Special Review

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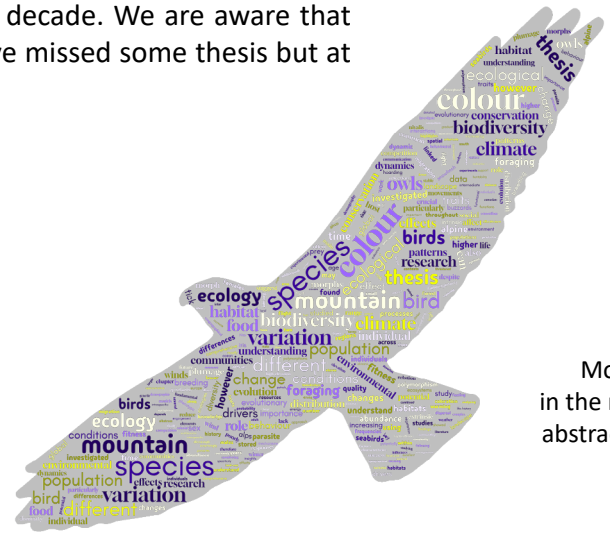
PHD DISSERTATION REVIEW IN ORNITHOLOGY (FIFTH EDITION)

INTRODUCTORY NOTE

In this fifth review section we are presenting the abstracts of some of the PhD-Dissertations defended by Italian PhD students between 2019/2020 and 2023/2024 academic years. In line with the previous edition we are including in this collection also the Italian students who undertook an international PhD programme developing its thesis in Europe or in collaboration with foreign institutions. This was absolutely needed since the number of Italian students looking at PhD opportunities abroad has been growing over the last decade. We are aware that we could have missed some thesis but at the same time we are confident that the review provides a comprehensive view of the research topics. The PhD-Dissertations are presented in alphabetical order by author's surname and, then, by year. We can appreciate that nowadays the students are highly motivated to publish their research producing a significant number of scientific articles. The Reference section below provides a comprehensive list of publications authored by the PhD students during their doctoral studies or shortly after.



Most frequently used words in the reviewed PhD-Dissertation abstracts. Figured made through WordClouds.com

THESIS 1

THE ROLE OF ECOLOGY IN THE EVOLUTION OF COLORATION IN OWLS

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ABSTRACT

Birds exhibit an extraordinary diversity in their colour patterns shaped by natural and sexual selection to fulfil communication, camouflage and/or protection functions. The factors promoting colour variation can be diverse and act differently on different traits and levels of organization. Therefore, to fully understand how ecology influences the evolution of colour diversity, it is necessary to consider holistic approaches combining multiple levels of study, including different traits and species with a wide range of ecological conditions. Owls display a remarkable diversity in colour patterns and morphology associated to a complex ecology, constituting an ideal system to understand the evolutionary causes of phenotypic variation. Using a multiple-scale approach, this thesis combined i) ecogeographical analyses at a world scale, ii) comparative analyses to control for the possible effects of common ancestry, and iii) field data of two species collected at the population level, to assess the relative importance of a number of ecological and evolutionary factors in determining colour variation in owls. Particularly, I investigated i) large scale geographic variability of melanin-based colour patterns in relation to environmental gradients in the frame of classic ecogeographical rules; ii) interspecific variability in colour polymorphism in relation to key ecological drivers; iii) the evolution of interspecific iris colour in relation to activity rhythm; and iv) the potential of iris coloration as a quality indicator in parent-offspring communication and other social contexts in Little Owls (Athene noctua) and Eurasian Scops Owl (Otus scops). My thesis showed that environmental variation may act in several ways promoting the evolution of colour variation in owls at different spatial scales. Specifically, it provided strong support for the idea that detectability in different light conditions, determined by both differences in activity rhythm and vegetation cover, may be a key driver of inter- and intraspecific colour variation in different traits in owls. Plumage attributes (i.e. melanin-based coloration and colour polymorphism) and iris colour are adaptive traits likely maintained by the selective advantage of camouflage under different light regimes or in terms of physiological adaptation to climatic and/or environmental conditions via different mechanisms. Finally, this research gave a first glimpse at the role of iris colour in communication in owls, suggesting that iris yellowness may potentially play a signalling role in social contexts. Evidently,

further experimental work is needed to better understand causes promoting evolution of colour variation and disentangle the role of colour in signalling individual quality in owls.

Thesis 2

MIGRATION STRATEGIES AND CIRCANNUAL PATTERNS OF HABITAT USE OF SNOWFINCHES (*MONTIFRINGILLA NIVALIS NIVALIS*) IN A PATCHY ALPINE LANDSCAPE

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ABSTRACT

Mountain regions are among the richest terrestrial ecosystems in terms of biodiversity and most threatened by anthropogenic modification and climate change. Species living in mountain regions are already responding through e.g. shifts in phenology or upslope migration. However, due to the complexity of species and community dynamics, the actual effects of climate change on mountain biodiversity are extremely difficult to predict. Moreover, the harshness of mountains hampers research activities, so we often lack knowledge of species ecology. In this thesis we studied the distribution range, the habitat specificity, the movement strategies and the group dynamics of one of the most emblematic alpine bird species, the snowfinch *Montifringilla nivalis nivalis*, focusing on the Western Europe populations. We introduced our study with an insight into the Holarctic mountain bird communities, their functional diversity and the functional uniqueness of their species, which resulted to be independent from the geographical distribution of mountain species. Moreover, it increases along the elevational gradient, following increasing specialization in high-elevation taxa adaptations. The current breeding distribution of the snowfinch is considerably greater than the potential distribution obtained by modelling breeding records with climatic, topographic and land-cover variables. Discrepancies are particularly evident in eastern Europe, where there is a lack of monitoring. Southern populations that live in lower elevation ranges, are more fragmented and isolated and could experience higher range contraction as a consequence of global warming. The species depends on high-elevation habitats throughout the year, although with a higher plasticity during winter, that allows it to cope with an unpredictable environment. Unpredictability of winter conditions at high elevations influences the snowfinch' movements as well. We found that the species undertakes wintering partial migration, connecting the

population of the Alps with those of the northern Iberian ranges, which could potentially reduce genetic drift, with important implications for the resilience and persistence of these populations. Yet, snowfinches seem to move when winter conditions in the Alps are harsher. Global warming might thus reduce migration propensity, with effects on population demography, structure and heterogeneity. Warmer conditions seem also to reduce the size and duration of flocks, potentially increasing the asynchrony with the peak of resource availability, with consequences on breeding performances. This doctoral thesis not only brings novel insights into the ecology of the snowfinch, but it also represents the starting point for future research on population connectivity and dynamics and on the species' responses to climate change.

Thesis 3

POLYMORPHIC COMMON BUZZARDS IN TIME AND SPACE

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Abstract
Visible phenotypic variations within a species, known as polymorphisms, are widespread in plants and animals. These traits, being heritable, provide excellent models for studying micro-evolutionary processes. Fitness, a key concept in evolutionary theory, measures an organism's contribution to the gene pool and helps biologists assess natural selection and microevolution. Morphs coexist at stable frequencies in nature, such as plumage polymorphism in 3.5% of bird species. However, the mechanisms behind the evolution and maintenance of such polymorphisms are often poorly understood. This thesis explores the evolutionary ecology of plumage colour variation in the Common buzzard (*Buteo buteo*). We quantified individual fitness in relation to plumage variation to understand the mechanisms maintaining intraspecific colour variation and its functions. Additionally, we analysed this polymorphism from both temporal and spatial perspectives. Initially, we described the type of polymorphism in buzzards, using pictures and pixel-based colour quantification. Our findings reveal continuous, unimodal variation ranging from very light to very dark individuals, rather than distinct categories. Morph types were stable throughout an individual's lifetime, despite minor darkening with age. Balancing selection likely maintains colour polymorphisms over evolutionary timescales. In buzzards, a proposed heterozygote advantage hypothesis suggested higher fitness in intermediate morphs compared to

light or dark homozygotes. Using social pedigrees of buzzards, we confirmed the high heritability of plumage colour but found no support for a simple Mendelian one-locus, two-allele inheritance model. Instead, plumage colour appears to be a quantitative polygenic trait. Analysing 20 years of reproductive data, we observed fitness differences among morphs, with intermediate morphs having the highest fitness. Assortative mating by morph was common, and such pairs had longer pair bonds and higher reproductive success. We also found an increase in intermediate morph frequencies over time. Finally, we studied the effect of plumage colour on dispersal behaviour using GPS-tracking data. Darker juveniles visited more areas during dispersal compared to lighter individuals, but colour did not affect other dispersal traits or habitat selection. For Common buzzards remarkably little is known about the geographical distribution of the morphs. Therefore, the "Buteo Morph" project was launched, where citizen scientists could enter their sightings and classify coloration in order to map morph distribution for the species on a large scale. Unpublished data show clinal variation in morph frequencies confirming anecdotal information about the presence of higher proportions of darker morphs in the south and increasing frequencies of lighter morphs in the north across their range in Europe.

Thesis 4

FOOD HOARDING OF AN AVIAN PREDATOR UNDER FOOD LIMITATION AND CLIMATE CHANGE

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Abstract
Hoarding behaviour (storing food for later use) has evolved to reduce the risk of starvation when resources are scarce. In this thesis, I studied the food-hoarding behaviour of Eurasian pygmy owls (*Glaucidium passerinum*) under spatio-temporally varying environmental conditions. I investigated differences between age and sex classes, the effect of intra-specific competition, predator responses to the abundance of the main prey, and the effect of climate on the behaviour. The data were collected starting in 2003 in western Finland, where the abundance of voles fluctuates in three-year population cycles. The number of stores per year and the biomass of prey items stored increased with vole abundance. Females and yearlings had larger and heavier stores than males and

adults, respectively. At times of low vole abundance, adult owls stored more small birds and fewer small mammals than yearlings. Females stored more small mammals than males, and showed a tendency to store fewer birds. The numbers of yearlings of both sexes and adult females increased with increasing vole abundance. Owls were less likely than expected to have a neighbour of the same class (sex or age) when the main prey was abundant, suggesting high sex- or age-specific competition. Food stores, however, were mostly larger when the nearest neighbour was of the same sex. In years of low vole abundance, increasing conspecific density reduced the total prey number stored by an owl, suggesting a high cost of competition. The thesis also reveals a strong effect of autumn and winter climate on food-hoarding pygmy owls and on the quality of the stored food. Pygmy owls may be partly able to adapt to climate change by delaying the initiation of food-hoarding. Numerous weather variables nonetheless affect their hoarding behaviour and the perishability of the cached food. Rotten food may be of poor quality and may be connected to a lower recapture probability. In female owls, rotted food hoards, often consumed, are linked with a lower future recapture probability, presumably indicating that they either die or emigrate permanently from the area. Detailed knowledge of age- and sex-related differences in hoarding behaviour under fluctuating abundances of the main prey can thus provide a fundamental tool to better understand the dynamics of a predator population and its response to climate change.

Thesis 5

INTRINSIC AND EXTRINSIC DRIVERS OF FORAGING MOVEMENTS IN COLONIAL BIRDS

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Abstract
Foraging is a central trait in species' life history, being tightly linked to individual fitness and therefore to population processes. To be successful, individuals should forage in a way that minimise energy expenditure and maximise energy intake. However, this balance depends on a mixture of different elements of intrinsic and extrinsic nature that drive foraging choices of individuals. Intrinsic drivers are elements inextricably linked to an individual's characteristics or qualities that often are a function of age or sex (e.g., dimorphism, social dominance). Extrinsic drivers are elements linked to the surrounding environment that can be abi-

otic (e.g., landscape features, weather), or biotic (e.g., heterospecific/conspecific presence, resources distribution). In this thesis I used a combination of bio-logging technologies and statistical modelling techniques to investigate in detail the drivers of foraging movements in different colonial bird species. Specifically, I investigated intrinsic and extrinsic drivers on sea and land (Chapters I and II), the effects of competition (Chapter III), the role of weather (Chapter IV), how food resources can be found in the sea (Chapter V) and its consequences (Chapter VI). My results suggest that a complex interplay of intrinsic and extrinsic drivers shape spatio-temporal foraging decisions in wild bird species, and their combined effect can be sometimes difficult to disentangle. Wind conditions, rainfall, morphological differences linked to sex, inter- and intra-specific competition all affect how individuals optimize their search for food, via the adoption of different behavioural tactics. Moreover, the search for food is particularly challenging in the marine environment, which is extremely dynamic and three-dimensional. Here, individuals could use a combination of static and dynamic features to locate prey aggregations. However, such features also aggregate contaminants such as microplastic, enhancing the risk of ingestion. In conclusion, understanding the connection between individual qualities, foraging movements and external agents is particularly important given the predicted global changes for future years. Ultimately, behavioural flexibility in foraging could be an important trait to successfully cope with such changes and could contribute to increasing the resilience of populations over time.

Thesis 6

INDIVIDUAL VARIATION IN AN ECTO-PARASITE-HOST SYSTEM: LIFE HISTORY, FITNESS AND EVOLUTIONARY POTENTIAL

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Abstract
Parasites and hosts constitute dynamic interactions exerting reciprocal selective pressures. Host-parasite interactions are thus ideal systems for the study of ecological and coevolutionary processes. However, while the effects of parasites on hosts have been extensively investigated, host-induced parasite evolution and parasite life history have been mostly neglected. In particular, knowledge on the amount of among- and within-individual variation between parasite traits is mostly unknown despite its fundamental importance to understand parasite performance and evolution. In this dissertation,

I report four experimental studies investigating several aspects of parasite individual variation in a songbird-tick system, namely the bird-specialized tree-hole tick *Ixodes arboricola* and its main host, the great tit *Parus major*. First, I investigated behavioural preferences for tick attachment sites on the bird body. Experiments were carried out using three tick species differing in ecology and host specificity both with and without bird grooming restrictions. The experimental findings as well as literature evidence suggest that ticks prefer to attach to the host head and actively move to this area when given the possibility. I hypothesize that this pattern is consistent throughout ixodid ticks feeding on birds. Second, I report how fundamental life-history traits affect individual tick success at every life stage, and estimate their phenotypic and genetic correlation between and within stages as well as the trait evolutionary potential (through animal models). Specifically, I investigated the following life-history traits: feeding time, engorgement weight, moulting time, and number of hatched eggs. Additionally, I accounted for the effect of tick sex, maternal effect, host identity, fasting time and batch. Results suggest differences in tick individual quality, for which engorgement weight seems to be a good proxy. Third, I investigated variation and heritability of host quality from the parasite perspective. Here, I measured to what extent hosts can affect tick performance and life history of larvae and nymphs both on- and off-host. I show that host individual characteristics significantly influenced larva and nymph attachment success. Additionally, hosts had a heritable effect on tick feeding time and, to a lower extent, on several other traits and success parameters. Lastly, I investigated whether *I. arboricola* males prefer to mate with heavier engorged females in order to obtain a higher fitness. Surprisingly, male mate choice experiments carried out in two different setups showed a lack of preference for heavier females. However, males seem to remember and avoid the mating partners they previously met.

Thesis 7

DYNAMIC SOARING IN THE WINDS OF CHANGE. THE EFFECTS OF WIND AND OCEANOGRAPHY ON THE POPULATION AND SPATIAL ECOLOGY OF SEABIRDS

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Abstract
Despite acting as central place foragers during breeding, most seabirds belonging

to the order Procellariiformes can perform foraging trips covering thousands of kilometres by extracting energy from the wind through a flight behaviour known as "dynamic soaring". The overarching aim of my thesis is to understand the pathways through which wind and oceanographic processes affect the demography, foraging ecology and spatial distribution of procellariiform seabirds. Focussing on the black-browed albatross (*Thalassarche melanophris*), we investigate the environmental drivers of demography. By developing integrated population models on a demographic database spanning nearly two decades, we found that the population breeding parameters were negatively impacted by ocean warming and positively affected by stronger winds, presumably through bottom-up environmental processes modulating food availability and accessibility. The population was highly sensitive to the survival rate of sub-adults, which comprised approximately half of the total population size. Our demographic investigation also revealed that albatross chick mortality events, clustered at small scales in time and space, suggest the role of an unidentified infectious disease prevalent in the study population. We documented a "habitat-mediated" pathway linking environmental conditions to the breeding processes of social monogamous seabirds. We found a higher prevalence of divorce in resource-poor years characterised by warmer sea surface temperatures, highlighting the direct disruptive effects of ocean warming on the social monogamous bonds of albatrosses. Our work then focussed on the role of winds in shaping the flight behaviour and the foraging ecology of the hypermobile Desertas petrel (*Pterodroma deserta*) and Bulwer's petrel (*Bulweria bulwerii*). Desertas petrels used favourable winds to maximise their ground speed and distance covered throughout their round-trip foraging movements. Bulwer's petrels, on the other hand, exploiting the stable North Atlantic trade winds, exhibited a striking selectivity for crosswinds. By engaging in crosswind zig-zag flight, they maximised both the distance travelled and the probability of detecting odour plumes along the round trip. Crucially, the movement patterns of these two species suggest that seabirds have a priori knowledge of the regional winds and can plan their round-trip with an expectation of predicted wind conditions and costs of flight. Collectively, the findings of my thesis highlight the sensitivity of seabirds to changes in oceanographic conditions and their reliance on winds. Given the accelerating pace of global change, monitoring the diagnostic responses of these "sentinels" of the global ocean is a conservation goal of utmost importance.

Thesis 8

INTERACTIONS BETWEEN ALPINE BIODIVERSITY, SNOW AND CLIMATE CHANGE

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Abstract

Mountain regions cover approximately a quarter of the Earth's surface, harbouring remarkable levels of biodiversity due to diverse habitats occurring along elevation gradients. These areas, exemplified by the Alps, are ideal for ecological research, offering different environmental conditions where to study animal communities. However, climate change and human activities threaten mountain ecosystems, making them among the most vulnerable worldwide. Despite their significance, mountain birds remain poorly studied due to logistical challenges in research. Focusing on European mountain bird assemblages, particularly in the Alps, this thesis examined various aspects of their ecology throughout the year. Starting from a comprehensive literature review, I identified the key drivers of population changes, highlighting direct threats such as mortality and habitat alteration as primary concerns, while the impacts of climate change were more difficult to detect, although increasing in time. Surprisingly, avalanches, despite their primary ecological role in mountain ecosystem dynamics, are poorly studied yet in this thesis I highlighted how they contribute positively to biodiversity by creating habitat mosaics that are suitable for a wide range of threatened species. In contrast, artificial disturbances like ski pistes can have adverse effects, reducing bird abundance and diversity due to habitat alteration. Nevertheless, with proper management, I argued that ski pistes could serve as refuges for certain open habitat species, particularly against vegetation encroachment. Detailed species-specific studies on mountain birds are lacking and thus one emblematic species, the Northern Wheatear *Oenanthe oenanthe* served as an excellent study species and sentinel for climate change at high-elevations. Crucial habitat requirements during different life stages emphasized the importance of maintaining traditional grazing practices to counteract vegetation changes induced by climate change and land abandonment. At last, the post-breeding migration period emerged as critical for mountain birds, with high-elevation habitats serving as crucial stopover sites rich in trophic resources. Understanding these dynamics is vital for conservation efforts, necessitating further research into habitat interactions and interspecies relationships. By exploring bird assemblages across elevation gradients and seasons, this thesis enhanced the understanding of mountain ecosystems and shed light on previously unknown relationships between bird species and habitats. It underscores the need for comprehensive conservation strategies, stressing the importance of studying ecosystems beyond the breeding season and extending research efforts to other taxa. In conclusion, this research contributed to the broader understanding of mountain bio-

diversity and calls for a holistic approach to conservation, encompassing various habitats and seasons.

Thesis 9

ASSESSING THE IMPACT OF HABITAT AND LANDSCAPE HETEROGENEITY AND LAND-USE CHARACTERISTICS ON MOUNTAIN BIRD COMMUNITIES, AND THE EFFECTIVENESS OF BIRDS AS INDICATOR OF OVERALL BIODIVERSITY

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Abstract
Birds are a crucial component of Alpine biodiversity, however, there is a lack of studies on their ecology. The effectiveness of birds as indicators of biodiversity patterns has been demonstrated in many contexts, but mountain birds remain poorly studied as possible proxies for the diversity of other taxa. This gap is exacerbated by the environment complexity, unique biodiversity, ecology, and the global changes affecting these regions. Many mountain birds inhabit heterogeneous habitats distributed across ecological gradients, posing challenges to comprehensive studies. Furthermore, the Alps are undergoing significant global changes impacting ecosystem functioning and ecological patterns. Understanding mountain bird ecology and their functions is crucial for effective conservation strategies. This thesis presents four studies analysing drivers affecting mountain bird communities, using diverse methodologies, examining functional and taxonomic indices, and exploring an entire ecological gradient or specific habitat types. The work investigates the effects of landscape composition, climate, and topography on bird communities across landscapes. It relies on data from South Tyrol and integrates different habitat, providing insights into Alpine ecological patterns. It highlights the crucial role of heterogeneity surrounding agricultural and urban/suburban landscapes, of natural/seminatural habitats, and of the continuity of forests. It utilizes remote sensing data to evaluate the impact of landscape heterogeneity and canopy height on bird communities in farmlands. This research highlights the importance of preserving landscape diversity to mitigate the effects of modern agriculture on bird biodiversity. The thesis assesses the role of different successional forest stages on the hazel grouse, a forest specialist species, in a Natura2000 area. The work highlights the

importance of understanding forest dynamics resulting from land-use changes and their implications for conservation. It addresses the impact of deadwood and tree-related microhabitats on bird and bat communities across forest types within South Tyrol. This work adopts a multi-taxon approach, emphasizing the complementary responses of different ecological indicators. It also assesses the potential of birds as reliable bioindicators for evaluating conservation measures and their ecological implications for Alpine biodiversity. Within this research I stress the significance of multi-taxon survey schemes to gain a comprehensive understanding of the whole biodiversity. In sum, this thesis contributes to the understanding of Alpine birds' ecology, their potential as ecological and taxa-based bioindicators, and the intricate relationship of ecological factors shaping their communities. It offers insights for the conservation of Alpine biodiversity and provides a foundation for future research and conservation efforts in the Alps and similar mountain regions.

Thesis 10

CARRY-OVER EFFECTS ACROSS LIFE STAGES IN RED KITES *MILVUS MILVUS*

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Abstract
Understanding behavioural differences among individuals and the mechanisms driving them is increasingly recognized as essential for explaining the demographic patterns of animal populations. Throughout life, external and internal conditions interact to shape distinct behavioural phenotypes, ultimately influencing individual fitness and population structure. However, studies that adopt such mechanistic, longitudinal perspectives remain scarce due to the difficulty of collecting detailed individual-level data. This thesis builds such a framework using an extensive GPS-tracking dataset of red kites (Milvus milvus) to explore how early-life conditions shape behavioural development, sociality, and survival across life stages. First, I examined the dynamics of sibling aggression during the nestling stage to understand how food availability and competition influence behavioural differentiation. Using a null-model approach, I found that red kite nestlings strategically adjust aggression according to daily fluctuations in food provisioning, and that these adjustments associate

with a skewed food allocation towards senior siblings when food is scarce, but allow for higher intake of youngest siblings, and thus catch-up growth, when conditions improve. These patterns suggest that food-driven aggression mediates both developmental trajectories and the formation of dominant–subordinate behavioural types. Next, I investigated how early-life nutritional conditions influence the emergence of social behaviour during dispersal. Combining a food supplementation experiment with social network and movement analyses, I found that last-hatched chicks—typically the least competitive—had the fewest social encounters after fledging. However, food supplementation reversed this pattern, leading to increased social interactions and spatial clustering in resource-rich areas. This demonstrates that early nutritional conditions can shape social and spatial phenotypes beyond independence, with implications for population structure. Further, I explored the drivers of variation in winter communal roosting behaviour, hypothesizing that these differences reflect cost–benefit trade-offs across life-history stages. Birds that joined communal roosts showed higher mobility and greater success in locating ephemeral food sources, suggesting enhanced foraging efficiency. Roost attendance declined with age and breeding onset, and was consistently lower in females, indicating that the benefits of communal behaviour vary with experience, sex, and reproductive status. Finally, I assessed the fitness consequences of early-life social phenotypes and found that high sociality was unexpectedly linked to lower survival, driven by increased mortality from collisions near roads. These findings reveal how anthropogenic environments can transform adaptive behaviours into ecological traps. Collectively, this work highlights the importance of integrating individual–environment interactions over time to understand how behavioural variation shapes population dynamics.

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