

ECOLOGY AND CONSERVATION OF EUROPEAN FOREST-DWELLING RAPTORS

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Plumage polymorphism in melanin-based coloration: a case study in the tawny owl *Strix aluco*

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Introduction

Phenotypic variation among individuals within the same population is common in most organisms, some individuals being, for example, larger, heavier or more colourful than others. Phenotypic variation is at heart of natural selection, and thus understanding how such variation is generated and maintained in natural populations is a central issue in evolutionary theory. And what does this phenotypic variation inform us about an individual, its environment and adaptation to it, are of major interests for field ecologists (Coleman *et al.*, 1994; Hallgrímsson & Hall, 2005). Genetically polymorphic traits are particularly relevant in this context since they are encoded by a limited number of alleles accounting for most of the inter-individual phenotypic variation.

The tight association between genotype and phenotype in polymorphic species allows researchers to carry out detailed studies on the effect of natural and sexual selection on evolutionary processes. Classical examples of genetic polymorphisms comprise blood types and eye coloration in human as well as melanin vs. peppered adult moths *Biston betularia* (Grant, 2004; for reviews in birds, see Galeotti *et al.*, 2003; Roulin, 2004). Colour polymorphic organisms provide a particularly promising study system because

of the dramatic colour variation within and between species (Endler, 1990) and its strong genetic control (e.g. insects: Majerus, 1998; anurans: Hoffman & Blouin, 2000; reptiles: Shine *et al.*, 1998; plants: Warren & Mackenzie, 2001; mammals: Majerus & Mundy, 2003; birds: Kruger & Lindstrom, 2001).

In this chapter, we review empirical studies carried out in the tawny owl *Strix aluco* with the aim of highlighting how the study of variation in melanin-based coloration can inform us about (i) the evolution and maintenance of genetic polymorphism in natural populations and about (ii) individual adaptation to heterogeneous environments.

Melanin-based coloration

Melanin is the most abundant pigment in animal taxa and is found in all of the main types of integuments among vertebrates (Ito & Fujita, 1985; Shiojiri *et al.*, 1999; Lesser *et al.*, 2001; Mundy *et al.*, 2002; Mundy & Kelly, 2003; Parichy, 2003; Hoekstra, 2006). Melanin-based coloration is determined by the deposition of two distinct pigments: grey to black eumelanin and yellow to reddish-brown pheomelanin. In birds, a comparative study found 334 species showing colour polymorphisms (3.5% of all birds), with higher occurrence in Strigiformes, Ciconiformes, Cuculiformes and Galliformes (Galeotti *et al.*, 2003). Well-known examples of melanin-based colour polymorphism include the ruff *Philomachus pugnax* (Lank *et al.*, 1995), the Arctic skua *Stercorarius parasiticus*, the snow goose *Anser caerulescens* (Mundy, 2005), the feral pigeon (Johnston & Janiga, 1995), the bananaquit *Coereba flaveola* (Theron *et al.*, 2001) and the common buzzard *Buteo buteo* (Kruger & Lindstrom, 2001). Nowadays, the distinction between discrete colour morphs and continuous variation in genetically-based coloration fades away since several colour polymorphic species display continuous variation in melanin expression (see for example: McGraw *et al.*, 2004, 2005; Hofmann *et al.*, 2007a,b).

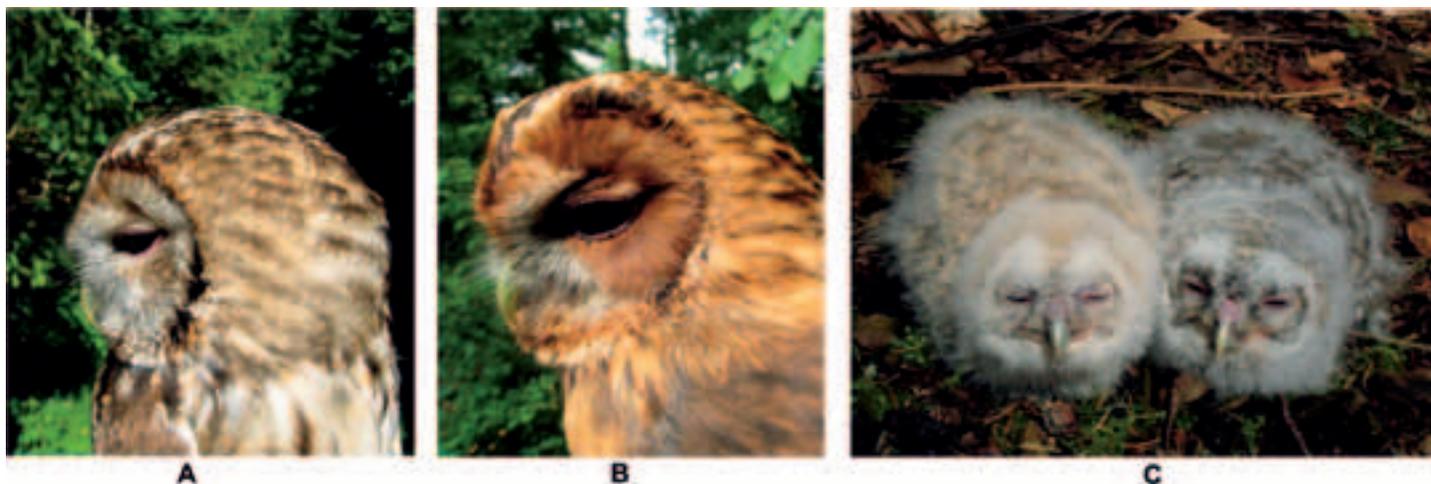


Figure 65: Illustration of the different level of pheomelanin expression in the tawny owl *Strix aluco*. Pictures A and B show a pale and a dark pheomelanin mother, respectively. Picture C illustrates two cross-fostered chicks, born from distinct parents, and that are displaying different melanin-based coloration.

Conversely to carotenoid pigments that cannot be endogenously synthesized in vertebrates, melanic pigments are synthesized *de novo* in specialized cells, the melanocytes, and inter-individual variation in melanin-based coloration is often under tight genetic control (Roulin & Dijkstra, 2003; Mundy & Kelly, 2003; Bize *et al.*, 2006; Hoekstra, 2006; but see Griffith *et al.*, 1999). Melanin synthesis involves the complex action of many genes, and their review is beyond the scope of this chapter (Bennett & Lamoreux, 2003; Slominski *et al.*, 2004; Millington, 2006). Of particular importance is the binding of melanocortin agonists, post-translational products of the proopiomelanocortin gene (*POMC*), and of its antagonist agouti-signalling protein (*ASIP*) to the specific receptor of the pigmentation process (*MC1R*) on the surface of melanocytes, which initiate the production of eu- and pheomelanin pigments, respectively. Mutations occurring within *MC1R* and *ASIP* genes have been shown to exert a major impact on plumage or coat coloration (Mundy & Kelly, 2003; Mundy, 2005; Nadeau *et al.*, 2007, 2008), and therefore melanin-based pigmentation is often considered as a phenotypic marker of alternative genotypes (Hoekstra, 2006). Nevertheless, comprehensive knowledge on the genetic basis of melanin-based coloration is restricted to a limited number of birds (Theron *et al.*, 2001; Mundy *et al.*, 2004; Mundy, 2005; Nadeau *et al.*, 2007, 2008; Hiragaki *et al.*, 2008; Bottje *et al.*, 2008) and the adaptive function of melanin-based colours remains poorly known (Parker, 2006; Hoekstra, 2006).

Plumage coloration in the tawny owl

The tawny owl *Strix aluco* displays large inter-individual variation in the degree of melanin-based plumage coloration (from pale to dark reddish-brown,

Fig. 65), such variation being explained to a large extent by the level of pheomelanin pigments (68% of total variance) deposited in feathers and to a lesser extent by the level of eumelanin pigments (21% of total variance; Gasparini *et al.*, 2009a). Three major methods have been used to assess the degree of melanin-based coloration in the tawny owl. Colour morphs can be directly scored in the field by human eyes (Galeotti & Sacchi, 2003; Roulin *et al.*, 2003; Brommer *et al.*, 2005), but unfortunately such scores are difficult to compare among studies since they rely strongly on the observer and it does not allow to assess the extent to which individual can change coloration between years. A better approach is to collect feathers on the back of individuals, a body part that displays substantial variation in reddishness, which can be measured either with the software ADOBE PHOTOSHOP, or with a spectrophotometer. These two alternative methods have the advantage to provide continuous colour scores (see Gasparini *et al.*, 2009a). Interestingly, a bimodal distribution of colour morphs can be observed (Fig. 66, see also Brommer *et al.*, 2005), suggesting the occurrence of two main morphs, so-called grey (pale pheomelanin) and reddish (dark pheomelanin), with some variation in the degree of pheomelanin within each morph. Expression of plumage coloration is neither sexually dimorphic (individuals of one sex are as likely to display a given coloration as an individual of the other sex; Galeotti & Cesaris, 1996; Roulin *et al.*, 2003; Brommer *et al.*, 2005; Fig. 66), nor sensitive to sibling competition (Roulin & Dijkstra, 2003; Roulin *et al.*, 2008b), but is found to be highly heritable, h^2 ranging from 0.72 in Finland (Brommer *et al.*, 2005)

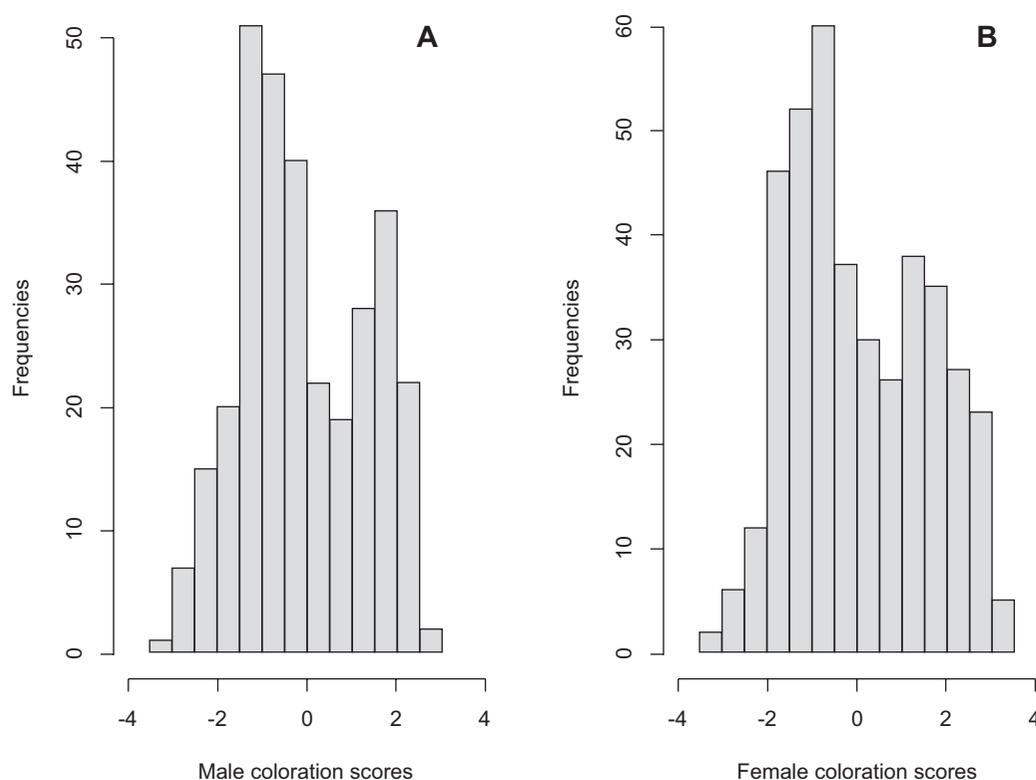


Figure 66: Frequency distribution of melanin-based plumage coloration in male (A) and female (B) tawny owls. Data are from 177 males and 208 females from a Swiss population. Coloration scores were obtained by measuring pictures of feathers with the software ADOBE PHOTOSHOP. Low scores stand for pale pheomelanic feathers (i.e. grey morphs) and high score for dark pale pheomelanic feathers (i.e. brown to reddish morphs).

to 0.93 in Switzerland (Gasparini *et al.*, 2009a; Table 49). Preliminary investigation of the genome architecture in the tawny owl was however unable to highlight important mutations within the coding sequence of key regulators of the melanogenesis (i.e. *MC1R* & *POMC*; own unpublished data in collaboration with N. Mundy for *MC1R*).

Adaptive function of melanin-based coloration

The issue of adaptive function of coloration has already been a major topic of discussion since Darwin and Wallace. In our review, a colour trait is defined as being adaptive when in some habitats or social conditions individuals displaying a particular coloration have a fitness benefit (in terms of growth, reproduction or survival) over other differently coloured individuals. This definition does not necessarily imply that coloration in itself drives adaptation since other naturally selected phenotypic traits can be genetically associated (see below). Recent reviews of the literature showed that the degree of melanin-based coloration frequently correlates with morphological, physiological, behavioural and life history traits (Jawor & Breitwisch, 2003; Roulin, 2004; Ducrest *et al.*, 2008). The proximate basis for such covariations to evolve in natural populations lies in three distinct reasons.

Melanin-based coloration may have an adaptive function if natural selection exerts its influence:

- (i) on coloration, which can be the case when coloration plays a role in foraging (Galeotti *et al.*, 2003; Roulin & Wink, 2004) and anti-predatory strategies (Jones, 1977; Johannesson & Ekendahl, 2002);
- (ii) on the melanic pigments, because of their effective chemico-physical properties that operate in antibiotic activity, resistance to solar radiation, oxidative stress or thermoregulation (Mackintosh, 2001; Slominski *et al.*, 2004; McGraw *et al.*, 2005; Clusella Trullas *et al.*, 2007);
- (iii) on phenotypic traits that are genetically correlated with coloration (Ducrest *et al.*, 2008).

In the latter case, selection is acting on genes that are closely associated with genes coding for coloration (genetic disequilibrium) or on genes with pleiotropic effects on coloration and other attributes. Hence, melanin-based coloration may also evolve as indirect response to selection exerted on alternative physiological, morphological or behavioural attributes (Kittilsen *et al.*, 2009), and thus may signal alternative life history or physiological strategies to cope with variation in habitats (for reviews: Galeotti *et al.*, 2003; Roulin, 2004; and see Roulin & Bize, 2007) or social environments (Rohwer, 1975, 1977).



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Table 49: Summary of published studies carried out on the covariation between pheomelanin-based plumage coloration and other phenotypic traits in the tawny owl. Within the studied parameter (in bold italic), different phenotypic traits (e.g. morphological, behavioural, physiological or life history traits) are associated. For each studied trait, we provide a number to be used in Figure 67, a description of the main results and a summary of the colour morph-dependant strategies (Dark = dark pheomelanin individuals; Pale = pale pheomelanin individuals), in order to present relative performance of these alternative strategies.

Studied parameters	Results		Reference
	Description	Summary	
Immune parameters			
1 Antibody production	Dark pheomelanin breeding females maintain a stronger level of antibody for a longer period of time compared to pale pheomelanin females	Dark>Pale	Gasparini <i>et al.</i> , 2009a
2	The same humoral challenge enhanced T-cell mediated immunity in dark reddish melanin nestlings while reducing it in pale reddish nestlings	Dark>Pale	Gasparini <i>et al.</i> , 2009b
3 Body mass after PHA vaccination	Nestlings born from dark pheomelanin mothers suffered greater body mass losses than those born from paler pheomelanin females	Pale>Dark	Piault <i>et al.</i> , 2009
4 Body mass after Tetravac vaccination	Dark pheomelanin breeding females suffered greater body mass losses than paler pheomelanin females	Pale>Dark	Gasparini <i>et al.</i> , 2009a
5 Blood parasites intensity	Dark pheomelanin adult owls hosted higher total parasite burden than pale pheomelanin adult owls	Pale>Dark	Galeotti & Sacchi, 2003
Genetic parameters			
6 Heritability	Expression of plumage coloration shows high heritability ($h^2 = 0.72$ to 0.93)	Dark=Pale	Brommer <i>et al.</i> , 2005; Gasparini <i>et al.</i> , 2009a
Hormone levels			
7 POMC prohormone	Pale pheomelanin females exhibit more circulating POMC prohormone than darker females when the brood size was experimentally enlarged but not when reduced	Pale>Dark	Roulin <i>et al.</i> , <i>in prep.</i>
Physiological parameter			
8 Oxygen consumption	Foster offspring raised by pale pheomelanin mothers showed a lower body mass than offspring raised by dark pheomelanin mothers, and also consumed more oxygen under laboratory conditions	Dark>Pale	Roulin <i>et al.</i> , 2005
Fitness components			
9 Body mass in relaxed environment	When fed <i>ad libitum</i> nestlings born from dark pheomelanin mothers converted food more efficiently into body mass than offspring born from paler pheomelanin mothers	Dark>Pale	Piault <i>et al.</i> , 2009
10	In some years, dark pheomelanin owls produced heavier offspring than paler pheomelanin individuals, while the reverse was true in other years	Dark=Pale	Roulin <i>et al.</i> , 2003
11	Nestlings sired by dark pheomelanin parents grew more rapidly in body mass in rich environments (i.e., experimentally reduced broods) than offspring sired by pale pheomelanin parents	Dark>Pale	Roulin <i>et al.</i> , 2008
12 Body mass in stressful environment	When food restricted nestlings born from dark pheomelanin mothers suffered greater body mass losses than those born from paler pheomelanin females	Pale>Dark	Piault <i>et al.</i> , 2009
13 Adult survival	In Italy, dark pheomelanin adults suffered a higher mortality in cool-dry years	Pale>Dark	Galeotti & Cesaris, 1996
14	In Italy, pale pheomelanin adults suffered a higher mortality in warm-wet years	Dark>Pale	Galeotti & Cesaris, 1996

Studied parameters	Results		Reference
	Description	Summary	
15	In Finland, pale pheomelanic morphs survived better than dark morphs	Pale>Dark	Brommer <i>et al.</i> , 2005
16	In a Swiss population, tawny owl survival was not associated with pheomelanic coloration		Roulin <i>et al.</i> , 2003
17	Probability of breeding	Proportion of dark pheomelanic females that were breeding was greater in years characterized by a low number of breeding pairs. Although not breeding every year, pale pheomelanic females produced offspring of higher quality	Dark≡Pale Roulin <i>et al.</i> , 2003
18	Fledgling production	Pale pheomelanic male and female owls had a higher lifetime production of fledglings	Pale>Dark Brommer <i>et al.</i> , 2005
19	Recruitment	Pale pheomelanic male owls produced more recruits during their lifetime than brown individuals	Pale>Dark Brommer <i>et al.</i> , 2005
Mating behavior			
20	Assortative mating	Pairing with respect to colour was not assortative	Dark≡Pale Brommer <i>et al.</i> , 2005; Roulin <i>et al.</i> , 2003
Environmental parameters			
21	Habitat background	Dark pheomelanic owls may be particularly cryptic in closed forest	Dark>Pale Galeotti & Sacchi, 2003

Potential adaptive functions of coloration in the tawny owl

Table 49 provides a survey of the empirical studies that investigated the potential adaptive function of melanin-based coloration in the tawny owl. Because melanin-based coloration, as well as pigment density or distribution, are experimentally difficult to manipulate, evidence of direct selection on these traits is lacking in natural populations. By contrast, several studies established covariations between melanin-based coloration and physiological, morphological and behavioural phenotypic traits, suggesting that the degree of plumage reddishness reflects adaptations to different environmental conditions. Hereafter, we discuss five major selective forces to which plumage coloration of tawny owls may signal an adaptation.

Cryptism. It has been proposed that reddish and grey morphs are more cryptic in closed and opened habitats, respectively (Majerus, 1998; Gehlbach & Gehlbach, 2000), suggesting an adaptive process based on the environmental background (Table 49). Indeed, such characteristic can confer fitness benefits by lowering the vulnerability to predators, enhancing foraging success and by minimizing the risks of mobbing from passerine birds (Negro *et al.*, 2007). Although Galeotti & Sacchi (2003) observed that dark pheomel-

anic lived in more closed forest habitats than paler individuals, data on numerous sites within distinct populations are needed to validate this hypothesis.

Adaptation to climate conditions. The tawny owl is a long-lived species (18-22 years; König *et al.*, 2008; <http://blx1.bto.org/birdfacts/results/bob7610.htm>) distributed throughout Eurasia and thus experiencing a wide range of climatic condition. Several studies have reported a relationship between adult survival and colour morphs, the direction of this relationship changing among years and countries/environments. In Italy, dark pheomelanic (i.e. so-called reddish morph) individuals were found dead more frequently in cool-dry years while pale pheomelanic (grey) ones were found dead more often in warm-wet years (Galeotti & Cesaris, 1996). This hypothesis is supported by another study conducted in Finland, pale pheomelanic owls have a better survival than darker individuals because of the cool-dry conditions occurring in this area (Brommer *et al.*, 2005). Interestingly this trend is changing partly because of the global climate warming (Karell *et al.*, *pers. comm.*). In contrast, in Switzerland adult survival was not associated with plumage coloration (Roulin *et al.*, 2003).

Adaptation to parasites. In Italy, dark reddish tawny owls hosted more endoparasites (*Haemoproteus*) than pale owls (Galeotti & Sacchi, 2003), but it re-



Grey morph of tawny owl captured for ringing. Iñigo Zuberogoitia.

mained unclear whether these observations were due to non-random habitat distribution of the different colour morphs. To clarify this issue, experimental immune challenges were performed in Switzerland and revealed that dark pheomelanic females maintained higher concentration of antibodies for a longer period of time than pale reddish ones (Gasparini *et al.*, 2009a). Similarly, another experiment done on the same population reported that the same humoral challenge enhanced T-cell mediated immunity in nestlings born from dark pheomelanic mothers while reducing it in nestlings born from paler pheomelanic mothers (Gasparini *et al.*, 2009b). These results suggest that the offspring of dark pheomelanic owls mount stronger immune responses either because (i) dark pheomelanic individuals inhabit environments where parasites are more abundant or virulent than in habitats occupied by pale reddish individuals (ii) and/or because dark pheomelanic individuals have a less efficient immune response and, in turn, are exposed for a longer time to parasites than pale pheomelanic individuals. Interestingly, resistance to parasitism by

dark pheomelanic individuals comes at a cost in terms of greater loss of body mass in both nestling and adult owls (Gasparini *et al.*, 2009a,b; Piauult *et al.*, 2009). This indicates that the cost/benefit trade-off of immunocompetence is differentially resolved by dark and pale reddish tawny owls.

Adaptation to variation in resources. The tawny owl preys mainly upon small rodents, such as the wood mice *Apodemus spp.* and bank vole *Clethrionomys glareolus* (Roulin *et al.*, 2008a), and rodent populations are known to show high density fluctuation over space and time (Karell *et al.*, 2009). Although nestling appetite did not correlate significantly with plumage coloration of the biological mother, an experimental manipulation of food supply to chicks demonstrated that offspring born from dark pheomelanic mothers grow in body mass faster than those born from pale pheomelanic mothers (Piauult *et al.*, 2009), whereas when preys were provided *ad libitum* the opposite pattern was found (i.e. offspring of pale mothers grow faster). In the same vein, a brood size manipulation experiment performed in the same Swiss population but

using other individuals (Roulin *et al.*, 2008b) pointed out that offspring from dark pheomelanic mothers grow quicker than offspring from pale pheomelanic mothers when brood size was experimentally reduced but not when enlarged (Roulin *et al.*, 2003, 2008b). In the aim of determining whether these morph-specific offspring growth patterns were associated with a difference in metabolic rate between offspring of red and grey mothers, Roulin *et al.* (2005) analysed nestling oxygen consumption and found that oxygen consumption was greater in offspring raised by grey foster mothers under warm temperature. Hence, growth and metabolic rates indicate that coloration is associated with phenotypic plasticity raising the interesting possibility that in periods when food is rare, such as during spells of rain, offspring of pale parents better cope with food depletion and once food conditions are restored offspring from dark parents can quickly catch

up in growth. Interestingly, both conclusions could explain why dark pheomelanic individuals were found to produce heavier offspring than pale reddish individuals in some years, and inversely in other years (Roulin *et al.*, 2003, 2004, 2005).

Adaptation to breeding conditions. Because physiological, behavioural and life-history traits are often closely associated, the four latter points can induce variation in reproductive parameters between pale and dark pheomelanic tawny owls. For instance, in Switzerland, darker pheomelanic females keep a constant resolution by breeding every year, whereas pale pheomelanic females are inclined to skip reproduction in poor years, which suggest a flexible decision rule according to environmental conditions (Roulin *et al.*, 2003). Although breeding less frequently, pale pheomelanic individuals produced more fledglings



Reddish morph individual of tawny owl in an oak forest. Iñigo Zuberogoitia.



and recruits than darker pheomelanic individuals in a Finnish population due to a longer life span (Brommer *et al.*, 2005).

Maintenance of polymorphism in melanin-based coloration

Melanin-based coloration can be non-neutral with respect to natural selection and is often associated with other phenotypic traits. Thus, selection on coloration and indirect selection on genetically correlated traits should induce changes in the frequency of colour morphs as recently observed in scops owl *Otus scops* (Galeotti *et al.*, 2009) and several other birds

(Roulin, 2004). The maintenance of colour polymorphism therefore requires some specific mechanisms. Hereafter, we briefly propose three hypotheses, which remain to be investigated in detail in the tawny owl.

First, heterogeneity in the environment can act as divergent selective force that promote the emergence and maintenance of alternative genetic colour morphs locally adapted to different habitats (Kassen, 2002; Galeotti *et al.*, 2003; Roulin, 2004; Sgro & Hoffmann, 2004; Byers, 2005; Chunco *et al.*, 2007). This process, also called 'local adaptation', states that alternative morphs are adapted to different habitats. In the particular case of disruptive selection (Ford, 1945;



Two siblings of tawny owl, dark and pale brown respectively. *Iñigo Zuberogoitia*.

Huxley, 1955; Lank, 2002), individuals at both edges of colour distribution are favoured because locally better adapted, leading to mono- or dimorphism over the long term (Brommer *et al.*, 2005). Second, without invoking frequency-dependent benefits of displaying a particular morph, one of the morphs is likely to become slightly fitter over the long run because of particular environmental conditions for instance. Under frequency-dependent selection, morphs perform less well when their frequency increase above the equilibrium frequency while their fitness increases when their frequency decreases. Classical example is the apostatic selection (Clarke, 1962), for which individuals displaying a new coloration enjoy an advantage

by being less rapidly detected either by their preys or by their predators than more common morphs (Bond, 2007). Finally, heterozygous individuals can have a fitness advantage over homozygous ones, called *heterosis*. This hypothesis of maintenance has been proposed to occur in the common buzzard (Kruger & Lindstrom, 2001), in which intermediate (i.e. heterozygous) breeding adults produce more offspring than light and dark (i.e. homozygous) conspecifics.

Conclusions

The study of evolution and maintenance of polymorphism in melanin-based coloration is a tremendous work, while empirical studies raised important questioning on the adaptive potential of colour morphs that still need to be tackled. Research on tawny owls show that the degree of pheomelanism covaries linearly with morphological, behavioural, physiological and life-history traits, which suggests therefore that individuals with different melanin-based coloration are best adapted to different environmental conditions. One plausible, albeit speculative, scenario is that colour polymorphism of adult tawny owls is maintained if spatial and temporal heterogeneity of the environment generate balancing selection favouring locally adapted individuals at different time scale (i.e. generations). Note also that, although we cannot firmly exclude disruptive selection or heterosis scenarios of maintenance of colour polymorphism in the tawny owl, empirical studies failed to demonstrate that selection favours either extreme morphs (Roulin *et al.*, 2003; Brommer *et al.*, 2005) or intermediately-coloured individuals (Piault *et al.*, 2009), respectively.

Life history theory points out that individuals have to allocate optimally their resources among all life history traits (Stearns, 1992) in order to maximize their fitness. Hence, trade-off resolution in resource allocation can be regarded as a decision rule that can differ between individuals (Wilson & Yoshimura, 1994). Accordingly, we showed that dark pheomelanic tawny owls tend to allocate resources equally among the different activities (e.g. body maintenance, parasite resistance, reproduction) independently of fluctuations in environmental factors, whereas pale pheomelanic individuals are more flexible in their decisions and limit associated costs by allocating resources accordingly to habitat quality and investing only in specific tasks in which they perform well. We thus temptingly define dark pheomelanic owls as adopting a '*specialist*' strategy, whereas we could consider paler owls as

adopting a ‘generalist’ strategy, which enables them to be more competitive during stressful conditions. In this context, the *specialist* morphs (reddish owls) are characterized by good performance under relaxed environmental conditions (i.e. low parasite densities, low competition, high food availability), but undergo the costs of these investments under stressful conditions as shown in Fig. 67 (e.g. low food-availability, high breeding competition). Conversely, stress-resistant generalist morphs adopt a strategy that enables them to perform well in harsh environmental conditions (Fig. 67). This scenario of maintenance still need to be verified but seems relevant at least in Switzerland, characterized by highly heterogeneous landscape and fluctuating environmental conditions across years. In Finland, environmental fluctuations are less frequent, which can justify the predominance of pale pheomelanic individuals, yet. However, in a global warming context, an increase of fluctuations are likely to occur as suggested by recent field observations (Karell *et al.*, 2011), which can lead to an adjustment of the distinct colour morph densities.

Perspectives

The reported covariations between pheomelanin-based coloration and fitness components (Table 49, Fig. 67) may have a genetic basis or be the outcome of non-random habitat distribution with respect to plumage coloration. A review of the literature points out to candidate genes potentially explaining the existence of such a trade-off: genes of the melanocortin system and the corresponding hormones are suggested to pleiotropically affect the degree of pheomelanin-based coloration and other phenotypic traits, including immunity, resistance to oxidative stress, regulation of the stress response, energy homeostasis, aggressiveness and sexual behaviour between distinct melanic morphs in vertebrates (Slominski *et al.*, 2004; Hoekstra, 2006; Ducrest *et al.*, 2008). In our preliminary investigations, we found that only pale pheomelanic individuals modulate melanocortin levels in relation to the quality of rearing conditions, which suggests that traits regulated by melanocortins are phenotypically plastic to a larger extent in pale than darker pheomelanic individuals (Roulin *et al.*, 2011; Table 49). In this case, the maintenance of locally adapted colour morphs with different norms of reactions is not only the product of balancing selection. From a proximate point of view, it could also be influenced either by mutations in the coding region of key genes involved in melanogenesis (e.g. *POMC*, *MC1R*, *ASIP*) or

by post-translational regulation of melanocortin levels. Since these hormones exert pleiotropic influences on several traits (metabolism, stress, aggression, oxidative stress or sexual functions) through the binding to specific receptors (*MC1-5Rs*), it is of major interest to study these inter-related traits together in order to obtain a complete overview.

Finally, the study of melanin-based coloration has also important implications for the understanding of animal ecology. In the particular case of the tawny owl, populations composed by distinct colour morphs may have different dynamics (Roulin, 2004), since pale pheomelanic females tend to skip reproduction more frequently than darker ones in Switzerland (Roulin *et al.*, 2003), but not in Finland (Brommer *et al.*, 2005). In addition, our review suggests that melanin-based coloration can signal resistance to stress factors, caused for example by anthropogenic disturbance or climate change. Thus, the study of variation in morph frequencies between populations or over long-term periods may provide a useful tool to detect environmental changes. In a context of climate warming, habitat fragmentation and decreasing biodiversity, such polymorphic species can thus be considered as valuable bioindicators of anthropogenic disturbances and climate change since alternative colour morphs appear to react in different ways to environmental changes.

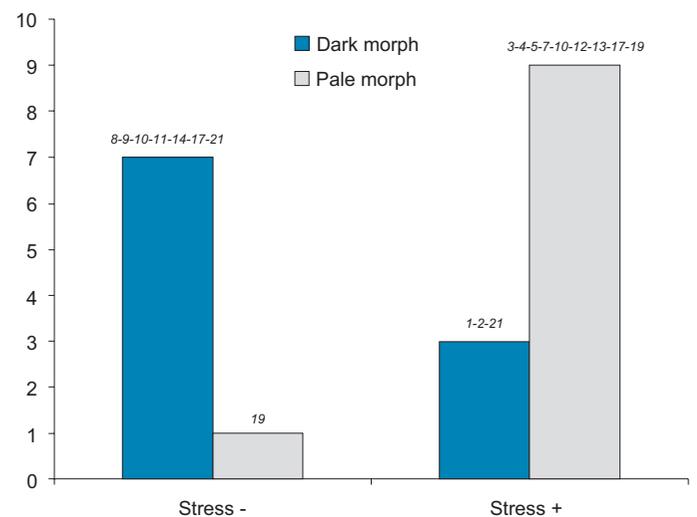


Figure 67: Number of studies indicating under which conditions (i.e. stressful or non-stressful situations) dark or pale reddish tawny owls are suggested to perform the best. Numbers above bars refer to studies reported in Table 49. ‘Stress -’ characterizes warm-wet climate conditions, low parasite densities, low level of sibling competition and high food availability, whereas ‘stress+’ defines cool-dry years, low food-availability, high level of sibling competition and food provided ad libitum).