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**AN EXPLORATION OF
ECOLOGICAL PROCESSES
UNDERLYING FITNESS
DIFFERENCES IN COLOUR
POLYMORPHIC TAWNY OWLS**

Charlotte Perrault



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ABSTRACT

Climate change affects temperature and landscapes, especially in northern latitudes where heavy winters are becoming less common. Changes in the environment can strongly affect animals locally adapted to their habitat. Camouflage and insulation play a key role in the survival of many animals. For predators, changes in camouflage abilities due to environmental changes can affect the probability of being detected by prey species, thereby affecting hunting success and predator-prey interactions. The tawny owl, *Strix aluco*, displays two genetically determined colour morphs, the grey and the brown morph, with some variation in the degree of pigmentation of pheomelanin in their plumage. Grey morphs have higher survival rates than brown morphs in snowy winters and are known to be more cryptic in snowy landscapes. In this thesis, I used experimental approaches to study camouflage effects on the behaviour of predators and prey. I investigated local adaptation by comparing phenotypic traits with genetic data. I first studied tawny owls' camouflage behaviour and space use in a novel environment. Neither morph showed evidence of background matching when using behavioural tests in controlled conditions. However, brown, tawny owls often perched in the exposed area, indicating boldness. Then, I assessed the significance of camouflage under variable environmental conditions by quantifying passerines' mobbing behaviour against stuffed owls during four different environmental conditions. The detection probability by potential prey never differs between the two morphs. However, the grey morph had a higher probability of being mobbed in the absence of snow cover than the brown morph and the mobbing probability was reversed in the presence of snow cover. Finally, I measured feather insulation capacities in nine different tawny owls' populations in Europe. The results showed only population differences in insulation capacities but no morph differences. Therefore, The two colour morphs experience differential benefits across snow conditions, which may help maintain colour morphs in the population, although further warming of winter climate is expected to shift tawny owls' population dynamics in northern latitudes.

KEYWORDS: Background matching, Behaviour, Boldness, Camouflage, crypsis, Climate change, Colour morph, Environmental adaptation, Feather, Genetics, Insulation, Phenotypic, Predator-prey interactions, Tawny owl, Temperature

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TIIVISTELMÄ

Ilmastonmuutos vaikuttaa lämpötilaan ja ympäristöön erityisesti pohjoisilla leveysasteilla, missä ankarat talvet ovat käymässä harvinaisemmiksi. Ympäristön muutokset voivat vaikuttaa voimakkaasti eläimiin, jotka ovat sopeutuneet paikalliseen elinympäristöönsä. Suojaväri ja lämmönsäätely ovat keskeisiä tekijöitä monien eläinten selviytymisessä. Petoeläimille kyky vaihtaa suojaväriä ympäristön muutosten vuoksi voi vaikuttaa todennäköisyyteen, että saalislajit havaitsevat ne, ja siten myös saalistuksen onnistumiseen ja peto-saalissuhteisiin. Lehtopöllöllä (*Strix aluco*) on kaksi geneettisesti määräytyvää värimuotoa: harmaa ja ruskea muoto, joiden höyhenpeitteen feomelaniinin pigmentaation aste vaihtelee jonkin verran. Harmaalla muodolla on korkeampi elonjäämisaste kuin ruskealla muodolla lumisina talvina, ja harmaan tiedetään maastoutuvan paremmin lumisiin maisemiin. Tässä väitöskirjassa käytin kokeellisia menetelmiä tutkiakseni suojaväriin vaikutuksia sekä petojen että niiden saaliiden käyttäytymiseen, ja tutkin paikallista sopeutumista vertailemalla fenotyyppejä piirteitä geneetisiin tietoihin. Ensiksi tutkin lehtopöllöjen suojavärikkäyttäytymistä ja tilankäyttöä uudessa ympäristössä. Käyttäytymiskokeiden kontrolloiduissa olosuhteissa kummallakaan muodolla ei ilmennyt sulautumista taustaan. Ruskeat lehtopöllöt olivat kuitenkin usein asettuneet avoimemmille alueille, mikä viittaa rohkeuteen. Tämän jälkeen arvioin suojaväriin merkitystä vaihtelevissa ympäristöolosuhteissa kvantifioimalla varpuslintujen häirintäkäyttäytymistä täytettyjä pöllöjä kohtaan neljässä eri ympäristöolosuhteessa. Saalislajien havaintotodennäköisyys ei eronnut värimuotojen välillä. Harmaalla muodolla oli kuitenkin suurempi todennäköisyys joutua häirityksi ilman lumipeitettä verrattuna ruskeaan muotoon, ja häirintätodennäköisyys oli päinvastainen lumipeitteen läsnäollessa molemmilla värimuodoilla. Lopuksi mittasin höyhenten eristyskykyä yhdeksässä lehtopöllöpopulaatiossa eri puolilla Eurooppaa. Tulokset osoittivat vain populaatioiden välisiä eroja eristyskyvyssä, mutta eivät eroja värimuotojen välillä. Näin ollen molemmat värimuodot hyötyvät eri tavoin lumisista olosuhteista, mikä saattaa auttaa ylläpitämään värimuotoja populaatiossa, vaikka talvien lämpenemisen odotetaan vaikuttavan lehtopöllöjen populaatiodynamiikkaan pohjoisilla leveysasteilla.

ASIASANAT: Taustaväriin mukautuminen, Käyttäytyminen, Rohkeus, Suojaväri, Maastoutuminen, Ilmastonmuutos, Värimuoto, Ympäristön sopeutuminen, Höyhen, Geneetiikka, Eristys, Fenotyyppinen, Peto-saalissuhteet, Lehtopöllö, Lämpötila

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RESUME

Le changement climatique entraîne une augmentation de la température et une modification des paysages, notamment dans les latitudes nordiques où les hivers rigoureux deviennent moins fréquents. Les changements environnementaux influencent les animaux localement adaptés à leur habitat. Le camouflage et l'isolation thermique jouent un rôle clé dans la survie de nombreux animaux. Pour les prédateurs, les capacités de camouflage peuvent affecter la probabilité d'être détectés par leurs proies potentielles, et ainsi influencer le succès de prédation et les interactions prédateur-proie. La chouette hulotte (*Strix aluco*) possède deux morphes : le gris et le brun, génétiquement déterminés par le degré de pigmentation de la phéomélanine dans leur plumage. Le morphe gris a un taux de survie plus élevé que le morphe brun lorsque la quantité de neige est importante et est plus cryptique dans les paysages enneigés. Dans cette thèse, j'ai utilisé des approches expérimentales pour étudier les effets du camouflage sur le comportement des prédateurs et de leurs proies, et j'ai examiné les adaptations environnementales en comparant des traits phénotypiques avec des données génétiques. J'ai d'abord étudié le comportement de camouflage des hulottes et leur utilisation de l'espace dans un nouvel environnement. Lors de mes tests comportementaux en conditions contrôlées, aucun des morphes n'a choisi de se poser sur le perchoir lui permettant d'être camouflé. Cependant, les chouettes brunes se posaient plus souvent dans des zones exposées, indiquant une différence de courage entre les deux morphes. Ensuite, j'ai évalué l'importance du camouflage en quantifiant le comportement anti-prédateur des passereaux sur des chouettes empaillés dans des conditions environnementales différentes. La probabilité de détection par les passereaux était la même chez les deux morphes. Cependant, le morphe gris avait une probabilité plus élevée d'être agressé en l'absence de neige, par rapport au morphe brun, et la probabilité d'agression était inversée en présence de neige. Enfin, j'ai mesuré les capacités d'isolation thermique des plumes dans neuf populations de hulottes en Europe. Les résultats ont montré des différences entre les populations en termes de capacités d'isolation, mais aucune différence entre les morphes. Les deux morphes de couleur bénéficient donc différemment des conditions neigeuses, ce qui peut aider à maintenir les morphes de couleur dans la population, bien que le réchauffement futur du climat hivernal devrait modifier la dynamique des populations de hulottes dans les latitudes nordiques.

MOTS CLEFS: Adaptation, Comportement, Courage, Camouflage, Crypsis, Changement climatique, Morphe, Environnement, Plume, Génétique, Isolation thermique, Phénotype, Interactions prédateur-proie, Chouette hulotte, Température

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Abbreviations

| | |
|----------|-----------------------|
| F_{ST} | Fixation index |
| P_{ST} | Phenotypic divergence |
| Q_{ST} | Genetic divergence |
| DNA | Deoxyribonucleic acid |

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I Perrault, C.; Morosinotto, C.; Brommer, J.E.; Karell, P. Melanin-based plumage coloration is associated with exposure in tawny owls under novel conditions. *Behavioral Ecology and Sociobiology*, 2023; 77:74.
- II Perrault, C.; Morosinotto, C.; Brommer, J.E.; Karell, P. Camouflage efficiency in a colour-polymorphic predator is dependent on environmental variation and snow presence in the wild. *Ecology and Evolution*, 2023; 13:12.
- III Perrault, C.; Baltazar Soares, M.; Morosinotto, C.; Karell, P.; Poprach, K.; Nilsson, L-O.; Eriksson, D.; Ericsson, P.; Grašytė, G.; Rumbutis, S.; Baroni, D.; Anderson, K.; Øien, I.; Casero, M.; Brommer, JE. Dressed for the weather: Tawny owl feather adaptations across a climatic gradient. *Manuscript*.

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1 Introduction

1.1 Adaptation and Fitness

Animals are locally adapted to their environment thanks to natural selection. Charles Darwin first introduced the theory of natural selection in *On the Origin of Species* (1859). Natural selection is a key evolutionary force shaping animal traits in nature. Natural selection can be defined as the processes increasing fitness based on an individual's characteristics (Fisher, 1930). Fitness is defined by an organism's ability to survive and reproduce in its environment (Fisher, 1930). The greater an individual's fitness is, the higher its chances of passing on its genes to the next generation. Reproductive success often serves as a proxy for fitness and depends on many factors in the wild. Success in reproduction heavily depends on an individual's ability to forage for food, evade predators, mate effectively, and produce viable offspring (Mills and Beatty 1979). Within a species, individuals may display a variety of traits, which can provide benefits or drawbacks depending on the surrounding environmental conditions (Mousseau and Roff 1987). Some of those inherited traits that can improve foraging or predation avoidance, for instance, can increase an individual's chances to survive and reproduce. When all other factors are equal, individuals possessing traits favoured by natural selection tend to live longer and have more offspring, passing these advantageous traits to future generations. With time, these beneficial traits become more common in the population, while disadvantageous ones might completely disappear. However, random factors and environmental conditions also affect fitness, influencing how natural selection acts on different genotypes and phenotypes (Mousseau and Roff, 1987).

Animals can also adjust their behaviour, physiology, or morphology in response to environmental changes via phenotypic plasticity (Agrawal, 2001). Phenotypic plasticity can be seen in responses to biotic stressors such as predation and mobbing risk (Kraft et al., 2006), but also in response to abiotic factors like temperature and climate (Brommer, 2011; Ghalambor et al., 2007; Piersma and Drent, 2003). For example, animals may alter their behaviour by changing their foraging habits or choosing different habitats, while physiological changes might include increasing feather insulation to cope with cold temperatures. A textbook example of phenotypic plasticity according to predation risk is the daphnia/tadpole example. Indeed, when

the predation risk increases (higher numbers of predators, higher numbers of killed prey, or higher concentrations of predator cues), changes in the anti-predator behaviour in *Daphnia* are perceived (Loose and Dawidowicz, 1994; Von Elert and Pohnert, 2000). Moreover, when predation risk increases, tadpoles increase their spatial avoidance of the predator (Anholt et al., 1996), reducing swimming speed (Anholt et al., 2000) and reducing their activity (Anholt et al., 2000, 1996; Petranka, 1989; Van Buskirk and Arioli, 2002). Different individuals within a species can show varying levels of flexibility, which in turn affects their fitness and ability to thrive amid environmental changes. It is essential to understand how animals adapt to their surroundings and to recognize that not all phenotypes respond in the same way to environmental changes. This understanding is crucial for evaluating their survival strategies (Bradshaw 2006).

1.2 Evolution of colour polymorphism

1.2.1 Generalities

Coloration is a trait shaped by various selective forces, including sexual selection, predation, frequency dependence, and social factors (Figure 1). First, sexual selection is playing a key role in coloration evolution, with individuals possessing bright or conspicuous traits often having an advantage to increase reproductive success, as these traits signal health or genetic quality to potential mates (Andersson, 1994). For instance, in guppies (*Poecilia reticulata*), females exhibit a preference for males with more colourful and vibrant colouration, driving sexual selection and influencing the evolution of male colour patterns (Kodric-Brown, 1985). Social factors also influence colour morphs, as shown in a study of the Western Fence Lizard (*Sceloporus occidentalis*) (Sinervo et al., 2001). They showed that throat colour variation in male lizards is linked to social status and aggressive interactions, with different morphs maintained by correlational selection. Certain traits associated with different social roles (e.g., territoriality vs. mate guarding) are favoured depending on the context. This study highlights how social dynamics contribute to the persistence of colour polymorphisms. Furthermore, frequency-dependent selection can maintain colour polymorphisms in populations, particularly when predators preferentially target the more common colour morphs, thus providing a survival advantage to rarer forms (Ayala and Campbell, 1974). Finally, predation is a crucial selective force shaping colour polymorphism, as cryptic coloration can help prey and predator species avoid detection.

In many species, colouration has evolved as an adaptation to the environment (Stevens and Merilaita, 2011). Camouflage plays a crucial role in the survival of prey species by allowing them to blend into their surroundings, making them less visible

to potential predators (Stevens and Merilaita, 2011). This cryptic colouration significantly enhances their chances of being detected. For example, prey species that exhibit colouration and patterns that match their habitat—such as leaves, bark, or soil—are more likely to remain unseen by predators. This strategy is particularly effective in environments with complex textures and patterns, where visual cues are abundant. It has been shown that great tits (*Parus major*) took twice as long to locate prey that matched the background (Merilaita and Lind, 2005). This finding highlights the importance of background matching, as it extends the detection time for predators and increases the likelihood of survival for cryptic prey.

Within a species, individuals may have different colourations suited to various habitats. Polymorphism can be defined as the occurrence of multiple distinct phenotypes within a population (Ford 1945, Figure 1) and has evolved as an adaptation to diverse climatic conditions, habitats, and environmental pressures (Figure 1). Colour polymorphism is rare but widely spread taxonomically (Hugall and Stuart-Fox, 2012). Multiple prey species have been shown to present colour polymorphism, such as spiders (Oxford and Gillespie, 1998), molluscs (Cook, 2017; Whiteley et al., 1997), crustaceans (Devin et al., 2004; Jormalainen et al., 1995) and vertebrates (Olendorf et al., 2006; Wentz and Phillips, 2003). Polymorphism allows species to thrive across different environments by offering specialised traits that improve survival and reproductive success. For example, certain colour morphs may be better camouflaged in some habitats, whereas other morphs would be better camouflaged in other habitats. Being well camouflaged allows potential prey to be invisible to predators and thus avoid predation. For predators, on the other hand, being invisible to the prey offers better hunting success, which will result in better survival and better fitness. Within the same species, polymorphism can evolve and be maintained if different morphs have different selective advantages in specific habitats or climatic conditions. A classic example of natural selection in a colour-polymorphic prey species is the peppered moth (*Biston betularia*), which has white and black morphs. In 19th-century Britain, industrial pollution darkened birch trees, making white moths more visible to predators when resting on the darkened trees. Black moths, however, gained a camouflage advantage in polluted areas, leading to an increase in black moths in their population. When pollution levels dropped, and trees returned to their natural colour, the white morph regained its advantage (Cook and Grant, 2000). The case of the peppered moth illustrates how natural selection through predation pressures varies among different phenotypes in a species, particularly in relation to their coloration and the shifts in environmental conditions (Cook et al., 2012).

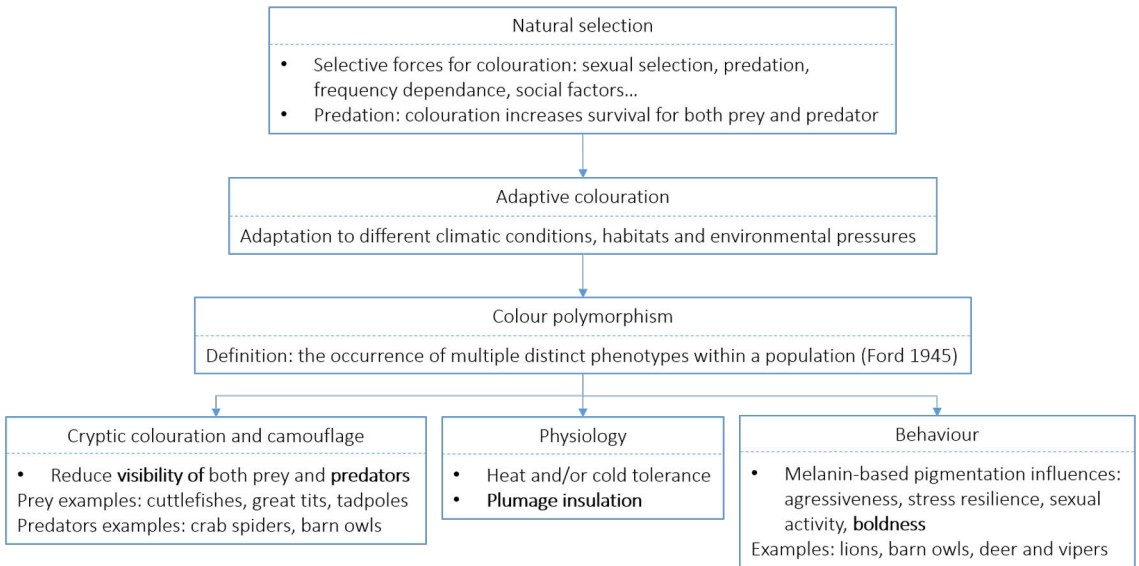


Figure 1. Graphical summary of the main general aspects of colour polymorphism. The focused elements studied in this thesis are highlighted in bold font.

Predators also benefit from camouflage since being invisible increases their hunting success (Figure 1). For example, the crab spider (*Misumena varia*) adopts the exact colouration of the flowers where its prey is feeding, becoming nearly invisible to its prey, which increases its hunting success and, thus, its fitness (Heiling et al., 2005). This type of camouflage is also known as cryptic colouration and is common in predator-prey dynamics. Cryptic colouration allows both predators and prey to blend into their surroundings. Cuttlefish, for instance, can change their colour and texture almost instantly to mimic their environment, lowering the risk of detection (Cuthill et al., 2017). In barn owls (*Tyto alba*), colour morphs range from white to red, and hunting success varies depending on environmental factors like moonlight. Research shows that white barn owls have higher hunting success during full moon nights because their plumage triggers prey to freeze longer, allowing them to capture more easily (San-Jose et al., 2019). In rodents, freezing behaviour is an anti-predator strategy that reduces detection probability. However, under bright moonlight, it can backfire, giving white-coloured morphs a hunting advantage.

Additionally, rare colour morphs may have an advantage due to apostatic selection. In predators, apostatic selection is a form of negative density-dependent selection where rare phenotypes are less easily recognised by potential prey (Clarke, 1962). In tawny owls, rare colour morphs may take longer for prey to identify, making it easier for them to catch prey (Paulson, 1973). After surviving an attack, prey can learn to distinguish between different colour morphs of predators (Roulin

and Wink, 2004). This recognition by potential prey will influence the hunting success of the identifiable colour morph (Roulin and Wink, 2004).

Predators benefit from camouflage beyond just being invisible to prey. Indeed, lower detectability also allows for avoiding harassment, such as mobbing by potential prey. Mobbing is an antipredator behaviour conducted by potential prey to make the predator leave the area (Curio, 1978). Predators try to avoid mobbing (Flasskamp, 1994). In the Australian powerful owl (*Ninox strenua*) and the European kestrel (*Falco tinnunculus*), persistent mobbing by potential prey forces individuals to change roost sites and select roosting habitats where mobbing occurs less frequently (Pavey and Smyth, 1998; Pettifor, 1990). Being harassed and then forced to move induces additional energy expenditure and may negatively affect predators' hunting success and increase their predation risk by alerting top predators.

1.2.2 Melanogenesis and Pleiotropy

In most colour-polymorphic species, melanin pigmentation genetically determines colouration (Roulin and Ducrest, 2013). Melanin pigmentation is responsible for producing black, grey, and brown colouration. More precisely, eumelanins produce dark brown, grey and black, whereas pheomelanins produce reddish and yellow colourations (Gill, 2007). Melanin production, or melanogenesis, is a complex process controlled by numerous genes and receptors (Ducrest et al., 2008; Emaresi et al., 2011). These receptors link the production of melanin with various other traits (Ducrest et al., 2008), and as a result, melanin-based colour polymorphism is often associated with additional characteristics in vertebrates. This phenomenon of a single gene affecting multiple traits is called pleiotropy (Paaby and Rockman 2013, Figure 1). The traits linked to melanogenesis can include morphological, physiological, behavioural, reproductive, or survival-related factors (Roulin, 2004). For instance, in barn owls (*Tyto alba*), offspring of darker-coloured mothers exhibit more robust immune responses compared to offspring from lighter-coloured mothers (Roulin et al., 2000). In lions (*Panthera leo*), darker males tend to be more aggressive and sexually active than lighter males (West and Packer, 2002). Ducrest et al. (2008) reviewed pleiotropic effects associated with melanism and showed that darker individuals may cope better with stress than paler individuals and, in some species, sustain higher metabolic rates. Additionally, the same study demonstrated that coloration is often linked to varying testosterone levels, with darker males frequently exhibiting higher testosterone levels than their lighter counterparts (Ducrest et al., 2008). Thus, individuals of different colours may be genetically predisposed to differ behaviourally, e.g. in terms of risk-taking behaviour or camouflage abilities, as well as physiologically, e.g. feathers' insulation properties. In cases where pleiotropy plays a role, natural selection may

act indirectly on colouration. Colour polymorphism can serve as an indicator of other traits that are genetically linked.

1.2.3 Colouration and Climate Change

Animals relying on coloration for survival will be significantly impacted by global warming and changes in seasonal patterns, such as reduced snow cover in winter. Climate change leads to habitat loss and shifts in seasonality, which are transforming ecosystems. Those changes often make previously advantageous adaptations less effective. Species reliant on environmental cues like snow for camouflage are especially vulnerable. For instance, the Arctic hare (*Lepus arcticus*) and the rock ptarmigan (*Lagopus muta*) change their winter coats to match snow colouration. As winter snow cover becomes unpredictable and uneven, adapted winter coats will be conspicuous in snow-deprived landscapes, making them easy to detect (Zimova et al., 2014).

Nevertheless, not only species that can change their winter coats will be affected by climate change. Animal colouration supposedly follows a rule of different colouration living in various climatic zones. Gloger's rule hypothesises that lighter colour animals live farther away from the equator compared to darker colour animals (Gloger, 1833). Dark-colour individuals are thus expected to be found in warm and wet climates, whereas light-colour individuals would be found in cold and dry climates (Delhey, 2019, 2017). Indeed, eumelanin deposition is supposed to be positively correlated to temperature and humidity increase, and pheomelanin deposition is also positively correlated with temperature but negatively correlated with humidity (Delhey, 2019, 2017). Climate change is predicted to shift wet and warm climatic zones, and thus, the colour frequencies of animals are expected to change as well. According to Gloger's rule, dark and light individuals will see their advantages shift, with darker individuals being favoured in regions facing an increase in temperature and humidity compared to lighter individuals. In owls' species, darker and redder owls are expected to be found near the equator and, thus, follow Gloger's rule (Passarotto et al., 2022b).

Colouration is an ideal phenotypic trait for studying the impact of environmental changes on animals. However, despite the substantial literature on protective colouration, it is still largely unclear how global environmental changes affect, for instance, the efficiency of colour used by predators (Grant and Grant, 2006) and how it may affect their niche use. Research on ecological processes driving fitness differences in colour polymorphic predators can enhance our understanding of how climate change will impact animal communities and dynamics.

1.2.4 The colour polymorphic tawny owl

Colour polymorphism is phylogenetically common among owl species (*Strigiformes*), where one-third of all described species are polymorphic in colour (Galeotti and Sacchi, 2003; Robinson et al., 2024).



Figure 2. Picture of a brown tawny owl (left) and a grey tawny owl (right).

The tawny owl, *Strix aluco*, displays two genetically determined colour morphs, the grey and the brown morph, with some variation in the degree of pigmentation within each morph (Brommer et al., 2005) (Figure 2). In tawny owls, plumage colouration is expressed via pheomelanin concentration, with the reddish colouration positively correlated with the concentration of pheomelanin and eumelanin pigments (Gasparini et al., 2009). Moreover, in the same study, feather colouration was highly heritable in tawny owls.

It has already been mentioned that pleiotropic effects are strong in colour polymorphic species (Ducrest et al., 2008). Many studies across different European populations of tawny owls have shown differences between the different colourations of tawny owls based on pleiotropic effects. First, when studying the genome of tawny owls and the associations between colour morph and other different genes coding for many traits, it has been shown that traits coding for cold environments adaptation were strongly associated with the grey morph (Baltazar-Soares et al., 2024). These results highlight the molecular basis for adaptation to cold environments likely explicitly linked to the grey morph and the strong covariation between colouration and physiology in tawny owls.

Indeed, many studies have found morph variation in physiology, appearance, and behaviour in tawny owls. First, there is a difference in hunting strategy between the colour morphs. Brown individuals have a higher diversity of prey delivered to the nest compared to grey individuals (Karell et al., 2021). However, this difference

depends on the availability of mammalian prey in their environment. The same study suggested that the brown morph is more generalist and reacts more to food supply variations than the grey. This hunting difference between the two morphs could benefit the brown morph since its strategy would allow better hunting success in an unpredictable environment. Indeed, prey choice depends on the availability of resources. However, individuals might perform prey searches and respond to variations in prey density differently if they have different camouflage abilities, different energy requirements or use different hunting habitats. Thus, their reproductive output and/or survival might be affected, and thus, their life history strategies.

Moreover, studies conducted in different European tawny owl populations have shown differences in immunity against parasites between colourations. Indeed, brown females present higher and long-lasting immune responses against blood parasites than grey females (Gasparini et al., 2009; Karell et al., 2011). In order to maintain a higher immune response, the brown females most likely spend more energy than the grey females (Gasparini et al., 2009). However, in an Italian tawny owl population, the brown morph was shown to host more blood parasites than the grey morph, and the immune response was higher in the grey morph than in the brown morph with the same parasite load (Galeotti and Sacchi, 2003).

For tawny owls, an infection can be costly and lead to, e.g., the shortening of telomeres. Indeed, telomere dynamics is a potential mediator of the costs of infections. Telomeres are stretches of non-coding DNA at the end of the chromosomes, and they shorten after each cell division (Blackburn, 2010) and when exposed to oxidative stress (Zglinicki, 2002). When telomeres become excessively short, the cell dies, leading to potential organ dysfunction and contributing to senescence and aging (Sahin et al., 2011). In tawny owls, telomere length is negatively correlated with the degree of pheomelanin colouration, and the rate of telomere shortening between breeding seasons was faster in darker pheomelanin individuals (Karell et al., 2017). The differences between the two colour morphs in telomere properties could explain the different life history strategies of the Finnish population. Indeed, it has already been shown that the early-life telomere length of individuals predicts future senescence of crucial reproductive traits such as clutch size and hatching success (Morland et al., 2023).

In Finland, grey tawny owls live longer and produce more offspring in their lifetime than brown ones (Brommer et al., 2005). However, brown pairs produce and raise heavier offspring than mixed (grey-brown) and grey pairs (Morosinotto et al., 2020). In Switzerland, grey females seem to skip breeding when the total number of breeding pairs is low. In cold breeding seasons, the number of breeding grey females increased (Roulin et al., 2003). Another study from Switzerland found that environmental factors, such as manipulated brood size, did not affect brown males'

reproductive effort while grey males adjusted their reproductive effort based on these conditions. Specifically, grey males produced more fledglings than brown males in enlarged broods, though no differences were observed with reduced brood sizes (Emaresi et al., 2014). The same study also highlighted lower survival rates in adult grey males compared to brown males. It is important to note that there is no associative mating between tawny owls' colour morphs (Brommer et al., 2005). Different patterns of life history strategies are thus being observed in different European populations, probably because of ecological and climatic contexts.

All those differences can indeed vary depending on the environment they live in and how this environment is changing over time. When the temperature decreases, the mortality rate might increase, whereas when the temperature increases, offspring production might increase. Similarly, under low food availability conditions, the cost of reproduction is expected to be higher, whereas, under high food availability conditions, reproduction will be accessible. The environment will drive differential behavioural responses of tawny owls' colour morphs. For instance, the two colour morphs show different dispersal distances according to the weather (Passarotto et al., 2022a). The grey morph covers longer distances in harsh winters compared to the brown morph, dispersing shorter distances.

Finally, it has been shown that there is a robust adverse selection against the brown tawny owl morph under harsh snow-rich winters, whereas both grey and brown tawny owl morphs survive equally in milder winters (Karell et al., 2011). This difference in survival between the two morphs depends on climate. However, it could also depend on several life-history strategies and the behavioural and physiological differences between the two colour morphs. However, it is essential to note that these variation aspects might not be parallel but could be part of the same pattern, e.g. climate could modify the behaviour or physiology and affect life history strategy. My thesis aims to understand the ecological processes underlying fitness differences in the colour-polymorphic tawny owls.

1.3 Plumage insulation

Plumage and feathers' structure, like colouration, can be a trait varying phenotypically due to different environmental adaptations. Feathers are a perfect trait for studying local adaptation in birds due to their diverse physiological and behavioural roles (Dyck, 1985; Terrill and Shultz, 2023). Feather morphology varies depending on the function, with the basic structure consisting of a central shaft (rachis) from which paired branches (barbs) are further subdivided into barbules (Prum, 1999). Thanks to the barbules locking themselves to each other, the barbs are attached, contributing to the feather's structural integrity. Body feathers, which provide insulation and waterproofing, are the most numerous in birds (Davenport et

al., 2009; Wetmore, 1936). The density of barbs and barbules influences the plumage's isolative capacity (Stettenheim, 2000). Birds in colder climates tend to have longer feathers with more plumulaceous parts and lower barb density to trap air between the body and the feathers (Barve et al., 2021; Pap et al., 2017), highlighting an adaptation to climatic conditions.

In addition to insulation, feather colour might affect their heat absorption. Darker feathers have been shown to absorb more heat due to melanin pigments, which reflect less light than lighter feathers (Rogalla et al., 2022). This result makes colour important for species in cold climates, like tawny owls. While the distribution of the two colour morphs across Europe is not fully understood, a recent study found that the proportion of brown morphs increases with warmer winter temperatures and decreases with higher winter precipitation and summer temperatures (Koskenpato et al., 2023). For nocturnal birds like owls, darker feathers may help with heat absorption during daytime when resting after nocturnal hunting. Despite these findings, there is still much to learn about how feathers within a species adapt to different environmental conditions. For instance, the proportion of plumulaceous feathers increases with elevation in house sparrows (*Passer domesticus*) (Barve et al., 2021). Similarly, great tits (*Parus major*) from northern populations had denser, shorter feathers with fewer plumulaceous barbs than those from southern populations, suggesting local adaptation (Broggi et al., 2011). Understanding how feather properties might result from local adaptation is crucial, especially in climate change. It has already been mentioned that the two morphs show different survival rates depending on the amount of snow in the environment, with the brown morph's survival significantly lower than the survival of the grey morph when the amount of snow is essential (Karell et al., 2011). Differences in the moult of flight feathers have been detected in our population in Finland (Karell et al., 2013). The brown tawny owl morph moulted flight feathers more often than the grey one. This may be because of different resource allocations of the morphs and brown morphs, which are more active, feather-consuming lifestyles and probably have higher metabolic rates. Moreover, tawny owls' colour morphs also differ in their feather properties in our Finnish population, with grey tawny owls having better insulation for the back feathers than brown tawny owls (Koskenpato et al., 2016). This difference in feather insulation could be a part of the explanation of why grey tawny owls show higher survival rates in cold Finnish winter.

To study local animal adaptation, phenotypic differentiations can be linked to genetic diversity across individuals in different environments, such as across a large geographical scale. The genetic differentiation between populations can be quantified with F_{ST} when the level of differentiation across populations is due to neutral processes such as genetic drift (Wright, 1943, 1931). In other words, populations experiencing high gene flow between them will have a low F_{ST} . In

natural populations, it is possible to quantify the level of divergence between the populations by calculating the P_{ST} from a quantitative trait such as feather measurements. Different levels of divergence can be observed by comparing F_{ST} and Q_{ST} (McKay and Latta, 2002; Merilä and Crnokrak, 2001). First, if $Q_{ST} > F_{ST}$, the genetic divergence for the trait is superior to expected via genetic drift alone, so natural selection favours different phenotypes in different populations. Then, when $Q_{ST} = F_{ST}$, the differentiation between the population observed is not entirely caused by genetic drift. Finally, if $Q_{ST} < F_{ST}$, natural selection favours identical phenotypes in the different populations. The P_{ST} is used in evolutionary and conservation biology as a proxy for Q_{ST} (Brommer, 2011). When using F_{ST} and P_{ST} , it is essential to note that all environmental factors cannot be excluded from explaining why some differentiation between populations is observed. Indeed, local adaptation means differences between populations due to genotypes, by definition. However, as I measure phenotypes in their natural environment, all observed differences in phenotype (within and across populations) could be due to plasticity. In birds, a perfect quantitative trait to study population differentiation is feathers.

1.4 Aims of the thesis

In my PhD, I study two ecological processes underlying fitness differences in colour polymorphic tawny owls. Specifically, my main study questions are: (Q.1) Is there a camouflage difference between brown and grey tawny owls, and do the two morphs use their potential camouflage abilities differently? (Q.2) Can camouflage or feather insulation differences explain the difference in survival in snowy winter? Previous work in the tawny owl's system has become textbook examples of evolutionary adaptations to climate change in nature. It is an excellent system to study cryptic colouration since it is a widespread predator in Europe with documented variation in colour morph fitness in different parts of its distribution (Emaresi et al., 2014; Roulin and Wink, 2004). By studying those two questions, I aim to understand which ecological processes are underlying fitness differences among the colour-polymorphic tawny owls.

- First, I tested tawny owls' camouflage abilities and how they use their space in captivity and a novel environment (**Chapter I**, Q.1, Figure 3). In an open field test, I used 19 captive tawny owls and studied their behaviour towards stressors (mobbing and predation). I hypothesised that both morphs would try to camouflage when exposed to predation risk and mobbing. On the other hand, when released in a novel environment, I expected the brown morph to be more prone to roost in the outer part of the experimental aviary due to the pheomelanin

association with aggressive behaviour (Da Silva et al., 2013; Ducrest et al., 2008) and thus boldness. Similarly, I expected the brown tawny owl morph to choose a more exposed perch in a familiar environment.

- Then, I investigated tawny owls' camouflage efficiency in the wild by studying antipredator behaviour towards them in different seasons (**Chapter II**, Q.1&2, Figure 3). I studied passerines' behaviour towards stuffed owls in four seasons (spring, autumn, winter without snow and winter with snow). In winter, I expected the grey tawny owl morph to be more difficult to detect only when there is snow in the environment since it is less conspicuous with this background (Koskenpato et al., 2020). Based on the findings of Koskenpato et al. (2020), I expected the brown morph to enjoy cryptic advantages in autumn and spring compared to the grey morph in such environments.
- Finally, I focused on the differences in plumage insulation capacities between the two morphs and nine different European populations (**Chapter III**, Q.2, Figure 3). Darker feather surfaces absorb more heat than light-coloured surfaces under exposure to the sun (Rogalla et al., 2022). Moreover, since back feathers have a lower insulation capacity in brown owls than in grey owls in Finland (Koskenpato et al., 2016), I expect that, across all our study populations, brown, tawny owls would have a higher density of barbs and barbules and shorter plumulaceous portion of their feathers (i.e. lower insulation capacity) compared to grey tawny owls. I compute the between-population differentiation in phenotypes (P_{ST}) of measured feather properties and compare it to the differentiation expected based on genetic drift alone (F_{ST}) to evaluate which, if any, of tawny owl feather properties show evidence of local adaptation.

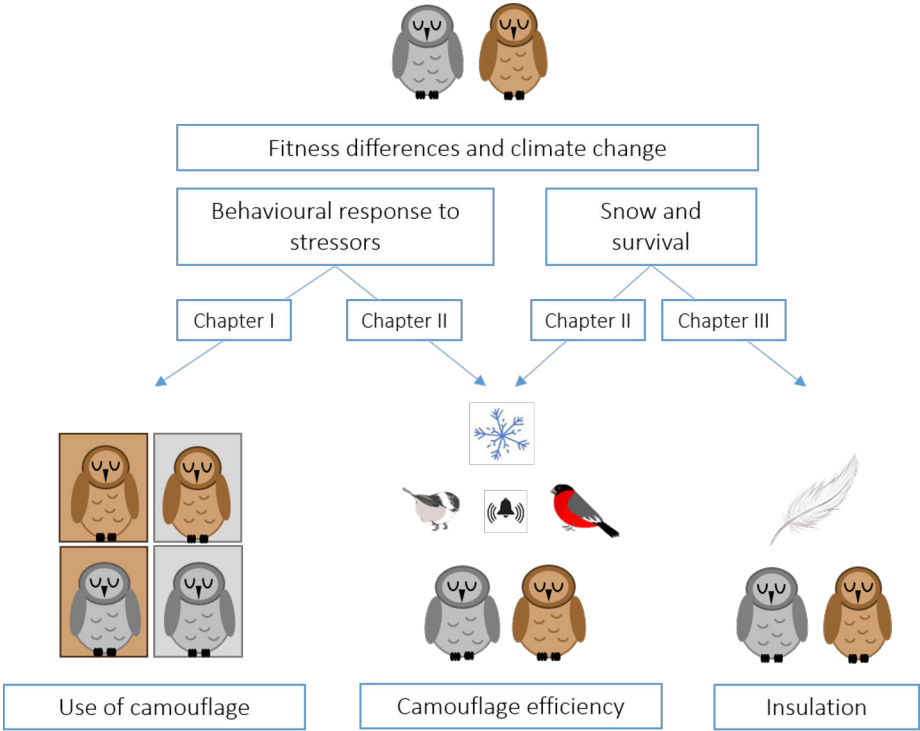


Figure 3. Graphical summary of the main general aspects studied in this thesis and the connection between the different chapters.

2 Materials and Methods

2.1 Tawny owls

2.1.1 Generalities about the Study Species

The tawny owl (*Strix aluco*) is a medium-sized owl species widely distributed across Europe, reaching its northernmost habitat limit in southern Finland (Francis and Saurola 2007, Figure 4). Tawny owls are usually found in mixed forests and cultural landscapes. They mainly prey on small mammals, with voles (*Microtus*) as their primary prey, but they can also consume birds and frogs. In that sense, their nesting success is strongly influenced by the abundance of small mammals (Karell et al., 2009; Petty, 1999). Tawny owls are territorial and maintain high mate fidelity (Saurola 1987). Both parents take care of the offspring with two distinct duties. Males provide food for the incubating female and the offspring, whereas females incubate the eggs and guard the nest (Mikkola, 1983; Sasvári et al., 2000). Tawny owls are predators but are not top predators, which leads to intraguild predation (Sergio et al., 2007).

Tawny owls display two distinct, melanin-based colour morphs: a pale grey morph (grey) and a reddish-brown morph (brown). These colourations follow a bimodal distribution, with intermediate colouration being rare (Brommer et al., 2005; Karell et al., 2011). The colour variation is primarily explained by pheomelanin pigmentation, but eumelanin pigmentation also contributes (Gasparini et al., 2009). The colour trait is highly heritable ($h^2 = 72\text{--}93$ depending on the study) and appears to follow a mendelian inheritance, with brown as the dominant allele in a one-locus, two-allele system (Brommer et al., 2005; Karell et al., 2011; Morosinotto et al., 2020). Mating between the colour morphs occurs randomly without preference, and both morphs are equally represented in males and females (Galeotti and Cesaris 1996).



Figure 4. Picture of a grey tawny owl in the experimental room of Chapter I.

2.1.2 Colour-scoring of the Tawny Owls

Several methods have been described in the literature to colour score the tawny owls' colour variation. These methods allow for either a continuous colouration score (Gasparini et al., 2009) or several colours with five distinct morphs (Da Silva et al., 2013; Emaresi et al., 2014), the three distinct morphs (Galeotti and Cesaris, 1996; Grašyte et al., 2017) and two distinct morphs (Brommer et al., 2005; Galeotti and Sacchi, 2003; Karell et al., 2011). Since the colouration of tawny owls follows a bimodal distribution, with most individuals being grey or reddish-brown (Brommer et al., 2005; Karell et al., 2011), I used the dichotomous approach and determined the individuals as two distinct morphs: grey or brown. To determine the colour morph of an individual, several parts of the tawny owl's body are scored, such as the facial disc, the chest, the back, and the overall impression by the amount of reddish brown perceived (Brommer et al., 2005). Each body part score was added to obtain a total score between 4 and 14, where 4 is the lightest grey, and 14 is the darkest reddish brown. If an individual's total score was between 4 and 9, it was considered grey; if the total score was between 10 and 14, it was considered brown. This colour-scoring method is highly repeatable (Brommer et al., 2005; Karell et al., 2011). In **Chapter III**, collaborators initially colour-score the owls using several other techniques. In Italy, colouration was scored using the same colour-scoring method as in Finland. Tawny owls' morphs from Scotland and Portugal were determined using the same colour scoring method as those of the Finnish population, using pictures of each individual. The other populations (Sweden, Norway, Slovenia, Republic Czech and Lithuania) were initially colour-scored using a different system

with several morphs identified. Still, individuals initially scored with other methods were converted into the same method as in the Finnish population. The conversion was done using a scale created from pictures for those populations. When the morph “rusty” was used, I considered those individuals brown.

2.1.3 Captive live Tawny Owls

In **Chapter I**, the first aim is to understand whether the two colour morphs used their camouflage abilities similarly. To do so, I imagined an experimental design to study the use of space and camouflage of tawny owls under potential stress inducers. The experiment was conducted in January 2021 on 19 adult captive tawny owls (11 grey (3 females and 8 males) and 8 brown morphs (3 females and 5 males), Figure 4). The owls were taken to captivity from their nest boxes just before fledging at the age of 23-27 days in spring 2020. Each owl came from a different nest. The owls were kept in a purpose-built aviary with separate identical aviary compartments (3m x3m x 6m, hereafter “home aviary”) at Lund University in Sweden (see below “roost site selection in home aviary” for the description of the aviary). At the beginning of the experiments, the owls were aged from 266 days to 288 days.

2.1.4 Stuffed Tawny Owls

In **Chapter II**, I aimed to understand how efficient the camouflage of the two different colour morphs of tawny owls was in various environments.



Figure 5. Picture of two stuffed tawny owls used in Chapter II, one brown (left) and one grey (right).

To study tawny owls' camouflage efficiency in the wild, I used four Tawny owls (*Strix aluco*) stuffed owls (two grey and two brown morphs, Figure 5). The stuffed owls were placed onto a wooden pole to mimic the roosting position of owls in their natural environment. The objective was to make the owls seem as wild as possible for the passerines to recognise.

2.1.5 Wild European Tawny Owls

To study insulation capacities with environmental variation, nine different populations of tawny owls across Europe were examined in **Chapter III** (Figure 6). The populations were from Finland, Sweden, Norway, Scotland, Italy, Portugal, Slovenia, Czech Republic, and Lithuania. Years of collection went from 2015 to 2023. A central point for each population was determined to get information on local weather such as Finland (central point Siuntio: 60°15'N, 24°15'E), Sweden (central point Karlsborg: 58°31'N, 14°31'E), Norway (central point Levanger: 63°43'N, 11°21'E), Lithuania (central point Kavarskas: 55°43'N, 24°92'E), Czech Republic (central point Olomouc: 49°69'N, 17°15'E), Italy (central point Cairo Montenotte: 44°37'E, 8°36'), Portugal (central point Faro: 36°98'N, -7°92'E), Scotland (central point Aberfoyle: 56°17'N, -4°36'E) and Slovenia (central point Mt. Krim: 45°58'N, 14°25'E).

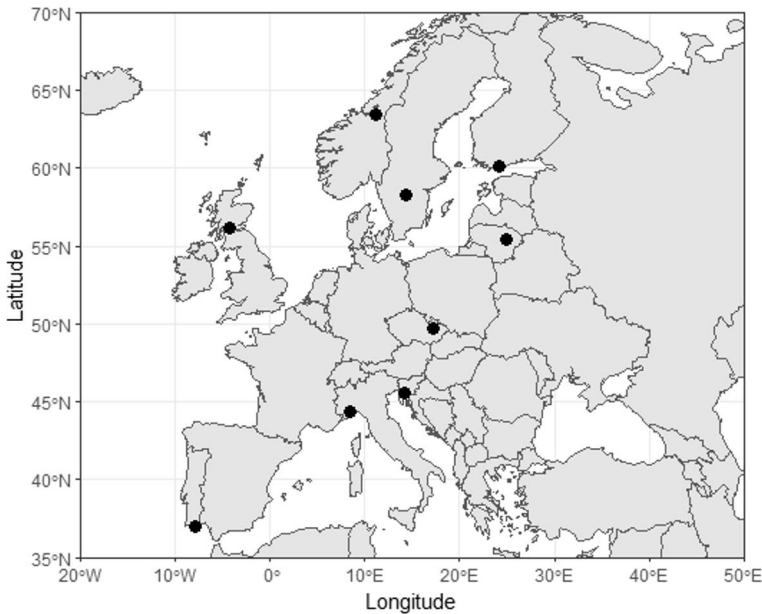


Figure 6. Map of Europe with the nine different tawny owls' populations represented in dots used in Chapter III.

2.2 Data collection

2.2.1 Roost site selection in Home Aviary

To detect tawny owls' space use in their familiar environment, when undisturbed by human presence, I observed owl roosting habits by recording pellets' position in the aviary (**Chapter I**). Owls regurgitate indigestible prey remains via the pellets (i.e. bones, teeth; Errington 1930; Glue 1970, Figure 7), usually while roosting. To identify the preferred perch for roosting, we collected owl pellets in the aviaries during the summer of 2020, from the 13th of June to the 13th of August, when the owls were still growing. Each week, two observers collected pellets. For five minutes, we were looking for pellets in the inner and outer parts of the aviary. Home aviaries were made in wood and the floor was covered in wooden pellets. Each home aviary had four different roosting options for the owls: two in an inner area and two in an outer area. All the home aviaries looked the same regarding the availability of perches in the inner or outer areas, but the disposition of perches differed from the experimental aviary. The location of the pellets inside the aviary was recorded. I used the number of pellets under a perch to measure the time the owl spent on that perch.



Figure 7. Picture of an owl pellet used in Chapter I.

2.2.2 Open field test

The experimental aviary of **Chapter I** (Figure 8) was created as an open-field test (Brown and Braithwaite, 2004; Carere et al., 2005; Dall and Griffith, 2014; Dingemanse et al., 2004; Peralas et al., 2017; Toscano et al., 2016; Yuen et al., 2017). The open-field test allows us to understand the owls' use of space, with multiple perching choices and two types of environments in the same aviary.



Figure 8. Picture of an owl roosting on the exposed perch of the experimental aviary in Chapter I.

Indeed, the aviary was composed of two parts, one covered by a roof and the other without a roof. The outer, exposed area had fences of metal wire on both sides and above and was thus more exposed to both predators and mobbers as well as climate (Figure 8 and 10). The inner part of the experimental aviary was composed of two different camouflage backgrounds made with camouflage nets painted in grey and brown colours, respectively. There were three perches in the experimental aviary: one with a grey camouflage background, one with a brown camouflage background and a perch in an exposed zone without background (Figure 9). The door was located in the upper right corner of the scheme (Figure 9) and was always covered by the camouflage background so that the owl could not perceive the door when inside the experimental aviary. The backgrounds were switched after each trial so that in every trial, each colour background was on the opposite side from the

previous trial. The speakers were placed in the inner corridor, just behind the fence of the aviary, and at the same height as the perches inside. Two speakers were used, one behind each background perch. There was no speaker next to the exposed perch.

For the open field tests, the owl was released into the aviary from the door (yellow arrow, Figure 9). One trial was divided into two distinct parts. First, space use was measured during the first 4 minutes after the owl entered the aviary. I was hidden from owl sight, recording perch use and any switching between perches by the owl.

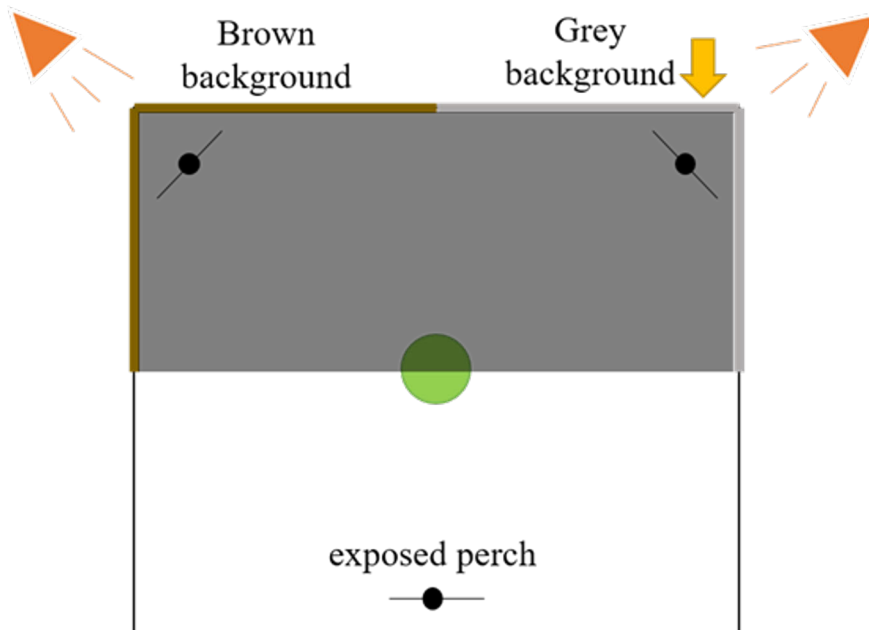


Figure 9. Scheme of the experimental aviary, seen from above. The black lines with a dot represent perches, and the orange devices represent speakers. A darker colour represents the inner part of the aviary. A yellow arrow represents the position of the door. The green circle represents where the visual cues were presented to the owls.

The exposed perch was located in the outer part of the aviary, and the two background perches were considered in the inner part.

Secondly, in the remaining 5 minutes and 40 seconds of the trial, a series of alternating cues of only playback or playback and visual cues combined were performed, each lasting 20 seconds. Each owl was tested 14 times in total, and the order in which each was tested during separate trials was randomised. Only playback cues (mobbing, predator, and control) were presented to the owl during the first five trials. The last nine trials were composed of playback and visual cues presented simultaneously (mobbing, predator, and control) (see Table 1). The visual cue was

pulled down at the same level as the owl's eyes when perched in the experimental aviary when the playback was on and pulled up against the ceiling when the playback was stopping.



Figure 10. Picture of an owl roosting on the brown background perch of the experimental room in Chapter I.

The owls could still see the visual cues up to the ceiling but flattened. All the playbacks (for the three treatment groups: mobbing, predator, and control) were made using sounds from the website xeno-canto (<https://www.xeno-canto.org/>). For mobbing, a mix of blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), willow tits (*Poecile montanus*), and thrushes (*Turdus spp.*) alarm calls from Europe were used since these are among the most common passerines in Northern Europe, where the study was performed. The soundtracks chosen for the mix had for each species 3 or more individuals calling. I created only one final soundtrack to be played for all the trials. The playback part, which in total lasted 5 minutes and 40 seconds, included nine sessions of 20 seconds playbacks separated by 20 seconds of silence in between each playback. The predator playback was made using northern goshawks (*Accipiter gentilis*) alarm playbacks, while the control playback was made using geese (*Anser anser*) alarm playbacks. Playback sessions lasted 20 seconds alternated with 20

seconds of silence as in the mobbing treatment. In total, one trial was composed of nine playback sessions.

The visual cues (mobbing passerines cue, predator cue, and control cue) were shapes hanging from the ceiling by a transparent string at a similar distance from each perch in the experimental aviary (Figure 9). The mobbing passerine cue consisted of four origami birds coloured as blue tits and great tits (Figure 11); the predator cue was a shape of a black bird of prey and the control cue was two circle shapes embedded together, one all black and one blue and yellow like the mobbing birds.



Figure 11. Picture of the origami birds representing the visual cue for mobbing behaviour in Chapter I.

I repeated the same treatment once for each owl. In the repeat, I switched background colours between the left and right side (i.e. one time grey background on the left side, one time brown background on the left side, Table 1).

Table 1. Table explaining the different trials of the experiment and how many times they have been conducted with the different cues (--: no observation).

| | mobbing | predator | control | total |
|---|---------|----------|---------|---------|
| <i>side of the aviary where the brown background is</i> | right | left | right | left |
| <i>playback only</i> | 1 time | 1 time | 1 time | 1 time |
| <i>visual cue + playback</i> | 2 times | 2 times | 2 times | 2 times |

Sessions were not conducted when weather (i.e. heavy snow, heavy rain, heavy wind) or when sounds in the environment might have interfered with the presentation of visual and auditory cues. The behaviour of the tawny owls (i.e. roosting site, number of switches between the perches, time spent on each perch) were both recorded with a camera and observed directly behind a fence outside of the experimental aviary where the owl could not see the observer. We defined a reaction to the cue to occur when the owl oriented its head towards the speakers and/or the visual cue. The playback and visual cue were simultaneously presented to the owls nine times in one trial. Each time, the observer recorded if the owl oriented its head towards the speaker and/or the visual cue, or not. I established a variable explaining the reaction of the owls to the cues: the “probability of reacting” out of the 9 stimuli, which takes into consideration how many times the owl responded to the stimuli during one trial (i.e. 0 or 1 reaction level, 9 repetitions per trial). The probability of reacting was then plotted as a percentage. The roosting site was recorded during the whole experiment. At the end of each trial, the observer approached the owl from the outer corridor next to the exposed perch to record its reaction (change perches: yes or no, choice of background perch if changing perches).

2.2.3 Camouflage experiments conducted in the wild

In **Chapter II**, I conducted experiments in the wild in the village Vassböle in South-western Finland (central point (Labbas): 60.126004°N 24.049494°E). Fourteen locations were selected within the area, separated from each other by an average of 380.73 meters (\pm 172.02 meters). A black feeder for bird seeds, a feeder for fat balls and a pole were installed at each location. Fat balls were provided during the winter times in order to attract more diverse communities of birds; this feeding resource is very attractive, especially during cold periods. For repeatability purposes, I also provided fat balls in all other seasons. The feeders were hanging from a tree, and a pole was pressed into the ground 10 (\pm 2) meters from them. Each feeder was filled

every week throughout all fieldwork seasons to attract the birds to the observation locations (Figure 12).



Figure 12. Picture of the refilling seeds process in one of the bird feeders in Chapter II.

The experiments were conducted four times: once during winter without snow cover (December 2019 to March 2020), once during spring (May 2021), once during autumn (September to October 2021), and once during winter with snow cover (January to February 2022) (Figure 13).

Every observation was made between 7:00 and 14:00, when the birds were most active. The time between two observations varied but was, on average, around 40 minutes. The experiments started in December 2019 with one observer. Between February and March, two observers were present. After March 2020, only one of the two observers performed the observations alone.



Figure 13. Pictures of one location from left to right in autumn, winter without snow and winter with snow in Chapter II.

Four tawny owl stuffed owls (two grey and two brown) were used during the experiments. They were attached to a wooden pole in order to mimic the roosting position. For each location five observations were conducted, one observation per each of the four stuffed owls (in random order) and a control (no stuffed owl). Arriving at one location, the observer(s) attached the stuffed owl pole with a rope to the pole already in place and took position equidistantly from the stuffed owl and the feeder to form a triangle from above (Figure 14).

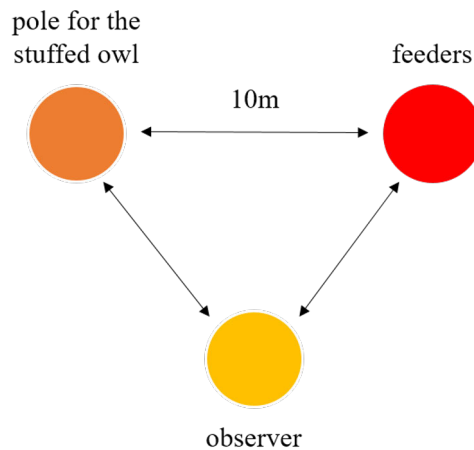


Figure 14. Scheme of the experimental design, seen from above in Chapter II.

After one minute, the observer took the hood off from the stuffed owl. When the observer was back to the observation spot, the observation officially started. During control, the same process, without the stuffed owl, was conducted to minimize the differences between the control and experimental trials. The aim was to have each morph tested 28 times in each season (14 locations * 2 stuffed owls). Due to technical

issues, the sample size varied a bit (Table 2). In addition to the 224 observations with a stuffed owl, there were 56 controls (14 locations * 4 seasons) and hence 280 trials were conducted in total.

Table 2. Table describing the number of trials per stuffed owl morph per season.

| | Brown stuffed owl | grey stuffed owl | total |
|----------------------------|-------------------|------------------|-------|
| <i>Spring</i> | 25 | 27 | 52 |
| <i>Autumn</i> | 27 | 28 | 55 |
| <i>winter without snow</i> | 29 | 28 | 57 |
| <i>winter with snow</i> | 30 | 30 | 60 |
| <i>total</i> | 111 | 113 | 224 |

During each trial, the behaviour of the mobbing birds was monitored. Behaviours observed were: the time until the first bird approaches the stuffed owl, its species, the time until the mob occurs and the distance of the approaching and mobbing birds from the stuffed owl. Several behavioural traits were considered and defined as:

- a *detection*, when a bird came closer to the stuffed owl, looking in its direction.
- a *mob* when at least three birds were all on the same tree, closer to the stuffed owl, clearly interested in the stuffed owl and looking in its direction and alarming.
- the *initial number of birds at the feeder*, describing the number of birds that were at the feeder when the observer(s) arrived at the observation location.

If mobbing occurred, the observer(s) waited five minutes after the mob stopped to end the observation. If no mobbing occurred, the trial was stopped after 30 minutes. The end of mobbing was defined as when the birds went back to the feeder or left the area. Environmental information was also recorded during each trial such as the wind intensity (scale from 1 to 3), the temperature, the light conditions (sunny or cloudy), and the snow depth (using a ruler in the snow five centimetres away from the stuffed owl placement).

2.2.4 Feathers

To study insulation differentiation between our nine European populations in **Chapter III**, four feathers per individual were collected, two feathers from the back (dorsal side) and two feathers from the chest (ventral side) (Figure 15). For some individuals, only one feather for the back or chest could be provided.



Figure 15. Picture of a dorsal feather (left) and a chest feather (right) in Chapter III.

Each feather was measured by hand with a ruler as well as its plumulaceous part without the rachis.

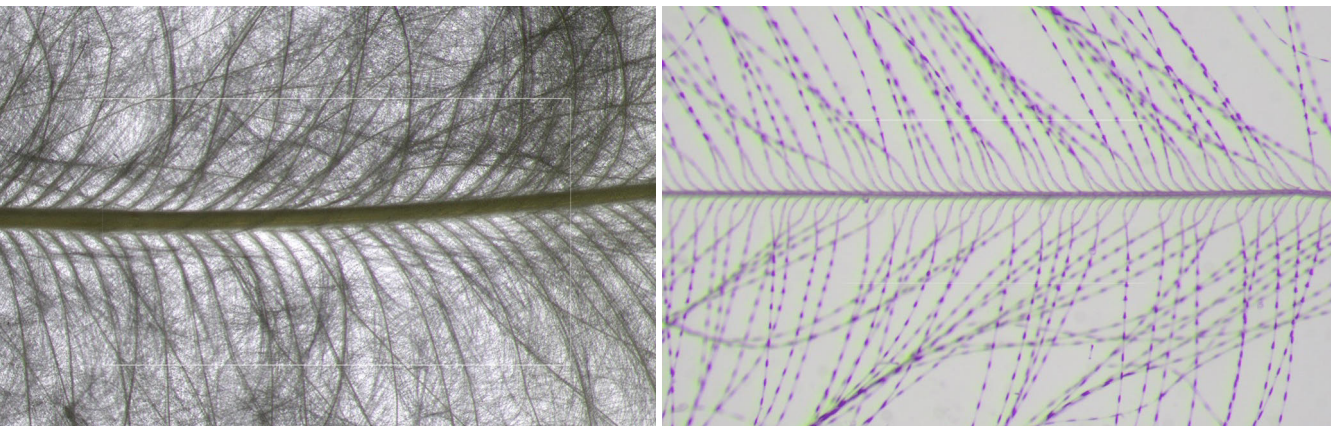


Figure 16. Microscope pictures of a feather (left, x10 magnification) and of a barb (right, x63 magnification) in Chapter III.

Microscope pictures were taken of the feathers and one barb of each feather (Figure 16). The microscope used was a Leica MZ10F Stereo. For the feather pictures, I used a magnification of x10, and for the barb pictures, x63. Each picture was taken from the middle part of the feather or the barb.

With ImageJ image analysis software (Schindelin et al., 2015), a square of 1cm^2 for barbs and 1mm^2 for barbules was drawn on each picture at the stem level. Using

a scale defined according to the microscope, the pixel distance was converted into centimetres (1cm=950 pixels, 1mm=765 pixels).

Two observers measured each feather with the ruler. One observer counted the number of barbs and barbules of feathers on the microscope pictures within the drawn square from five populations out of nine, and another observer counted on the microscope pictures from the remaining four populations out of nine. For a subset of 39 feathers from random populations, two observers counted barbs and barbules. The correlation in the counts made by these two observers was very high (barbs: $r=0.95$, $pvalue<0.001$, $N=19$; barbules: $r=0.99$, $pvalue<0.001$, $N=20$).

2.2.5 Sampling and DNA extraction

The DNA used in my thesis came from multiple tissues, mostly due to constraints on performing invasive sampling (collection of blood, muscle tissue, etc.) imposed on birds in the countries from which these tawny owl populations originated.

Thus, DNA from individuals from Slovenia, the United Kingdom, Norway, Italy, and the Czech Republic was extracted from buccal swabs (IsoHelix™) that allowed the sample of epithelial cells in tawny owls' mouths. DNA from individuals from Finland was extracted from fresh blood maintained in a non-coagulation solvent. DNA from Lithuania was extracted dry blood droops persevered in filter paper. The only exception was Portugal, where DNA was obtained from muscle tissue. This is because our collaborator in the country was a Wildlife Rehabilitation and Research Centre that granted access to their deceased owls. My collaborator established a standardized DNA protocol across samples, which consisted of a customized version of the salt extraction protocol (Aljanabi and Martinez, 1997) to increase DNA yield.

All samples were genotyped with eight microsatellite markers using a multiplex PCR approach (Saladin et al., 2007; Thode et al., 2002). PCR was carried out in three 12 μ l reactions using the QIAGEN Multiplex PCR Kit (Qiagen Inc. Valencia, CA, USA) with an annealing temperature of 55 °C and a primer concentration of 0.2 μ M. To improve the microsatellite peak profiles, a GTTT tail was added to the 5' end of each reverse primer (Brownstein et al., 1996), as seen in the supplementary materials, Table S1.

DNA amplifications were performed on Applied Biosystems 2720 thermal cyclers and the size of the fragments was determined by capillary electrophoresis on an ABI Prism™ 3130xl genetic analysis instrument. The peak profiles of the pooled samples could then be separated during scoring and visual inspection, using GeneMarker™ version 2.4.0 (SoftGenetics). Laboratory work for microsatellite genotyping was carried out by the Center of Evolutionary Applications (University of Turku, Finland).

2.3 Statistical analysis

All statistical analyses were performed using R software version 4.1.2 (2021-11-01) (<http://www.R-project.org/>). Values were considered as statistically significant when $P < 0.05$.

In **Chapter I**, I used Generalized Linear Mixed-Effects Models (GLMM) for all the models, using the function ‘glmer’ implemented in package ‘lme4’ (Bates et al., 2015) in R (R Development team 2019). Individual ID was consistently included as a random factor and I considered morph (scored as a binary variable: G = grey, B = brown) as a fixed factor. For all the models involving behaviour in the experimental room, I included as fixed factors: the number of previous trials to control for the habituation of the room, sex, time of the day (morning or afternoon) and disturbance (binomial variable, i.e. wind, people talking nearby, truck passing by the nearest road) because they could affect the behaviour of the owls. First, the efficiency of active background choice was analysed as a binomial GLMM, such as the use of the matching background corresponding to the owl colour morph (1) versus the non-matching background or the exposed perch (0). The exposed perch data was combined in this analysis with the non-matching background choices since many owls were choosing this perch (119 cases out of 266), making the analyses stronger when keeping those observations. The same data were used to study the binomial use of space in the experimental room, such as the use of the outer part of the experimental room (exposed perch, 1) versus the inner part of the experimental room (either grey or brown background, 0). The reaction level of the owls to mobbing cue, predator cue and control cue was analysed as a binomial GLMM. The type of playback (mobbing, predation, or control) was considered a fixed factor, to test if the owls would react differently. I also controlled for the presence of a visual cue (binomial variable) by including it as a fixed factor.

The proportion of pellets found in the outer part of the aviary (open, no roof) compared to the inner part (hidden, with roof) was modelled as a binomial GLMM. The proportion of pellets found in the outer part of the aviary (i.e. under the outer perch) compared to the inner part of the aviary was calculated using the function `cbind` (Bates et al., 2015) in R. To control for the weather effect, I included the number of rainy days during the week before the collection as a fixed factor. I also corrected the impact of sex and the collection week as fixed factors since pellets were collected during owls’ growth.

In **Chapter II**, in order to assess the efficiency of the owl stuffed owl presence, I conducted a Pearson's Chi-squared test with Yates' continuity correction comparing owl detection with and without the stuffed owl being present. For all the probability models, I used Generalized Linear Mixed Models using Template Model Builder (GLMMTMB), using the function ‘glmmTMB’ implemented in package ‘glmmTMB’ (Brooks et al., 2017) in R (R Development team 2019). Location ID

was consistently included as a random factor, and I considered morph (scored as a binary variable: G = grey, B = brown) to be a factorial fixed effect. I further included fixed factors: the initial number of birds at the feeder before the experiment started, the season, and the moment of the day (morning or afternoon). I included perturbation as a factorial variable scoring whether any perturbation (wind, rain, snow, people talking nearby, truck passing by the nearest road) occurred or not during the trial, because these could affect the behaviour of the passerines. The detection and mobbing probabilities were analysed as binomial GLMM scoring detection or mobbing as 1 and non-detection or non-mobbing as 0. The effect of snow cover within the winter season on mobbing probability was tested using only the data from winter without snow and winter with snow using a binomial GLMM.

In **Chapter III**, all feather traits were analysed using mixed models. The model included a year of sampling as factorial fixed effects, and for the length of the plumulaceous part of the feather, I also included the total feather length. Initial models were constructed including all levels of repeated measures as random effects. That is, for the number of barbs and barbules I included population and ID of the sampled individual as random effects. For the length of the plumulaceous feather, I included the population, ID of the sampled individual and ID of the measurement. Thus, these models partitioned the variance (conditional on the fixed effects) into between-population, between-individual and (for plumulaceous feathers) between repeated measures on the same individual.

For the computation of the differentiation between population (P_{ST}), we used as response variables the mean values for the number of barbs and barbules and the mean length of the plumulaceous part of the feather for each individual over all measures. Fixed effects in the model were as described above, except that the mean total feather length was used as fixed effect in the analysis of the plumulaceous part of the feathers. Random effect included was population and the P_{ST} was computed as

$$P_{ST} = \frac{\sigma^2(pop)}{\sigma^2(pop) + \sigma^2(res)}, \quad (1)$$

where $\sigma^2(pop)$ and $\sigma^2(res)$ are the between population and residual REML variances respectively as inferred by the above described mixed model. The analysis of the differentiation of morphs (brown coded as 1; grey as 0) across populations was analysed in a mixed model with binomial error distribution and logit link implemented in AsReml (VSN International). The proportion of variance across population was computed on the logit scale following Nakagawa and Schielzeth (2010).

Models were implemented in the package sommer (Covarrubias-Pazarán, 2016) in R. Uncertainty (standard error) of the ratio of variances, such as e.g., P_{ST} (eq. 1) or the proportion of variance due to between-individual variance (i.e., repeatability), was inferred using the delta method as implemented in the package sommer. Mean values for the number of barbs and barbules were calculated for each individual.

3 Results and discussion

3.1 Behavioural response to stressors

In the open field test conducted in **Chapter I**, I evaluated tawny owls' roosting site selection as well as their use of camouflage. The results revealed that the probability that owls chose to roost in the outer part of the experimental aviary depended strongly on the colour morph of the tawny owl. Brown tawny owls had a higher probability of using the outer area of the experimental aviary than the grey tawny owls (Figure 17). Furthermore, stressful cues such as predator or mobbing did not change tawny owls' roosting site (except in 19 cases out of 262). This could indicate that the open field test was already a stress-inducing place for tawny owls. Moreover, grey tawny owls were more likely to select the perch with a matching background compared to brown tawny owls (binomial GLM: Estimate \pm SE = 1.57 ± 0.47 , df = 1, Chisq = 11.26, $P < 0.001$). However, this difference in background matching choice is mainly explained by brown tawny owls using more the exposed perch (without a camouflage background) compared to grey tawny owls. Nevertheless, while grey tawny owls were using the three perches approximately randomly in equal proportions, the brown morph used the perch with the matching brown background the least frequently (<10%).

In order to understand how tawny owls would use their environment in a non-stressful environment, I estimated the time spent on different perches available in their home aviaries with the weekly number of pellets found under each perch (**Chapter I**). I found that the proportion of pellets found under the outer area compared to the inner area did not differ between the two morphs, nor between males and females (Figure 17). These two results highlight the difference in space use between the two morphs depending on the environment they are occupying. In the supposed non-stressful environment, the home aviary, both morphs are using their space the same way. However, in a supposed stressful environment, the open field test, brown tawny owls show a higher probability of roosting in the experimental room's outer area than grey tawny owls. Wild animals may improve their camouflage efficiency through active background choice (Stevens et al., 2017). However, I find here that, under novel conditions, both morphs rapidly chose where to perch independently on the camouflage background and did not change perch during the

presentation of the cue. Yet, camouflage is key for nocturnal predators like tawny owls, as it would allow them to not be detected during the daytime by mobbers or predators. For tawny owls, it has been shown that human observers detect the brown morph with a higher probability and faster than the grey morph (Koskenpato et al., 2020). However, our results show that the brown morph does not behaviourally compensate for its poorer camouflage by using camouflaged roosting perches.

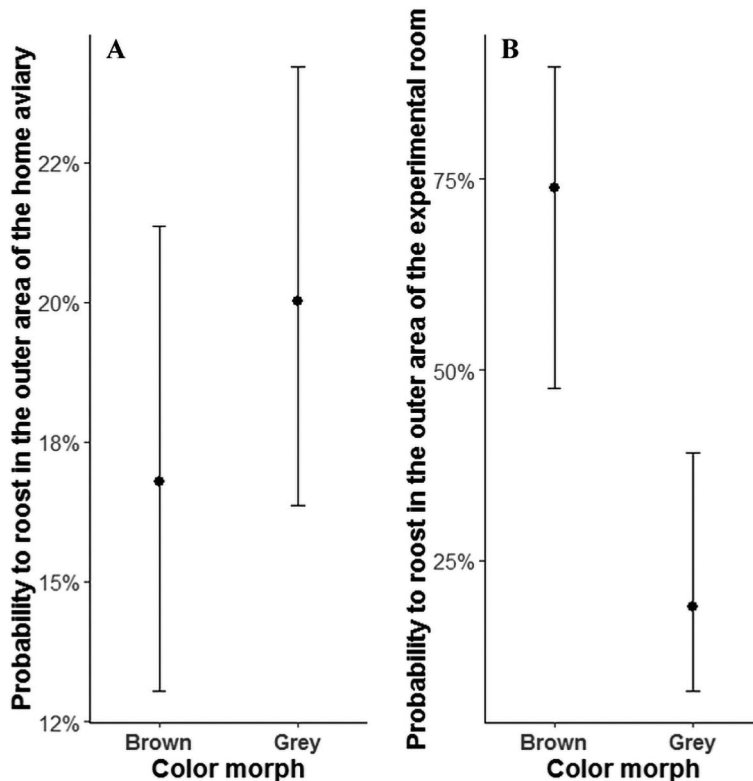


Figure 17. (A) Least squares means with 95% confidence intervals of the probability to roost in the outer area of the home aviary, according to colour morph (brown or grey) (B) Least squares means with 95% confidence intervals of the probability to roost in the outer area of the experimental aviary, according to colour morph (brown or grey). Figure issued from Perrault et al. (2023), **Chapter I**.

In the wild, being more exposed can be a disadvantage since it leads to an increase in encounters with predators and mobbers, with diurnal predators being responsible for 73% of owls' mortality (Sunde et al., 2003). Being more prone to be exposed could also indicate being bolder in general and thus be an ecological advantage. Indeed, being bolder could help to explore, protect territories, and disperse more. However, the two morphs show no difference in dispersal patterns,

neither at natal dispersal (Passarotto et al., 2022a) nor in breeding dispersal (Passarotto et al., 2023). Behaviourally speaking, it has also been shown that the two morphs display different aggression levels and boldness (Da Silva et al., 2013). Boldness can be defined as the willingness of individuals to engage in risky behaviour (Ward et al., 2004). Boldness is often tested using behavioural tests such as the novel object experiment or an open field test (Brown and Braithwaite, 2004; Carere et al., 2005; Dall and Griffith, 2014; Dingemanse et al., 2004; Perals et al., 2017; Toscano et al., 2016; Yuen et al., 2017). In the open field test, risk-taking is measured by the amount of time an individual spends out in the open (i.e. away from the protected inner area with walls of the open field). Choosing to roost in the exposed area of the experimental aviary (**Chapter I**) strongly suggests choosing the riskier choice to roost since it would lead to greater exposure to potential predators and mobbing birds.

Choosing different types of exposure to roost could also imply a various choice of habitats to breed, rest and prey. For the latter, the colour morphs of the two tawny owls have been shown to present different hunting strategies (Karell et al., 2021). Indeed, they showed that brown, tawny owls are more generalist when hunting than grey tawny owls in years with low mammalian prey abundance. This hunting habit and, thus, diet difference could be a beneficial strategy to cope with unpredictable environmental variations such as low prey abundance. Being able to hunt in open habitats could present an ecological advantage, and it has already been shown that polymorphic species are more prone to live in open/closed habitats than in intermediate habitats (Passarotto et al., 2022b). However, Galeotti and Cesaris (1996) did not find that tawny owl colour morphs would differ in their habitat choice, which is unexpected, with our results showing that both morphs are using different types of habitat in a novel environment. Such morph-specific exposure behaviour can be correlated with the distribution of morphs and intra-specific competition for resources, which are all expected according to the theory of the evolution and maintenance of colour polymorphism (reviewed in Roulin 2004).

Moreover, the open-field test allows us to test for the boldness of the individuals. Being more prone to exposure is a proxy for bold behaviour. In this particular case, being bold can be an advantage for the individuals of a population. It has been shown in a review of over 40 animal species that melanism is, in general, associated with aggressive and bold behaviour (Ducrest et al., 2008). In tawny owls, the association between pigmentation and boldness in the wild is partly supported by breeding adult females guarding the nest site when offspring are big enough to be thermoregulated. It indeed has been shown that darker-coloured (brown) tawny owl females are more likely to be present at the nest when a human intruder approaches compared to lighter-coloured (grey) females in the late nestling period (Da Silva et al., 2013). However, Brommer et al. (2014) did not find such an association while studying nest

defence during incubation. In that sense, brown, tawny owls are more prone to expose themselves and thus be more visible to potential predators and mobbing birds, but they can also be favoured by boldness in the guarding nest process.

It is important to note that our findings are based on tawny owls taken into captivity from their nest, and we can thus assume that their experience of mobbing harassment or predators is limited. Before the start of the experiment, the tawny owls experienced raptors flying over the facilities and small birds such as blue and great tits coming into their home aviaries. Moreover, it has been shown that naïve raptors with less experience react significantly less than experienced ones to mobbing sounds (Consla and Mumme, 2012). Thus, the more advantageous perching choice for roosting to escape mobbing or predation might be learned instead of innate. This camouflage learning also occurs in nature because tawny owls choose less exposed places to roost after encountering goshawks (*Accipiter gentili*) (Sunde et al., 2003). Moreover, it has been shown in pied flycatchers (*Ficedula hypoleuca*) that their nesting choice was dependant on the position of their predator's nest (Thomson et al. 2006). This habitat choice depending on predators in the wild explain the lack of space use I observed in their home aviaries. Nevertheless, I find that both tawny owls' morphs react the same way to predation risk and mobbing in our setup, simulating both stressors. Hence, our findings highlight that young and naïve brown, tawny owls may have higher costs of predation and mobbing due to a lack of camouflage. We already know that the mortality in young tawny owls leaving the nest is very high (Sunde, 2005), with 36% of young dying within 55 days after leaving the nest. Predation from mammalian and avian predators is the most important cause of death (Overskaug et al., 1999). When tawny owls are juvenile and naïve, a poor ability to camouflage may have consequences for morph-specific survival. However, in our Finnish population, they showed that the survival of juvenile tawny owls after leaving the nest was not morph-dependent. Indeed, there was no morph-specific recruitment pattern, with offspring of brown and grey recruited in similar numbers in the population (Morosinotto et al., 2020). Of particular interest is, therefore, to what extent the two tawny owl colour morphs are differentially detectable by wild birds (**Chapter II**) and how they actively react to those stressors in the wild.

3.2 Camouflage efficiency in the wild

In **Chapter II**, I studied the camouflage efficiency of the two different colour morphs in the wild using stuffed owls and recording antipredator behaviour from passerines. First, antipredator responses (i.e. birds approaching the stuffed owl, birds mobbing) were recorded only when a stuffed owl was presented (experimental) and never when no owl stuffed owl was presented (control) (experimental 189/224,

control 0/52; Chi-square = 135.31, df = 1, $p < .0001$) indicating the well-functioning of my experiment. I conducted the experiment in four different seasons to create four different environment types. I showed that the reduced detectability of grey tawny owl morphs in snowy conditions, as previously observed using photographs and human observers (Koskenpato et al., 2020), is likely applicable in ecologically relevant scenarios. Specifically, when assessing the effect of snow on mobbing behaviour, grey tawny owls had a significantly higher likelihood of being mobbed during snow-free winters but a significantly lower likelihood of being mobbed in snowy winters compared to brown tawny owls (Table 3, Figure 18). Additionally, brown morphs experienced lower mobbing rates during the spring and autumn than grey morphs. Even if the probability for the owl stuffed owl to be detected by the passerines varied enormously across seasons (Analysis of deviance type II Wald Chi-square test; $\text{Chisq}=10.97$, $\text{df}=2$, $P<0.01$), detection did not differ between the two morphs, and the interaction between morph and season was not significant.

Table 3. Analysis of Deviance Table (Type II Wald chi-square tests) of a Generalized Linear Mixed Model analyzing the mobbing probability of the stuffed owl by the mobbing birds in the winter season with or without snow cover ($n=117$). The model includes the morph of the owl stuffed owl (grey/brown) and environmental information such as the season (Table 2: winter with snow, winter without snow; Table 3: spring, autumn), the initial number of birds present at the location, moment of the day (morning/afternoon) and perturbation (yes/no). The model includes an interaction between season and morph. The location is considered a random factor. Significant fixed terms are indicated in bold font. Table issued from Perrault et al. (2023), **Chapter II**.

| Variables | Df | Chisq | P |
|--|-----------|--------------|----------------|
| <i>Morph</i> | 1 | 0.02 | 0.90 |
| <i>Season</i> | 1 | 1.91 | 0.17 |
| <i>Perturbation</i> | 1 | 0.87 | 0.35 |
| <i>Moment of the day</i> | 1 | 0.94 | 0.33 |
| <i>Initial number of birds at the feeder</i> | 1 | 1.44 | 0.23 |
| <i>Morph * Season</i> | 1 | 4.35 | <.05 |

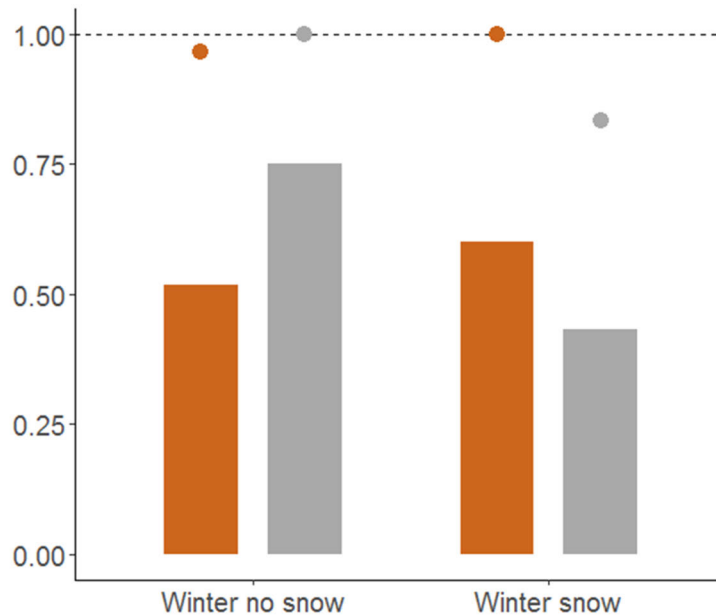


Figure 18. The proportion of all trials in which the stuffed owl was detected (dots) or mobbed (bars) (Y axis) when the stuffed owl was brown (plotted with brown colour) or grey (plotted in grey colour) in winter without snow (“no snow”) or a winter with snow (“snow”). The dashed line indicates probability of one. Plotted are the raw data, see Table 2 for analysis. The number of trials is indicated in the bars. Figure issued from Perrault et al. (2023), **Chapter II**.

During the daytime, nocturnal predators are resting from their hunting night. Having a higher probability of being detected and mobbed by passerines during the daytime can thus become an issue. Indeed, diurnally active small passerines may find and mob them. When roosting in an exposed place (**Chapter I**), the tawny owl is detected and harassed and must move to another spot (Hendrichsen et al., 2006). Being forced to move from one spot to the other means using and losing energy that would have been available e.g. for hunting the coming night. On the one hand, our findings, therefore, imply that brown, tawny owls may suffer higher costs than grey tawny owls, depending on whether there is snow or not during the energetically demanding winter season. On the other hand, the brown tawny owl morph appears well camouflaged in other seasons. It is important to note that in our study population, the survival of brown tawny owls is drastically lowered compared to the survival of grey tawny owls under snow-rich conditions (Karell et al., 2011) which is consistent with the notion that snow-rich winters are critical for survival. Camouflage and hiding are particularly important in winter since the probability of detection is high, independently of the morphs. I previously showed in a behavioural experimental setup that brown tawny owls were more likely to use exposed perches

than grey tawny owls after release in a novel environment (**Chapter I**). Thus, the two morphs might display different strategies in order to avoid predation risk and mobbing. However, in **Chapter I**, the two colour morphs responded the same way to predator and mobbing cues.

In conclusion, my findings show that the lowered detection of the grey tawny owl morphs under snowy conditions, as found earlier using pictures and human observers (Koskenpato et al., 2020), is likely to be operational under ecologically relevant conditions. Indeed, when investigating snow's impact on mobbing probability, grey tawny owls have a significantly higher probability of being mobbed in winter without snow cover but have a significantly lower probability of being mobbed in winter with snow cover compared to brown tawny owls.

3.3 Plumage insulation capacity

In **Chapter III**, I showed that there was little genetic differentiation between populations for the plumage colouration. Indeed, plumage colour differentiation between populations was in line with what would be expected from genetic drift (P_{ST} on the logit scale = 5%, Figure 19). This result highlights the high gene flow between the European populations. Genetic drift is a random process that changes allele frequencies within a population (Wright, 1943, 1931). Over time, genetic drift can result in the fixation or loss of alleles, contributing to genetic differentiation between populations that were originally similar. When population differentiation matches what would be expected from genetic drift, it suggests that the differentiation is consistent with neutral evolutionary processes (Wright, 1931). This means the differences have likely arisen due to random changes rather than selection. Gloger's rule links animal colouration with climatic variation, with the darker-coloured animals predicted to live in warmer and wet environments (Delhey, 2017). Prior research suggests that tawny owl colouration does not strictly follow Gloger's rule, indicating a more complex system influenced by various factors (Koskenpato et al., 2023). However, our sample sizes were likely too small to accurately assess the phenotypic variation in the other feather traits and in colouration variation, and more individuals per population are needed to reliably estimate the proportion of light versus dark morphs.

Regarding the other phenotypic differentiation studied in **Chapter III**, I showed that tawny owl morphs differ in their insulation capacity only in terms of the plumulaceous length in their back feathers. Specifically, grey tawny owls have shorter plumulaceous sections in their back feathers compared to brown tawny owls, a result that contradicts a previous study from Finland (Koskenpato et al., 2016). The difference in results between our two studies may be attributed to the involvement

of multiple observers in our study, differences in statistical approaches, sample sizes, and the year of data collection.

Additionally, I found differences in tawny owl body feather properties across European populations. Our microsatellite study revealed low genetic differentiation between populations ($F_{ST} = 0.022$; 95% CI 0.005–0.039, Figure 19), indicating substantial gene flow, consistent with the generally low differentiation seen among bird populations (Barrowclough, 1980). Based on neutral divergence alone, I would expect minimal phenotypic differentiation. However, tawny owl populations showed differences in the size of the plumulaceous part of the feathers, as well as microscopic feather traits like barb densities (except in back feathers) and barbule densities (Figure 19). The differentiation in these traits (P_{ST}) ranged from 14% to 42%, far exceeding the neutral genetic differentiation (F_{ST}).

Feather trait differentiation between populations was more pronounced in chest feathers than in back feathers. The plumulaceous sections of the back feathers, but not chest feathers, were larger in colder populations, with the Norwegian population particularly standing out. Only back feathers exhibited a north-south gradient, with northern, colder populations having longer plumulaceous sections than southern, warmer populations. This supports the idea that birds in colder environments have longer feathers with larger plumulaceous portions (Barve et al., 2021; Pap et al., 2017), a trait that may enhance insulation in harsh winters. One explanation for why only the plumulaceous length of back feathers correlates with winter temperatures could be that the lungs are closer to the back, making better insulation in this region essential to protect vital organs from cold air (Farner and King, 2013). Additionally, birds' chest and abdominal cavities contain fat storage cells that may assist with front insulation (Blem, 1976). While further research is needed to understand how feather insulation affects fitness and its genetic basis, our results suggest that feather properties may reflect local adaptation, possibly driven by climate.

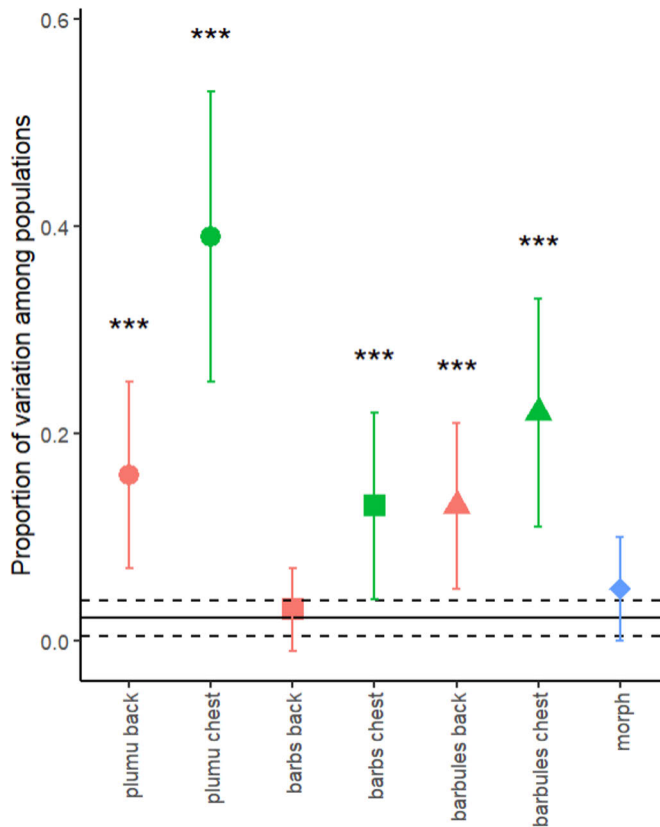


Figure 19. The different proportion of variance between populations (P_{ST}) and their standard errors for the plumulaceous length (filled circles), the number of barbs (filled squares) and barbules (filled triangles). The green colour indicates the chest feathers, the orange colour the back feathers and the blue colour the morph of individuals. Stars are indicating significance in the LRT test with “***” meaning $p < 0.001$. The F_{ST} is represented with a horizontal line and the dotted lines represent the 95% confidence interval of the F_{ST} .

Birds in colder environments tend to have lower barb and barbule densities to trap more air (Barve et al., 2021; Pap et al., 2017). In our study, populations differed in barb density only in chest feathers, with Finland, Slovenia, and Sweden populations showing lower barb densities compared to others. However, barb density did not appear to be climate-related across tawny owl populations. Interestingly, there was substantial differentiation in barbule density between populations (23% for chest feathers and 13% for back feathers, Figure 19), though this variation was not associated with winter climate, suggesting the influence of population-specific factors on this microscopic feather trait.

Overall, the studies showed that the grey tawny owl is highly dependent on snowy winters for effective camouflage during daytime roosting. With global warming leading to less snowy winters in northern latitudes, the grey morph may lose its camouflage advantage in winter. For colour polymorphic species with morphs adapted to specific environmental conditions, climate change poses a significant challenge to their ability to camouflage and maintain their ecological advantages. Species adapted to cold environments, including colour-polymorphic ones, may face substantial declines in response to these environmental changes (Mills et al., 2018; Zimova et al., 2016).

To conclude, my finding based on samples of several European populations is contrary to the previous study made in Finland (Koskenpato et al., 2016), which showed differences in back feather insulations between the two colour morphs. Taken together, my experiments underline that the crypsis of the grey morph is highly context-specific; the grey morph is only mobbed less by small passerines than the brown morph when there is snow. The two colour morphs, therefore, experience differential benefits across snow conditions, which may help to maintain colour morphs in the population, although further warming of winter climate will reduce the potential for camouflage for grey tawny owls in northern latitudes.

3.4 Strengths and limits of the thesis

This thesis deals with the study of behaviour, such as antipredator behaviour and camouflage, in a predator species. Most of the camouflage studies are focusing on the influence of camouflage on prey species and their survival. Being invisible to the predators is well known and studied but being invisible to prey and mobbers is less described in the literature (Stevens and Merilaita, 2011). My studies allowed us to understand more about the behaviour of predators towards stressors like mobbers or predation, as well as the impact of predator camouflage in the wild. During this thesis, I studied the camouflage aspect from both a predator and a potential prey point of view. Indeed, I had the chance to work with captive owls and to study their behaviour towards stressors in a controlled environment. Additionally, I observed passerines' behaviour towards a potential predator in the wild using stuffed owls. Moreover, I also got the opportunity to work with many co-authors around Europe and collaborate to study the different feather properties around Europe. This study shows that collaboration over large spatial scales is possible and opens the opportunity to study other trait differentiation or feather differentiation for multiple bird species. Museum samples, for instance, could offer good opportunities for this type of large-scale studies on feathers differentiation either within or in between populations/species.

Working in both controlled and wild environments made my studies more solid but these experiments presented some limits. In **Chapter I**, I decided to use an open-field test. When using open field tests, any methodological biases are important to consider (Brown and Braithwaite, 2004; Carere et al., 2005; Dall and Griffith, 2014; Dingemanse et al., 2004; Peralas et al., 2017; Toscano et al., 2016; Yuen et al., 2017). For instance, in our experimental design the location of the speakers could have had an impact on owls' roosting choice. However, during the trials, all owls were settled (except for 19 owls out of 262) after approximately two minutes of habituation in the experimental aviary, which was before the audio treatment started, meaning that the location of speakers did not influence the experiment. We could also note the door location as a potential bias in the owls' choice. However, it seems unlikely that the position of the releasing door, could have influenced owls' roosting decision. Indeed, the door was always covered by a camouflage net during the experiment so that the owl could not see the door once in the experimental aviary. At the end of each trial, I was approaching the experimental aviary from the direction of the exposed perch and was visible to the owl. Seeing me approaching them, the owls perching on the outer perch always fled to an inner perch. At that moment, while the inner part with the door could be potentially as stressful for the owls as the outer exposed part, the outer one should have been perceived as even more stressful since the owl could see me approaching. Moreover, when the owls were perching in the outer exposed part of the home aviaries (similar in structure to the exposed area in the experimental aviary), the owls performed antipredator behaviour (elongated cryptic pose) when facing birds of prey flying above the aviaries (personal observations). Thus, the owls were aware of the potential danger they were facing when choosing the exposed outer perch. I, therefore, interpret that brown owls are likely bolder, and not shier than grey owls when choosing to perch in the exposed part of the aviary.

In **Chapter II**, I conducted experiments in the wild using stuffed tawny owls. The environment was thus not controlled. Controlled environments however, can present advantages but also disadvantages, like the limitations I faced in **Chapter I**. In addition, since this experiment required a lot of time and investment, I only had the chance to conduct it for one entire year. To make the results stronger, it would have been good to increase the replicates of this experiment or increase the number of seasons. The fact that in some seasons, one of the two morphs was detected all the time (probability=1) made the statistical analyses more difficult to perform. Moreover, I could have included a positive control, such as an object that did not have the shape of the owl, or an owl with a very different colouration. However, I would argue that the existing pole present at each site was sufficient to state the presence of an unknown object in the passerine's environments when conducting the non-owl controls. Indeed, the pole was a good control because it was positioned

exactly in the same spot and represented the absence of the predator, like the branch where the predator generally roosts but is empty at that particular moment. I would also argue that using a different shape could have also biased a response as a “novel object” added to the environment could have influenced the passerines’ response only because of the object’s novelty. Moreover, more observers should have been included in the experiments to avoid bias or make the observer blind to the owl’s colour morph during the experiment.

In **Chapter III**, I had the chance to work with many co-authors from different countries in Europe. This collaboration allowed me to compare multiple tawny owl populations living in different environments. However, sample collecting was sometimes complicated due to experimental constraints. While measuring the feathers, I realised that the differences between feathers taken from the same individual were large. The study would have been more relevant if more feathers from each individual had been collected to reduce the within-individual variance in terms of the plumulaceous length of the feather. Moreover, to understand the variability of the barbs and barbules measure, it would have been beneficial for the study to have repeated measures (different feathers from the same individual).

Moreover, our finding of population differentiation in most feather properties exceeding the neutral divergence expectation suggests that these properties could have been shaped by selection and thus be a signature of local adaptation. All these feather properties affect the insulation capacity of the plumage suggesting that populations may be adapted to their local climatic condition. However, I find that only the plumulaceous part of the back feathers decreases in populations with higher mean winter temperature suggesting that other aspects than winter climate are important factors driving inter-population differentiation among feather properties. It has been shown on down feathers that the same feather properties were more adapted to wet/marine environment whether than cold harsh environments (Pap et al., 2020). Nevertheless, a weakness of the $P_{ST} - F_{ST}$ comparison used here is that much (potentially all) of the observed differences between populations can be directly caused by the difference in the environmental conditions between the populations rather than produced via natural selection in adapting to that environmental condition. At present, we lack information on the genetic basis of these feather traits, hampering an assessment of their potential to adapt.

4 Conclusion and future perspectives

My thesis allowed me to highlight significant differences between the two tawny owl morphs in their behaviour, such as camouflage abilities, use of space and reaction to stressors, but also their camouflage efficiency in different environments, and their insulation capacities. In **Chapter I**, I showed that brown tawny owls are more likely to roost in exposed areas, potentially increasing their risk of being predated and mobbed. I thus assumed the brown morph to be bolder than the grey morph since it was exposing itself more to danger. On the other hand, grey tawny owls showed a preference to perch in closed areas. In **Chapter II**, I showed that the effectiveness of camouflage in tawny owls is highly context-dependent. Particularly in winter when snow presence will affect which of the two morphs will be mobbed more. Thus, brown tawny owls are easily detected in snowy landscapes and do not compensate for their poorer camouflage by trying to camouflage. Our results align with previous studies indicating that grey tawny owls have higher survival in snowy winters (Karell et al., 2011) compared to brown tawny owls and that brown tawny owls are easier to spot by humans when snow is present in the background (Koskenpato et al., 2020). Small passerines were more likely to detect and mob brown morphs in snowy conditions, whereas grey morphs faced greater mobbing pressure in non-snowy conditions. My results reveal how the efficiency of each morph's camouflage changes with seasonal variations, with snow playing a critical role in camouflage abilities. In **Chapter III**, I showed differentiation in feather insulation properties across European populations, with northern populations having longer, better-insulated feathers. Interestingly, while I observed regional differences in feather traits, they were not directly linked to plumage colouration, and the grey and brown morphs showed comparable insulation capacities.

Despite these promising results obtained in my thesis, questions remain. Additional research is needed to better understand tawny owls' use of space in the wild. With GPS loggers for instance, we could be able to trace how both morphs are using their environment in terms of reproduction, resting times, and mobbing or predation. It would also be important to be able to detect wild mobbing events and study tawny owls' behaviour towards those stressors. When planning the experiments for **Chapter I**, I initially wanted to also test the owls for stress, with

either cortisol or glucocorticoid test levels. However, it appeared to be too difficult and might have been biased by the fact that they were already stressed when being manipulated by me. There is abundant room for further progress in determining differences in stress response and coping strategies of tawny owls to understand the mechanisms behind the behaviours observed. Based on our present results I would predict that the two colour morphs have similar baseline levels of corticosterone, as suggested by overall similar behaviour in a familiar environment, but may differ in their induced levels of corticosterone when facing novelty or stress.

In **Chapter II**, I showed that there are indeed differences in mobbing events between the two morphs during different periods in the year. Future studies on whether the ecological process of detection and mobbing by small passerine prey in winter can create selective pressure on colour morph survival in the wild are therefore recommended. Our findings would also benefit from replication or, ideally, experimental manipulation of snow cover as our comparison is made across different winters with and without snow. Hence, the presence/absence of snow cover thus is confounded with and uncontrolled for annual differences in our experiments.

In **Chapter III**, I showed that tawny owl feather properties vary across European populations, showing differentiation in plumulaceous size and microscopic features like barb and barbule density. While back feather variations align with a north-south gradient, suggesting adaptation to colder climates, chest feathers show less clear patterns. Future research should investigate the genetic basis of these traits and explore other factors beyond climate influencing feather differentiation. Our approach in **Chapter III** appears promising to identify properties of feathers that could be shaped by adaption although more work is needed in the future. Of major importance is a better understanding of the genetic basis of these traits as well as replication of the same studies on other species will be needed if assuming the evolution to be convergent for these traits. To develop a full picture of population differentiation for feathers traits, additional studies will be needed that consider my findings.

In conclusion, my thesis highlights the vulnerability of colour-polymorphic species, like tawny owls, to climate change. Species adapted to specific environmental conditions will face increased pressures as their local environment changes, potentially leading to declines in populations that rely on camouflage to survive. Understanding the interplay between behaviour, camouflage, thermal insulation, and environmental change is crucial for predicting the future of these polymorphic species in a rapidly changing world.

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