

**THE ORIGINS OF COMMUNAL ROOSTING BEHAVIOUR 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: The benefits of being a social butterfly – Evolution of Communal Roosting Behaviour in Birds C**

## **1.1 Introduction**

Understanding why species differ in their social behaviour has fascinated biologists for years (Wrangham & Rubenstein, 2014). Sociality is documented not only in several taxa (e.g., fish, mammals, birds) but also in different aspects of their ecology (e.g., birds mating in leks, kettle of raptors migrating together, lions hunting and foraging together). The occurrence of the wide array of social behaviours in wildlife suggests there are set benefits to socializing with conspecifics. For instance, 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). 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). The benefits of sociality are also widely documented in colonial seabirds, where hundreds of breeding pairs gather on islands for breeding and chick-rearing, and search for food around the colonies as proposed by the central-place foraging model (Ashmole, 1963; Houston, 1985; Monier, 2024). Research has shown how individuals from a colony use information from others to find feeding sites (Camphuysen et al., 2006, Bairos-Novak et al., 2015) , and there is empirical evidence that demonstrates the benefits of such behaviour (Thiebault et al., 2014a; Thiebault et al., 2014b). Whether intentional or inadvertent (e.g., (Bijleveld et al., 2010), there is a transfer of information from informed to naïve individuals in the colony such that the latter benefit from being in the group (Weimerskirch et al., 2010). In time, roles could change, and the naïve can gain new information. In this way, remaining social benefits the group collectively.

Other aspects of the ecology of wildlife have also been studied through the lens of social behaviour. For example, 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. During migration, individuals can guide themselves through previous personal experience (asocial learning, sensu Laland, 2004), but to gain such experience individuals need to invest significant amount of time and energy (Németh & Moore, 2014). More importantly, the information gained through time can be outdated when navigating in unpredictable environments. To reduce the risk and uncertainties of these new surroundings, individuals need to constantly gather information about the immediate and changing environment. In this context, observing other individuals and their behaviour (social learning) provides a shortcut to acquiring information (Németh & Moore, 2014). This transfer of information may reduce predation risk, increase foraging efficiency, and therefore play an important role in the collective decision-making (Aikens et al. 2022). Despite its evident benefits during migration, this information transfer mechanism can also be seen in local movements. A study conducted by Kano et al. (2021) shows how homing pigeons (*Columbia livia domestica*) increase reliance on social cues during collective navigation likely to reduce predation risk. Altogether, these examples provide insight into how individuals leverage sociality to gain information outside of their perceptual range to make more accurate or efficient decisions.

One interesting form of social behaviour is that of communal roosting (hereon CR). 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). 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 roosting is seen in species like crows and ravens, vultures, eagles, parrots, swallows, some falcons, etc. Communal roosts aggregations vary in size, and while there is not a specific threshold value to classify a roost, the values usually fluctuate from tens to millions of individuals (Everding & Jones, 2006; Laughlin et al., 2014). Composition of a roost may also vary between species and even populations. Some studies report individuals remain faithful to one particular roosting site (Everding & Jones, 2006; Laughlin et al., 2014; Leyrer et al., 2006), whereas others report fluid compositions of the roosts (Conklin & Colwell, 2007). The composition may vary in different populations as well. For instance, a study by Caccamise & Morrison (1986) showed that some individuals of European Starlings  (*Sturnus vulgaris*) showed high fidelity for their roost sites whereas others shifted between a major and a minor roost. What constitutes a roost is also variable. Some species roost on one or a patch of trees close to each other (Seixas & Mourão, 2018), others roost along cliffsides (Donázar & Feijóo, 2002), and in some cases even in human structures (Novaes & Cintra, 2013). Similarly, sizes also vary. For instance, a study done in Snow Geese (*Chen caerulescens*) considered a communal roost of a size of 5km2 (Béchet et al., 2010). For the purpose of this research, because I am not collecting behavioural data myself but instead relying on secondary data, I will use communal roosting as referred by the authors in the literature, which frequently refers to aggregations of 10 or more individuals.

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) the evolution this seemingly paradoxical behaviour (see Waser1981). At a first glance, the prevalence of this behaviour may appear striking given the apparent little benefits of sharing space and resources with individuals that in many cases – unlike colonial seabirds- are not family. Yet, as discussed above, there clear examples of how sociality -through information transfer- benefits individuals in a group when acting cohesively. A question is raised: what are the benefits of CR?

Several hypotheses have been proposed to explain the origins of communal roosting. First, it has 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). For instance, a classic study on Common Bushtits (*Psaltriparus minimus*) showed that with colder temperatures, individuals tend to gather together with and reduce their metabolism, which is associated to energy conservation (Chaplin, 1982). Gilbert et al., (2010) provide a comprehensive summary on the energetic benefits of huddling (or communal roosting), with concrete examples from the literature. While there might be energetic benefits of huddling in a roost site, the evidence is inconclusive. In fact, one study done with Chimney Swifts (*Chaetura pelagica*) found the opposite pattern – high ambient temperatures seemed to intensify huddling (Farquhar et al., 2018), which they argued could be a consequence of a reduction of insect abundance (correlated with high temperatures). Other studies have even observed that communal roosting implied traveling far to communal roosts instead of roosting locally, which uses more energy than that gained from possible thermoregulation (Beauchamp, 1999; Gyllin et al., 1977). Furthermore, if thermoregulation was the primary benefit of CR; one would expect it to occur mostly in areas with cold weather such like higher latitudes. Nonetheless, several studies demonstrate the use of communal roosts in mild (Moleón et al., 2011) or even warm weather conditions (Jaggard et al., 2015; Seixas & Mourão, 2018). Noteworthy, most of the examples summarized by Gilbert et al., (2010) of the benefits of huddling due to cold temperatures come from studies with penguins in Antarctica, which experience extreme weather conditions. In particular, the studies done on Emperor Penguins (*Aptenodytes forsteri*) show that the increase in huddling occurs not only in the winter, but that it also coincides during the breeding period, in which males undergo a four-month fast. While these examples can clearly explain the need for huddling during the winter, penguins have a unique and distinct ecology from landbirds, thus, these findings might not be scalable to the majority of species.

A second hypothesis is that CRB 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 doesn’t have conclusive evidence. For instance, a study done on Whimbrels (*Numenius phaeopus*) suggested that the selection of roosting sites was best explained by access to feeding resources and isolation from potential predators (Johnston‐González & Abril, 2019). Although predator avoidance is suggested as one mechanism, foraging efficiency was still an important one, and therefore they cannot be disentangled. Another study by Rosa et al., (2006) showed that in their study area, for some species of waders, predator avoidance was the main driver for roost selection. It is worth mentioning that in their study, the two potential roost sites had low prey availability overall. Even more important, their assessment of prey availability was done within less than 1m2 from the roosting site. Hence, the scope of this study is very local and limited in interpretation. To introduce more controversy, research also supports the idea that larger groups (due to sociality in a roost) can increase detectability for predators (Ward & Webster, 2016), suggesting that being cryptic may be a more beneficial tactic to reduce predator avoidance. In addition, this hypothesis is not well supported in the case of species that do not have ecological predators like large birds, raptors (e.g., Swainson hawk *Buteo swaisoni*) or vultures (Coleman and Fraser, 1986), thus it cannot fully support the evolution of this behaviour in all the taxa in which it is observed. As outlined by Beauchamp (2010) in his review, the benefits of predator avoidance might be acting in conjunction with increased foraging efficiency, rather than acting alone.

A third explanation for the evolution of communal roosting behaviour is related to foraging efficiency. The ideas of colonial breeding and central-place foraging observed in seabirds were extended to the sociality of communal roosts, where non-breeding individuals gather with conspecifics to spend the resting period (Ward & Zahavi 1973, Wright et al. 2003). 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 was 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). Since its proposal, the ICH has raised controversy in the literature (Barta, 2001). Some studies seem to support this hypothesis (Harel et al., 2017; Papageorgiou et al., 2024; Wright et al., 2003), while others have found no evidence (e.g., Mock et al., 1988). Conversely, these latter studies have found other mechanisms by which individuals share information like local enhancement (e.g., Cortés-Avizanda et al., 2014). During local enhancement, information is transferred when an individual cues on another already feeding individual. A study done on Torresian Crows (*Corvus orru*) found that this was the most likely main mechanism for information transfer given that the feeding areas were located close to the roost (Everding & Jones, 2006). While there are intricacies to the different mechanisms by which information is transferred, they may be acting together in some cases (Dermody et al., 2011). Ultimately, it is well documented in the literature that information transfer to increase foraging efficiency is a sound explanation for the evolution of communal roosting.

~~Examples from the literature show that when conditions are challenging, animals incur in territorial defense. For instance, a study done on striped mice (~~*~~Rhabdomys pumilio~~*~~) shows that they are highly aggressive and territorial to defend a critical food resource that becomes seasonally scarce (Schradin, 2004). Despite the apparent advantages of territorial defence,~~

If the foraging hypothesis (regardless of the specific mechanism) holds true, and indeed communal roosting increases foraging efficiency for individuals, one may ask why don’t all species incur in this behaviour? While CRB brings benefits for foraging, there are trade-offs associated with this behaviour. In terms of foraging, the main trade-off is the need to share the resource with others. As such, 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 behaviour more than others. Scavengers are a notable example given the nature of their unpredictable food sources (Harel et al. 2017). The lack of predictability of when and where a resource may appear makes it hard for them to defend territories. In these cases, using information already available to others may significantly reduce their time searching. In fact, not coincidentally, several studies of communal roosting have been done on scavengers. 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. Species that have a high dispersal have larger home-ranges. Thus, their search for food in the landscape requires a larger time and energy investment. For such species, relying on social information from conspecifics may be more beneficial than actively defending a territory against them. Indeed, Sheard et al. (2020) found that dispersal ability (as measured through the Hand-Wing Index) was negatively correlated with territoriality. By navigating larger areas, species also acquire more information from feeding areas (Buckley 1997), which may be useful for them to assess which are the most profitable ones. 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, especially if the main mechanism for information is via the ICH and not local enhancement. In the former, individuals need to remember the location of food patches to return to them so that the information gained is valuable for other members (Weimerskirch et al., 2010). Hence, it would be expected that species with greater spatial memory will be able to retain information better, making several successful foraging trips, which can give cues to others at a roost (G Hernández-Montero et al. 2020).

Perhaps less evident would be the influence of ***mass.*** Because larger species tend to have higher energetic demands, their foraging efficiency needs to be crucially high to meet these requirements. An interesting study by Blumstein & Møller (2008) investigated the relationship between sociality and longevity- which is well-known to be correlated with mass. Their results didn’t support the idea that these two variables are correlated. However, their proxy for sociality was cooperative breeding only, and their sample size limited to birds of North America only. It is worth replicating these efforts on a larger scale research, and using other forms of sociality such as that of CRB.

Certainly, there are within-species variables that may also affect the persistence of CRB such as age-class. From the lens of foraging efficiency, juveniles are much more prone to roost communally as they are less experienced in finding food. However, those variations occur at a population level, at thus are beyond the scope of the current research. At a species level, however, all the aforementioned variables (***trophic level, dispersal ability, memory and mass***) combined could be acting together to promote the evolution of this behaviour as hinted by the literature.

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 this group. 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 his sample size comprised less than 5% of the total bird’s species in the world. More importantly, his study 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). For instance, aquatic birds like waterfowl feed primarily on fish. Fish are constrained in movement within a lake, which makes their occurrence more predictable. Research has also suggested that resource dynamics such as resource pulses may have a greater effect in terrestrial ecosystems than aquatic ones (Liem, 1990; Nowlin et al., 2008). Although communal roosting is seen in aquatic bird species like herons and egrets, the driver for CRB in these groups may be less driven by foraging only (e.g., Youcefi et al., 2019). These difference in dynamic of their feeding role and ecology make the results hard to extrapolate to landbirds. Noteworthy, at the time of Beauchamp’s study, information on feeding guild, social behaviour 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 behaviour across different phylogenies.

Even after Beauchamp’s 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. Furthermore, several studies have focused their attention in using the ICH as the main mechanistic pathway of benefitting from CRB to increase foraging efficiency. 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 behaviour for the fitness of individuals regardless of how they achieve it. 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.

## **1.2 The unique nature of avian foraging ecology**

A relevant question remains unanswered – why are birds an interesting study system to study communal roosting behaviour? The answer has both ecological and pragmatic rationales. Firstly, the frequency of occurrence of communal roosting behaviour is higher than that of any other taxa. Birds, unlike most mammals (with the exception of bats), have a greater capacity to navigate the landscape without being limited by terrestrial anthropogenic barriers. In fact, 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 an important limiting factor as compared to terrestrial wildlife. Why, then, the need for communal roosting instead of defending a territory? It is inevitable to think that there are overlooked benefits to this behaviour. Yet, despite their dispersal ability, birds cannot exceed in their food intake since that would compromise their flying abilities. As such, cost-benefits of when and where to eat need to be carefully assessed before engaging in foraging. Thus, feeding needs to occur in less quantity but more frequency. In other words, it is more important to find greater number of resources by several individuals and sharing them than one individual taking control over a large food patch. Perhaps the paradox of communal roosting lies in the proposed counterintuitive advantages of group foraging, as opposed to looking for resources individually.

In addition, birds have radiated to inhabit a wide array of regions and habitats, and have also adopted a diversity of diets and feeding strategies. Yet, CRB is observed in birds regardless of the feeding guild, strategy, dietary type, etc., or region they exist in. In fact, this behaviour has evolved in species that do not share a common ancestor (e.g., Old World and New World vultures). Altogether, these lines of evidence suggest that there are factors that are favoring the evolution of this behaviour.

## **1.3 Movement ecology and bird foraging behaviour**

Despite long-standing interest in the factors that shape bird foraging behaviour, it is still poorly understood how internal traits and external conditions jointly shape avian foraging movement (Mallon et al. 2020). Specifically, bird foraging behaviour has been studied mostly through direct observations. Because such methods are highly time-consuming, these studies have addressed the foraging behaviour of specific taxa only (e.g., Smith et al. 2012). Scaling such studies at a global level would be merely impossible given the amount of time and resources required.

With the advance of tracking technology, however, different approaches can be used to make inferences on foraging behaviour. 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 behaviour, 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 behaviour, as proposed by Ward & Zahavi through the ICH.

## **1.4 Biological variables as potential explanations of the origins of CRB**

## **1.4.1 Memory and CRB**

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 behaviour, 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 behaviour. 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 behaviour, 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.

## **1.4.2 Hand Wing Index and CRB**

Dispersal plays a key role in several ecological processes, and it is a major factor driving community assembly (MacArthur & Wilson, 1967). Despite its importance, little has been studied around the underpinning drivers of dispersal variation in birds (Dieckmann et al., 1999). Because studying dispersal from standard methods is so time-consuming, they are difficult to scale up to larger number of species (Sheard et al., 2020). Thus, indices are the most useful way to estimate dispersal. One of the most used indices in bird research is Hand-Wing index. HWI is a metric of bird wings’ aspect and its ratio, and it is used as a proxy for flight efficiency and dispersal ability (as summarized by Sheard et al., 2020).

In his study of the ICH, Ward & Zahavi (1973) proposed that communal roosting can be correlated to dispersion for foraging which has been supported by other studies. For instance, 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. 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, it could also be argued that an efficient flight mode is the driver of aerial lifestyle (e.g., Reliance on CRB) and not vice versa. Using HWI to understand how dispersal ability relates to CRB could provide a more comprehensive understanding of the drivers of this form of sociality.

### 1.4.3 Mass and CRB

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 between body mass and metabolic rate 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).

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 ideas to suggest communal roosting is positively correlated to body mass. Theoretically, a precise measure of metabolic rate would be more accurate to explore the relationship between energetic demands and the need for communal roosting. However, just like with dispersal ability, these measurements are costly and invasive, and these measurements are not currently available for the vast majority of species. Using mass as a proxy for energetic demands is useful for research done at larger scales, as proposed by the scope of this thesis.

### 1.4.3 Trophic guild and CRB

Trophic guild is inherently tightly related to foraging strategies. All of the trophic guilds, carnivores are notorious actively hunting their prey. Because they feed on organisms that are in higher levels of the food chain as compared to herbivores, more energy is lost to the environment as entropy in the process (Golley, 1960), which means they need more food supply constantly. For this reason, they are usually highly territorial. Scavengers, on the contrary, do not hunt for food, and instead they feed on carrion. This characteristic makes it hard for them to defend a territory, as the regeneration of the resource is hard to predict. Scavengers can be further divided into facultative and obligate scavengers (Aguilera-Alcalá et al., 2020), with the latter feeding exclusively on dead carrion (less foraging plasticity).

Although CRB has been widely documented in a vast array of species, it is interesting to note that the vast majority of scavengers exhibit this behaviour (e.g. ravens, crows, several vultures), whereas the behavior is less predominant in carnivores. 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). Indeed, most studies done on CRB and the ICH focus on scavengers. Obligate scavengers are of particular interest in the study of communal roosting, as they are the guild that would most evidently benefit the most from this behaviour. Although this thesis will not focus the efforts on this guild solely, further research may want to focus on this group to further disentangle the drivers and intricacies of this behaviour.

## **1.7 CRB 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 behaviour 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 behaviour 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 that have evolved this behaviour over evolutionary timescales. 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 well-documented in the scientific literature that birds have been widely studied under the foraging ecology lens. Some recent studies have looked into the relationship of communal roosting behaviour and foraging ecology. In spite of this progress in our understanding of the role of sociality in ecological foraging, assessing these relationships at a global scale remains unaddressed. While I will build on Beauchamp’s work, this thesis aims to greatly extend the scope of the work by increasing the dataset and the predictor variables, as well as updating the knowledge on CRB. Hence, this thesis breaks new ground by answering this overarching question.

Here, I will compile biological variables (HWI, mass, trophic guild and brain size) and test the relationship between these and communal roosting behaviour. 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 Behaviour (CRB) 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 to tease apart the competing hypotheses.

## **1.9 Thesis aims and structure**

The overall aim of my thesis is to discuss drivers of communal roosting behaviour and the potential implications on foraging efficiency in land birds. The present section (Chapter 1) provides the general framework for this thesis. Each chapter is designed to function independently while responding to the overarching research question. Consequently, repetitive elements will appear throughout this thesis as a result of the stand-alone nature of each chapter for later publication. For example, the introduction sections of Chapter 2 and Chapter 3, contain elements from Chapter 1 as an introductory chapter.

*Chapter 1* includes a literature review on movement ecology of wildlife, with particular focus on bird foraging behaviour. *Chapter 2* is focused on understanding variables that affect the prevalence of communal roosting behaviour (CRB) in birds. *Chapter 3* uses 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 behaviour has fascinated biologists for years (Wrangham & Rubenstein, 2014). From mating to foraging, there are diverse examples of social behaviour 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 is evidence that sociality plays an important role in shaping learning, and that this learning can create local cultures in a population (Aplin, 2019) , with behaviours 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 behaviour 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. First, it has 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). If thermoregulation was the primary benefit of CRB, one would expect it to occur more frequently in areas with extreme cold weather such like higher latitudes. Yet, this is not what is observed, with XXXXX (Beauchamp, 1999; Gyllin et al., 1977). Another hypothesis is that CRB 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 was 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 behaviour 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 behaviour. A question arises, then: Can the evolution of communal roosting behaviour 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 behaviour 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 behaviour across different phylogenies.

Even after Beauchamp’s 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 behaviour 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 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.

Because this data is not centralized in one database, I proposed a process to increase the efficiency of the search given the large volume of data. 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 behaviour 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 behaviour, 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 behaviour has been widely studied and documented, in which case I assigned it as 1. For other species, the behaviour 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 behaviour (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.

### 2.2.2 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).

### 2.2.3 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 incorporate phylogenetic relationships between species in the regression models, I obtained 100 phylogenies from VertLife (Jetz et al., 2012). From these 100 trees, I then constructed a consensus tree via least squares using the function ls.consensus (Lapointe & Cucumel, 1997) from the phytools package (Revell, 2012). To estimate the phylogenetic signal (Pagel’s λ ) of the trait data in the phylogenetic tree, I used the phylosig function from the phytools package. This value was then used to rescale the variance-covariance matrix constructed using the function vcv.phylo. The rescaled matrix was then used for posterior modeling.

The tip labels associated to the phylogenetic data from the computed trees was compared against my dataset from AVONET and I only kept the species for which there was phylogenetic data available. When names didn’t match but referred to the same species, I manually reviewed the names in AviBase (Lepage et al., 2014) to review for changes in the nomenclature and changed them accordingly to match the phylogenetic dataset. The remaining species (8354) were used for posterior analysis.

### 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 behaviour may have evolved differently in each guild. To calculate the phylogenetic signal of the trait in the evolutionary tree, I first calculated the variance-covariance

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 forty chains and 1000 000 iterations. Because of the large sample size of my data (946), I used priors to help initial guesses of the model. I used the coefficient estimates of the model without phylogenetic as a random effect. The mean values obtained where then used as priors in the final model. I used Cauchy distribution for the parameters probability as it has heavier tails thereby relaxing the assumption and weight of the priors.

###### **2.2.4.1 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).

###### **2.2.4.2 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. This was done to make test this model against one including brain size as a predictor using the same data.

The second model was fitted 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).

Table 1. Predictor variables included in each model tested and size of data used for each model

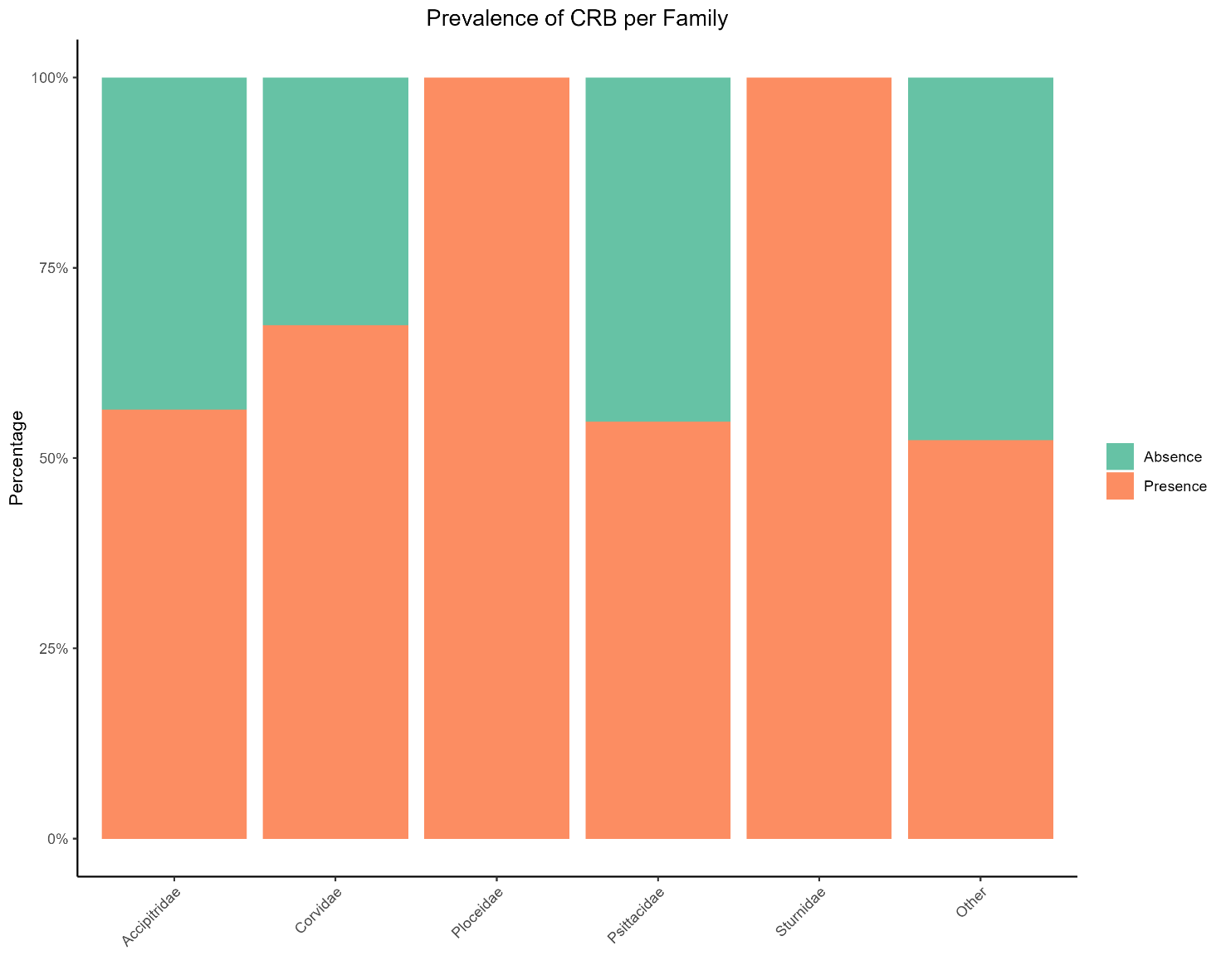
|  |  |  |
| --- | --- | --- |
| Model name | Predictor variables included | Number of species |
| Null\_model | phylogeny | 946 |
| Global model | HWI, body mass, trophic guild, phylogeny | 946 |
| Subset\_global\_model | HWI, body mass, trophic guild, phylogeny | 300 |
| Subset\_global\_model\_brainsize | HWI, body mass, trophic guild, phylogeny, residuals brainmass/bodymass | 300 |
| Model\_4 | HWI, body mass, trophic guild, phylogeny, brain mass, brainmass:bodymass | 300 |

**2.2.5 Ancestry Analysis**

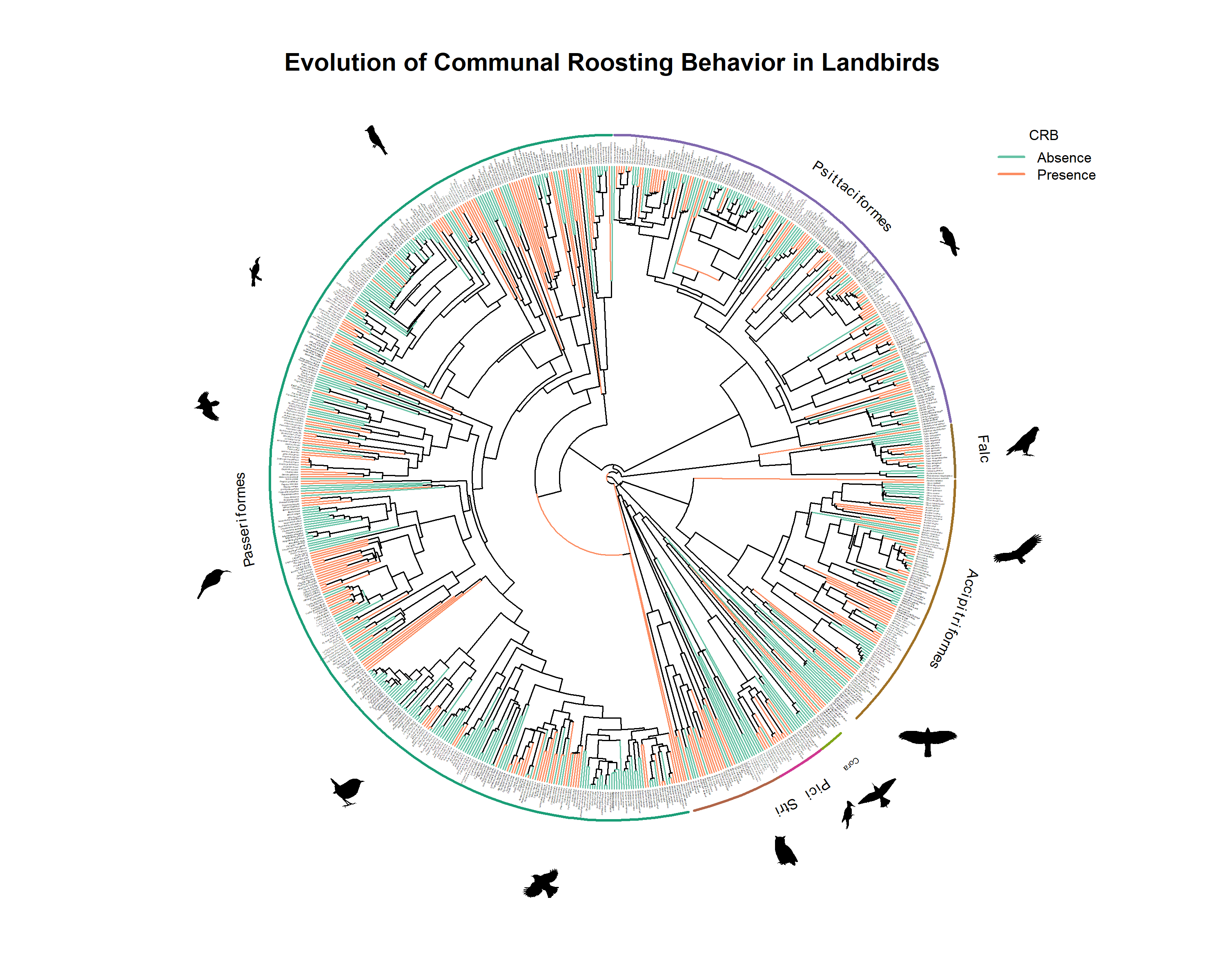
## **2.3 Results**

### 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 show the convergence evolution of this behaviour. Data were collected through Birds of the World and a Google scholar search.*

### 2.3.3 Biological variables and CRB

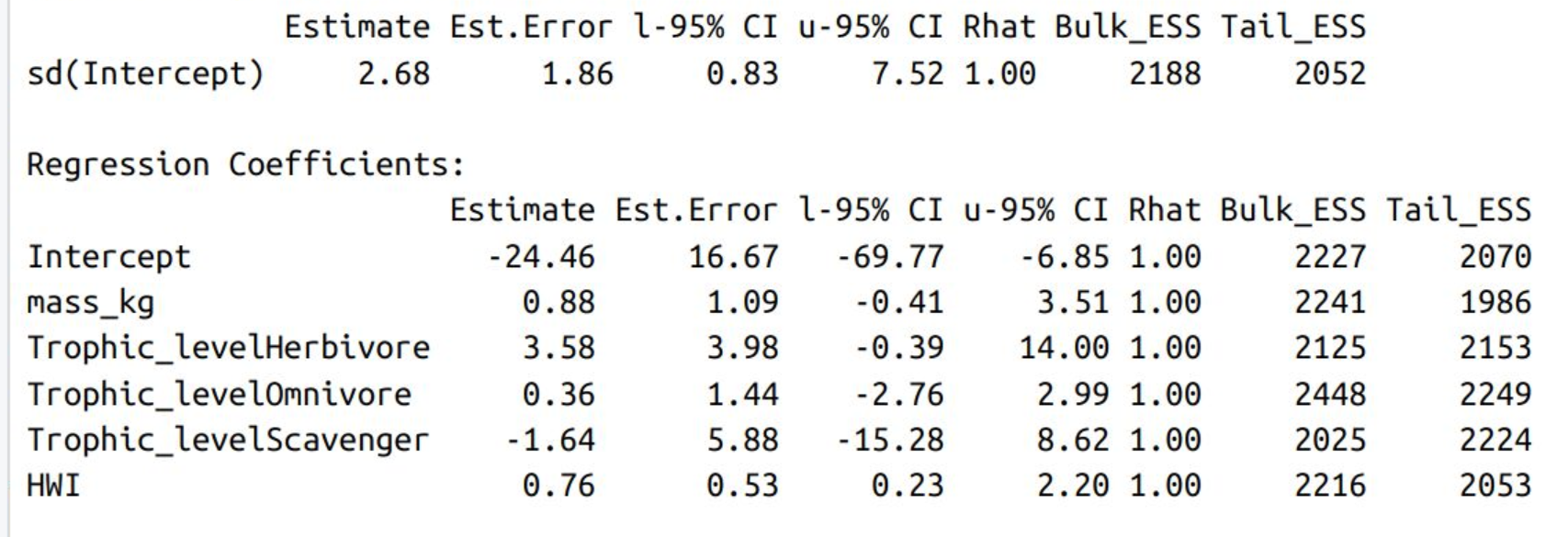
Overall, Handwing Index and Mass showed a positive trend with CRB, with prevalence of CRB increasing as how HWI and Mass increased, and a greater prevalence of CRB in scavengers as compared to other trophic guilds (Figures 2.3-2.5, Appendix 1).

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 and the coefficients.

**

#### **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).

YOU WILL HAVE TO CITE AND REFUTE THIS PAPER:

<https://meridian.allenpress.com/rapt/article/52/4/407/429769/Evolution-of-Communal-Roosting-A-Social-Refuge>

ALSO REFUTE PATCH SITTING HYPOTHESIS

<https://www.sciencedirect.com/science/article/pii/S0169204604001288#aep-section-id9>

### 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).

*HERE mention that IN RAPTORS FOR INSTANCE, CRB IS MOSTLY DOCUMENTED IN JUVENILES., WHICH SUGGESTS FOR NAÏVE INDIVIDUALS THAT ARE LESS ABLE TO HUNT/DEFEND/DISPERSE CRB IS A GREAT OPTION. THIS LEVEL OF DETAIL IS OBVIOUSLY NOT IN THE DATA OF THE MODELS BUT WORTH DISCUSSING*

### 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

## **1.4 Predictability of resources and foraging behaviour**

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 are less likely lead to territorial behaviour (Grant 1993). Interestingly, many scavengers forage in groups, leading to wonder if there are any benefits to this social behaviour given the nature of their unpredictable food sources.

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.

THIS STATEMENT IS HARD TO PROVE OR REFUTE BECAUSE ASSESSING THE OCCURRENCE BASED ON LATITUDE WOIULD BE TPOO CHALLENGING SINCE MANY SPECIES OCCUR IN A WIDE RANGE OF LATITUDES.

ADD AND EXPAND ON THIS

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 behaviour 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 behaviour and hierarchies within and across species. For instance, a study conducted in East Africa with seven types of scavenger species showed that there is 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 behaviour and hierarchies established. Interestingly, this high competition has in turn led to the evolution of specific behaviours 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.

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 behaviour with shared communal roosts among individuals.

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## **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 behaviour. 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**

Yet, regardless of its specific origins, there is evidence that sociality plays an important role in shaping learning, and that this learning can create local cultures in a population (Aplin, 2019) , with behaviours 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).

USEFUL TO SAY THAT ROOSTS ALSO FORM PART OF LEARNING TO NAVIGATE THE LANDSCAPE USING THERMALS TO FORAGING AREAS

Given their obligate scavenging nature, old and new world vultures rely highly on communal roosting behaviour. 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), behaviour (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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SUPPLEMENTARY MATERIAL

A TABLE WITH ALL THE REFERENCES USED FOR BRAIN SIZE

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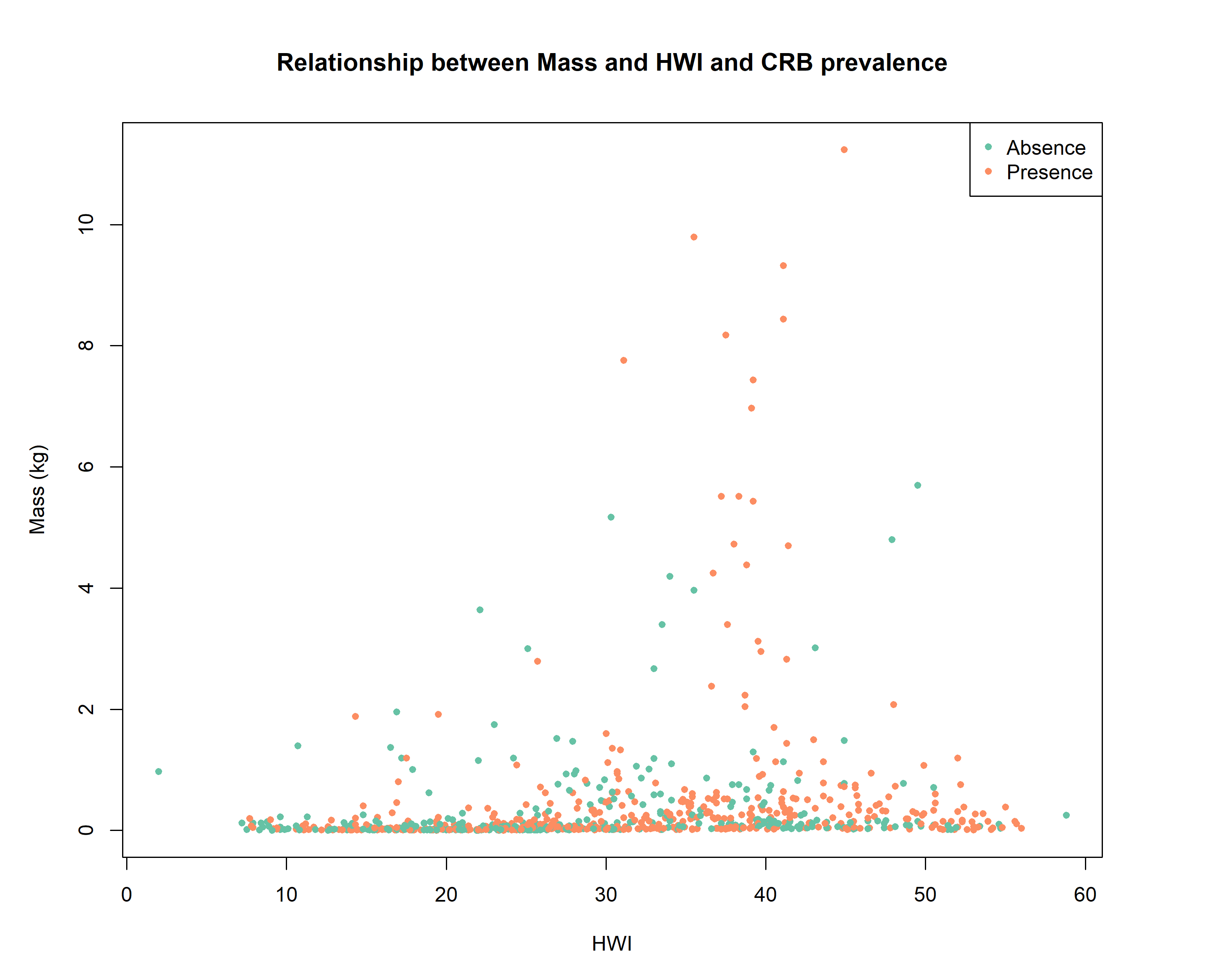
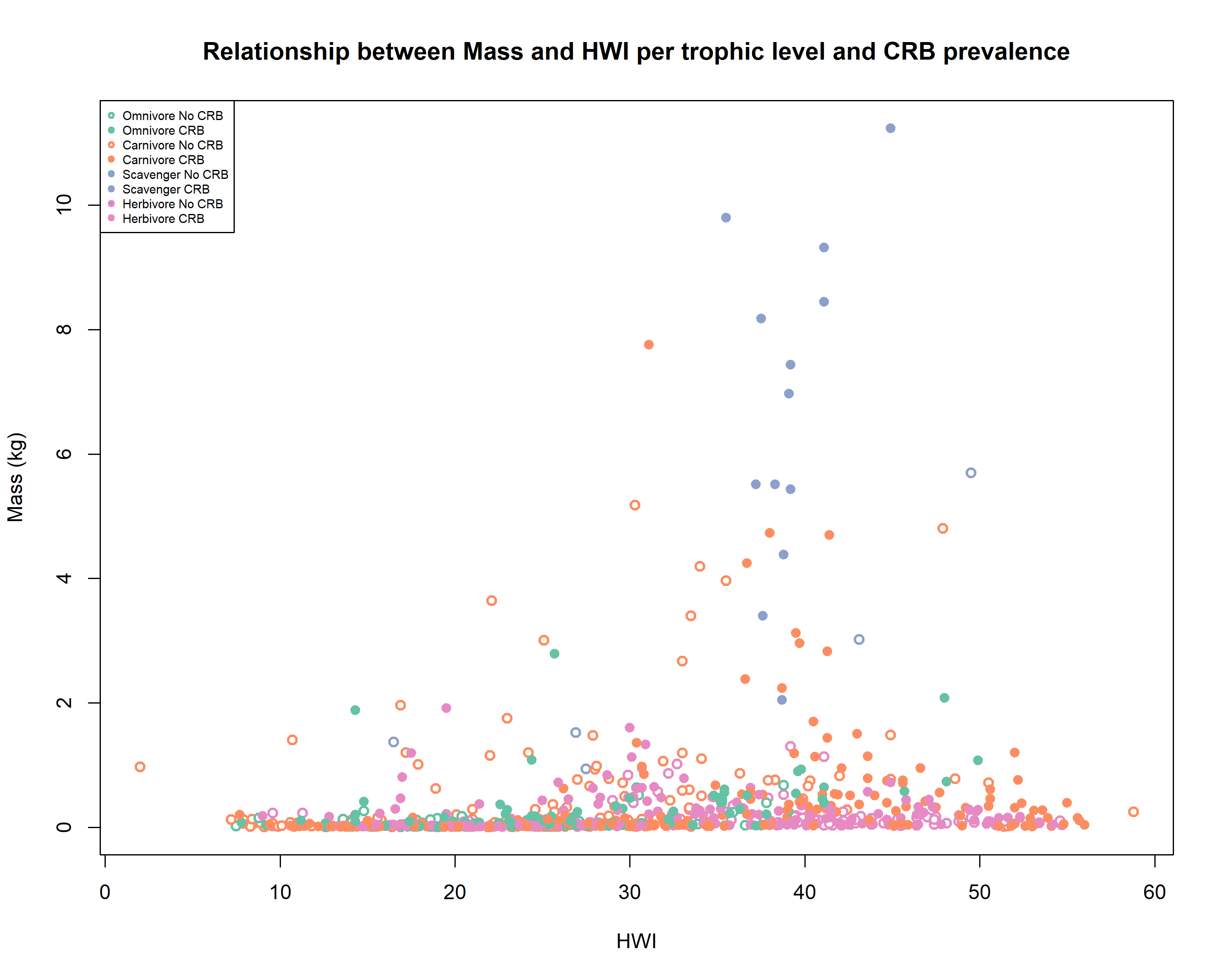
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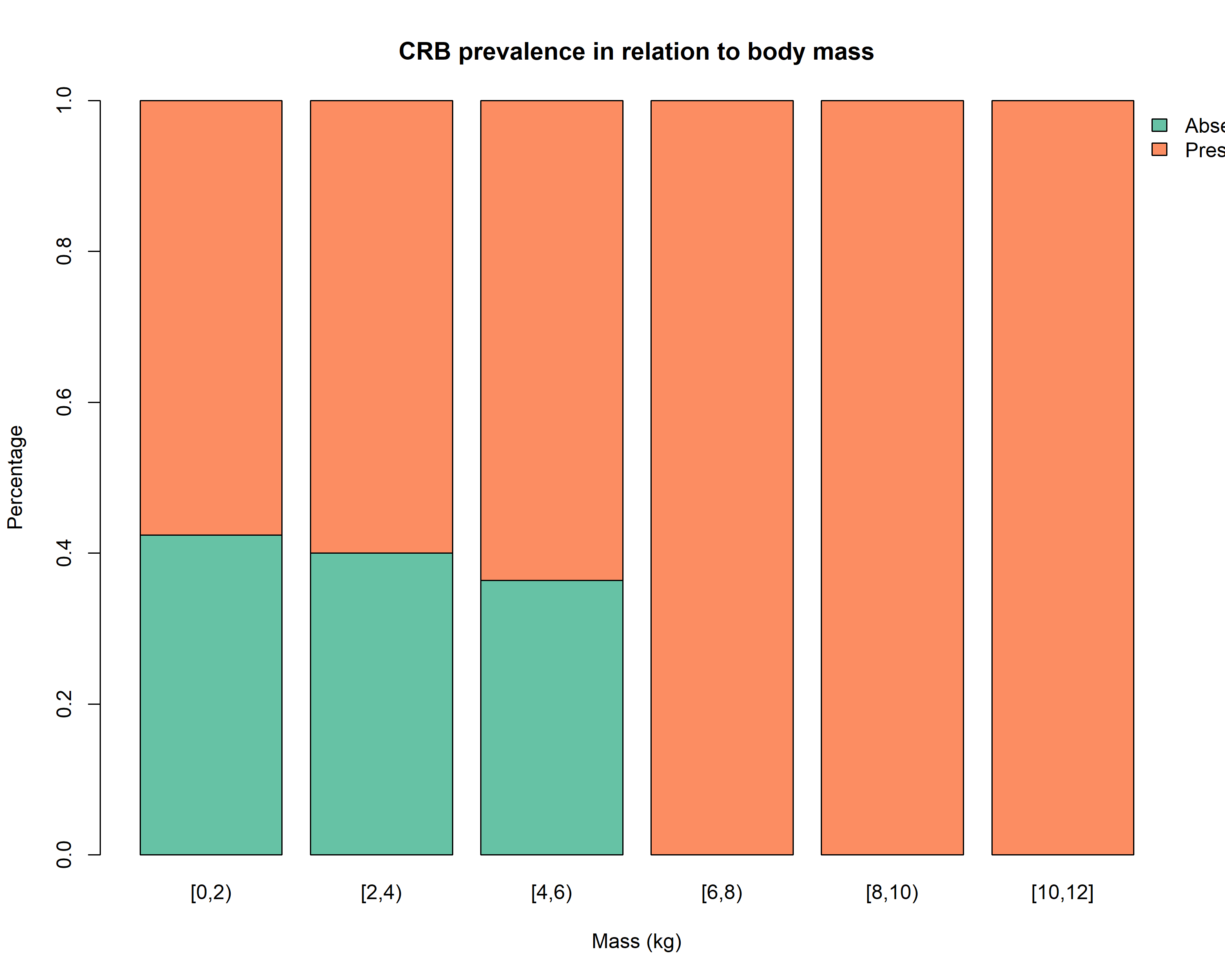
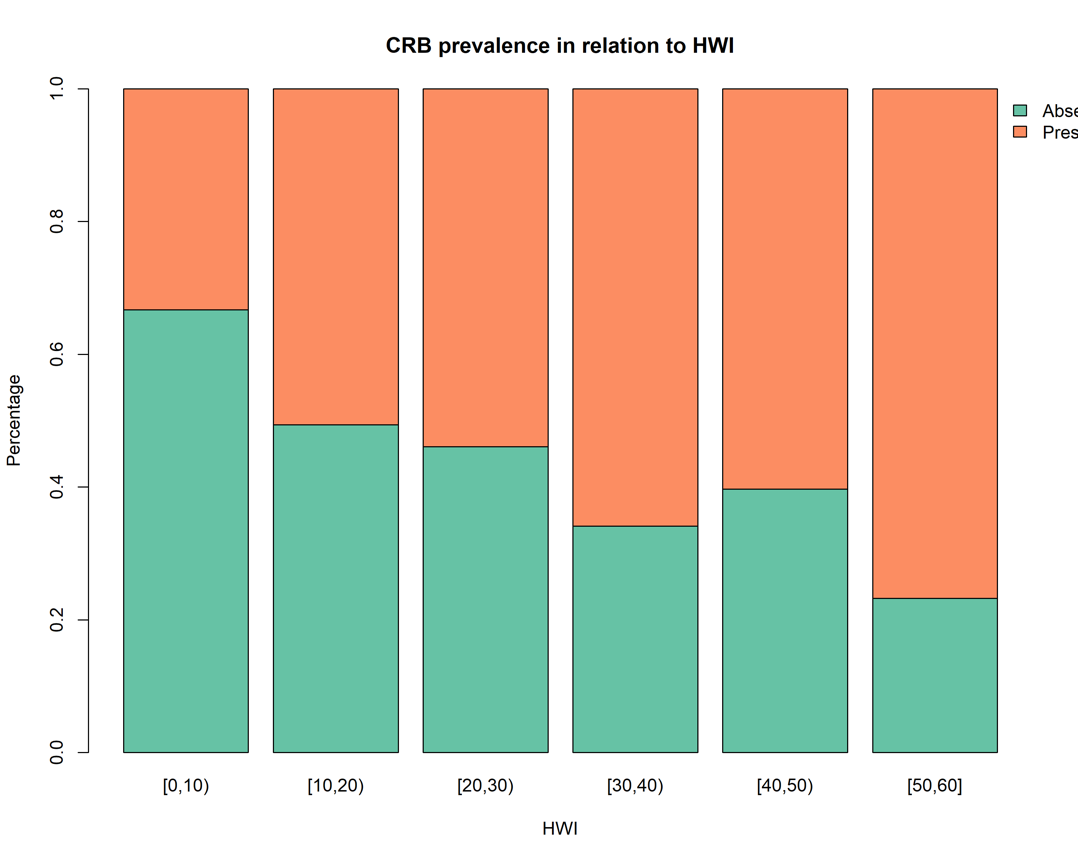
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# **Appendices**

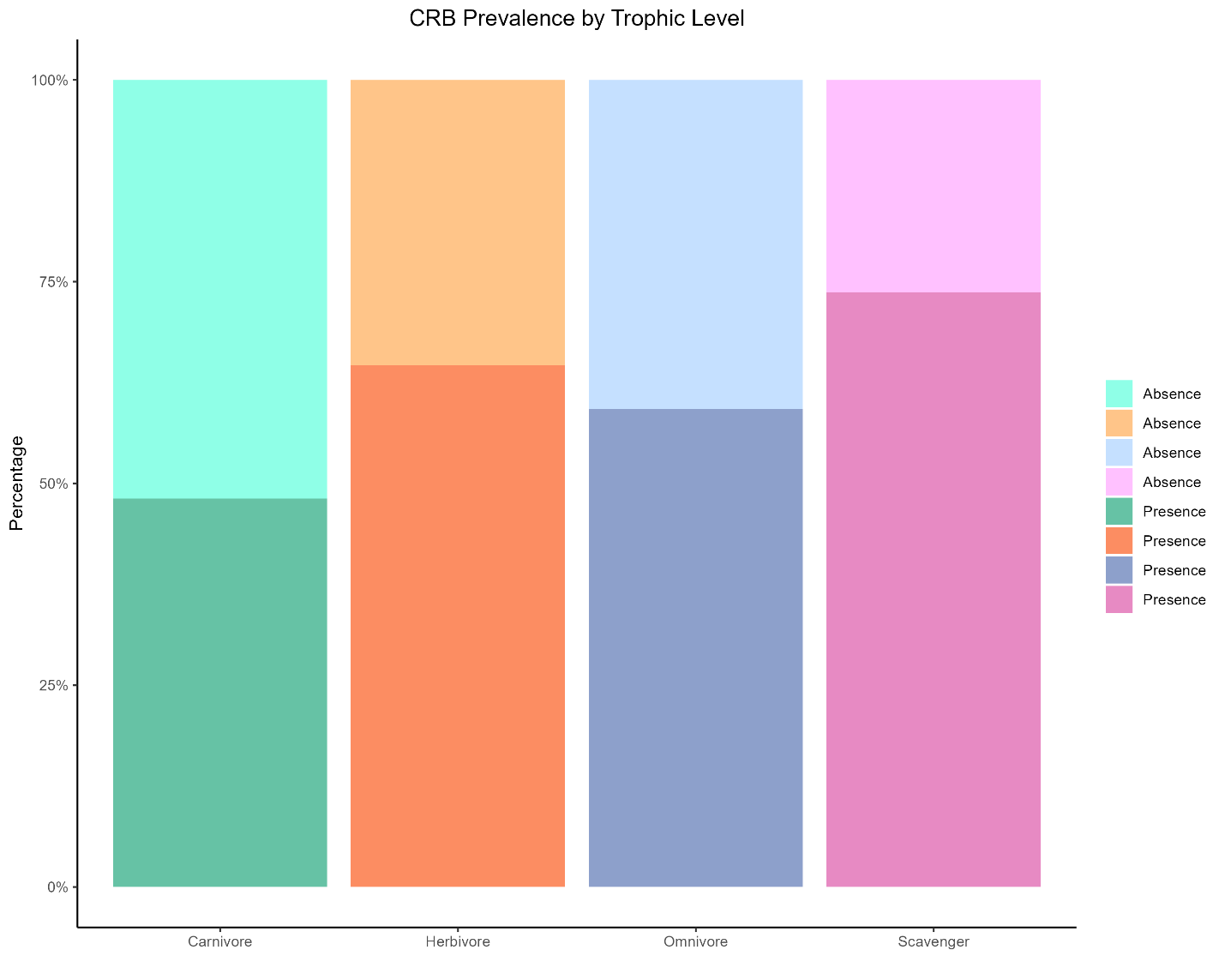
## **Appendix 1: Supplementary figures**



***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 behaviour. 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.*

## **Appendix 2: Code**

All code and figures used for Chapter 2 of this thesis can be found on the GitHub repository at <https://github.com/QuantitativeEcologyLab/MSc.-Communal-roosting-behav>