# **Chapter 2: Sharing is caring - The evolution of communal roosting behavior in birds**

**Introduction**

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**Key word: local enhancement**

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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). This behavior is striking given the apparent little benefits of sharing space and resources with unrelated individuals. Yet, it is seen in species across many taxa, including fish (Clough and Ladle 1997), mammals (Kunz, 1982) and birds (Eiserer 1984). 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, or set therefore, that support(s) this behavior.

It has been argued that these roosts are sites where naïve individuals can potentially exchange information with more experienced individuals on the location of food sources. This concept is formalized by Ward and Zahavi (1973) via the Information Center Hypothesis (ICH). Some prerequisites have been proposed by Mock (1988) to successfully test the ICH. First, *site fidelity*: individuals commute from specific roost sites to a recently detected carcass. Second, *differential success*: individuals differ in the information they have regarding food locations a given moment. In other words, there are informed and naïve individuals. Third, *signal transfer*: informed individuals may be identified by others through reliable physical (e.g., visual cues) or behavioral signals, either intentionally or inadvertently. This will allow for uninformed individuals to follow informed individuals. Fourth, *tolerance:* food resources are typically larger than the feeding capacity of a single individual, leading to satiation. Hence, information on location of food sources has little costs for the informed individual. Lastly, it is assumed that the cost of being a follower has an overall positive payoff than exploring for food individually. If the ICH holds true, individuals that exhibit communal roosting behavior are expected to have increased foraging efficiency than those who do not (e.g., Harel et al. 2017). Undoubtedly, this would be beneficial for scavengers given the high competition for their pulsed food resources (Van Overveld et al. 2022).

In an attempt to answer this question, the drivers for the communal roosting behavior in 201 bird species were tested by Beauchamp (1999), and his findings suggested that increased foraging efficiency was the most likely cause for communal roosting behavior. Other studies on specific species support this idea (Dermody et al. 2011). The conclusions on the aforementioned studies altogether open a new avenue for research to test this hypothesis in several other systems. Although the ICH has been well studied conceptually, these ideas have not been tested yet on a broader taxonomic scale after Beauchamp’s study, and a general understanding of the factors influencing avian communal roosting behaviour remain unknown. Using the comparative method, this chapter will focus on answering the following research question: what biological variables affect the prevalence of communal roosting behavior in landbirds?

**Methods**

*Communal roosting behavior*

To evaluate the relationship between biological variables and the evolution of communal roosting behavior in landbirds (Brusatte et al. 2015), I first collected data on communal roosting behavior. To do so, I gathered information on each species profile in Birds of the World, as it is the most comprehensive centralized database for birds’ natural history. When the information was not available for a given species, I used online databases and research papers using keywords like ‘*species name and communal roosting*’, ‘*species name and social roosting*’, and ‘*species name and social behavior*’. I then used the first five pages in google scholar to look for publications on the selected species. In parallel, I used Python's BeautifulSoup to web scrape Wikipedia for the number of literature references per species. The number of references where then clustered into three groups: not enough information (0-2 references), medium amount of information (3-5 references), and a lot of information (6-10). Clusters 1 and 2 where then used with web scraping tools to extract data from Wikipedia, OpenAlex, and Scopus. The manually collected data served as a benchmark to evaluate the accuracy of the web scraping results. The references in the output were then used to look for information on communal roosting behavior. This accelerated the search by dismissing species for which the number of references are negligible (cluster 1).

Communal roosting behavior will be classified as a Bernoulli variable where 0 is non-roosting behavior, and 1 is complete roosting behavior. Species for which this behavior is not properly documented will be classified as data deficient, and excluded from the analysis.

*Phylogenetic data*

I used the comparative method to explore the evolutionary relationship between physiological and biological traits and the communal roosting behavior in landbirds (*sensu* Felsenstein 1985) comprising roughly 8373 species. To access phylogenetic data and relationships between species, I used Trees from <https://vertlife.org/>. For each species we generated 100 trees and the information was then used to construct a phylogenetic diagram.

*Biological variables*

To test for the biological variables driving the evolution of communal roosting behavior, I selected four main traits: body mass (kg) following Beauchamp (1999), Hand-wing index (HWI), trophic guild and residuals of body size to brain size ratio (as a proxy for memory). A rationale as to why these potential explanatory variables were selected follows:

* Trophic guild: Trophic guild follows a comparable pattern, where scavengers are expected to rely more on CRB given the unpredictable nature of their food sources (Harel et al. 2017). Data from Trophic guild will be obtained through AVONET, an online database for all bird species. Complementary information will be used to adjust for these categories where pertains.
* Hand-wing Index (HWI): Hand-wing index is a metric of dispersal ability in birds (Arango et al., 2022) and therefore it indicates the capacity of a species to scout looking for food sources. Where HWI is high, CRB may bring more benefits as they might access food location over broader areas that can be then accessed by others through information sharing (Buckley 1997). Hand-wing Index values will be obtained through AVONET.
* Memory: Memory was chosen as, for species to share information, memory on the location of the food source is required to be later passed on (G Hernández-Montero et al. 2020). To test for this variable, residuals of relative brain size (absolute brain size in relation to body mass) were used following van Overbeld et al. (2022).
* Mass: Finally, mass was selected *a priori* from a larger pool of co-variates to reduce correlation between parameters. For instance, body mass, average lifespan and clutch size can potentially have an effect on communal roosting behavior given that larger, long-lived species tend to rely on information sharing to meet their greater energetic demands. Mass values will be obtained through AVONET.

Figure 2.1 below shows the anticipated relationships between avian communal roosting behavior and the variables tested.

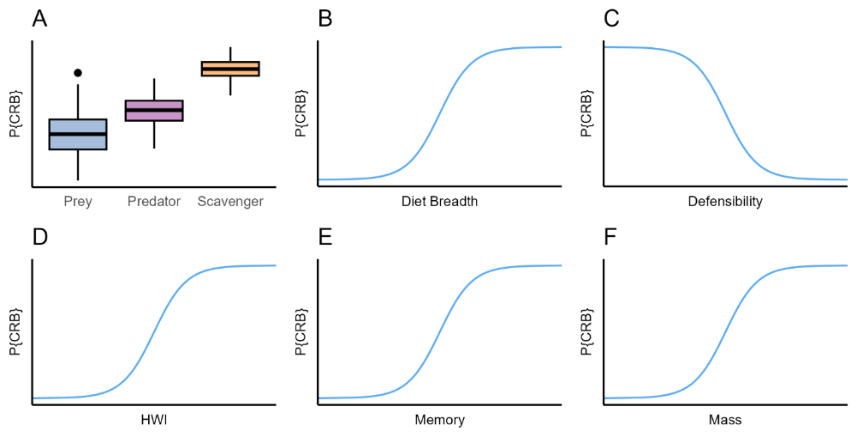


Figure 2.1. Anticipated relationships between the selected biological traits and the probability of Communal Roosting Behavior (p{CRB}). A) Trophic guild and Probability of Communal Roosting Behavior, where it will be considerably more probable in scavengers than in other trophic guilds. B-F show continuous biological variables and the expected relationship with P{CRB}.

*Competing hypotheses*

Although the aforementioned variables are suggested important drivers of CRB, other confounding variables may influence in the evolution of this behavior. 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. Furthermore, CRB might be beneficial during the winter in higher latitudes for temperature regulation. Hence, we cannot discard the ultimate causes in the evolution of this behavior for such species.

Another possible explanation to the evolution of communal roosting behavior is related to predictability of food sources available in the landscape. When food sources are unpredictable, species may benefit more from information sharing as per the ICH. Similarly, dietary breadth may have an effect on CRB. A wider dietary breadth effectively means less need to defend a territory. From a cost-benefit perspective, a wider dietary breadth means there are more benefits of sharing location of food sources than defending a widely available resource.

*Statistical analyses*

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

Eq. 1

Where CRB is the Communal Roosting Behavior, and is the regression coefficient that determines the relationship between the variables. The model was fitted in R using the *brms* package using a binomial error distribution.

We used …number of warmup chains, iterations. No priors were selected for the model as we decided to let the data guide the model instead of introducing biases.

**Results**

*Web Scraping*

OpenAlex had approximately a 14% accuracy, compared to SCOPUS which had a 15% accuracy to the manually checked list of species.

*Phylogenetic tree and CRB*

*Biological variables and CRB*

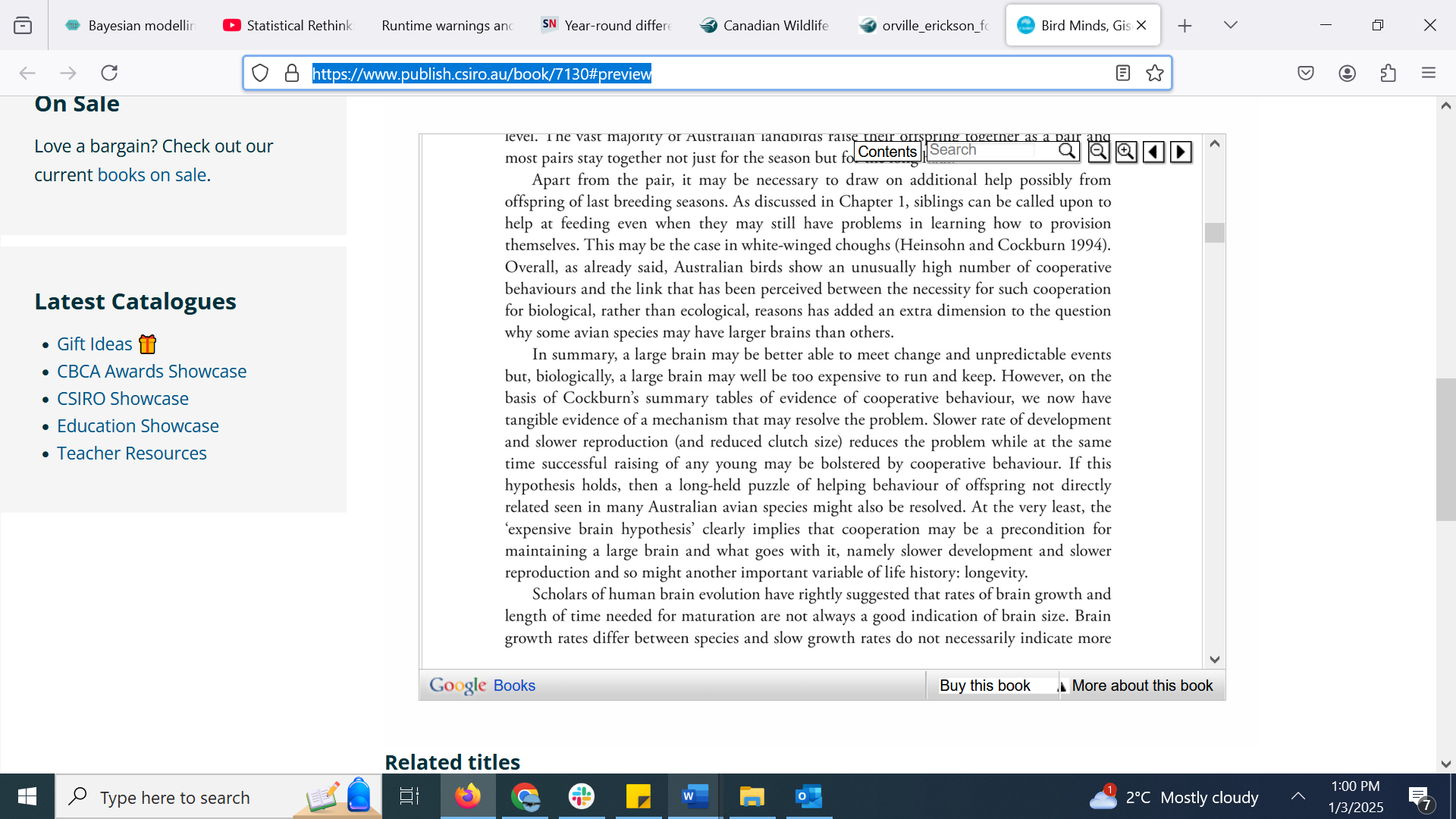
**Discussion**

**Thoughts as I am reading:**

**Could communal roosting be more frequent in less predictable landscapes (eg more natural?) versus more stable (human-dominated, that have carrion more available) in condors or other scavengers? Can we test this with movement data?**

Although brain size has been used as a proxy for intelligence, there are several arguments that challenge this idea. For instance,

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**Memory and Communal Roosting Behavior**

As detailed in the main text, I expect to see a positive relationship between memory and the prevalence of CRB. The rationale behind this expectation is that for individuals to be able to share information on the location of feeding sources when they roost together, they require the capacity to remember the locations of food items and return to those sites on subsequent foraging trips (Ward and Zahavi 1973, Dywer et al. 2018). The predictions for this variable are shown below.

I predict that the probability of CRB will increase linearly with memory because as proposed by the ICH, communal roosting behavior is a trait that is evolutionary favorable to increase foraging efficiency. Although the variables are expected to have a linear relationship, the link function used for the model is a logistic one since probabilities can range only between 0 and 1, hence, the I expect that the relationship will behave like an *s* shape with a saturation point in which the probability of CRB reaches its maximum value of 1 despite increases in memory.

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, to the best of my knowledge, data on hippocampus volume for all bird species are not readily available, which limits the scope of its application. Because lab experimentation is not feasible for the scope of this work, I will instead rely on the residuals of the brain mass to body mass relationship as a proxy for memory. I am opting to work with these residuals, rather than brain size directly, due to the strong correlation between brain size and body size (Smaers et al. 2021). Though not an explicit measure of memory, these residuals 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.

*Confounding variables and alternative hypotheses*

Although I hypothesize that greater memory is an important evolutionary exaptation (Gould & Vrba 1982) for CRB, memory 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 behavior since I also expect an effect of trophic guild, where scavengers are expected to make greater use of communal roosts (see Fig. 2.1 A). To determine the extent to which this correlation may be an issue, I will first estimate the correlation between the brain size residuals and feeding guild before fitting the model, and appropriate action will be taken based on the magnitude of the correlation coefficient (Dormann et al. 2013). For instance, parameter estimates for correlated variables are unbiased on average, but suffer from high variance due to identifiability issues, thus a sufficiently large sample size would serve as a viable solution, particularly for weakly correlated variables. For more extreme correlations, much of the information in the variables is effectively redundant, meaning that selecting only the variable that makes most biological sense, while dropping other correlated variables is likely the optimal choice. In the unlikely event that a large number of the variables I will be working with are correlated, I can consider a Principal Component Analysis (PCA) to generate statistically independent variables, though the biological interpretability of the covariates can be compromised and this will only serve as a final option, should the aforementioned two prove infeasible.

Though correlated parameters will require special care, perhaps more challenging is the fact that I am using the brain size residuals as a proxy for memory, while these are also related to other aspects such as cognition (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 behavior 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. Though this limitation cannot be overcome in this thesis, results will be interpreted with caution and contrasted against these alternative biological drivers.

Similarly, memory may lead to other behaviors 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. Hence, greater memory might not necessarily correlate to communal roosting behavior nor sociality. Thus, to complement my analysis, I will be collecting additional data on food caching behavior of birds. With these data, I can test whether this variable (food caching behavior) has a strong effect on deviating the correlation between memory and CRB. If the latter is observed, then memory might could have a greater correlation to food caching than CRB.

Furthermore, I am predicting that memory and probability of CRB have a linear relationship. Yet, it may also happen that the expected relationship behaves differently. For instance, that the relationship may be quadratic, or exhibit some other form of non-linearity. A possible example would be if memory (as measured via a proxy) is greater in large eagles than vultures, then a possible quadratic trend could be observed, in which case there would be limitations to the hypothesis proposed and the reasoning behind it. Although this wouldn’t obscure the trend *per se*, it would require careful model validation and may limit the scope of the conclusions I can draw from them.

Though little can be done to correct for these underlying assumptions statistically, extra care will be taken when interpreting these results such that limitations are acknowledged. For instance, I will aim to identify pairs of species with experimental evidence of good cognition but poor memory (e.g., Biegler et al. 2001), and vice versa to serve as contrasts in my discussion. I will also discuss how memory and other aspects of social behavior might come into play, such as memory and food hoarding as opposed to communal roosting.

*Predictability and diet breadth*

Access to regular food sources is a determinant factor on populations fitness. It is not surprising therefore that species that feed on carrion tend to exhibit communal roosting behavior. This can be explained to the fact that their food source is limited and unpredicitable, which makes it impossible for these species to defend a territory.

For example, it has been documented that food availability may induce communal roosting behavior in highly territorial species (Great-Horned Owl). This is because high predictability and availability of food in a farm location makes it easy for everyone to access resources without the need to compete for a territory. <https://doi.org/10.3356/JRR-13-47.1>.

LOOK FOR RESEARCH DONE ON OTHER TERRITORIAL SPECIES AND WHAT THEY FOUND. TAKE PERHAPS SNOWY OWLS!

Although terrestrial productivity at a global scale can be measured through NDVI and the variability of NDVI can act as a proxy for predictability, that measure is seldom useful for the current research since several species exist on a vast geographic range with contrasting productivities. INCLUDE AN EXAMPLE OF SPECIES AND ITS GEOGRAPHIC RANGE. Moreover, productivity and predictability 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.

The same challenges arise for an accurate measure of dietary breadth. For instance, when assessing the dietary breadth of an insectivore, do we include all insect species it feeds on, or clump insects into one type of diet item? It becomes even more confusing when trying to classify scavengers’ diet that may feed on carcasses only, but of several kind of species. From a conceptual and empirical point of view, this measurement is not feasible at a global scale,

OTHER MEASURES OF SOCIALITY ARE NOT APPROACHED HERE (EG SPECIES MAY HAVE GOOD MEMORY BUT DO NOT EXHIBIT CRB, INSTEAD ARE PERHAPS COMMUNAL NESTING). ALSO, BIG MEMORY CAN BE ASSOCIATED WITH FOOD HOARDING, AND NOT WITH CRB.

**Future work**

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 (EG MENTION STUDIES), but other species remain underrepresented in the study of memory. Finally, testing the idea that species exhibiting communal roosting behavior 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.

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