

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

MSc. research proposal

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# **Abstract**

# **Lay Summary**

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# **List of Abbreviations**

|  |  |
| --- | --- |
| CRB | Communal Roosting Behaviour |
| DIC | Deviance Information Criteria |
| HWI | Hand-wing Index |
| ICH | Information Center Hypothesis |
| UBCO | University of British Columbia, Okanagan Campus |
| pCRB | Probability of Communal Roosting Behaviour |
|  |  |

# **Acknowledgments**

# **Dedication**

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

## **1.1 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 mechanistic 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.

## **1.2 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.

## **1.3 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.

## **1.4 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.

## **1.5 Sociality 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.

## **1.6 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.

## **1.7 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.

## **1.8 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.

## **1.9 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 2: Sharing is caring - The evolution of communal roosting behaviour in birds**

## **2.1 Introduction**

Understanding why species differ in their social behavior has fascinated biologists for years (Wrangham & Rubenstein, 2014). From mating to foraging, there are diverse examples of social behavior across taxa encompassing fish, mammals, and birds. Several hypotheses have been proposed to explain the origins of sociality in animals. Yet, regardless of its specific origins, there’s evidence that sociality plays an important role in shaping learning, and that this learning can create local cultures in a population (Aplin, 2019) , with behaviors that may persist several hundreds of years (e.g. evidence of stone tool use in chimpanzees, *Pan troglodytes* (Haslam et al., 2009; Luncz et al., 2015; Mercader et al., 2007).

One interesting form of social behavior in many animals is that of communal roosting (hereon CR). Communal roosting is seen in species across many taxa, including fish (Clough and Ladle 1997), mammals (Kunz, 1982) and birds (Eiserer 1984). In birds, communal roosts are aggregations of unrelated individuals (either con- or heterospecific) that spend the resting period (either diurnal or nocturnal) together (Laughlin et al. 2014). The prevalence of this behaviour is striking given the apparent little benefits of sharing space and resources with individuals that in many cases are not family. Despite this, the frequency and diverse range of species in which communal roosting occurs suggest that it has evolved independently on numerous occasions, and that there should be an underlying mechanism that support(s) this seemingly paradoxical behaviour.

Several hypotheses have been proposed to explain the origins of communal roosting. One idea that has support from the literature is protection from weather. It’s been suggested that several species use communal roosts to huddle together as a way to find protection from extreme environmental temperatures (Farquhar et al., 2018; Gilbert et al., 2010, Chaplin, 1982). However, if this was the case, the behavior will be more likely to occur in areas with extreme cold weather such like higher latitudes, although this is not what we see in the current observed patterns (Beauchamp, 1999; Gyllin et al., 1977). Another well-supported idea is that communal roosting behaviour acts as a mechanism for predator avoidance (Weatherhead, 1983). Although this idea is reasonably documented for some species (McGowan et al., 2006; J. B. Williams, 1994), it has contradicting evidence in the case of species that do not have ecological predators like large birds or raptors (Coleman and Fraser, 1986), thus it cannot fully support the evolution of this behaviour in all the taxa in which it is observed.

A third explanation for the evolution of communal roosting behaviour is related to foraging efficiency. It has been argued that these roosts are sites where naïve individuals can potentially exchange information with more experienced individuals on the location of food sources. This concept is formalized by Ward and Zahavi (1973) via the Information Center Hypothesis (ICH). This hypothesis states that there is a difference in knowledge between informed individuals and naïve individuals on the location of food sources, and that when roosting together there is a signal transfer (either intentional or inadvertently) such that naïve individuals can follow informed ones to feeding sites. If there is enough food for individuals to share, the cost of being a follower has an overall positive payoff than exploring for food individually (Mock 1988).

If the ICH holds true, individuals that exhibit communal roosting behaviour are expected to have increased foraging efficiency than those who do not (e.g., Harel et al. 2017). While the evidence is still inconclusive, this is the most supported hypothesis. Following the ICH, this behaviour would undoubtedly be beneficial for a wide array of species given the inherent relevance of feeding. However, not every bird species would benefit equally from the presence of CRB. Some biological traits may have favoured the evolution of this behaviour to promote more successful foraging. For instance, some trophic guilds may benefit from this behavior more than others. Scavengers are a notable example given the nature of their unpredictable food sources (Harel et al. 2017). Even within scavengers, there might be a differential pattern between obligate and facultative scavengers where the former would critically benefit from since the competition of these pulsed food resources is higher (Van Overveld et al. 2022). Similarly, dispersal ability may also determine CRB. If a species has a high capacity to disperse, it would acquire more information from feeding areas in the landscape while scouting, and therefore may be able to gain information worth sharing in a roost (Buckley 1997). But gaining instantaneous information from the landscape is not enough for information transfer later in a roost. For this information to be useful for efficient foraging, memory is also crucial. Hence, it would be expected that species with greater spatial memory will be able to retain information better, making several successful foraging trips, and therefore pass on this information at a roost (G Hernández-Montero et al. 2020). Perhaps less evident would be the influence of mass. Larger species usually have a longer lifespan and bigger clutch sizes. Because these species tend to have higher energetic demands, their foraging efficiency needs to be crucially high to meet these demands. Although this may suggest that they would benefit more from roosting communally, this relationship may be less clear given that other strategies can also increase foraging efficiency such as high territoriality. However, all the aforementioned variables combined could be acting together to promote the evolution of this behavior. A question arises, then: Can the evolution of communal roosting behavior in landbirds be explained from these specific biological variables?

In an attempt to understand the evolution of communal roosting in birds, Beauchamp (1999) tested ecological variables that might drive the evolution of CRB in birds. He selected mass, diet type, and territoriality in 437 bird species on different taxa. His findings suggested that increased foraging efficiency was the most likely cause for communal roosting behaviour. Other studies on specific species support this idea (Curk et al., 2025; Dermody et al. 2011, Harel et al., 2017; Sassi et al., 2024). Despite his comprehensive study, his work focused on all birds whose phylogeny had been widely documented at the time, and therefore he worked with a limited sample size. He also included waterbirds. While this may not be a problem per se, waterbirds’ feeding ecology differ in nature than those of terrestrial birds (e.g. Twining et al., 2019), and resource dynamics such as resource pulses may have a greater effect in terrestrial ecosystems than aquatic ones (Liem, 1990; Nowlin et al., 2008). Thus, this group should be studied separately to prevent the patterns from being obscured. Noteworthy, at the time of Beauchamp’s study, information on feeding guild, social behavior and phylogeny were still limited. Access to new information offers the possibility to answer a similar yet more extensive research question to understand the evolutionary origins of this behavior across different phylogenies.

Even after Beauchamp’s robust study, the evidence for foraging efficiency as the main driver of communal roosting has been stated as not conclusive for some of the species in which it has been tested. However, there is a caveat to this statement. Most of these studies have been conducted in a single species only, and most cases in a limited timeframe. While these approaches help us understand the mechanistic of the ICH itself, it limits the scope to understand the overarching drivers underpinning CRB. From an evolutionary perspective, the latter is important because it gives us information on the reliance of this behavior for the fitness of a species. Despite the seemingly importance of understanding the evolution of CRB, to the date, this question has not been tested yet on a broader taxonomic scale after Beauchamp’s study. These remaining unknowns open a new avenue for research, which are the aim of the present thesis. Using the comparative method, this chapter will focus on answering the following research question: Are mass, trophic guild, memory and dispersal ability strong explanatory drivers of communal roosting behaviour in landbirds?

## **2.2 Methods**

### 2.2.1 Biological variables

To test for the biological variables driving the evolution of communal roosting behaviour, I selected four main traits: body mass (kg) following Beauchamp (1999), Hand-wing index (HWI) as a measure of dispersal ability (Arango et al., 2022), trophic guild and residuals of body size to brain size ratio (as a proxy for memory, van Overbeld et al. 2022).

Hand-wing Index, Mass and Trophic guild were obtained from AVONET, and brain size (mass and volume) values were obtained from several databases from the literature, including published papers and private databases (e.g., Franklin et al., 2014; Guay & Iwaniuk, 2008, Supplementary material S1).

###### **2.2.1.1 Global model**

To test for the importance of biological variables on Communal Roosting Behaviour, I tested five different models. The first set of models used all data available (946 species), and I compared the null hypothesis – in which CRB is only explained by phylogenetic relatedness, and the biological variables model (HWI, mass, trophic guild).

###### **2.2.1.2 Subset models**

The second set of models used only a subset of species (300), which include only the species for which we have brain size data. Brain size was obtained in volume (mm3) and mass (kg) from different sources (Supplementary S2). Because brain size and brain volume were highly correlated (0.9), brain volume was dropped to avoid collinearity. Brain mass was selected over brain volume as it had more raw data available. A linear model was fitted between both variables using the ‘lm’ function and used to predict brain mass for those species for which only brain volume was available. To correct for collinearity between brain mass and body mass, I fitted a linear model between the two variables. The residuals of the model were used as the predictor rather than brain mass itself (Van Overveld et al., 2022). The first model was the same model than before but only on a smaller sample size. The second model was ran adding the residuals of brain mass against body mass as a predictor variable. A third model was ran using an additional interaction term between brain mass and body mass instead of the residuals. Models were compared using DIC. (Table 1).

|  |  |  |
| --- | --- | --- |
| Model name | Predictor variables included | Number of species |
| Null\_model | phylogeny | 946 |
| Model\_1 | HWI, body mass, trophic guild, phylogeny | 946 |
| Model\_2 | HWI, body mass, trophic guild, phylogeny | 300 |
| Model\_3 | HWI, body mass, trophic guild, phylogeny, residuals brainmass/bodymass | 300 |
| Model\_4 | HWI, body mass, trophic guild, phylogeny, brain mass, brainmass:bodymass | 300 |

### 2.2.2 Communal roosting behaviour

To evaluate the relationship between biological variables and the evolution of communal roosting behaviour in landbirds (Brusatte et al. 2015), I first collected data on communal roosting behaviour.

To do so, I used Python's BeautifulSoup to web scrape Wikipedia for the number of literature references for all the selected species. I then classified the species in three main clusters based on the number of references found for each of them in their Wikipedia profile: not enough information (0-2 references), medium amount of information (3-5 references), and a lot of information (6-10). Clusters 2 and 3 were then used with web scraping tools to extract data on communal roosting behavior from Wikipedia, OpenAlex, and Scopus. The references in the output were then used to streamline the information search on communal roosting behaviour for these species. This step also accelerated the search by dismissing species for which the number of references is negligible (cluster 1).

For clusters 2 and 3 (and above), I gathered information on each species profile in Birds of the World, as it is the most comprehensive centralized database for birds’ natural history. I especially thoroughly read information on social behavior, foraging, and non-breeding sections. When the information was not available for a given species in this database, I used online databases and research papers using the following keywords in Google Scholar: ‘*species name AND communal roosting*’, ‘*species name AND social roosting*’, and ‘*species name and social behaviour*’. I then used the first five pages in the Google scholar search for each of the combinations to look for publications on the topic and the selected species in combination with the outputs of the web-scraping search. The publications were then accessed and read to extract the information.

Communal roosting behaviour was classified as a discrete binary variable where 0 is non-roosting behaviour (absence), and 1 is evidence of communal roosting behaviour (presence). For some species, the behavior has been widely studied and documented, in which case I assigned it as 1. For other species, the behavior has not been properly studied, but there is scattered evidence of individuals being observed roosting together in a given population. This was classified as a 1 for CRB as well. For other species, it is clearly stated that they do not exhibit the behavior (e.g. highly territorial), or that they do so only when they are breeding for mating purposes. In these cases, they were treated as a 0. Finally, for some other species the behaviour is not properly documented or has confusing information. For instance, some species indicate they flock together when foraging, but there is no explicit evidence or suggestion that they roosted together before gathering in flocks. In these cases, I classified them as data deficient using a conservative approach, and were therefore excluded from the analysis. After curating the information, the dataset comprised of 946 species that were used for subsequent analyses.

### 2.2.3 Phylogenetic data

To account for the effect of phylogenetic relatedness, I used the comparative method (*sensu* Felsenstein 1985) to explore the evolutionary relationship between physiological and biological traits and the communal roosting behaviour in landbirds comprising roughly 9076 species. The comparative method provides a framework to use evolutionary branches instead of species as the datapoints to leverage autocorrelation.

To access phylogenetic data and relationships between species, I used Trees from VertLife (Jetz et al., 2012). I generated 100 trees and the information was then used to construct a consensus tree using the function ls.consensus from the phytools package.

### 2.2.4 Statistical analyses

The evolutionary relationship between communal roosting behaviour (CRB) and was modelled using Equation 1.

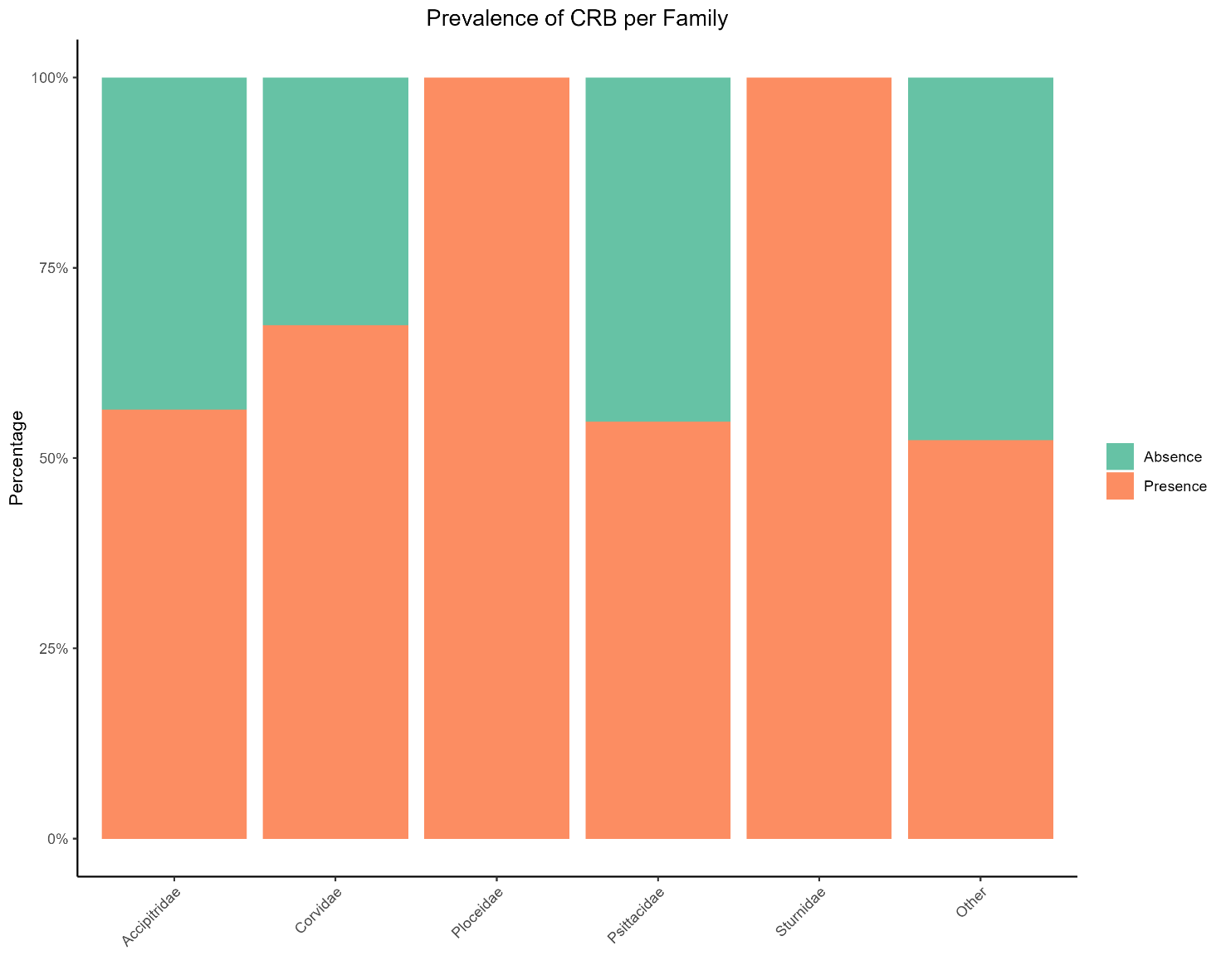
Eq. 1

Where CRB is the Communal Roosting Behaviour, and is the regression coefficient that determines the relationship between the variables. Phylogeny was included as a random effect as the evolution of this behavior may have evolved differently in each guild. The model was fitted in R using the *brms* package as it allows for flexibility to handle binary data and includes phylogenetic structure as a random effect. I used a Bernoulli family distribution and the *logit link* function for the response variable as the probability of CRB should saturate at 1 despite increases in the predictors. The model was run with eight chains and 1000000 iterations. Given the large sample size in our model (946), I did not use priors only so that the data informed the model without introducing biases.

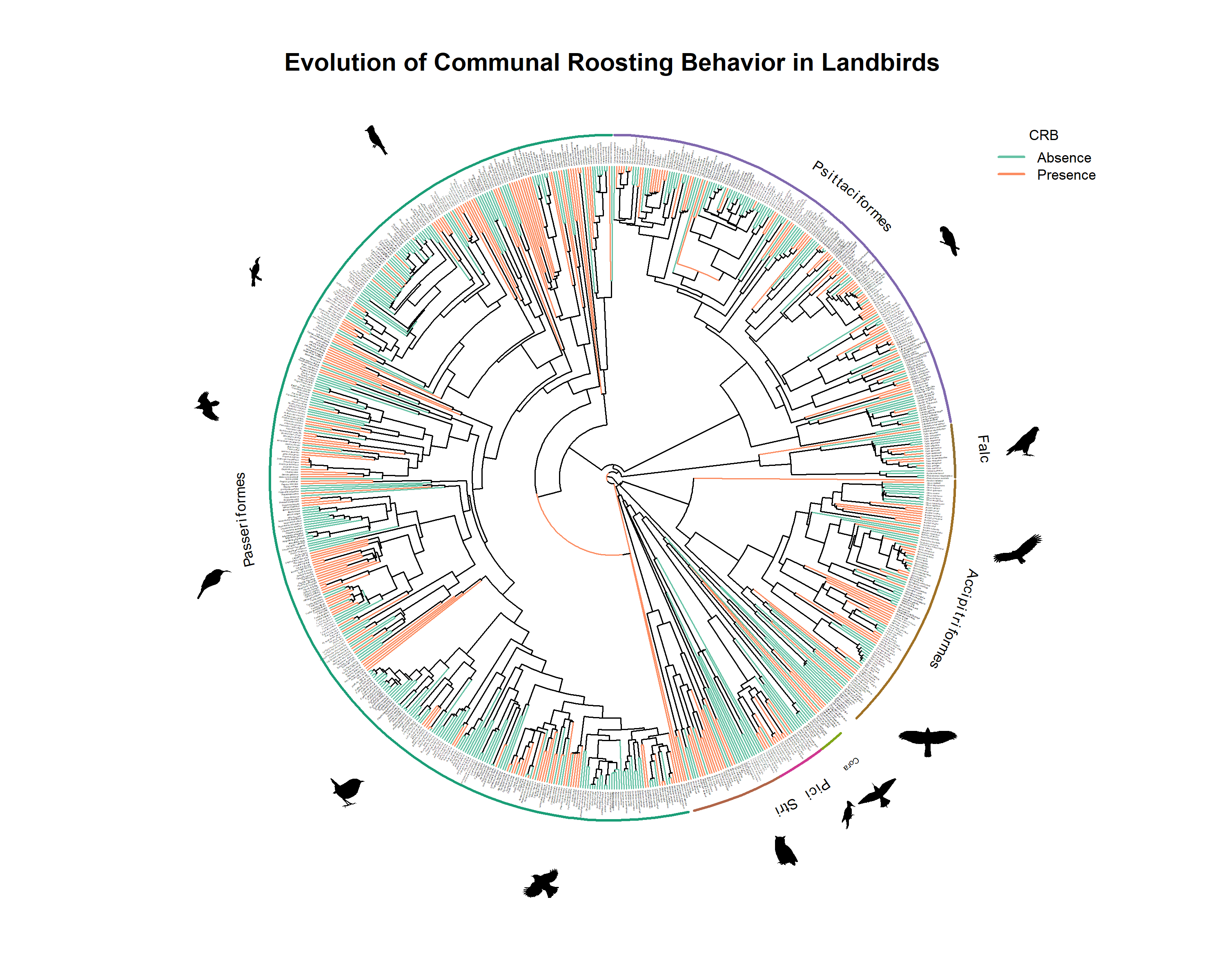
## **2.3 Results**

### 2.3.1 The distribution of Communal Roosting

Of the 946 species for which Communal Roosting Behaviour was classified, 42.1% showed absence of CRB and 57.9% showed presence of CRB which means my sample was evenly distributed. Communal roosting was predominant in families Sturnidae, Psittacidae, Accipitridae and Corvidae (Figure 2.1). Figure 2.2 shows the evolution of CRB in different taxonomic groups.



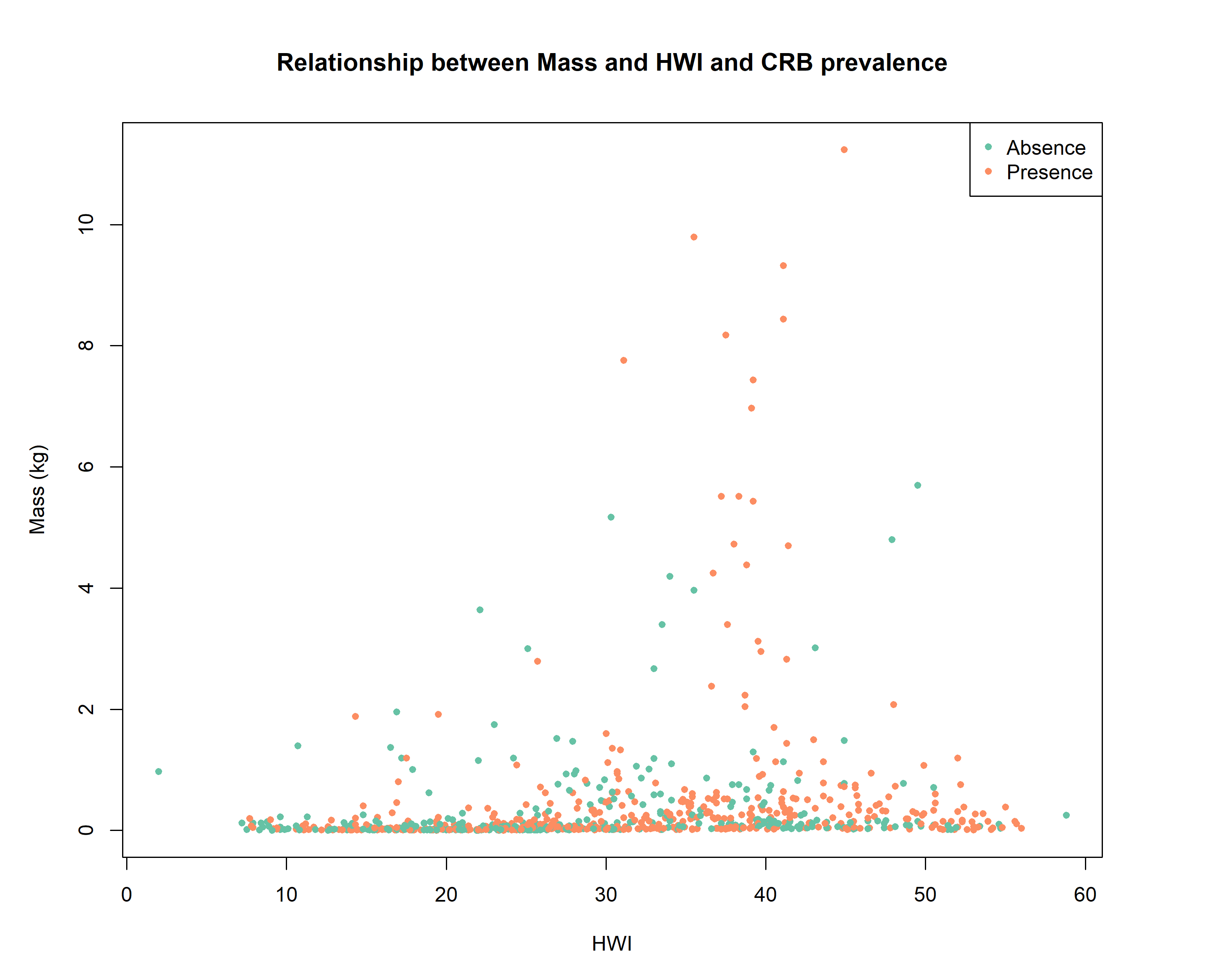
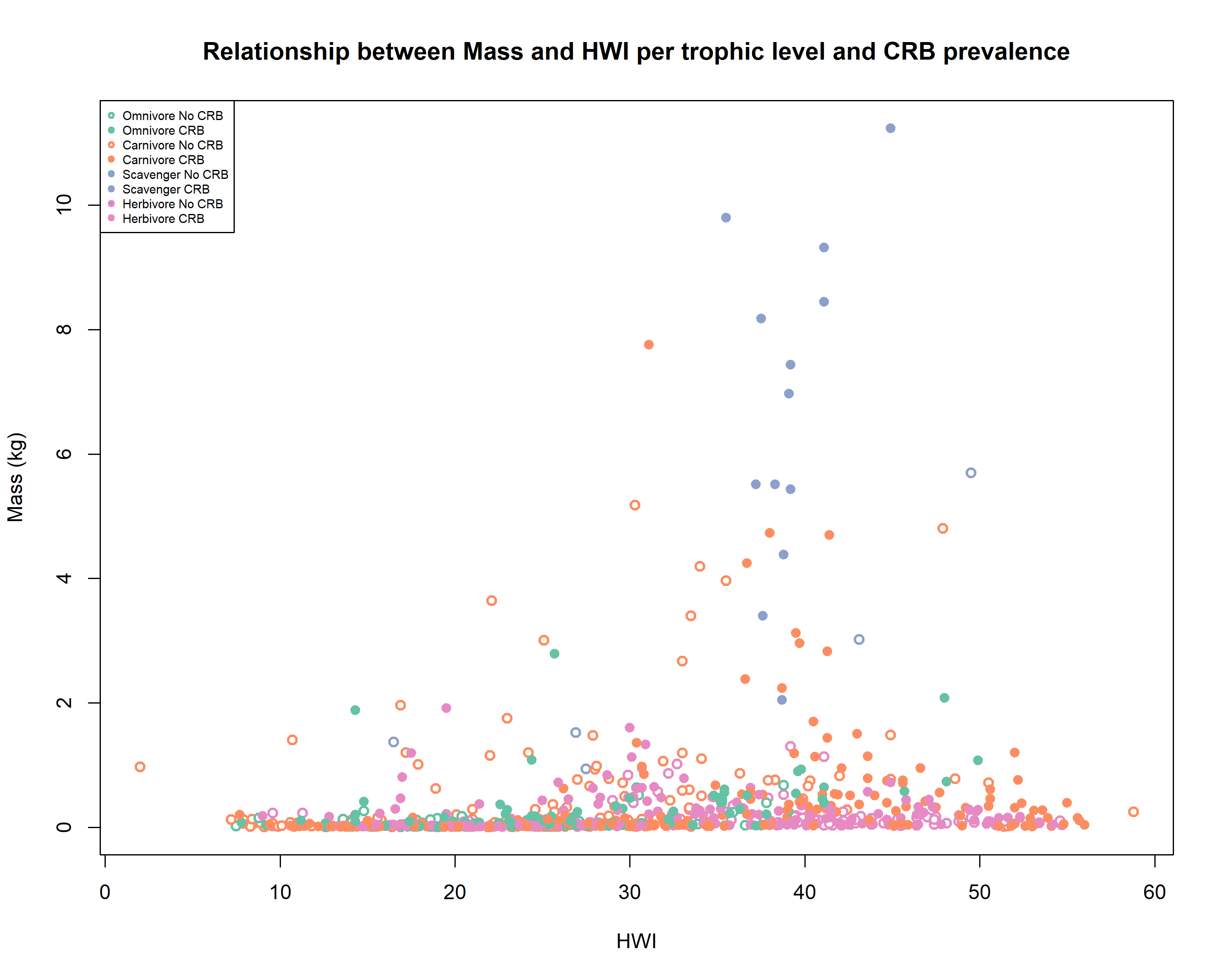
***Figure 2.1*** *Prevalence of Communal Roosting Behaviour in Families with greater representation (25> species).*



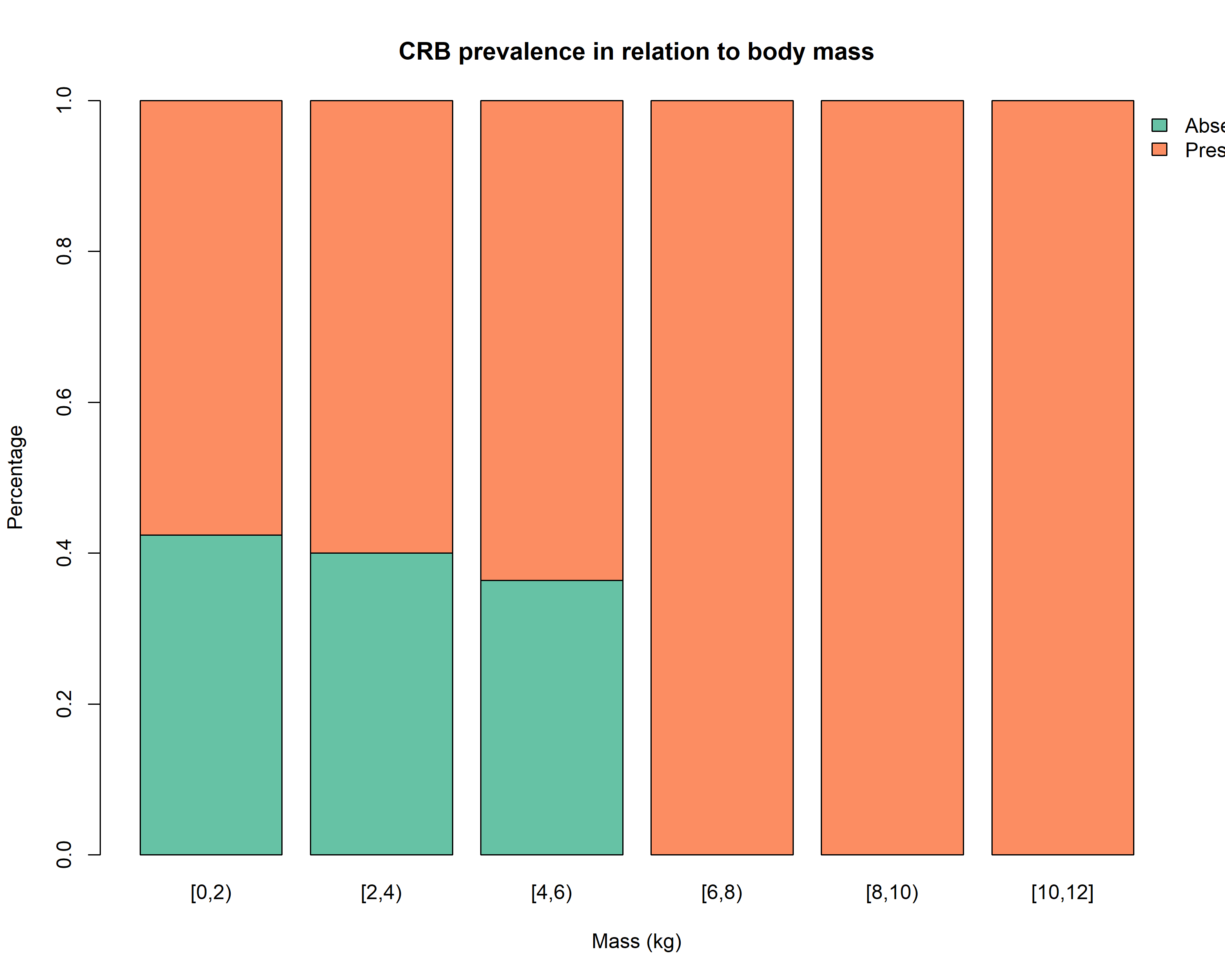
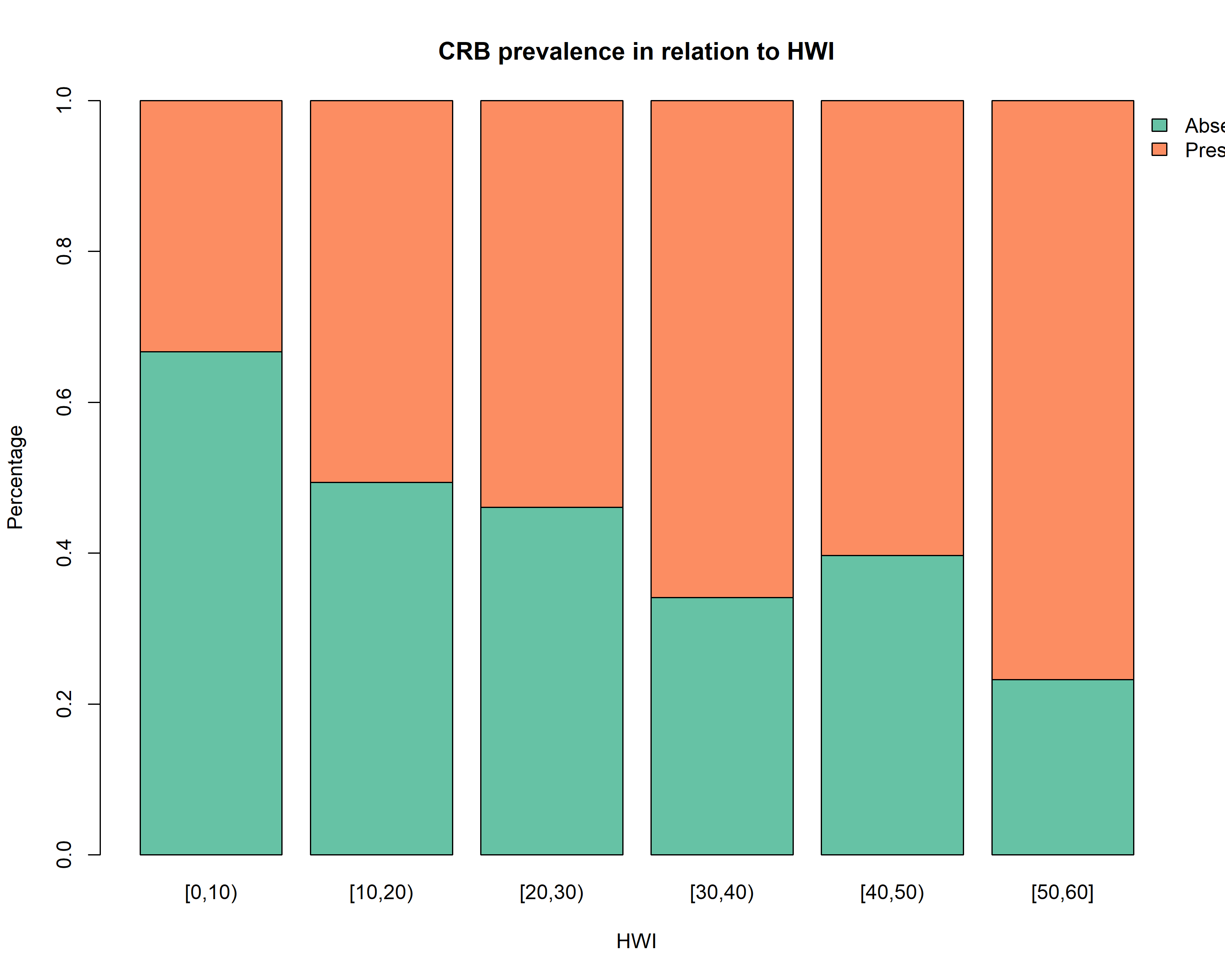
***Figure 2.2*** *Evolution of Communal Roosting Behaviour in Core Land Birds across different taxa. Data shows the convergence evolution of this behavior. Data was collected through Birds of the World and a Google scholar search.*

### 2.3.3 Biological variables and CRB

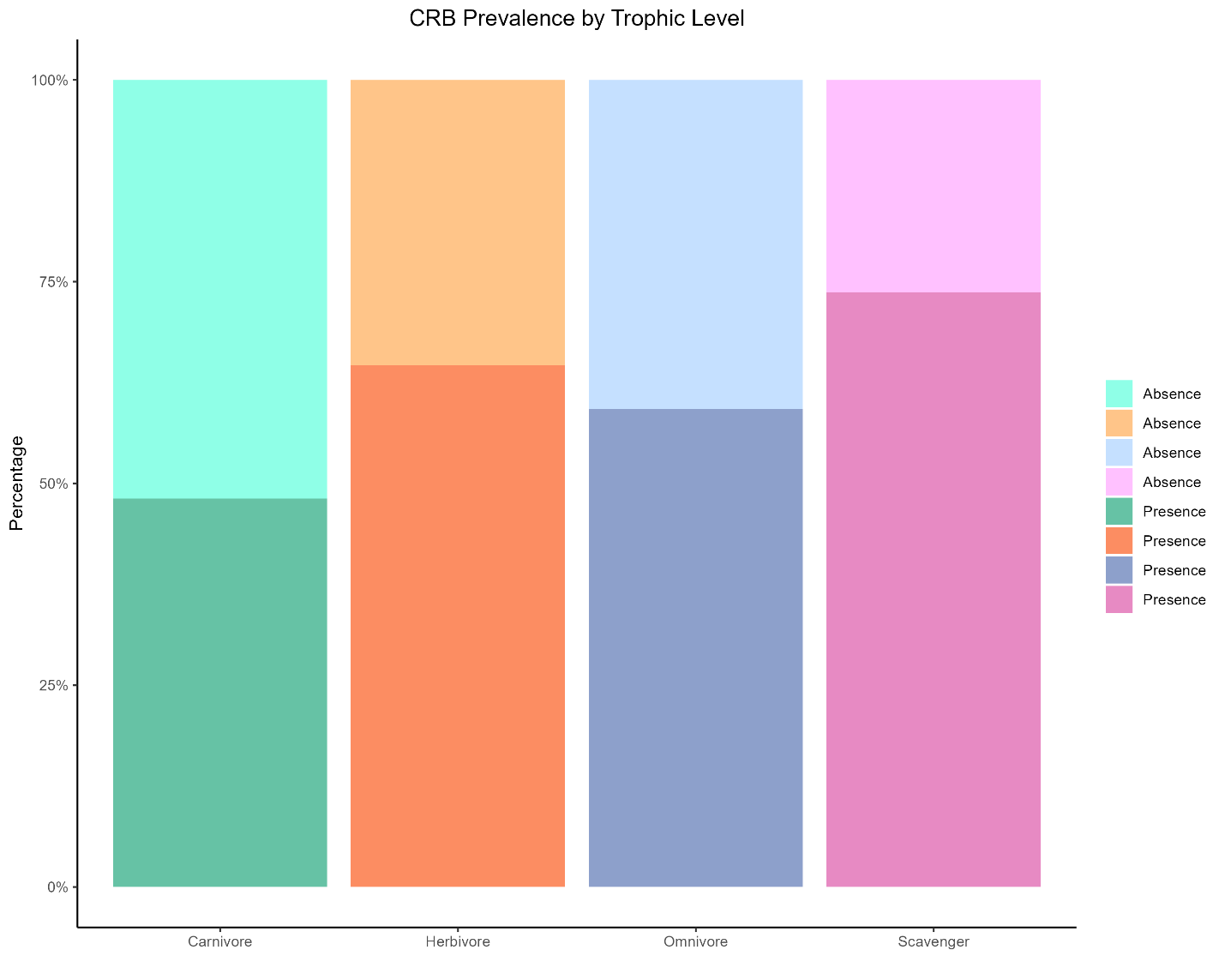
Overall, Handwing Index and Mass showed a positive trend with CRB, with prevalence of CRB increasing as how HWI and Mass increased, and a greater prevalence of CRB in scavengers as compared to other trophic guilds (Figures 2.3-2.5).



***Figure 2.3*** *Panel* ***a*** *show the Prevalence of Communal Roosting Behaviour in Core Land Birds in relation to HWI and mass. Data shows the convergence evolution of this behavior. Panel* ***b*** *show the sane as above including trophic levels.*



***Figure 2.4*** *Prevalence of Communal Roosting Behaviour in Core Land Birds in relation to HWI (****panel a****), and mass (****panel b****).*

***Figure 2.5*** *Prevalence of Communal Roosting Behaviour in Core Land Birds in relation to Trophic Level.*

The first set of models favored the model with biological variables over the null model (259.5 Model\_1 over null model, Figure 2.3). These suggests that overall, phylogeny alone cannot explain the evolution of this behaviour. However, Rhat values in my model are currently greater than 1(Figure 2.4), which suggest the model has not converged properly so results of the model should be cautiously interpreted.

Figure 2.7 Model comparison between global (all data model) and null model.

*Waiting for models*

Figure 2.6. Summary of global model.

*Waiting for models*

#### **2.3.4 Transition to CRB - Section on ancestry of the behaviour**

*Waiting for models*

## **2.4 Discussion**

Communal Roosting Behaviour has been widely documented in different taxa with several explanations for this behaviour. The results suggest that the evolution of CRB evolved in several clades that do not share a direct common ancestor, suggesting convergence evolution of the trait. Additionally, our findings suggest that the ICH is the most likely hypothesis to explain this behaviour given its predominance on species across all taxa and that inhabit a wide array of environments with contrasting weather conditions (e.g., Mindt et al., 2024, Preston, 2005; Saldanha et al., 2019).

### 2.4.1 Hand Wing Index and Communal Roosting Behaviour

The results supported the idea of a positive relationship between HWI and pCRB. These findings support the hypothesis of dispersing ability to promote this form of behaviour, which has been discussed by other authors. For example, a study done by (Caccamise & Morrison, 1986)) suggests that European starlings (*Sturnus vulgaris*) gather in aggregations near supplementary feeding areas (SFA) to reduce the energetic cost of traveling to food sources. The rationale is that even if the individuals can commute long distances to feed in distant areas, they may benefit from roosting near the SFA. Hence, it is plausible to suggest that species that have high dispersal ability used to find food sources have evolved communal roosting behaviour to reduce the energetic cost of feeding. Indeed, the sole idea of having supplemental feeding areas rests on the assumption that species can and have to disperse further away from their territories. In this study, the authors propose that individuals are more faithful to roosts near SFA rather than a stable communal roost. Nevertheless, the benefits of roosting (regardless of which type of roost) are inherently the same (e.g., Sonerud et al. 2002) support this hypothesis. In a recent study, Weeks et al. (2022) reported a strong correlation in birds between species with aerial lifestyle and HWI, arguing that species that rely highly on aerial lifestyles (e.g., commuting between roosting sites and foraging areas) have developed more efficient flight. Although they suggest that aerial lifestyle and efficient flight coevolve, here I propose that efficient flight mode is the driver of aerial lifestyle (e.g., Reliance on CRB) and not vice versa.

### 2.4.2 Mass and Communal Roosting Behaviour

Body mass has long been recognized to affect lifespan (Healy et al., 2014) and therefore metabolic rate (Kleiber 1932; Peters, 1983); Hudson et al., 2013; Nagy et al., 1999). A comprehensive literature review done by (Hudson et al., 2013) outlines the studies done on this matter, highlighting the idea that there is variation on how the relationship scales between clades (e.g., birds, mammals, amphibians). While the scale at which body mass and metabolic rate relate is still being debated, it is reasonable to say that the greater the body size, the higher metabolic rates needed to sustain that amount of mass (Gillooly et al., 2001). For instance, high metabolic rates has been correlated to behaviours like torpor in hummingbirds, and food hoarding in several birds and mammals (Day & Bartness, 2003). The results of this study show that communal roosting behaviour is positively correlated to body mass, perhaps since by increasing foraging efficiency, communal roosting acts as a mechanism to reduce energetic costs (metabolic rate). There is evidence that suggests that communal roosting behaviour is positively related to longevity in parrots (Munshi-South & Wilkinson, 2006). Likewise, longevity is positively related to body mass (Healy et al., 2014). Therefore, it is possible to extend these results to suggest communal roosting is positively correlated to body mass as shown by my results. An extension of this idea could be tested by measuring metabolic rate in particular, rather than body mass. Specifically, mass-specific metabolic rate (Suarez & Gass, 2002) could shed light into more accurate relationship. However, these measures are not available for the vast majority of species.

### 2.4.3 Trophic level and Communal Roosting Behaviour

My model shows that trophic level scavenger has a significant effect on CRB (although not any of the other trophic levels). This is not surprising considering the vast number of scavengers that have been documented to exhibit communal roosting (e.g., ravens, vultures). Because communal roosting has been found to increase foraging efficiency, it is reasonable to suggest that species that rely on ephemeral and unpredictable spatial-temporal food sources are particularly prone to take advantage of communal roosting (Kohles et al., 2022). However, communal roosting has evolved in other trophic levels as well. For instance, several seed parrots also show communal roosting (Munshi-South & Wilkinson, 2006). This may be indeed to increase group-foraging efficiency, but additional benefits may arise from this behaviour. A study conducted on starlings (*Sturnus vulgaris*) where access to food was manipulated showed that receivers (naïve individuals) reacted to senders (e.g., individuals with access to food) by changing their foraging effort, as well as their vigilant activity. Therefore, species that have natural predators also benefit from CRB (Fern�ndez-Juricic & Kacelnik, 2004).

### 2.4.4. Brain size and Communal Roosting Behaviour

Social behaviours that rely on memory have been widely documented for birds (e.g., Boeckle & Bugnyar, 2012; Penndorf et al., 2023). The results of this study suggest that memory is positively correlated with Communal Roosting Behaviour. Memory, in particular spatial memory, is important for individuals to be able to benefit from CRB efficiently since they require the capacity to remember the locations of food items, and return to those sits on subsequent foraging trips (Ward and Zahavi 1973, Dywer et al. 2018), as well as returning back to their communal roosts. A study conducted on bats showed that spatial memory together with social cues were key for individuals to track the resources efficiently (Lourie et al., 2024). Other study in bats showed how they relied on spatial memory to find their communal roosts (Hernández-Montero et al., 2020). Clearly, spatial memory has been well established as a mechanism for food finding in wildlife (Brodbeck, 1994; Marzluff, 2010; McGREGOR & Healy, 1999). Testing for this relationship requires a measure of memory that can be obtained and compared across a wide range of taxa. Unfortunately, direct measures of memory are challenging to obtain, and typically require some form of recall experiments (Brady et al. 2023) or data that might not be available for all species. For instance, it has been suggested that hippocampus volume is a good proxy for spatial memory in birds (Garamszegi and Ens 2004). However, data on hippocampus volume for all bird species are not readily available, which limits the scope of its application. Because lab experimentation was not feasible for the scope of this work, I used the residuals of the brain mass to body mass relationship as a proxy for memory. Residuals were chosen over brain size due to the strong correlation between brain size and body size (Smaers et al. 2021). Though not an explicit measure of memory, these residuals have been showed to correlate with individual cognitive capacity under experimental settings (Burns et al. 2008, Benson-Amram et al. 2016), and also relate to food caching in birds (Garamszegi and Ens 2004). Collectively, these lines of evidence support the use of the brain mass to body mass residuals as a robust proxy for memory in birds.

### 2.4.5 Alternative predictors: Predictability of food sources and food abundance

Access to regular food sources is a determinant factor on populations fitness. It is not surprising therefore that species that feed on ephemeral food sources tend to exhibit communal roosting behaviour. This can be explained to the fact that their food source is limited and unpredictable, which makes it impossible for these species to defend a territory. Therefore, as proposed by the ICH, sharing information on food sources is especially beneficial for such species. This phenomenon has been observed in species with different feeding strategies. For instance, a study by (Farquhar et al., 2018) showed that the increase in probability in communal roosting (huddling) of Chimney swifts (*Chaetura pelagica*) was associated to higher temperatures, which was correlated to lower prey availability. Similarly, Brown & Brown (1996) showed that cliff swallows (*Petrochelidon pyrrhonota*) tend to form large aggregations near ephemeral but abundant insect patches. Predictability of food sources expands beyond the nature of the trophic guild itself and suggests that for example, for a given scavenger species, if their food source is predictable (e.g., dumpsites), the need to exhibit communal roosting might decrease. Yet, using opportunistic more reliable food sources has seldom evolved in geologic timescales. Thus, while some plasticity of CRB may be observed in recent years for some species, the origin of the behaviour or lack thereof cannot be attributed to these human-induced scenarios.

Similarly, food abundance may have an effect on CRB. A wider amount of available food sources effectively means less need to defend a territory. From a cost-benefit perspective, greater abundance of food sources means there are more benefits of sharing location of food sources than defending a territory for a widely available resource (as long as all individuals can access the resource). For example, it has been documented that food availability may induce communal roosting behaviour in highly territorial species (Great-Horned Owl). This is because high availability of food in a farm location makes it easy for everyone to access resources without the need to compete for it ((Robinson & Davis, 2014). One could argue that a greater amount of food resources may mean less need to communal roost since the food is available for everyone. This may hold true to some extent, in which case perhaps communal roosting is favored only after a threshold is reached in which every individual has enough access to the resource (e.g., Buckley, 1997), and in which case communal roosting may be bringing other benefits than information sharing (e.g., a quadratic relationship). A comprehensive review was done by Kohles et al. (2022) and they propose a framework in which social information benefits can be tested as a function of the type or abundance and predictability of resource that was tested on bats. This framework may be useful to test birds’ sociality in the same fashion to complement my research.

Noteworthy, ambient temperature seems to be an important predictor variable as well, where CRB might be beneficial during the winter in higher latitudes for temperature regulation. For instance, when there is food scarcity, communal roosting might be induced as a way to reduce heat loss (Lubbe et al., 2018). Hence, food availability may also be confounded with ambient temperature. While it is possible that in these scenarios, the evolution of CRB could be driven by environmental rather than biological factors, the likelihood is low given that habitats have been subject to dramatic climate variabilities in the last 10 000 years (Alley & Agustsdottir, 2005), so we cannot assume that current environmental conditions drove the evolution of CRB in species seen today.

Finally, while communal roosting has most likely evolved to increase foraging efficiency in flock-living birds (Sonerud et al., 2002), we cannot discard that the behaviour has been maintained because it also may decrease predation risk (Gilbert et al., 2010), thermal stress (e.g., Wojciechowski et al., 2011), and the cost of mate assessment (Beauchamp 1999; Blanco and Tella 1999) as suggested by other alternative hypothesis.

### 2.4.6 Limitations

Although the aforementioned variables are suggested important drivers of CRB, other confounding variables may influence in the evolution of this behaviour. For instance, while it is true that the ICH may hold true for several scavenger species, prey species may also benefit from this phenomenon to share information of potential predators. Similarly, a major challenge of memory as a predictor is that it could be correlated to trophic guild, another predictor variable that has been proposed for the model. In particular, several vultures and corvids have good memory and cognitive abilities for problem solving (Weir et al. 2002, Lefebvre et al. 2004, Van Overveld et al. 2022). Because all vultures and many corvids (e.g., ravens, crows, magpies) are also scavengers, the coincidence (or correlation) between trophic guild and cognitive abilities may hinder my capacity to link memory and communal roosting behaviour.

Another limiting factor is the use of brain size residuals as a proxy for memory since these are also related to other aspects such as cognition (Biegler et al. 2001, Burns et al. 2008, Benson-Amram et al. 2016), intelligence (Dickie & Roth 2016) or other biological traits like life expectancy (Smeele et al. 2022). Thus, there is a risk that a relationship between brain size residuals and roosting behaviour may be due to correlates with other variables other than memory *per se*. Alternatively, other patterns could obscure the relationship between the proposed variables. For instance, research has suggested that neuronal connections are more accurately related to cognitive abilities than is brain volume (Logan et al. 2018). Nonetheless, neuronal connections might not necessarily be positively correlated with brain mass to body mass residuals, which would limit the use of the latter as a proxy. Albeit, the density of neuronal connections is significantly more complicated to measure and it requires an invasive approach far beyond the scope of my research. Similarly, memory may lead to other behaviours that are not necessarily communal roosting under the foraging efficiency hypothesis. For instance, greater memory could lead to food hoarding (Clayton & Krebs 1995). Here, individuals do not rely on sociality to successfully access foraging sites, although they do rely on memory. Alternatively, memory (or intelligence) could increase the ability to rely on local enhancement (Everding & Jones, 2006), where individuals don’t exhibit communal roosting but rather loose aggregation that rely on visual cues of conspecifics to find food. Hence, greater memory might not necessarily correlate to communal roosting behaviour alone. Further research should expand on this hypothesis using the data collected as part of this research.

Finally, there is a limitation in my ability to detect CRB. For instance, a study conducted in fish showed that their social cohesion varied depending on the state of hunger. Individuals that were food-deprived were less likely to join shoals, possibly to reduce competition with conspecifics (Killen et al., 2016). This suggests that the tendency to exhibit a social behaviour state that increases foraging efficiency (e.g., communal roosting) may also be determined by the degree of urgency of feeding. A study conducted on American Robins found that the patterns of communal roosting behaviour were consistent with food finding (more communal roosting by juveniles, more communal roosting later in the season, foraging areas used on consecutive days were farther apart after robins roosted communally, and home ranges were bigger for robins that used the communal roost more, Benson et al., 2012). It is worth noting that this condition does not suffice to drive the evolution of the behaviour itself in a species, but instead affect the frequency of the behaviour, which may hinder ability to detect it, which would ultimately impact the outcome of my model. In my model, CRB was classified as a binary response variable (0,1), however, as data becomes more available, it would be interesting to test biological (and ecological) variables against the frequency of CRB (as a percentage). Yet again, this information is not currently available for the vast majority of species.

### 2.4.7 Future work

One of the major limitations of this study is the available information on communal roosting for several bird species. A large volume of research is conducted on a handful few species only. Conducting more field observations on understudied species may help to bridge that information gap. Another approach to do so would be the use of weather radar data (e.g., Cheng et al., 2020), but this approach is limited to where weather radars are available.

Additionally, whilst the current research shed light on relevant drivers of CRB, further examination of the proposed variables should be tested to increase the accuracy of the predictions and better understand the biological processes behind the correlation. For instance, we acknowledge that the proxy used for memory is a limiting factor. Assessing the same correlation with other measures of memory (e.g., hippocampus size) may provide more accurate results. Furthermore, testing these models with empirical data from a random sample of species may also help to validate the models proposed. Significant work has been done on corvids and parrots, but other species remain underrepresented in the study of memory.

Testing the effects of ecological drivers (e.g., food abundance and predictability) is also a relevant task. Although terrestrial productivity at a global scale can be measured through NDVI and this measure can act as a proxy for abundance of food sources, that measure is seldom useful for the current research since several species exist on a vast geographic range with contrasting productivities. For instance, Peregrine falcons (*Falco peregrinus*) exist in every continent except Antarctica (Birdlife International, 2021). This makes it impossible to model their associated habitat productivity without oversimplifying the model. Thus, adopting a conservative approach, this variable was not considered here. However, doing a more detailed analysis at a local scale could take this into consideration. Moreover, coupled with weather, productivity of habitats has changed over time, often at geological scales. Hence, using current productivity might not be representable to determine the evolution of CRB. Even if we establish a correlation, causation could not be concluded.

Abundance of food sources has another challenge: number or resources and dietary breadth. A question arises of whether resource abundance of number of different items is more important. For instance, is it more important for Great-Horned Owls to have more mice or different prey sources despite low numbers of each? In addition, measuring dietary breadth poses its own challenges given that the level at which we group the diet items has a direct impact on the estimation of dietary breadth. Take, for example, a seed eater. Are seeds an item in the diet, or are each type of seed important? Although from a nutritional point of view these are important questions to consider, that is beyond the scope of the current research. From a conceptual and empirical point of view, this measurement is not feasible at a global scale.

Finally, testing the idea that species exhibiting communal roosting behaviour are more efficient at finding food sources would provide valuable information to expand the current research. This can be feasibly done with movement data using ballistic length scales as a proxy for foraging efficiency, or experimental designs placing feeding stations in the landscape coupled with movement data.

# **Chapter 3: The need for ecological studies in social species**

## **3.1 Introduction**

Sociality is widely observed in the animal kingdom, and it has been documented that social behavior enhances learning (Aikens et al. 2022). From migration to mating and chick-rearing, sociality seems to bring benefits to all individuals in the group. While the role of sociality in grouping is still not fully understood, is increasingly recognized that many birds and mammals live in social systems that are structured by long-term affiliative and agonistic relations (Kappeler, 2019; Massen, 2018). Feeding in groups is a foraging strategy that brings numerous benefits to group members, such as increasing the likelihood of locating food and enhancing vigilance for predator detection (Marinero et al., 2018). These benefits may increase survival of individuals and overall fitness.

Among animals, social grouping has been mainly studied in mammals. Conversely, in birds, these studies are somewhat limited. Among birds, most studies have been conducted in corvids given their notably sociality and cognitive skills (Emery et al., 2007; Emery & Clayton, 2004). Corvids establish strong social relationships and social hierarchies, and they show sophisticated reasoning and problem-solving abilities. These fascinating features, however, have not been studied in other bird species.

Vultures, just like corvids, are scavengers. Similarly, vultures are also highly social species. Among this group, several species have been documented using communal roosts where several individuals gather for the resting period (Campbell, 2015; Van Overveld, Gangoso, et al., 2020), as well as individuals gathering around carcasses when foraging. Beyond this example of sociality, there is also research done in despotic behavior and hierarchies within and across species. For instance, a study conducted in East Africa with seven types of scavenger species showed that there’s niche partitioning between the species in the study system (Kendall, 2013). In concrete, the author found that species that have greatest search efficiency or greater sociality (e.g. Bateleurs, Ruppell’s, Lappet-faced, and White-backed vultures) had access to patches of better quality than their counterparts, hence establishing dominance. Likewise, a study done on Andean Condors (*Vultur gryphus*) shows that sex, age and pigmentation drive hierarchy in this highly despotic species. As seen above, while sociality may benefit individuals in a group, it may also increase competition in the group for food resources, which is particularly important when resources are limited (Moreno-Opo et al., 2020).

## **3.2 Why vultures?**

Vultures, unlike corvids, are obligate scavengers. This means that they depend entirely on carrion for their energy supply. Carrion is an ephemeral resource heterogeneously distributed and often limited in space and time (Barton et al., 2013; DeVault et al., 2003; Ostfeld & Keesing, 2000). Because of its scattered and unpredictable nature, competition at these feeding sites is high with agonistic behavior and hierarchies established. Interestingly, this high competition has in turn led to the evolution of specific behaviors to reduce competition for resources such that the community finds balance. Such mechanisms include niche segregation among the different species (Savolainen et al., 1988; Schuette et al., 2013). Albeit, when dominance is established in individuals of the same species, niche partitioning becomes less likely. From a conservation point of view, this is important two reasons. First, if resources are limited, population may select in favor of adult individuals, which may decrease juvenile recruitment thereby impacting the population fitness. Second, if resource partitioning does not occur within a species or a guild and individuals are forced to gather around one resource, a significant portion of the population may be prone to threats while feeding.

## **3.3 A note on the Information Center Hypothesis**

In Chapter 2, I highlighted the importance of communal roosts as a place where individuals gain access to location of food sources, as explained by the Information Center Hypothesis. It is important to say that the information transfer is usually unintentional. This is relevant because transferring information about a food source location does not inform about the quality of the resource itself. If individuals are foraging on suboptimal food sources and other individuals in the roost follow, this could have a severe impact at a population level. Several roosts for vultures are located near anthropogenic food sources like garbage dumps given their greater predictability such that it is less energetically costly to access food, despite its poor quality. Noteworthy, vultures are among the most threatened group of birds in the world, most species showing steep declines in their population (McClure et al., 2018). Notably, these declines are exacerbated due to their gregarious behavior. When individuals follow others and forage together at a single carcass, it amplifies the risk of mass mortality when the carcass is poisoned (D. Ogada et al., 2016; D. L. Ogada, 2014; Santangeli et al., 2016)). Thus, the use of social information when feeding may become an ecological trap (Curk et al., 2025) with cascading effects.

## **3.4 Size matters: The Andean Condor – A peculiar case study**

Given their obligate scavenging nature, old and new world vultures rely highly on communal roosting behavior. In black vultures, for instance, individuals may roost up to 200 individuals together. These large roosts provide several opportunities to access foraging sites by increasing accuracy of the food location by following more knowledgeable individuals (Sassi et al., 2024), leading to more cost-efficient movement (Rafacz & Templeton, 2003; H. J. Williams & Safi, 2021). Evidently, the larger the size of the roost, the greater probabilities to find communal food sources. In the wild, however, these opportunities are constrained by population sizes of the species in question.

With a wingspan of 320 cm, females weighting up to 11 kg and males up to 15 kg (Houston et al. 2020), the Andean Condor (*Vultur gryphus*) is the heaviest extant soaring bird. It is an obligate scavenger, and a highly social species (Donázar et al. 1999), that uses communal roosts when they are not breeding, with aggregations adding up to 50 individuals. Despite their widespread distribution, large portions of the population are concentrated in specific locations, where these communal roosts exist.

Like other vultures, Andean Condors are also obligate soarers. This means they rely on thermal updrafts to search for carcasses. When foraging, these birds gain altitude by riding a thermal updraft (hot air masses created as a consequence of heated surface that rises), and they use it to move in the landscape in search for food (Sassi et al., 2024). This remarkably energy-efficient flight mode allows them to reduce energy expenditure. Given their size and feeding guild, Andean Condors highly benefit from this flight strategy. Some geographical features promote the occurrence of thermals like cliffs and slope inclination and aspect (Scacco et al., 2019). It is likely that when selecting a communal roosting site, they select roosts that will allow them to exploit these thermals to commute to and from foraging grounds. In fact, a study by Sassi et. al (2024) shows that vultures movement decisions relied highly on social information.

Collectively, all of these lines of evidence suggest that communal roosting sites are crucial for the population structure and dynamics in Andean Condors. Much has been hypothesized about the importance of communal roosts for information sharing and feeding resources. Nonetheless, more research is needed to understand how the information transfer operates in these roosts, and how valuable each connection is for information transfer. As concluded by(Curk et al., 2025), the value of social information was only evident with a large number of vultures in the area. These findings stress the need to have healthy populations that can self-sustain (Van Overveld, Blanco, et al., 2020), especially as natural food becomes more limited.

Undoubtedly, communal roosts are areas of high conservation priority (Dermody et al., 2011). As with many other vultures, Andean Condor populations are decreasing throughout its range, with all major threats being anthropogenic. In particular, habitat loss, poisoning due to human-wildlife conflict and wind power development are of greater concern, which frequently act synergistically. Because of their size, ecology (e.g., long lifespan, low reproductive rates, obligate soaring species – which requires longer learning periods (Hertel et al., 2023)), scavengers), behavior (social species), and conservation status (globally Vulnerable), this emblematic Andean species is a peculiar study system and good model (Poessel et al., 2018) to test the hypotheses on the effects of sociality on foraging efficiency as they represent an extreme in the spectrum of extant flying birds.

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A TABLE WITH ALL THE REFERENCES USED FOR BRAIN SIZE

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