of a major mutation).

Foraging behaviours are probably the best example whereby plasticity triggers new directions of evolution, which are unlikely to be achieved in other ways (Price et al., 2003). There are at least three differences between colour patterns and foraging behaviours that make directions of evolution in colouration likely to be less strongly influenced by plasticity. First, whereas novel foraging behaviours likely affect survival and persistence of populations in novel environments (Sol et al., 2005), sexually selected traits by the nature of their strong frequency dependence are likely to have much weaker influences on population survival. For example, it has been

generally difficult to detect an effect of plumage dichromatism in birds on extinction (Morrow and Pitcher, 2003). A number of studies did find that plumage dichromatism reduced the probability of that species becoming established in new locations following introductions by humans (McLain et al., 1999; Bessa-Gomes et al., 2003). However, the most recent analyses based on a large dataset, and controlling for introduction effort, did not find such an association. Instead, measures of foraging flexibility were found to be the only important variables affecting introduction success (Cassey et al., 2004; Sol et al., 2005).

The second difference between color patterns and foraging behaviors is that it seems likely that genetic variation underlying development of form (including colour patterns) lies along roughly the same axis as phenotypically induced environmental variation. More generally, phenocopies, whereby environmental perturbations mimic genetic mutations, are a common feature of development, attributed to the fact that genetic and environmental influences affect similar developmental processes (Zuckerkandl and Villet, 1998; West-Eberhard, 2003). An example is that the colour of the European great tit raised in captivity (e.g. Fig. 3) resembles that of the great tit from India (Gompertz, 1968). This means that although plasticity affects rate of evolution it will have less effect on directions of evolution. Finally, major mutations affecting color that differentiate species have been discovered (Price, 2002). In particular the MC1R gene affects both intensity and pattern of melanization in a number of groups. Melanism itself can be produced by a single point mutation (Mundy, 2005), suggesting that in this case at least, mutation was the driving force behind the origin of the melanic plumage.

In a specific example of the evolution of melanin-based patterns, Yeh studied a tail pattern in the dark-eyed junco *Junco hyenalis* determined by the presence/absence of melanin in patches of the outer tail feathers (Yeh, 2004). She studied different populations that had been separated for only about ten generations, but one population (occupying a novel environment) had 20% less white in the tail than the other. She raised juveniles from an early age in outdoor aviaries and found that the differences in the amount of white in the tail were retained through successive moults. The change therefore appears to have been a result of genetic evolution, and there is little evidence that plasticity in the amount of white in the tail has played any role in the evolution of mean levels of white.
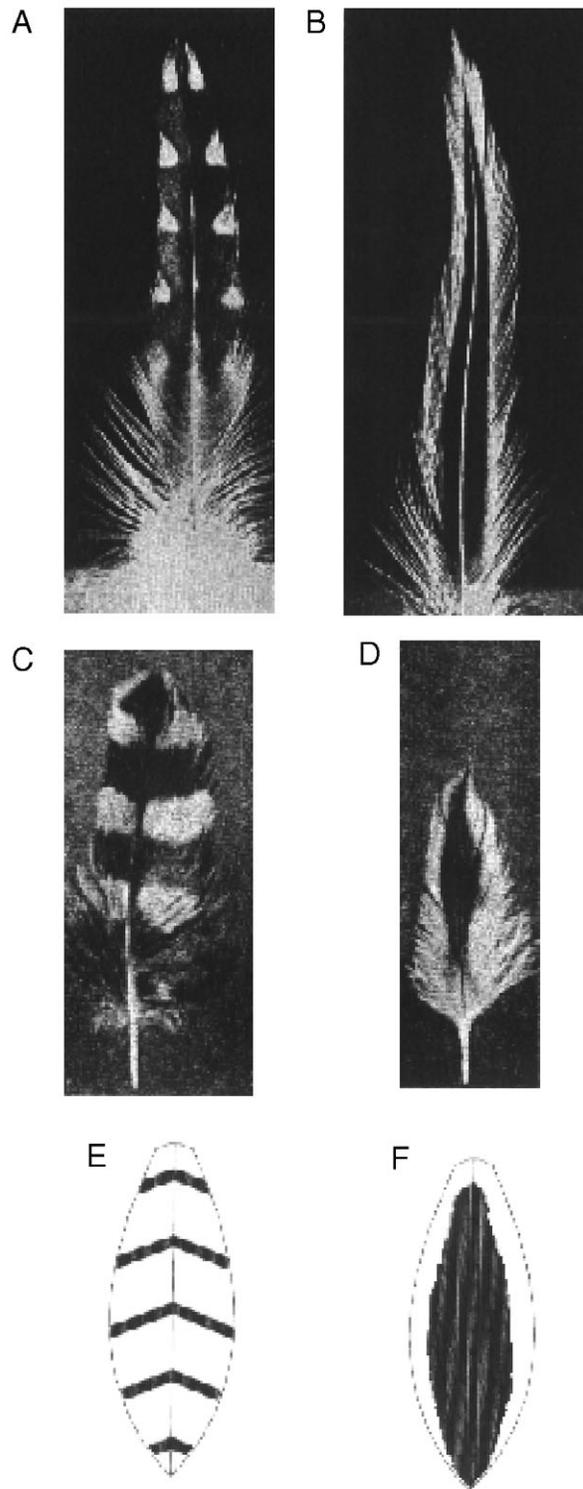

Fig. 6. Examples of melanin pigment patterns produced by experimental manipulation (A–D) and computer simulation (E,F). (A,B) Ornamental feather from the neck region of a male Brown Leghorn chicken receiving 1.5 mg of a subcutaneous injection of thyroxin every sixth day during growth of the feather (Lillie, 1932) (A); (B) control feather from the same region. (C,D) Normal feather from the wing covert of a short eared owl (C), and (D) a feather from the same covert induced to grow after removal of the thyroid gland [from Voitkevich (Voitkevich, 1966), p.183]. (E,F) Two patterns produced in computer simulations of diffusion and interactions between two molecules ('activator' and 'inhibitor') on a growing feather (Prum and Williamson, 2002). The activator stimulates production of both activator and inhibitor. Inhibitor diffuses faster than, and inhibits, activator. Dark areas are locations where the activator is above a certain concentration. One important difference between the two simulations is that the diffusion rate of inhibitor is higher when the longitudinal patch is produced. Both these patterns are commonly observed across feather tracts of different species of birds (Prum and Williamson, 2002).

However, plasticity in behavioural traits, including number of clutches laid in the season (Yeh and Price, 2004) and territorial responses to song playback (Newman et al., 2006), have likely generated novel selection pressures on the tail pattern (P. J. Yeh and T.D.P., unpublished observations). Thus in this study plasticity in behavioural traits is invoked as being an important cause of the reduction in tail pattern, by influencing directions and intensity of selection.

Although phenotypic plasticity must play a critical role in some cases of population differentiation, natural and sexual selection will also operate in the absence of any plastic responses. This makes it difficult to ascribe a definite role to plasticity in any particular case, even striking examples such as the tool-using behaviour of the woodpecker finch. In the case of colour patterns, the large influence of diet on carotenoids implies that entry into a novel environment should cause simultaneous developmental changes in many individuals, implying that plasticity likely plays some role in driving further genetic differentiation. Such influences of diet are not so apparent for melanin patterns, and environmental perturbations that produce large changes may perhaps be confined to single individuals and die out with them. Here genetic mutations that produce similar phenotypes may play a more direct role in generating population differentiation.

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