

**THE ORIGINS OF COMMUNAL ROOSTING BEHAVIOR IN BIRDS**

MSc. research proposal

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March2025

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# **Chapter 1: Movement ecology and foraging behavior**

*Movement ecology in wildlife – an overview*

Movement is ubiquitous throughout the life cycle of countless species. It is an essential characteristic of life that shapes ecological processes for living organisms and systems (Nathan et al., 2008, 2022) including the search for food (Garsehelis & Pelton 1981 , Zuberogoitia et al. 2012) ), mates , breeding areas (Gregory et al. 2010), or other important resources, as well as the avoidance of detrimental factors such as predators (Fortin et al. 2005, Smith et al. 2023), disease, or competitors ([Hayward](https://journals.co.za/doi/epdf/10.10520/EJC117325) & Slotow 2009 ). Put simply, an individual's movement and the patterns and consequences derived therefrom are an outcome of their behavior. Movement can thus be considered a fundamental component of many species’ ecology, and, consequently, of key interest in many scientific fields within ecology. The unifying framework under which this is studied is termed ‘*movement ecology*’, where research into this area is typically focused either towards describing the natural history of heretofore undocumented movement behavior (e.g., Florko et al. 2023), or exploring the extent to which an animal’s movement might reflect the way it perceives and therefore reacts to its environment (Benhamou, 2014; Teitelbaum et al., 2020).

Although the movement processes may be more evident during the breeding period of animals, habitat quality (e.g., availability of resources) also drives animal movement throughout the whole annual cycle. For many species (but see Geremia et al., 2019) this variation in movement patterns is usually closely synchronized with the spatial and temporal arrangement of the landscape (Wiens 1989; Levin 1992; Chave 2013, Mezzini et al. 2023). In other words, fluctuations in resource availability in time and space (Bell et al. 1993), coupled with an individual’s change in requirements (Parrish 2000, Groscolas & Robin 2001, Brown et al. 2004, Hedenström 2006, Kidd-Weaer et al. 2020), will conspire to shape the movement that drives habitat use (Johnson 1980), sometimes favoring range residency (Burt et al. 1943, Alston et al. 2022) and other times favoring movement shifts (Mueller & Fagan 2008; Van Moorter et al. 2009; Owen-Smith et al. 2010). For instance, it has been widely documented that the migratory patterns of many species are governed by fluctuations in food resources (Gauthreaux 1982, Thorup et al. 2017, Sotillo et al. 2019). An example of this is seen in peregrine falcons (*Falco peregrinus*) migrating from northern North America to central and South America following other species’ migration (e.g., shorebirds) since the latter are an important prey item in their diet (Ydenberg et al. 2004, Watts & Truitt 2021, Ydenberg et al. 2023. Whilst resource availability evidently drives movements over relatively large spatio-temporal scales with impacts on species’ biogeographic ranges and their population-level spatial structuring (e.g., migration), it can also occur at a smaller spatio-temporal scale (range-resident species), but show a similar pattern to migration behavior nevertheless. For example, as described by Benhamou (2013), in the late dry season in Niger, buffalo (*Syncerus caffer*) restrict their movements in the vicinity of a few permanent water holes but leave these overexploited areas as soon as the first rains come to settle in more productive regions (Cornelis et al. 2011). These changes in location induced by the tracking of resources in the landscape can even be seen at a smaller scale when resource depletion and renewal make animals return to particular feeding areas (Benhamou & Riotte-Lambert 2012). An example of this behavior is displayed by hummingbirds that forage using different flower patches and complete a circuit as the nectar is renewed (Tello-Ramos et al. 2015) with cycles happening on the order of hours or less.

Clearly, the arrangement of important resources and concomitant changes in community structure across a landscape drive patterns of animal movement. Though individuals have many needs beyond nutrition (e.g., finding reproductive partners, sleeping, etc.), foraging is likely a key aspect of movement given that energy acquisition is essential for all heterotrophic species, which ultimately drives all other life processes. Hence, foraging ecology might be crucial to understand the mechanistics underpinning animal behavior. Given the vital importance of foraging, I will focus my thesis on this aspect of ecology, with particular attention on birds. In this opening chapter, I aim to review the current state of knowledge on movement ecology of wildlife to set the grounds for my research. I will also identify gaps that remain to be addressed as a framework for my work. Specifically, I will 1) summarize the literature on movement ecology related to foraging behavior with particular attention on birds, 2) discuss social behavior in wildlife as a way to increase foraging efficiency, and 3) identify knowledge gaps and suggest future directions to address these.

*The unique nature of avian foraging ecology*

A relevant question remains unanswered – why are birds an interesting study system to answer the research questions here proposed? The answer has both ecological and pragmatic rationales. First, birds, unlike most mammals, have a greater capacity to navigate the landscape without being limited by terrestrial anthropogenic barriers, and they also display different types of movements (e.g., flying modes). For instance, many birds rely on thermals or updrafts to gain elevation and velocity which allows them to travel long distances with little energy expenditure. This aided movement implies that flying long distances to feeding sources may not be a limiting factor. Furthermore, because birds need to fly as a main type of locomotion, they can’t exaggerate on their food intake unlike mammals, or else their movement will be limited. Therefore, their energy intake needs to be properly managed, which ultimately means that foraging needs to happen more regularly but in less quantities. Altogether, these variables make feeding a complex process where several factors need to be considered in the decision-making of where and when to feed.

In addition, many species of birds’ forage in groups, either by hunting or scavenging together. It has been discussed in the literature that foraging in groups helps individuals maximize foraging efficiency, which ultimately may increase a populations fitness. In particular, scavenging is an interesting feeding strategy. Several bird species rely on scavenging (e.g., corvids, some eagles, etc.), and although this behavior is not unique to the bird taxa, obligate scavengers (species that feed solely on carrion) are very rare in other groups of animals. And yet, this behavior seems to have evolved in birds more than once in groups with no common ancestors (Old World and New World vultures). This suggests that there are factors that are favoring the evolution of this strategy. Strikingly, several species of obligate scavengers have complex social networks. It is worth asking whether sociality plays a vital role in the foraging efficiency of this group.

From a pragmatic perspective, there are extensive datasets existing for birds, compiled and organized in a standardized manner, and at a global scale. These reasons provide a unique opportunity to answer research questions at a large scale and identify trends at the taxa level.

*Movement ecology and bird foraging behavior*

Despite long-standing interest in the factors that shape animal foraging behavior, it is still poorly understood how internal traits and external conditions jointly shape avian foraging movement (Mallon et al. 2020). Specifically, bird foraging behavior has been through direct observations. Because such methods are highly time-consuming, these studies have addressed the foraging behavior of specific taxa only (e.g., Smith et al. 2012), but research done on overarching questions aimed at unravelling the underpinning drivers of avian foraging ecology - especially across taxa - is not.

With the advance of tracking technology, however, different approaches can be used to make inferences on foraging behavior. For example, in mammals GPS data have been used to determine foraging based on velocities of movement (see Owen-Smith et al. 2012). Furthermore, using long-term data allows us to make predictions of important feeding grounds, especially for territorial species. Another study done with storks (*Ciconia ciconia*) confer information on the feeding areas during their life cycle and estimated the frequency of landfill use by the studied populations (Flack et al. 2016) using tracking data. Alternatively, a research paper on Andean Condors by Perrig et al. (2020) used GPS locations to identify probable foraging areas based on distance from roosting sites, velocity values and time of the day. There is a need to generate foundations on the types of movement associated to foraging behavior, especially given that the data are becoming more readily available.

Though individuals have many needs beyond nutrition (e.g., finding reproductive partners, sleeping, etc.), foraging is likely a key aspect of movement given that energy acquisition is essential for all heterotrophic species, which ultimately drives all other life processes. Hence, foraging ecology might be crucial to understand the mechanisms underpinning animal behavior. Given the vital importance of foraging, I will focus on my thesis on this aspect of ecology. In this opening chapter, I aim to review the current state of knowledge on potential drivers affecting foraging behavior of birds, and possible gaps that remain to be addressed to guide my work.

*Predictability of resources and foraging behavior*

To defend a feeding territory implies that there are benefits of doing so, one of them being energetic rewards (Ord 2021). Hence, it is expected that individuals with higher energetic demands (e.g., apex predators) will be more territorial than species in lower trophic guilds, all else being equal. Species with very specific niches and scarce or scattered food availability will also be more prone to defend territories because competition for these resources is likely to be stronger. As such, the greater the diet breadth of species, the less territorial they would be. However, when resources are unpredictable in the landscape, defending a feeding territory is no longer reasonable, and this is the case for many scavengers. Many scavenger species are large in size (vultures, ravens) which translates to high energetic demands, and yet they rely on unpredictable food patches, which naturally, cannot lead to territorial behavior (Grant 1993). Interestingly, many scavenger species forage in groups, leading to wonder if there are any benefits to this social behavior given the nature of their unpredictable food sources.

*Social structure and foraging behavior*

Evidence of social learning is growing across the animal kingdom (Aikens et al. 2022) with several studies looking at social behavior during migration. A phenomenon that has been widely studied through the lens of social behavior is migration. During migration, animals need to make complex decisions about where and when to migrate. These decisions may have a direct impact on survival and fitness, and hence it is a challenging process even for adult experienced individuals. Despite individuals acquiring previous knowledge that provides general guidance during migration, this information can be outdated when navigating in unpredictable environments. In these scenarios, relying on social interactions or collective behavior may play an important role in decision-making (Aikens et al. 2022). Research from long-distance migrants suggests that long-range communication can enhance foraging efficiency and navigation (e.g., blue whales *Balaenoptera musculus*). Evidence also suggests that large groups can benefit from collective sensing. For example, collective attention in flocks of homing pigeons (*Columbia livia domestica*) improves predator detection and navigation (Kano et al. 2021). Similarly, collective sensing in massive flocks of passenger pigeons (*Ectopistes migratorius*) may have helped birds locate spatially and temporally unpredictable food patches (Guiry et al. 2020, Aikens et al. 2022). This provides insight as to how individuals leverage sociality to gain information outside of their perceptual range to make more accurate or efficient decisions during migration.

The benefits of social behavior, however, do not apply to migrating species alone. It has been discussed in the literature that one possible benefit from breeding in colonies is enhanced efficiency in exploiting an unevenly distributed food supply (Fisher 1954), which is supported by findings in Brewer’s Blackbird *Euphagus cyanocephalus* (Horn 1968). In addition, there is evidence to suggest that non-breeding sites like communal roosts do indeed act as information centers where individuals share information on foraging sites (Ward & Zahavi 1973, Wright et al. 2003). Thus, the sociality of communal roosting can be correlated to dispersion for foraging (Ward & Zahavi 1973). Here, vultures are an interesting system for several reasons. First, their unique feeding habits, since they are the only terrestrial vertebrate that is an obligate carrion consumer (van Overveld et al. 2020), second, because both New World Vultures and Old World Vultures – two independent lineages- converged to similar foraging habits (Van Overveld et al. 2022), and third, most- if not all- vulture species present some degree of social behavior with shared communal roosts among individuals.

*Memory and foraging behavior*

To navigate the landscape successfully, animals use cues in their environments like odor, sound, location and attributes in the landscape to guide their movement (e.g., Berberi et al. 2023). The process of acquiring this information, processing it and use it to make decisions is referred to as learning (Rolls, 2014; Anderson, 2015; Dukas, 2017, Kashetsky et al. 2021), and the term used for information retention is called memory (Rolls, 2014; Anderson, 2015; Dukas, 2017). This acquisition of knowledge is then used to evaluate whether to execute specific actions. For instance, an individual may decide whether or not to access a foraging area based on an assessment of the costs and benefits of doing so. Repeating this process and assessing the decision based on these costs or benefits suggest a learning process. Only recently has the field of movement ecology increased consideration of learning as part of animal decision-making when navigating the landscape (Fagan et al., 2013, 2017; Avgar et al., 2015; Lewis et al., 2021). For example, a study by Ranc et al. 2020 showed that memory played an important role in movement patterns for reintroduced roe deer (*Capreolus capreolus*) within their home range; the deer showed a higher preference for areas that were previously visited. Another study in blue whales showed that they rely highly on memory for migration and foraging areas (Abrahms et al. 2019). Models have been also developed to suggest how memory can play a role in establishing boundaries of a home range (Van Moorter et al. 2009, Börger et al. 2008). Furthermore, a study by Potts and Lewis (2016) proposes a model to approach how animal movement can lead to territoriality determined by memory processes. Evidently, memory determines an important part of animal behavior, especially for long-lived species (Fagan et al. 2013). It is therefore reasonable to suggest that foraging is partially driven by learning processes as well. A classic example is that of feeding stations for vultures in Africa and Europe. For many vulture species that are in peril, supplementary feeding stations have been implemented to reduce poisoning threats. Once a group of individuals finds a feeding station, they will come back to use it frequently, given that the food is reliably there. This is a clear example of a memory process in foraging behavior. However, in a more complex scenario, with natural food availability, learning processes may function differently as food sources are usually scattered in the landscape, thus, animals might need to remember not one but many potential feeding grounds. One question arises, though: how does memory affect foraging efficiency for those species that feed on unpredictable food sources? If the food cannot be predicted, is memory all that relevant in finding them? Here, it can be argued that for scavengers that exhibit communal roosting behavior, short-term memory plays a role when finding and then sharing information with other individuals. Exploring the relationship between these two variables could open the door for further research questions in terms of the role of communal roosting in foraging success of a population, which ultimately has conservation implications.

*Foraging ecology and conservation implications*

Understanding how animals navigate the landscape for foraging is especially important for vulnerable and threatened species like top predators (e.g., raptors and species of conservation concern in general). For instance, predicting when and where an eagle is likely to hunt can help to design effective conservation strategies that work for the species under threat and the people whose livestock is predated. This can then be transformed into management strategies to reduce predation that would otherwise lead to human-wildlife conflict (Allen & Singh 2016). Other scenarios where foraging behavior is relevant for conservation strategies are seen in highly social species like vultures. Worldwide, vultures are one of the most threatened groups within birds (McClure et al. 2018). One of the major threats for this group is the persistence of toxic substances in the carcasses they feed on. For example, it has been well-documented that poisoned baits represent a pressing concern to Andean Condors (*Vultur gryphus*) throughout its distribution. Another classic example is the iconic problem of lead poisoning in California Condors (Finkelstein et al. 2012). For old-world vultures, the main threat remains the use of toxic baits containing drugs used for cattle and poisoning (Green et al. 2004). This is particularly sensitive because given the nature of scavengers feeding ecology, they rely on patchy and unpredictable food sources. Thus, if the unevenly distributed food sources available pose a threat, these species have few alternative options to obtain their energy from, and the metabolic cost of living can be unaffordable. Under this scenario, communal roosting behavior is critical to exchange information on both food availability and threats in the area, such that protecting these roosting areas might be key to long-term survival of different populations. Noteworthy, these communal roost sites are relevant not only as habitat *per se*, but also as social-hubs that might be crucial for decision-making of the population. This is especially true for highly social species. Here, the proposed idea is that for a social population to remain functional, the networks of the social construct need to be conserved as well. Hence, high-quality communal roosts and healthy population numbers are essential to sustain a viable long-term population.

*Knowledge gaps and future directions*

It is unquestionable that birds are among the most studied species in the planet. While foraging has been widely studied in this group, the relevance of social behavior in foraging has not been as popular. Furthermore, in spite of having a vast amount of information on the foraging ecology for several species of birds, organizing and processing all this information together to draw conclusions on the determinant biological variables that shape foraging behavior, especially across taxa, remains an overlooked task. Hence, to the best of my knowledge, this thesis will pioneer in answering some of these overarching questions.

Here, I will compile biological variables and test the relationship between these and communal roosting behavior. While I will not be able to prove causation, the research will provide a starting point for future studies to build on, where causation can be explored. This database will also provide the grounds for future studies to test how Communal Roosting Behavior impacts foraging efficiency with the aid of tracking data. In addition, it could also be explored if the prevalence of CRB is also related to possible weather variables.

**Thesis aims and structure**

The overall aim of my thesis is to discuss drivers of communal roosting behavior and the potential implications on foraging efficiency in land birds.

*Chapter 1* will include a literature review on movement ecology of wildlife, with particular focus on bird foraging behavior. *Chapter 2* will be focused on understanding variables that affect the prevalence of communal roosting behavior (CRB) in birds. *Chapter 3* will use the previous chapters to highlight the value of sociality for foraging efficiency through the lens of Andean Condor (*Vultur gryphus*) conservation. *Chapter 4* describes the project timeline as well as my progress to date.

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