PHD-DISSERTATION REVIEWS IN ORNITHOLOGY  
(2019-2020 academic year)  
Edited by Francisco VALERA

This section includes the abstracts of some of the PhD-Dissertations submitted in Spain during the 2019-2020 academic year as well as some others not published in earlier volumes of Ardeola. They are in alphabetical order by University where they were presented and, then, by year and alphabetical order of the author’s surname. This section also includes a link to access the full version of the reviewed thesis when available.

Esta sección incluye los resúmenes de algunas de las Tesis Doctorales en Ornitología defendidas en España en el curso 2019-2020 junto con otras no recogidas en reseñas anteriores. Se ha seguido una ordenación alfabética por universidades y, dentro de ellas, por año y autor. También se incluye un vínculo que permite acceder a la versión completa de la tesis reseñada en caso de que esté disponible.

Informative note:
In its section PhD-Dissertations Reviews in Ornithology, Ardeola reports any studies on ornithological issues presented in our country. The section is intended as an updated overview of the latest ornithological research performed mainly in Spain. In spite of the efforts of the editor to compile all the theses, we are aware that the collaboration of researchers (supervisors and doctorates) is needed to give a full view of ornithological research in Spain. We therefore invite the scientific community to report on their results (address: ardeola@seo.org). The Scientific Committee of SEO/BirdLife grants a biannual prize to the best Ph Dissertation included in this section. The prize is awarded in the corresponding Spanish Ornithological Conference. We are looking forward to hearing from you, also as proof of the relevance and quality of ornithological research in Spain.

Nota informativa:
Ardeola recoge en su sección Reseña de Tesis Doctorales en Ornitología aquellas tesis leídas en nuestro país que estudian temas ornitológicos con el fin de informar sobre las más recientes investigaciones desarrolladas, fundamentalmente en España, en este campo científico. A pesar de los esfuerzos que realizamos para reseñar todas las tesis concluidas, somos conscientes de que un registro completo y actual de las mismas requiere de la colaboración de los investigadores (directores y doctorandos). Por ello invitamos a todos aquellos implicados en la realización de tesis en ornitología a que nos informen de sus resultados (dirección: ardeola@seo.org). El Comité Científico de SEO/BirdLife otorga con carácter bienal un premio a la mejor tesis doctoral reseñada en esta sección, que es entregado en el Congreso Español de Ornitología correspondiente. Esperamos vuestras noticias como buena señal de la pujanza de la investigación ornitológica en nuestro país.
Breeding cliff-nesting birds at mining sites: management recommendations.

Key words: bird services, ecological traps, habitat preferences, mining restoration, secondary users.

Abstract:
To build infrastructures, we rely on the construction sector, which produces aggregates and cement through mining activity. The reconciliation of the extractive activity and conservation of natural values is a crucial issue. Currently, our capacity to return ecosystems affected by mining activities to their original situation is limited. An alternative to restoration is the creation of ecosystems for fauna of conservation concern. Cliff-nesting birds (birds that rely primarily on rocky or sandy walls to breed) colonize human-created environments such as mining sites (quarries and aggregate pits from the cement and aggregate sector). However, mining restoration often fails to consider the cliff-nesting fauna that may have colonized these areas. Furthermore, previous work has failed to address how important these man-made habitats are for the conservation of cliff-nesting birds, and how to manage their presence during the active phases of the mining sites. The aim of this thesis is to study the cliff-nesting bird community at mining sites, and to give management recommendations to enhance biodiversity by improving breeding habitats for cliff-nesting bird species in Mediterranean areas of Spain. We expect mining sites to have the potential of accommodating a varied community of cliff-nesting birds. We studied three aspects to manage these communities: (i) the potential risk of generating trap habitats by excess of predation; (ii) the process of breeding habitat selection and habitat preferences of cliff-nesting birds at different scales; and (iii) the ecological services of cliff-nesting birds that could be applied to restoration. To do this, we carried out a large-scale survey in 2016 and 2017, in 29 mining sites during the breeding season in Spain, to study the abundance, richness and diversity of the cliff-nesting communities. The mining sites were representative of the environmental diversity of the study area. Then, we selected two model species. We studied the Eagle Owl’s *Bubo bubo* presence and diet in mining sites and outlined restoration and management considerations for cliff-nesting birds to avoid excess predation pressure. We selected the Sand Martin *Riparia riparia* to analyze the ecology and habitat selection of cliff-nesting species in mining sites, and to established measures to reconcile mining activity with their breeding populations. We also studied the provision of engineer ecosystem services of birds applicable to restoration actions, as a way of improving the local biodiversity of cliff-nesting birds, by studying the Sand Martin’s burrowing activity at mining sites. Our results indicate that mining sites have a varied community of cliff-nesting birds and that, for some species, these sites could be relevant as breeding habitats. We determined that the Eagle Owl is a specialist predator in the mining sites, with rabbits *Oryctolagus cuniculus* as its main prey, and that their frequent presence in these sites does not generate a risk of excess of predation of the cliff-nesting community. We observed that Sand Martins showed habitat preferences at the different studied scales, and that this information could be used to design management recommendations and restoration actions for this species. Finally, we observed that the burrowing activity of the Sand Martin generated holes that were
colonized by secondary cavity-user birds, the Rock Sparrow *Petronia petronia* being the most abundant species. With this work, we aimed to explore alternatives to conventional restoration actions, to improve vulnerable biodiversity and to reconcile fauna with mining activity. Our study supports incorporating actions to promote cliffs, together with managing the mining sites to form a heterogeneous mosaic of habitats that satisfy the requirements of the cliff-nesting species (roosting, feeding, etc.). Finally, the study of these complementary habitats inside and outside the mining sites should be pursued in future lines of research, to improve the management and conservation of cliff-nesting species in mining sites.


**Universidad Autónoma de Madrid**

Alfonso Íñiguez, Sergio  
E-mail: srgalfonso@gmail.com  
Supervisors: Gil Pérez, D. and Pérez Rodríguez, L.

**Early bird development modulators: the role of steroids and oxidative stress on ageing.**  
*Moduladores del desarrollo temprano en aves: el papel de los esteroides y del estrés oxidativo sobre el envejecimiento.*

Key words: androgens, competition, development, *Sturnus unicolor*, yolk.  
**Palabras clave:** andrógenos, competencia, desarrollo, *Sturnus unicolor*, yema.

**Abstract:**

Life history traits are a set of morphological, physiological or behavioural features or changes that occur through the organism’s life and ultimately determine its fitness. The expression of these life history traits is often subject to trade-offs whose resolution promotes the existence of different life history strategies. These trade-offs often involve physiological mechanisms that must be addressed in order to fully understand their origin and evolutionary significance. These mechanisms may include, for instance, the direct effects (and associated costs) of certain hormones or the increased production of reactive oxygen species as a result of some physiological processes, which may constitute a significant cost that constraints the expression of some life history traits. These processes can exert profound effects during early development, when the organism is experiencing a series of fast and deep changes that will ultimately determine its adult phenotype and lifetime fitness. Thus, understanding the effect of early life conditions on key components of individual physiology (e.g. growth rate, oxidative stress levels, rate of cellular ageing) constitutes a central issue in Evolutionary Ecology. In this thesis we experimentally analysed the impact of some components of early life conditions (prenatal and postnatal exposure to androgens, degree of brood competition, impact of oxidative stress) on different relevant physiological traits of the developing individual (growth, oxidative status, physiological stress, immunocompetence, cellular ageing). To do so, we performed a series of experiments under natural conditions using the Spotless Starling *Sturnus unicolor* as study species. We found that harsh conditions during early development (i.e. increased competition levels via experimental manipulation of brood size) results in impaired nestling growth, particularly among females, which are probably under competitive disadvantage within the broods due to the sexual dimorphism in this species. These conditions also result in increased physiological stress—as reflected by corticosterone levels—, and negatively impacted telomere dynamics, thus reflecting an impact on the rate of cellular ageing during this early period of life. We also found that experimentally increased exposure to androgens (either during prenatal development—via egg injections—or after hatching—via hormone implants)— caused changes in growth trajectories, but exerted no significant effects.
on immunocompetence or oxidative status. We also found that increased exposure to oxidative stress during early development impairs nestling growth and exerts contrasted effects on different branches of the immune system, stimulating humoral innate immunity and tending to suppress cell-mediated immune responses. The latter effect may suggest an adaptive allocation of resources among components of the immune system that are subject to a trade-off. Finally, we found no support for the widely accepted notion that oxidative stress is the main mechanism explaining individual variability in telomere length. Other processes, like cell proliferation rate, could be relatively more important at least during the characteristic telomere attrition process associated to early development. The last contribution of this thesis is a call for caution when trying to infer oxidative status of individuals by using one or few biomarkers of oxidative stress: despite the magnitude of our experimental induction of oxidative stress via Diquat injections—as revealed by clear effects on individual growth—, this was not captured by two widely used markers of oxidative stress (malondialdehyde concentration and trolox equivalent antioxidant capacity of plasma). This warns against simplistic approaches to oxidative stress responses, and claims for the use of multiple markers of oxidative damage and/or tracking their variations in different tissues.


Universidad de Barcelona

Cruz Flores, Marta
E-mail: martacruzflores@gmail.com
Supervisors: Ramos García, R. and González-Solís, J.

Life history of a long-lived, migratory species.

[ Estrategia de vida de una especie longeva y migratoria. ]

Key words: demography, life history strategies, movement ecology, seabirds, stable isotope analysis.

Palabras clave: análisis de isótopos estables, aves marinas, demografía, ecología del movimiento, estrategias vitales.

Abstract:

Oceans are suffering from rapid environmental change, pointing to the need of multi-year studies on species that can inform us about the strength and direction of these changes. Oceanic environments are remarkably difficult to study, thus studying the Life History (LH) strategy of an oceanic predator may shed new light on the links between the oceanic environment, trophic resources and how these are used for survival, growth, and fecundity. These topics can be studied through different disciplines, such as demography, movement and trophic ecology, for which rapid technological and theoretical advances have opened new avenues of research. The improvements in capture-mark-recapture models, the increasing use of stable isotopes analysis (SIA) in diet and migration studies, together with the size reduction in tracking devices, offer the opportunity to study LH strategies of small species previously inaccessible. With the present thesis, I aimed to study the LH strategy of a small, long-lived, oceanic and migratory species, the Bulwer’s Petrel *Bulweria bulwerii*, in the Atlantic Ocean. Specifically, I aimed to delve into their foraging and migratory strategies and to understand the implications of reproduction on their trophic ecology and survival. Our results revealed that during the breeding period Bulwer’s Petrels foraged mainly around the Canarian and Azorean waters to feed on mesopelagic prey. I showed that reproduction implies constraints (at spatial, activity, and trophic levels) and can carry a cost on survival, especially for females, while males seem to reduce this cost through sabbatical years. We evaluated and confirmed the po-
tential of SIA as a good geographic marker to study migratory movements of marine predators. Bulwer’s Petrels migrated to two main non-breeding areas, the Central and the South Atlantic, which implied different phenological and migratory strategies. This species showed to be resilient to environment changes during the non-breeding season, but more sensitive to them during the breeding season, resulting in a lower survival in years with higher sea surface temperature. Indeed, we inferred the increasing temperature of the oceans will sharply decrease Bulwer’s Petrel survival, compromising their populations viability, and making them an excellent sentinel of the changes occurring in oceanic food webs.


Morera Pujol, Virginia
E-mail: morera.virginia@gmail.com
Supervisors: Ramos García, R. and González-Solís, J.

Multi-colony approaches to study migratory and foraging strategies in pelagic seabirds.

[Una aproximación multi-colonia al estudio de las estrategias migratorias y de búsqueda de alimento en aves pelágicas.]

Key words: animal movement, foraging movements, migration, seabirds, shearwaters.

Palabras clave: aves marinas, migración, movimiento animal, movimientos de alimentación, pardelas.

Abstract:

Movement is a widespread characteristic in the animal kingdom—occurring at many spatiotemporal scales—with consequences at an individual, population, species, and even ecosystem level. It is a very diverse character, with many different drivers that stem from the way in which individuals interact with their environment. Of these, one of the most important is the distribution of resources, particularly for migratory and foraging movements. In migration, the search for an optimal environment involves movement at large spatiotemporal scales, following seasonal changes in resource distribution. In foraging movements, the search for resources happens at small spatiotemporal scales, and involves different strategies to optimise the search and capture of food, including the ability to obtain foraging cues from conspecifics. In seabirds, movement—at large and local scales—has deep repercussions in their life-history traits, evolutionary history, morphology, physiology and behaviour, which makes them a very valuable study group to understand the role, the causes and consequences of migratory and foraging movements in the ecology of marine top-predators. The study of migratory and foraging movements has been revolutionised by the development of smaller, cheaper and better tracking devices, promoting multi-colony, population and even species approaches to the study of animal movement. Yet, it also comes with a set of methodological challenges that have to be addressed in order to make unbiased inferences of space and habitat use at population or species level from individual movement data.

In this thesis, we develop methods to test the possible biases introduced by the use of individual tracking data to infer distribution at a population or species level. We then apply these tools to a multi-colony dataset of non-breeding locations of Cory’s (Calonectris borealis), Scopoli’s (C. diomedea) and Cape Verde (C. edwardsii) Shearwaters, to study their migratory connectivity and non-breeding habitat segregation at the colony, population and species level. Lastly, we apply state-of-the-art spatial models to study foraging distributions of three neighbouring colonies of Cory’s Shearwaters, detect the segregation among them and unravel the environmental and behavioural drivers of this segregation. I developed several functions in the R environment aimed at the detection of the effects of individual site fidelity and

Ardeola 68(1), 2021, 219-239
temporal variability in the inference of spatial use at a colony or population level, and to calculate the degree in which the movements of a single population can be representative of those of the entire species. These tools are applicable to individual movement data regardless of the species or tracking device. We also used these tools to demonstrate the spatial and ecological segregation between the non-breeding distributions of three taxa of _Calonectris_ Shearwaters studied, as well as detecting a stronger degree of migratory connectivity at a population than at a colony level. The later result indicates that individuals of different colonies within a population mix in the non-breeding areas, but birds from different populations do not, which has important implications for their population dynamics and for their conservation and management. Lastly, we demonstrated segregation among the foraging distributions of three neighbouring colonies of Cory’s Shearwaters, both in the waters surrounding the colony and in distant, foraging grounds. We found evidence of both environmental and behavioural drivers behind this segregation, and suggest a mechanism through which transfer of information between individuals can be shaping the distributions of foraging seabirds. This thesis provides relevant tools for the field of movement ecology, as they can be used for analysing movements of mobile species, regardless of species, tracking device or spatiotemporal scale. In addition, they are relevant for the field of seabird ecology as they provide insights into the causes of space and habitat use in long-ranging pelagic seabirds.


Zajková, Zuzana
E-mail: zuzulaz@gmail.com
Supervisors: González-Solís, J. and Bartumeus, F.

Movement ecology in pelagic seabirds.

Key words: at-sea behaviour, bio-logging, geolocation, migration, phenology.

Abstract:

Movement is a fundamental component of behaviour and thus both are inextricably linked, so variation in movement patterns usually reflects different behaviours. The way individuals allocate time budgets to different behaviours within circadian rhythms and over the annual cycle will ultimately provide knowledge about evolutionary processes and adaptive capacity, which is also important to proper conservation actions of endangered species. Seabird movements have been studied over the last 20 years with the wide deployment of geolocator-immersion loggers, but wet-dry data seem underused according to literature published. Along four chapters this thesis presents novel insights about movements and behaviour of four little-known seabird species from the Atlantic Ocean: Boyd’s Shearwater (*Puffinus boydi*), Common Tern (*Sterna hirundo*), Atlantic Petrel (*Pterodroma incerta*) and Cory’s Shearwater (*Calonectris borealis*). Using wet-dry data alone or combined with positional data we uncovered the timing of major life cycle events and revealed circadian and circa-anual activity patterns of such species. In highly mobile migratory seabirds, the existence of radically different behavioural contexts linked to phenology and the need to exploit different marine environments over the year lead to different behavioural budgets. In the last chapter, we present a new analytical protocol based on state-of-the-art algorithms to decipher behaviours from wet-dry data. We reveal the hierarchical and modular nature of seabird behaviour at an unprecedented level of detail and used cutting-edge data visualization to highlight key insights. Our framework paves the way to use behavioural
annotation for addressing old and new questions of interest in ecology from new perspectives using geolocator-immersion sensors. Overall, through this thesis, I highlight the irreplaceable utility of wet-dry data to get unique insights in ecology and behaviour over the annual cycle of seabirds, a difficult-to-observe group of birds that remain out of the human sight most of their life. Geolocator-immersion sensors continue to be the most extended loggers to track year-round movements of seabirds, since they ensure the welfare of tagged individuals. Therefore, the results compiled in this thesis should encourage researchers to incorporate the use of wet-dry data within hypothesis-driven frameworks, which surely would contribute to increase our knowledge of seabird ecology at sea.


Universidad de Extremadura

Abad Gómez-Pantoja, José Mª
E-mail: abadjm@unex.es
Supervisors: Masero Osorio, J.A. and Villegas Sánchez, M.A.

Ecoimmunology in long-distance migratory birds: metabolic costs and sex-related effects.
[Ecoinmunología en aves migratorias de largas distancias: costes metabólicos y efectos ligados al sexo.]

Key words: basal metabolic rate, ecoimmunology, habitat, migration, shorebirds.

Palabras clave: ecoimmunología, hábitat, líquidos, migración, tasa metabólica basal.

Abstract:
The immune system is a complex and flexible defence system that evolved to protect animals from invading pathogens and cellular maintenance. It is essential for survival, but also a costly system that competes for resources with other costly activities, generating trade-offs and even reducing host fitness. Thus, the investment in the immune system and the strength of the immune response should be optimized in relation to the surrounding environment, resources available and individual phenotypes to balance their costs and benefits. Charadriiformes is a highly diverse order in terms of ecological strategies, being a good study model to test how different environmental factors may influence the immune system of long-distance migratory birds. This thesis aimed to improve our understanding of the costs of the immune system and the environmental factors that may shape the immune response of migratory waterbirds through the annual cycle. To fulfil this general aim, the following aspects were addressed: (i) the transfer of maternal antibodies is one of the non-genetic strategies by which mothers may influence the development of their offspring. We took blood samples from recently hatched Gull-billed Tern Gelochelidon nilotica chicks, and quantified the concentration of maternal antibodies. Mothers transferred significantly more maternal antibodies to males than to females, and the plasma levels of these antibodies were positively related to early survival of offspring. By this sex-related transfer, mothers might favour the survival of males, probably the more sensitive gender, during the early stages of their development. (ii) the activation of the immune system entails potential metabolic costs. We determined the time course of the primary and secondary humoral immune response against sheep red blood cells in non-breeding Little ringed Plovers Charadrius dubius, and estimated the associated energy costs in terms of basal metabolic rate (BMR). The injection with this non-pathogenic antigen elicited the production of specific antibodies that, in both responses, peaked six days post-injection. The plasma levels of antibodies during the secondary response were 29% higher than during the primary response, but the difference was non-significant. BMR did not significantly vary during the primary immune.
response, but peaked three days post-injection during the secondary response, increasing significantly by 21%. Conversely, plover body mass decreased significantly along the primary immune response, but did not vary along the secondary response, which may point to an energy reallocation strategy during the primary immune response. Interestingly, the BMR peak occurred before the antibody peak, which supports that the activation of the immune response is more costly than the production of specific antibodies. (iii) The increase of salinity is a major concern for coastal and freshwater wetlands that may affect many migratory animals during the non-breeding season. Osmoregulation imposes significant energy costs to organisms, and it may influence physiological traits such as the strength of the immune response. We investigated whether the salinity of African wetlands may induce residual effects that carry over and influence physiological condition in the Black-tailed Godwits Limosa limosa limosa during their northward migration through Europe. Through the analysis of feather stable isotope values, we found that overwintering males and females occupied West African wetlands with a broad salinity gradient, with females using mostly freshwater wetlands. Only in males, salinity of African wetlands was related with differences in the pro-inflammatory immune response to phytohemagglutinin (PHA) and size-corrected body mass of godwits staging in Europe. These findings provide a new perspective onto the processes by which wetland salinity could potentially influence population dynamics through sex-dependent carry-over effects, and how migratory species may respond to current and future environmental changes. (iv) Migration may help hosts to reduce the impact and costs associated to pathogens, and this could be especially effective for shorebirds (Charadrii). This waterbird group shows a strong dichotomy in the areas used for breeding and wintering, and while Arctic breeders winter in marine areas, southern breeders tend to use more freshwater areas. These different migratory strategies have been associated with a differential parasite pressure in the environment, being lower in marine habitats, and have led to the hypothesis that shorebird marine species have a lower level of immunocompetence than freshwater species. We tested this hypothesis by comparing the pro-inflammatory response to PHA and its associated energy costs in Dunlins Calidris alpina, a long migratory shorebird breeding in sub-arctic latitudes and wintering mostly, but not exclusively, in marine habitats. We found that the pro-inflammatory response of dunlins overwintering in marine habitats was significantly lower than that of dunlins overwintering in freshwater areas. Associated to this lower pro-inflammatory response, marine dunlins did not vary their BMR and reduced significantly their body mass. Conversely, dunlins from freshwater habitats significantly increased their BMR and did not vary their body mass. These findings support the hypothesis according to which the selection pressures exerted by parasites have a role in the evolution of migration strategies of shorebirds.


Universidad de Granada

Azcárate García, Manuel
E-mail: mazcarategarcia@gmail.com
Supervisors: Soler Cruz, J.J. and Ruiz Rodríguez, M.M.

Signalling and evolutionary responses to bacterial environments in birds. The case of the Spotless Starling (Sturnus unicolor).

Key words: animal communication, bacteria, ectoparasitism, nest bacterial environment, sexual signalling.

Ardeola 68(1), 2021, 219-239
Palabras clave: ambiente bacteriano del nido, bacterias, comunicación animal, ectoparasitismo, señales sexuales.

Abstract:

Birds are continuously making decisions; the food to eat, the partner to mate, or the host to parasitize. Decision-making has enormous fitness consequences and, at least partially, is modulated by the information received from the environment, including that from clues and signals emitted by other organisms. By definition, the signals function in contexts of social communication and are beneficial for both senders and receivers, while the inadvertently information provided by clues, only benefits to receivers. In both cases, eavesdropping on these cues by undesirable organisms may have significant negative effects on the emitters and, thus, constrain the evolution of related traits. Microorganisms might also play a role in contexts of communication as it has been highlighted in recent years. Bacteria are in continuous interaction with birds, and might, for instance, produce volatile components used in chemical communication. Also, there are many species that inflict severe negative effects to their hosts, including death. Therefore, in a communication context, the evolution of signals and behaviours aimed to reliably showing the ability of individuals to cope with microorganisms will be favoured in host populations. Understanding the evolution of clues and signals, and therefore the selective pressures that may have favoured, maintained, or restricted their development, is essential to understanding the functioning of these traits in particular, and of animal communication in general. The main objectives of the thesis are embodied within the context of information and communication that is sometimes mediated by microorganisms. We mainly worked on different clues and signals of the Spotless Starlings (Sturnus unicolor) that directly or indirectly may be related to microorganisms, in contexts of parasitism, predation and social communication. Specifically, we experimentally studied: (i) the use of visual clues of ectoparasitism by brood parasite females when choosing the host nest to parasitize; (ii) the use of chemical clues by predators and ectoparasites by experimental breaking of faecal sacs of starling nestlings in their nests; (iii) interspecific variation in wear and susceptibility to bacterial degradation of nestling feathers and whether it covaried with nest bacterial environment. Furthermore, in scenarios of sexual selection, we checked: (iv) the relationships between colouration of secondary sexual traits (beak, feathers and legs) and variables related to antimicrobial defences and reproductive success in females; (v) the effects of experimentally shortened starling throat feathers on indicators of phenotypic and genetic quality (the length and dynamics of telomeres), and (vi) the association between two secondary sexual characteristics (length of throat feathers and colour of starling male beak) in a framework of multiple signalling. The main results are that the presence of experimental spots in starling eggshells, simulating those produced by the ectoparasite Carnus hemapterus, affected nest choice by conspecific brood parasitic females. The preferred host nests for brood parasitism were those without clues of ectoparasitism. We also showed that the experimental breakage of faecal sacs increased nest bacterial loads, affected negatively nestlings development, and positively the probability of depredation and, although not significantly, that of ectoparasitism. These results suggest that behaviours associated with parental removal of faecal sacs from nests have evolved, at least partially, to avoid the negative effects of pathogenic bacteria, and to eliminate the chemical clues that facilitate nest detection by predators and ectoparasites. Moreover, when comparing feathers and nest bacterial environment of 16 bird species we detected consistent interspecific
differences in nest bacterial loads that co-varied with interspecific differences in the susceptibility of feathers to degradation by keratinolytic bacteria, and with feather wear. These results therefore suggest that species-specific bacterial environments determine the integrity of the feathers and their capacity to resist bacterial degradation. This information can be transmitted to conspecifics. Regarding the objectives related to signals functioning in sexual communication contexts, we found that the plasma antimicrobial capacity of females (mediated by natural antibodies), and the amount of uropigial secretion produced, were positively related to their reproductive success, and that those antimicrobial capabilities are related to the coloration of the integuments (feathers, beak and legs). Therefore, these colorations might function as sexually selected signals indicating immune capacity of females during mating. In addition, our results showed negative relationships between the male ornamental throat feathers and telomere length and dynamic one year after manipulation. However, these associations disappeared when considering feather length after the experimental shortening. These results suggest that the detected associations were not due to a direct effect of feather length but to age since older males would have shorter telomeres and longer throat feathers. Finally, experimental feathers shortening produced statistically significant effects on the coloration of the base of the beak the following year. This coloration was positively related to body condition and the natural length of ornamental throat feathers, suggesting a sexual signalling function of this character. These results support, for the first time, a causal link between the expressions of two sexually dimorphic traits, which is essential for understanding their functionality within the multiple signals framework. Altogether, my thesis contributes to the understanding of the evolution of animal communication and signalling in contexts of ectoparasitism, brood parasitism, depre-
dation and social and sexual communication. The originality of some results opens new possibilities and lines of research, such as those highlighting the role of microorganisms in these contexts through experimental approaches.


Díaz Lora, Silvia
E-mail: silviadiazlora@ugr.es;
silvia_monte2@hotmail.com
Supervisors: Martín-Vivaldi Martínez, M. and Martínez Bueno, M.
Cosmetic colorations and bacteria in contexts of sexual selection in Hoopoes and Hornbills. [Coloraciones cosméticas y bacterias en contextos de selección sexual de abubillas y calaos.]
Key words: cosmetic coloration, Hornbills, symbiotic bacteria, Upupa epops, uropygial gland secretion.
Palabras clave: bacterias simbiontes, Calaos, coloración cosmética, secreción de la glándula uropigial, Upupa epops.

Abstract:
Bacteria are common symbionts of macroorganisms frequently establishing mutualistic associations, in which both the symbiont and the host get benefits. One of these benefits is protection of the host against pathogens, by means of defensive substances that the bacteria synthesize. The microbial community associated with the host may be different among individuals of the same species and, consequently, be a property that causes differences in the abilities of those individuals. These differences could be of interest to potential partners and, thus, the production of signals associated with this quality could be under selection. Thus, the quality of an individual’s microbiome could be the information transmitted by some existing sexual signals in hosts of beneficial bacteria. The evolution and maintenance of the signals depends on the reliability of the information transmitted. In this scenario, it would be
expected the evolution of signals dependent on the symbiotic bacteria hosted, through the colours caused by the metabolites of the bacteria. An example could be the European Hoopoe (*Upupa epops*). Its uropygial gland secretion harbors bacteria producing antimicrobial substances that are responsible for the brown color of the secretion and of the eggshells, since females actively stain them with the secretion. The fact that the association with bacteria in Hoopoes is temporary and linked to the nest environment raises the question of how they obtain their bacterioma each season. One possibility would be the acquisition of symbionts that may remain in reservoirs in the nests used by other hoopoes the previous years. In such a case, it would be beneficial for the Hoopoes to be able to detect those nests and select them for nesting. The existence of symbionts in the uropygial secretion of birds could be a more widespread phenomenon. In the order *Bucerotiformes*, a sister clade of *Upupiformes* formed by 61 species of Hornbills, some species have coloured uropygial secretions, which they use to stain different parts of their body, possibly with an ornamental function. However, it is not known whether their pigmented secretions are linked to the presence of microbial communities in the uropygial gland, as described in hoopoes. In Hornbills and Hoopoes, only females incubate and take care of the nestlings while they are small, and the males provide all the food in that period. Therefore, it is expected that the reproductive investment depends on the quality of their partner. In Hornbills, stained secretions are used by both sexes throughout the year, and therefore they could act as pre-mating signals. However, in the Hoopoes, the colored secretions with bacteria are only present in the females, after pairing, while they are inside the nest, and therefore, they could function as post-mating signals to obtain a greater male investment. The hypothesis of this thesis is that the uropygial glands of Hoopoes and Hornbills harbor communities of symbiotic bacteria differing among individuals, and, that some signal traits have been selected to show their quality. The objectives are to test the following predictions: (i) Hoopoes can incorporate into their gland beneficial bacteria from the material of reused nests, and thus, they would select nests previously used by other Hoopoes; (ii) cosmetic eggshell color in Hoopoes are used by males to infer the quality of females. Therefore, males will make a greater reproductive effort when they are paired with females that have higher quality secretions; (iii) the pigmented uropygial secretions of Hornbills will show evidence of presence of bacteria more frequently than the non-pigmented ones. To test these predictions, we performed an experiment manipulating the presence of material from nests previously used by Hoopoes; and a cross-fostering experiment of clutches between pairs of females in a wild population of Guadix (Spain). The third prediction was tested with bacterial samples taken from 13 species of Hornbills housed in different zoos in Spain, Portugal and France. The Hoopoes preferred nest boxes containing soft material versus empty ones, regardless if the added material came from previously used Hoopoe nests. The characteristics of the experimental material did not affect reproductive success, but they affected bacterial loads of the eggshells and the composition of the bacterial community of the uropygial gland. This is the first time that an effect of the nest material on the uropygial secretion bacteriome is shown in Hoopoes. All the results supported the general hypothesis that in Hoopoes and Hornbills, cosmetic colorations of the uropygial secretion may be selected as quality signals associated with the possession of symbiotic bacterial communities. Male Hoopoes responded to the changes in the eggshells cosmetic color investing less with more saturated color, which is negatively related to the abundance of symbiotic bacteria in the female’s secretion. This is the first experimental demonstration of the benefits associated with
the female cosmetic signal in Hoopoes. In Hornbills, we confirm for the first time that some species maintain symbiosis with bacteria in their secretions. Contrary to expectations, bacteria were not abundant in colored secretions. However, some of their symbionts may be responsible for the pigmentation of the secretion. In addition, the comparative study of the ornaments of Hornbills shows associations with the presence and abundance of groups of bacteria, both pathogenic and producing defensive substances, and interactions between these bacterial groups. Together, these findings suggest that Hornbills are a new study model of great interest to understand the evolution of mutualistic symbiosis with bacteria in birds, as well as of signals associated with that relationship.


Veiga Neto, Jesús
E-mail: jveiga@eeza.csic.es ; veiga.ew@gmail.com
Supervisors: Valera Hernández, F. and Moreno Rueda, G.

Determinants of the host-parasite relationship in a system formed by a cavity-nesting bird and its ectoparasites in an arid ecosystem.

Key words: arid areas, Carnus hemapterus, ectoparasites, host colonization, host-parasite, vectors.

Palabras clave: Carnus hemapterus, colonización del hospedador, ectopárasitos, parásito-hospedador, vectores.

Abstract:

Parasites are strongly influenced by numerous abiotic and biotic factors operating at different temporal and spatial scales. To understand parasites dynamics, host-parasite interactions and the underlying mechanisms of such interactions it is necessary to study how those factors influence parasites and their relationships with the hosts at the various scales. Here we study the effect of off-host and host-related factors on the relationship between a cavity-nesting bird species, the European Roller (Coracias garrulus) and its ectoparasites, mainly the haematophagous fly Carnus hemapterus. The main factors considered in this study involve habitat characteristics at the mesoscale (the host nest and the immediate surroundings) like nest-site type (a major source of habitat heterogeneity in our study area) as well as host and parasite density, breeding phenology of the host (i.e. seasonal effects) and host total brood mass (as a surrogate of cues for the parasites). We study the effect of these factors on the colonization success and distribution (prevalence and abundance) of the most common ectoparasite (Carnus hemapterus). However, since a given host species usually harbours several parasite species, the approach “one host-one parasite” overlooks the effect of the interactions among parasites that mainly occur at the infracommunity level. Therefore, we also explore the effect of the above-mentioned factors on the ectoparasite infracommunity of the European Roller. Our study is performed in a semi-arid environment, therefore contributing to our knowledge of host-parasite interactions in such habitats that are underrepresented in the scientific literature. Both to fill the gaps on the basic biology of the study species and to build up our study on solid foundations, we also explore basic aspects of the natural history of Carnus hemapterus such as the characteristics of the pupal stage of the ectoparasite or its life span during the dispersal stage (closely related to colonization success). We found that carnid flies have a very short life span during the dispersal stage (less than four days), in spite of which they are able to colonize ca. 100% of the host nests. Its longevity during this period increases with body size, environmental humidity and with access to food (flowers).
Nest-site type influences colonization success of carrion flies, so that it is higher in nest boxes on sandstone cliffs-farmhouses than in nest boxes on trees. Colonization success also increased with host density and host brood mass but decreased as the season progressed. Interestingly, parasite density had no effect on host colonization success. Nest-site type also explained differences among nests in composition of the ectoparasite infracomunity and in abundance of various ectoparasite species. These variables were not affected by the spatial structure, nor by brood mass. However, host breeding phenology affects the ectoparasite infracomunity differences in abundance, acting mainly over *Carnus hemapterus*. Our results also reveal that it is necessary to consider the non-infective stages of parasites when analysing host-parasite relationships since they are important for understanding habitat selection criteria, host-range and processes regulating coexistence with other species. In our study system, the observed patterns of prevalence and abundance of imagos and pupae of three supposedly generalist ectoparasites (*Carnus hemapterus* and the louse flies *Pseudolynchia canariensis* and *Ornithophila metallic)* suggest that, for some parasite species, the requirements of non-infective stages may be more restrictive than the ones of the parasitic stages. Since some of the ectoparasites here studied are vectors of haemoparasites and since the identification of associations host-vector-pathogens is critical for understanding the ecology of diseases, we studied the likely vectorial role of biting midges (Fam. *Ceratopogonidae*). We found that *Culicoides paolae* and *C. circumpictus* were common visitors in nests of various species of troglodyte birds. These midges feed on various bird species and harbour four lineages of *Haemoproteus*. Thus, they can play an important role in the transmission of *Haemoproteus* in the study area. Finally, this study reveals that the infracomunity of ectoparasites of a cavity-nesting bird species in a semi-arid environment is rich (made up of at least species of eight different families, including a recently introduced species, *C. paolae*), with some species being particularly abundant. We conclude that socioenvironmental characteristics at small scale are major determinants of the spatial distribution of nest-based ectoparasites in an arid environment.


**Universidad Pablo de Olavide**

Baños Villalba, Adrián
Supervisors: Edelaar, W. and Tella Escobedo, J.L.

**Mechanisms of adaptation to a changing world.**

*Mecanismos de adaptación a un mundo cambiante.*

Key words: adaptation to the environment, biodiversity, threatened species.

*Palabras clave: adaptación al medio, biodiversidad, especies amenazadas.*

**Abstract:**

The current extinction rate of species on Earth is greater than any of the mass extinctions registered in the fossil record in its entire history. This increased biodiversity loss is caused one way or the other by the human species. Changes in land use, climate or biological invasions are acting worldwide. In this context, understanding the mechanisms by which organisms adapt to the environment and the ecological and evolutionary consequences that these entail is a key factor. In this thesis, this question is approached from two different perspectives. The first one (Section 1) assesses how populations of invasive species adapt to a new environment. Before a population becomes invasive in a non-native area, it must first have passed through the earlier stages of invasion (capture, transport and introduction) before its establishment in
this area. These stages could be acting as selective filters of individual variation. In this way, the introduced individuals would not be a random sub-sample of the native population of origin. This could have a great impact on their invasive potential. However, what happens in these earliest invasion stages has hardly ever been studied. To test the hypothesis that selection acts already early during a biological invasion, we followed the individuals of two invasive bird species from their native habitat in Senegal and during these early stages of a potential invasion. We indeed found that selection acts on variation in a gene related to behaviour (Chapter I). In addition, we found that selection also acts on many other phenotypic characteristics that could have a great importance for invasive potential, such as sex, age, body size, brain size, beak size and shape, body condition, stress hormone levels and behaviour (Chapter II). The second perspective (Section 2) assesses how native populations adapt to environmental changes. For this we studied all the possible mechanisms of adaptation (natural selection, phenotypic plasticity, habitat choice and environment adjustment), but especially focusing on matching habitat choice. This mechanism is based on the non-random dispersal of individuals due to an assessment of variation in their local performance, such that individuals settle down in those habitats that best match their phenotypes. Despite its eco-evolutionary importance, this mechanism has received almost no research attention. In this thesis, we study how a native population of grasshoppers has adapted in camouflage (a classic form of adaptation to the environment) in the colonization of a new urban environment (one of the most drastic changes in the habitat). We found a population divergence on a micro-geographic scale (differently coloured grasshoppers on distinctly coloured urban substrates) despite the existence of a lot of (presumably homogenising) movement by individuals. In Chapter III, we demonstrate that habitat choice, and not other mechanisms such as natural selection or phenotypic plasticity, is the main mechanism that has caused the recent local evolution of camouflage and the micro-geographic population divergence. In addition, we found that habitat choice acts also at a much finer scale, in which individuals improve their camouflage by aligning with certain substrate patterns depending on their degree of colour matching with the substrate, making it a flexible way to increase performance on different spatial scales (Chapter IV). However, this matching between phenotype and environment can also be achieved through phenotypic plasticity. In Chapter V we show that grasshoppers are able to change their body coloration through successive molts to resemble the substrate on which they live. The degree to which they do so is affected by the risk of predation they are exposed to: experimental increase of risk resulted in an increased phenotypic adjustment. Taken together, this thesis demonstrates in a convincing and quantitative manner the existence and importance of two neglected mechanisms of adaptation of populations to environmental changes, thereby increasing our understanding of how invasive and native populations adapt to change and ecological opportunities in an increasingly changing world.


Álvarez-Blanco, Paloma
E-mail: palomaoviedo@hotmail.com
Supervisors: Cerdá Sureda, X. and Angulo Agudo, E.

Ecosystem responses to the Argentine ant invasion: Effects on vertebrates.

[Respuestas del ecosistema ante la invasión de la hormiga argentina: Efectos en vertebrados.]

Key words: chemical weapons, invasion ecology hypotheses, Linepithema humile, predator-prey relationships, subtle effects.
Palabras clave: armas químicas, efectos sutiles, hipótesis de la ecología de las invasiones, Linepithema humile, relaciones depredador-presa.

Abstract: Biological invasions are one of the main drivers of biodiversity loss. Certain effects of invasive species are commonly overlooked and potentially compromise the structure and function of ecosystems in unpredictable ways. This thesis takes advantage of the vast knowledge of the invasive Argentine ant, Linepithema humile, to focus on subtle and indirect effects on the recipient ecosystems, specifically on native vertebrates (amphibians, birds) in Doñana National Park (southern Spain). This tiny intruder is notorious for displacing the native ant community in the ecosystems it has successfully invaded. Therefore, this thesis assesses whether the effects of potential prey depletion scale to higher trophic levels. Although the Argentine ant lacks recognized weapons, it is well known for its aggressiveness when outcompeting native ants. I evaluated whether native vertebrates at their most vulnerable stages are susceptible to being attacked or disturbed by the invasive ant and if they suffer from lethal or sublethal effects that hamper their development. These issues were addressed through field sampling and monitoring, field and laboratory experiments, and analyses of chemical, isotopic, histological, physiological, and behavioural parameters. My results reveal the Argentine ant invasion has negative impacts on native vertebrates in Doñana at different levels. For example, the native amphibians studied here have altered their diet, by shifting to non-ant preys in infested areas. Additionally, vertebrates in their early stages of development showed poor body condition under experimental (juvenile amphibians) and field (chicks) conditions when they were fed a diet supplemented with Argentine ants or raised in invaded areas. Furthermore, both myrmecophagous species, such as the Natterjack Toad, Epidalea calamita, and non-ant predators, such as the Great Tit, Parus major, modified their habitat use in invaded compared to uninvaded areas, although for different reasons (foraging and breeding, respectively). Finally, I demonstrate, for the first time in the literature, that the invasive Argentine ant has a powerful venom –iridomyrmecin– that is able to paralyze and kill native vertebrates, specifically juvenile amphibians. This unexpected finding deserves special attention, as it may play a key role in the previously demonstrated negative effects/invasiveness of this species. Overall, this thesis reveals overlooked indirect and subtle effects of an invasive species at different ecosystem levels, but also yields novel information about the mechanisms underlying these effects.


Torres Medina, Fernando
E-mail: fernantor1@gmail.com
Supervisors: Blas García, J. and Marchant, T.A.

Stress ecology and adrenocortical function in White Stork (Ciconia ciconia).

Palabras clave: cigüeña blanca, corticosterone, eje Hipotálamo-Pituitaria-Adrenal.

Abstract: In birds, the Hypothalamic-Pituitary-Adrenal (HPA) endocrine axis is involved in the secretion of corticosterone, the main stress hormone in this group of vertebrates. Under normal conditions, plasma corticosterone levels fluctuate within a lower range of baseline levels that allows adjusting physiology, morphology and behavior to the predictable
energy demands of the environment. In contrast, corticosterone levels typically increase to a higher range of stress-induced levels in response to disturbance, facilitating adaptive changes aimed at maintaining homeostasis while overcoming the perturbation. Repeated or longer-term exposure to disturbance may generate chronic stress, causing deregulation of the HPA axis with imbalanced corticosterone production. This thesis had several major goals. First, I aimed to study the effect of human presence in nature as a potential source of chronic stress in birds. Corticosterone levels were quantified in White Stork (Ciconia ciconia) nestlings exposed to different degrees of human presence and the self-inhibitory mechanism of corticosterone secretion (i.e., negative feedback) was experimentally induced through dexamethasone treatment. Results showed differences in the adrenocortical activity of storks exposed to humans compared to conspecifics living free of anthropogenic presence, as reflected by the lower feather corticosterone levels in the latter group. Such differences were not found when comparing blood corticosterone levels, likely because (contrary to feathers) circulating hormones only reflect short-term physiological trajectories. These results did not provide evidence for chronic stress among human-exposed storks and suggested a reduced exposure to stress events in areas with human presence. As a second goal, I addressed the mechanism responsible for an age-related attenuation in the adrenocortical response to stress typically displayed by altricial birds during post-natal development. Such attenuation of the response to stress has been postulated as an evolutionary mechanism to prevent long-term corticosterone elevations, which may jeopardize growth and development at early ages, when nestlings’ physiological and behavioral abilities to cope with disturbances are limited. Two hypotheses have been proposed to explain the mechanism underlying this pattern: (i) a progressive age-related growth and maturat-

ion of the HPA axis (Maturation Hypothesis), or (ii) a gradual attenuation in the intensity of the negative feedback in the HPA axis (Negative Feedback Attenuation Hypothesis). This question was addressed by inducing negative feedback through dexamethasone treatment in White Stork nestlings. Results indicated a positive effect of age on plasma corticosterone elevations in response to stress, but no age effects on negative feedback, suggesting that the progressive maturation of HPA axis tissues is the proximal mechanism responsible of the attenuation pattern. The third goal tested the effects of subcutaneous corticosterone implants on adrenocortical function in nestling and adult White Storks. Implants are regularly used in evolutionary and behavioral endocrinology studies to simulate chronic corticosterone elevations (over several days) and study subsequent effects on specific biological traits. Contrary to our predictions, our implant experiments resulted in decreased baseline and stress-induced levels of plasma corticosterone. A review of 50 previously published avian studies revealed that baseline corticosterone levels generally increase (72% of the experiments) while stress-induced levels decrease (78% of the experiments) after implant treatment. The results of this review placed in context our results and contributed to expand the prevailing assumptions in the use of implants because: (i) baseline levels showed a quadratic association with implant dose across bird species (and decreased levels may thus occur at both high and low doses), and (ii) corticosterone implants also decreased stress-induced levels, thus producing stress-hyporesponsive phenotypes. This review also revealed important study biases in the use of implants by avian researchers. In summary, this thesis studied the effect of external and internal factors on avian adrenocortical function, examined the proximal mechanisms that allow this function and generated practical knowledge for further research.


Ardeola 68(1), 2021, 219-239
Abstract:

Rise of agriculture during the Mesolithic-Neolithic transition gave birth to a new biotope, the farmland, which in a few thousand years reached a planetary scale at the expense of natural ecosystems. This widespread land use change implied a demise of many avian species as their natural habitats were replaced by crops and grazing lands. However, it became into a new habitat for some grassland birds who were able to shift from their natural habitats to human-made environments. Some avian species found there a land of opportunity, among them a few Buttonquail (Turnicidae) species. However, the recent farmland intensification is leading to a general decline of these species. In this PhD we use the Andalusian Buttonquail (Turnix sylvaticus sylvaticus) as a case study. This species has been able to cope with traditional farming and until recently has had a wide distribution in the western Mediterranean countries but currently is in the verge of extinction. Starting from a global and historical scale approach, contextualizing the taxon at biogeographic and taxonomic levels, we arrive at the “in situ” study of the only population that still survives. In Section 1 we create an index to evaluate the concern status of all Turnicidae species and subspecies by using the BirdLife distribution areas and data from the eBird citizen science platform. We also describe the asymmetric heterochromia in the iris of this family and other pale-eyed bird species as a feature to aid vision by regulating the light entering the eye. In Section 2 we establish the historical evolution of the extinction process in Europe and North Africa, to model and evaluate the historical distribution based on environmental variables and then study the population in Morocco to determine the population size at different times, to evaluate the population trend and to describe habitat selection and reproductive biology. Extinction risk is often associated with species intrinsic traits such as bigger size, higher trophic level, narrower habitat niche or smaller distribution areas. Despite this, fast extinctions can also occur in species apparently not matching any of these traits. Here we describe how this taxon with a former wide range, high reproductive rates, a low trophic level in the food chain, small size and apparently coarse habitat requirements, is close to extinction. By niche modelling we outline its historical distribution and then we explore at a regional scale (Andalusia) the role of historical land use changes and human population trend in the rapid decline of the species. PCA analysis of environmental variables showed that its distribution was mainly determined by low continentality and aridity. Since the 19th century, the decline in the extent of occurrence has been above 99.99%. PCA analysis of land use changes showed that areas with a higher probability of historical presence have suffered more intense agriculture intensification, afforestation processes and higher human population pressure and development. Conservation efforts should focus on maintaining coexistence of the species with the human being. The last populations of threatened taxa usually survive in low-impacted areas, whose protection and management is critical for its conservation. However, they can also be located in humanized and highly dynamic areas, whose management can be extremely challenging. Here, we show how the last Andalusian Buttonquail population is...
restricted to a small, strongly used agricultural area (4,675 ha) in the Atlantic coast of Morocco, where the birds adapt their life cycle to a fast crop rotation. Buttonquails occupy crops during the flowering and fruiting stages, thus changing the preferred crop types along the year, although alfalfa fields were occupied all the year round. We used estimated occupancy rates in different crops to obtain seasonal (2017) and year-to-year population estimates (2011, 2014 and 2017). Numbers showed wide seasonal fluctuations: lowest in winter and maximum in summer (112 to 719 individuals). Year-to-year summer estimates also showed wide variations and large uncertainties, ranging between a maximum 1,890 estimated in 2011 and a minimum in 2014 with 492 individuals. The last population estimate available was 596 individuals in 2017. The area is suffering a rapid shift from traditional irrigation farming towards practices more akin to commercial industrial agriculture. The conservation of this critically endangered taxon is highly dependent on the maintenance of traditional farming practices and a rational on-site agricultural modernization. Understanding the breeding cycle of wildlife is essential to afford conservation strategies. This is especially important for barely studied species and urgent for those in a serious risk of extinction. We performed 2302 sampling events to determine the occurrence and breeding of the species. Breeding season lasted from February to October. The species bred in 17 different crops but it did not use cucumber and artichoke fields. However, a strong selection for alfalfa, pumpkin and maize fields was evidenced. Nests were on average 82mm × 71.4mm grass lined structures built on a ground scrape. Eggs had 26.14mm mean maximum length, 20.24 mean diameter and weighted 5.9g. All complete clutches had four eggs and the hatching rate was 3.42. All monitored nest successfully reared at least one chick. Clutch size and hatching rate matched the standards for other Buttonquail populations and species. Thus, the causes of the decline must be found in other stages of the reproductive cycle. Additional studies are needed to reveal chick and juvenile survival.


Universidad del País Vasco / Euskal Herriko Unibertsitatea

García Barón, María Isabel
E-mail: isa.garciabaron@gmail.com
Supervisors: Louzao Arsuaga, M. and Santos Vázquez, M.B.

Integrating marine megafauna into ecosystem-based management: a multidisciplinary approach applied to southern European waters.

Key words: ecological modelling, marine megafauna, marine protected areas, oceanographic surveys, systematic conservation planning.

Abstract:

Marine megafauna show high risk of extinction worldwide, raising awareness of the need of priority conservation strategies to ensure their protection. To reverse this situation, information on the spatio-temporal patterns of the pressures that affect the marine environment and an assessment of their severity are urgently needed to inform biodiversity and habitats conservation, devise appropriate mitigation measures and advise spatial planning decision processes. In this context and to anticipate the response of the ecosystems in the face of growing pressures, a holistic
management approach, such as the Ecosystem-Based Management (EBM) with an integral vision of the ecosystem is required. Implementing the EBM approach requires multidisciplinary data collection, monitoring of the system state, behaviour, and functioning, development of methods to organize, display, and illustrate the relationships of ecosystem components and methodological developments of transdisciplinary nature to synthesis data, multipurpose and integrative in order to inform management measures. This thesis was focused on the Bay of Biscay (BoB) and the North and North-Western Iberian coast where the marine megafauna is suffering increasing disturbances due to anthropogenic pressures and there is evidence of the increasing impacts of climate change. Thus, the main aim of the thesis was to assess the impacts of human activities on marine megafauna by integrating their spatial ecology into EBM. By focusing on seabirds and cetaceans inhabiting the BoB, the thesis developed an integrative ecological framework based on multidisciplinary approaches to identify threats, develop environmental indicators, establish baseline values, obtain estimates of spatio-temporal abundance, assess the coherence of Marine Protected Areas (MPAs) networks and, in addition, examine the value of long-term series for MPA robustness. Firstly, this thesis collected information of the impact of the main threats affecting seabirds and cetaceans in the BoB and developed a two-fold approach to identify the main pressures affecting directly or indirectly cetacean and seabird species. Whilst seabirds are particularly sensitive to oil spills, bycatch and marine litter, cetaceans are especially vulnerable to bycatch, vessel collision, and pollution-related threats. This type of assessment studies can aid in the identification of priority areas and/or species where management measures should be applied to ensure that the goal of the Marine Strategy Framework Directive (MSFD), sustainable conservation of the marine environment, is reached. Secondly, an example of the combination of multiple pelagic components was shown to provide an integral assessment to advance EBM by developing a methodological approach to identify biologically appropriate oceanographic and prey landscape predictors to jointly consider both the spatial and vertical dimensions of oceanographic habitats. This approach, which can be applied to any marine species, was developed using as case study the Sooty and the Great Shearwaters Arduenna grisea and A. gravis. The species abundance patterns were influenced by oceanographic conditions and prey accessibility integrated above the depth of maximum temperature gradient for Sooty Shearwaters and at the surface for Great Shearwaters, leading to a vertical segregation. Similarly, both species showed a spatial segregation in relation to shelf areas versus oceanic areas. The first abundance estimates for both species during September in the BoB are provided. Thirdly, this thesis identified the Essential Ocean Variables (EOVs) that shape the environmental envelope of the North and North-Western Spanish seabird and cetacean’s community and delineate their High Value Biodiversity Areas (HVBAs) taking advantage of the sightings collected during annual oceanographic surveys. The sea surface temperature and the chlorophyll-a concentration were identified as EOVs, driving the environmental envelope and shaping the HVBAs. HVBAs were located mainly over the North-Western Spanish waters and decreased towards the inner BoB remaining spatially stable over the ten-years study period. The use of this information can facilitate the establishment of baseline values to predict and detect the effect of multiple threats on HVBAs, as well as to fulfill the emergent need for sound spatial information to support the implementation of marine spatial planning. Fourthly, the difficulty of protecting highly mobile species that cross multiple jurisdic-
tional boundaries and multiple non-specific MPAs was addressed by assessing whether the current MPAs network in the area offers protection to the Fin Whale *Balaenoptera physalus*. Results showed that the main critical area for Fin Whales was located over the South-Eastern part of the BoB, an area that is currently only marginally covered by three MPAs. Based on these results, a trans-boundary MPA was proposed for this species in the BoB. Finally, the value of time-series data was assessed by exploring whether priority areas for the conservation of megafauna species (i.e. seabirds and cetaceans) remain consistent regardless of the amount of data considered. The results provide a method for calculating the minimum number of monitoring years required to establish an effective MPA network, which we recommend for future spatial prioritization exercises for highly mobile species. All the results obtained in this thesis share a practical goal as they focus on the biodiversity and ecosystem conservation aspects of the EBM, which needs multidisciplinary studies involving different approaches and study techniques. With the aim of operationalising the EBM within the current European legislation, the results intend to integrate new ecosystem components such as marine megafauna into EBM to inform conservation and management measures in the context of the MSFD overall aim, which is to enable sustainable use of marine goods and services.


**Universidad de Sevilla**

Luna Fernández, Álvaro
E-mail: alvalufer@gmail.com
Supervisors: Carrete, M., Sanz Aguilar, A. and Tella Escobedo, J.L.

**The urbanization process and its effect on the dispersal of birds: the case of the Burrowing Owl (Athene cunicularia).**

**Key words:** *Athene cunicularia*, dispersal strategy, reproduction, survival, urban ecology.

**Palabras clave:** *Athene cunicularia*, ecología urbana, estrategias de dispersión, reproducción, supervivencia.

**Abstract:**

Urbanization has become one of the greatest global landscape transformations. Usually, the spread of cities creates new habitats starkly different from the natural ones it replaces, and simplifies and homogenizes animal communities. Despite this general trend, some species are able to thrive and even prosper in urban ecosystems. Among birds, for example, nearly 20% of the roughly 10,000 described species can be found in cities. Thus, understanding the factors that allow certain individuals and species to persist within these landscapes, as well as the consequences for their population dynamics and structure, is as important as identifying the drivers of species loss. Dispersal, a fundamental event with influence on the demography and structure of populations, is among the main ecological processes that may be altered by urbanization. However, few studies have assessed the differences in this process between conspecifics living in their original habitats and those inhabiting cities. This thesis focuses on the dispersal of the Burrowing Owl (*Athene cunicularia*) in the city of Bahía Blanca (Argentina) and its rural surroundings. There, a specific monitoring program conducted annually from 2006 to 2019 has surveyed ca. 2,500 urban and ca. 3,200 rural nests of this species, recording reproductive parameters and marking ca. 2,000 adults and nestlings. This long-term study has been complemented with individual measurements of Burrowing Owls behavior. Specifically, we recorded the individual variation in the susceptibility to
humans. This personality trait is included within a range of behaviors that encompasses risk taking, aggressiveness, and exploration and dispersal propensity, playing a role in the colonization of cities. The main hypothesis is that individuals disperse according to their phenotypes, although their dispersal decisions may be also influenced by the heterogeneous selective pressures observed in the study area. Furthermore, the coexistence of different dispersal strategies may play a positive or negative role in term of individual fitness, with potential effects in the population dynamic. Thus, the aim of this study is to understand the influence of individual cues (behavior, sex and age) and environmental factors (quality of natal and breeding zones, predation pressure and habitat type) in dispersal strategies of Burrowing Owls in adjacent but deeply different habitats, the city and their immediate rural area. Moreover, we assess whether dispersal decisions influence the biological effectiveness of individuals in both habitats in terms of reproductive parameters and survival. In Chapter 1 we focused on natal dispersal. We found that urban Burrowing Owl dispersed nearer than rural ones. Moreover, females, bold individuals and those born in poor quality territories dispersed farther. Females and rural individuals who settled far from their natal territories improved their reproductive output in their first breeding attempt, and this extended to both sexes and habitats when we consider productivity throughout the entire life. On the contrary, females that dispersed farther showed lower local survival. In Chapter 2 we explored the development of cooperative breeding, an uncommon strategy in this monogamous owl. We showed that cooperative families were mainly composed by three adults. The extra individuals were generally males born the last breeding season in the same territory, who delayed their dispersal to help their parents. The contribution of helpers can increase food provisioning, as evidenced by the fact that nestlings born in cooperative breeding units had a better physical condition. Cooperative breeding occurred more frequently in highly productive areas in which a greater number of conspecifics aggregated: the city and high quality rural areas. Furthermore, territories with helpers collaborating in reproductive tasks showed higher breeding success. The offspring raised in cooperative families had only a slight increase in their survival probabilities, compared with juveniles raised in common pairs. Survival showed temporal variations and the main factors driving survival differences were age and habitat: adults showed higher survival than juveniles, who had a higher survival in urban than in rural habitats. Finally, in Chapter 3, we studied breeding dispersal. We observed that a significant part of the population remained faithful to the same territory. Distances covered by dispersing individuals were shorter than those observed in natal dispersal. In general, females dispersed more frequently and travelled farther than males. Again, urban individuals were less prone to disperse, settling closer from the previous nest. In rural areas, individuals that suffered predation or breeding failure in a given territory, dispersed more frequently. However, bold individuals dispersed less than fearful ones, probably due to the higher ability of the former to cope with the disturbances suffered during the breeding period. The influence of behavior disappeared in the urban environment, where the main determinant of site fidelity was conspecific density.