

Literature Review 3: Annotated Bibliography

Ordering: The annotated bibliographies featured in this document are ordered under two headings that were organized according to similarity in their defining points. The flow begins with more broad studies that looked at environmental ecology where the environment in some way shapes this behaviour, followed by more specific topics that investigated the behaviour as a function of nesting success strategies.

Factors influencing environmental ecology:

Ekman, J., & Ericson, P. G. (2006). Out of Gondwanaland; the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies.

Proceedings of the Royal Society. B, Biological Sciences, 273(1590), 1117–1125.

<https://doi.org/10.1098/rspb.2005.3431>

Summary: Spurred by previous research detailing historic predisposition for cooperative breeding, as well as the lack of research into the ecological context at which the behaviour presents in, Ekman & Ericson (2006) sought to explore corvid evolutionary history to delve deeper into what ecological factors contribute to this behaviour. In addition, they investigated how this breeding behaviour responded to a factor such as latitude by completing a comparative analysis between ancestry and a southern hemisphere origin. To accomplish this, they focused on family cohesion and alloparental care in the context of phylogenetic trees. They then used the

Discrete algorithm to obtain a reconstruction of the maximum-likelihood of the ancestral states with the correlated character evolution. Subsequent reconstructions and analyses were run on those correlated character evolution. From this, they found cooperative breeding occurred more frequently in corvids that had a habitat distribution encompassing tropical or subtropical environments in the Southern Hemisphere. This latitudinal distribution provided some evidence for a correlation between climatic areas and the type of breeding system present. However, it was also theorized that this phenomenon could be attributed to selection against cooperative breeding in northern distributions where this behaviours evolution was limited in some way. They also determined that cooperative breeding as it occurs in corvids is highly plastic which shows that many selection forces are involved in the behaviour's response to latitude. This was significant because it showed that breeding systems such as cooperative breeding have environmental sensitivity where foraging conditions and social environment changes can manipulate the type of cohesion present in bird populations. In addition, it showed that latitude and the environment play a role in the expression of this behaviour. Future studies are needed to investigate whether adverse climatic changes could cause cooperative breeders to change their strategies.

Contribution: This article was chosen because it advances the understanding of how the environment influences the expression of cooperative breeding in corvids. The research study did not support a previous hypothesis that predicted breeding system shifts correlated with more open habitats. Instead, corvids that displayed cooperative breeding behaviour were determined to encounter variable habitats. The article provided future areas of research such as looking into the full explanation concerning the paucity of cooperative breeding.

Baglione, V., Marcos, J. M., Canestrari, D., Griesser, M., Andreotti, G., Bardini, C., & Bogliani, G. (2005). Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? *The Journal of Animal Ecology*, 74(5), 842–851. <https://doi.org/10.1111/j.1365-2656.2005.00983.x>

Summary: Inspired by a previous model that predicted scarcity in breeding opportunities might result in cooperative breeding behaviour, as well as previous studies that displayed how year-round residency might facilitate this behaviour, Baglione et al. (2005) sought to compare two crow populations with differing dispersal and social organization to test whether a lack of breeding vacancies influences dispersal. They also investigated whether year-round residency would better predict for the delayed dispersal behaviour that is necessary in cooperative breeding. To do this, two crow populations from northern Italy and from northern Spain were studied. The population from Italy was non-cooperative and lived year-round in non-territorial flocks, whereas the Spanish population was cooperative with resident territoriality. Birds were tagged and followed over the study area, with behavioural observations taken over a period of five weeks to document any parental-offspring aggression. The number of competitors per breeding vacancy was measured alongside various surveys, bird counts, and other measurements/observations. Territoriality was assessed using crow foraging distribution and territory overlap. From these observations, they found that habitat saturation and cooperative breeding occurrence were not highly associated. They also determined that the relationship between territory turnover and saturation was more complex than believed previously, as slow turnover was associated more often with lower habitat saturations. Finally, they suggested that year-round residency likely played a larger role in delayed dispersal expression, as parental presence in the natal territory may confer benefits such as predator protection and resources to

juveniles. This study was significant because it provided evidence for why some species experience delayed dispersal and cooperative breeding and others do not. In addition, it showed that habitat saturation may not be the predictor for dispersal for this population of crows. Future studies are needed to investigate more than two populations to remove potential random bias from the results.

Contribution: This article was chosen because it advances the understanding of the ecological factors influencing delayed dispersal and cooperative breeding in populations of crows. The study showed that year-round territoriality likely confers greater advantages for birds that delay their dispersal, while populations that do not do this may be less territorial. This study supported previous studies that investigated factors shaping the social organization of crows, especially in terms of factors promoting year-round residency. The study puts forward future areas of exploration, such as determining whether these results hold with more populations studied.

Bresgunova, O. A. (2013). Cooperative breeding in corvids (Passeriformes, Corvidae). *Biology Bulletin*, 43, 693-706. <https://doi.org/10.1134/S1062359016070049>

Summary: With the knowledge that cooperative breeding required delayed dispersal and extended parent and offspring relations, Bregunova (2013) aimed to review corvid cooperative breeding literature and explored factors that could contribute to delayed dispersal and cooperative breeding in corvid species and populations. The review was conducted using a systematic review of published literature that excluded information regarding behavioural variants such as adoption and adult-adult feeding. From the literature compilation, many observations and findings were shown. Regarding the occurrence of these

behaviours, it was shown that helping behaviours are common in male birds relative to females. For helper bird hormonal status, it was determined that levels of sex hormones were significantly lower in helpers relative to breeding pairs. The sedentariness of certain species preserved family grouping due to the lack of migration. Regarding ecology, it was inferred that habitat stability and the shortage of potential nesting sites were involved in the maintenance of the sedentary lifestyle of some species, thereby keeping them confined to one location with their kin. This also relates to the idea of adult tolerance of juveniles, whereby increased social interactions supported familial attachment and extended parenting that would likely influence delayed dispersal behaviour. It was also determined that helping behaviours could likely arise through traditional learning as a form of culture. Finally, year-round group living, and cost-benefit analysis further developed the notion that extended familial interactions and kin selection would have influenced cooperative breeding. Inferences from this collapsed into the idea that ecology and territorial patterns keep corvids localized, which thereby increases social interactions and therefore leads into helping behaviours and delayed dispersal. The review concluded by addressing the need for long-term studies that would aid in the complete identification of delayed dispersal and cooperative breeding that this review set out to accomplish.

Contribution: This review article was chosen due to its deep investigation into the factors that contribute to or influence delayed dispersal, and therefore cooperative breeding, in the family of *Corvidae*. It also contributed to the advancement of this field and topic due to its inclusion of hypotheses and inferred explanations as a reaction to the compiled literature information summarized in the paper. Finally, the paper posited future areas of study that currently lacked information, which included long-term studies of both marked and unmarked corvids to fully identify the factors influencing cooperative breeding.

Canário, F., Mtos, S., & Soler, M. (2004). Environmental constraints and cooperative breeding in the azure-winged magpie. *The Condor*, 103(3), 608-617.

<https://doi.org/10.1650/7454>

Summary: With the knowledge from previous studies that poor conditions could drive birds towards indirect fitness benefits by assisting kin with their offspring, Canário et al. (2004) investigated the effect that ecological constraints may have on cooperative breeding in Iberian Azure-winged magpies (*Cyanopica cyanus*). They looked at breeding performance and helping behaviour when the climate conditions varied. The study occurred over two years in southeastern Portugal, with nests inspected during breeding season periodically to assess for various nest features such as brood size and nest success, in addition to monitoring for depredated/deserted nests. Measurements of nestling wing and tarsus length, as well as body mass, were conducted. Adult birds were tagged. Observational data on parental care, as well as weather data, were also acquired. From this, they determined that nests with helpers performed better in both years. It was evident because those nests saw increased fledgling production, likely due to the increased rate of food provisioning and nest visits compared to nests without helpers. They also observed that the year with poor conditions and reduced food availability led to increased helper number at nests relative to the year with better conditions. It implied two things: that there was a strong year effect and that poor conditions led to more failed breeders that could redirect their fitness efforts towards helping breeding kin. The study was significant because it showed that geographic variation and environmental studies could aid in determining the mechanics and reasoning behind this behaviour in corvids. Future studies should focus on the benefits that helpers obtain from participating in this behaviour to understand other possible drivers of cooperative breeding.

Contribution: This article was chosen because it provided insight into how weather conditions could impact helper presence. It also showed how increased helper presence led to increased breeding success and provisioning for magpie fledglings. The research supports previous research on how changes in fitness, as with the poor conditions of one of the years, could influence failed breeders to redirect help towards successful breeders. The work posited that future investigation should focus on the other advantages that helpers may obtain from cooperative breeding. It also would like future studies to investigate other key factors influencing the behaviour.

Baglione, V., Canestrari, D., Marcos, J. M., Griesser, M., & Ekman, J. (2002). History, environment and social behaviour: experimentally induced cooperative breeding in the Carrion Crow. *Proceedings: Biological Sciences*, 269(1497), 1247-1251.

<https://doi.org/10.1098/rspb.2002.2016>

Summary: With the knowledge that the carrion crow (*Corvus corone corone*) had great variation in the level of cooperative breeding between different populations, Baglione et al. (2002) sought to experimentally determine if cooperative breeding occurred in response to current environmental conditions. To accomplish this, they transplanted 39 eggs from a Swiss population where cooperative breeding and offspring retention was absent to a population in Northern Spain that were known to cooperatively breed. The eggs and resulting hatchlings were marked and tracked to identify the individuals. Blood samples were drawn, and behavioural data was observed for about 3 hrs/week during the breeding season; the data collected was then taken for further statistical analysis. From this, they found that the environment in which chicks were

reared had a significant impact on delayed dispersal, which has an important role in cooperative breeding behaviour. In addition, they also found that during breeding season, some transplanted juveniles chose to remain with the resident birds of their natal territory, with a few juvenile females exhibiting helping behaviour such as feeding and nest defense. This study was significant as it exhibited how the rearing environment played a role in the occurrence of helping behaviour in carrion crow populations. It also provided evidence that there was a causal relationship between cooperative breeding behaviour expression and the current environmental conditions in which the crows lived. It also showed that the difference in behaviour between the populations was likely due to plasticity rather than constraints imposed by phylogeny. Future studies are needed to determine what the specific factors are that would drive cooperative breeding and helping behaviour expression in the carrion crow. In addition, more research needs to be done on what roles territoriality and constrained breeding vacancies have in the determination of offspring retention in this species.

Contribution: This article was chosen because it advances the understanding of the role that the environment plays in social behavioural evolution in different populations of carrion crow (*Corvus corone corone*). The results in the article support previous theories that have posited that the current environment plays a deterministic role in determining which species or populations will exhibit cooperative breeding behaviour. However, this study challenges a constraints model of explanation that placed constrained suitable breeding vacancies as an important factor influencing offspring retention. The work posited that investigation should focus on the role that constrained suitable breeding vacancies have on this behaviour.

Factors influencing nesting success:

Innes, K. E., & Johnston, R. E. (1996). Cooperative breeding in the white-throated magpie-jay. How do auxiliaries influence nesting success? *Animal Behaviour*, 51(3), 519–533.

<https://doi.org/10.1006/anbe.1996.0057>

Summary: With the knowledge from previous studies that helpers, birds that have delayed their dispersal in favour of assisting a brooding pair with their offspring, could have an influence on egg-laying, nest predation reduction and nestling starvation reduction, Innes & Johnston (1996) investigated how helpers influenced the reproductive success in the white-throated magpie-jay (*Calocitta Formosa*). To accomplish this, field work was conducted in Costa Rica over three breeding seasons. Helpers were classified under three categories based on observational data detailing their movements and nesting effort contributions. During this study, 152 birds were tagged with leg bands and weighed, and other distinguishing characteristics were noted down. Group size and composition data, as well as reproductive success and nest loss sources were observed through close monitoring. Data was analyzed using various statistical tests including ANOVA and t-tests. The results obtained from this data indicated that every stage in the nesting cycle of these birds was enhanced in some way by helpers. In addition, there was a positive association between full-time helper number and nesting success. Egg-laying onset, egg predation, and hatching failure were also found to be significantly influenced by helpers. Nests with helpers had earlier egg-laying, reduced nest predation, and reduced hatching failure. This study was significant because it offered clear evidence that helpers had an influence on the overall nesting success in this population of magpie-jays. It also supported the anti-predator hypothesis because the results displayed reduced nest predation in nests with helpers. Finally, it

demonstrated that hatching success was primarily influenced by two parameters: egg predation and hatching failure. Additional research should be focused on determining helper influence on hatchability in other cooperatively breeding species to ascertain and validate the results. In addition, future research should investigate helping effort variation as a factor in reproductive success in other species.

Contribution: This article was chosen because it provided insight into the types of help that helpers provide in a cooperatively breeding species. In addition, it demonstrated that predation may be a key component in why this behaviour occurs in the wild due to its significant relation to many reproductive parameters. The research supports previous studies that looked at helper influence on laying onset but contradicted a study that looked at helper influence on hatchability in a different species. Future areas of exploration put forward by the study included testing the anti-predator hypothesis in other cooperatively breeding species.

Ren, Q.-M., Luo, S., Du, X.-J., Chen, G.-L., & Du, B. (2016). Helper effects in the azure-winged magpie *Cyanopica cyana* in relation to highly-clumped nesting pattern and high frequency of conspecific nest raiding. *Journal of Avian Biology*, 47(4), 449-456.

<https://doi.org/10.1111/jav.00783>

Summary: With the knowledge from previous studies that the variable benefits of cooperative breeding could influence corvid breeding strategies, Ren et al. (2016) investigated the drivers influencing different types of assistive behaviour in the azure-winged magpie (*Cyanopicus cyana*). For two years in Gansu Province, China, researchers captured and tagged adult birds. Measurements of their body mass, beak, and tarsus length were also taken. Blood was extracted

at this time to determine sex using PCR techniques. Next, the nests were located and checked daily during the laying period to determine clutch size. Measurements of the egg and nestling mass were taken until the birds were fledged. Adult behaviour was recorded at the nests using video recording equipment. These videos, as well as the other data compiled from the study, were subsequently analyzed. From these observations, the research team determined that helper presence did not directly influence the clutch size, potentially due to other factors such as female bird condition before egg-laying. They also found that helpers contributed almost half of the courtship-feeding to incubating females, which may have allowed these females to maintain better body conditions. Another result was that nestlings with helpers present were larger at fledging than those without helpers, which could improve nesting success and survivability. They also found that food supply was likely not limiting in this population as both assisted and unassisted breeding pairs had similar provisioning rates. Finally, they determined that predation was likely the largest influencer in this behaviour as helpers reduced nest predation. This was significant because it demonstrated that the helper effect correlated with nest raiding, a leading cause of nest failure in this population. Future studies are needed to determine whether these results hold in other populations or species.

Contribution: This article was chosen because it provided insight into the drivers of cooperative breeding. It provided evidence that predation was the leading cause of nest failure, which would influence the bird population to use helpers to aid in nest success. The study supported previous research that reported that the presence of helpers had no visible effect on clutch size. It did not support the model of a previous study that predicted food provisioning as the leading influencer

of helper effects. Future areas of exploration were proposed including the reason behind the equal provisioning of brood pairs with and without helpers.

Canestrari, D., Marcos, J. M., & Baglione, V. (2009). Cooperative breeding in carrion crows reduced the rate of brood parasitism by great spotted cuckoos. *Animal Behaviour*, 77(5), 1337- 1344. <https://doi.org/10.1016/j.anbehav.2009.02.009>

Summary: With the knowledge that cooperative breeding species may be targeted by brood-parasites such as cuckoos due to increased provisioning, but that helper presence could also aid in nest defense against parasites, Canestrari et al. (2009) investigated how cooperative breeding in crows may either positively or negatively impact cuckoos, and investigated the costs associated with brood-parasitism on carrion crows (*Corvus corone corone*). They focused on how the group size of the host influenced factors such as parasitism rate, parasite egg laying opportunities, parasite reproductive success, and the role that parasitism had on host reproductive success. To do this, the group conducted a 12-year study in Northern Spain where hatching sequence and success were observed and recorded. During breeding season, group size and composition were monitored in addition to measuring the time that the incubating females spent in or outside of the nest. Statistical analyses were then conducted on the collected data to investigate and determine the parameters outlined in the objective. From this, they determined that more nests were parasitized when the parasitism rate increased, but that the number of parasite eggs was independent of group size. They also determined that parasite egg-laying opportunities declined as the group size of the host increased and that the reproductive success of the parasite was found to positively correlate with group size. Finally, they found that parasitic

egg presence did not have a significant effect on the number of host fledglings, but that host reproductive success instead correlated with host egg number and group size. This study was significant as it demonstrated a potential factor influencing cooperative breeding in carrion crows, specifically that increased group sizes reduced the likelihood of brood parasitism passively. Future studies are needed to determine the exact role that helpers have in the defense of the nest.

Contribution: This article was chosen because it advances the understanding of the passive defense role that helpers had against parasites. The research goes against previous studies that believed the higher preference of brood-parasites on unassisted pairs was due to superior quality in these nests; the results instead found that these unassisted nests had higher nest failure rates relative to assisted nests. The work also posits future areas of exploration, including what the generality of the results could mean when compared to other cooperative breeders, as well as the determination of the circumstances that affect brood parasitism in these social birds.

Wascher, C. A. F., Canestrari, D., & Baglione, V. (2019). Affiliative social relationship and coccidian oocyst excretion in a cooperatively breeding bird species. *Animal Behaviour*, 158, 121-130. <https://doi.org/10.1016/j.anbehav.2019.10.009>

Summary: In response to the knowledge that the social environment of group living animals could affect their health, Wascher et al. (2019) investigated the relationship between the social relationship quality of captive carrion crows (*Corvus corone*) and the occurrence of parasites in their excretion, specifically coccidians. They focused on how certain social parameters such as

relationship quality, relatedness, group size, and dominance rank affected parasite egg/oocyst excretion patterns. To accomplish this, 36 crows were separated into groups reminiscent of those in the wild and spatially isolated to allow for group data collection. They resided within a four-compartment outdoor aviary in Spain over the span of seven years and provided daily food and water. Droppings were obtained on a regular schedule, but sanitation never occurred to allow for parasitism. Behavioural data were observed and taken for further statistical analysis and the droppings were examined and stored to determine the number of positive parasite samples. From this, they found that approximately 31% of the total dropping samples contained coccidian oocysts. They also determined that strong social bonds, large group size, and bird relatedness had a statistically significant effect on the proportion of samples containing coccidian oocysts. These parameters showed that it lowered the probability of gastrointestinal parasite occurrence. For the remaining parameters of sex and dominance rank, there were no significant relations to the number of samples with parasites. This study was significant as it provided further insight into the fitness advantages of quality social bonds in carrion crows. Future studies are needed to determine the true causality in this relationship as well as the other advantages and trade-offs that sociality and cooperative breeding may have. Additionally, research needs to be done on how this relationship may occur in wild populations of carrion crows and how it may affect these results.

Contribution: This article was chosen because it advances the understanding of how social factors that result from cooperative breeding may have an advantageous effect against coccidian parasitism in carrion crow (*Corvus corone*) groups. The research supports previous studies on the direct and indirect fitness benefits of cooperatively breeding social groups such as crows that could be extrapolated to include other species such as primates. The work also posits future areas

of exploration, including behaviour causality determination in addition to advantages and trade-offs that sociality may have on the health of both corvids and other species that exhibit similar pro-social behaviours.

Valencia, J., Solis, E., Sorci, G., & de la Cruz, C. (2006). Positive correlation between helpers at nest and nestling immune response in a cooperative breeding bird. *Behavioral Ecology and Sociobiology*, 60(3), 399–404. <https://doi.org/10.1007/s00265-006-0179-z>

Summary: In response to the knowledge that helpers in cooperative breeding species could positively impact the fitness of offspring, Valencia et al. (2006) investigated the role that helpers had on the immune response of azure-winged magpie (*Cyanopica cyanus*) nestlings. They focused on determining if there was a causality between helper presence and nesting immune response and explored whether nestling body mass variation could be explained by helper-induced nestling immune response. To do this, the immune response for nestlings in the Iberian study area was measured over two consecutive breeding periods. This was accomplished by injecting 11-day old nestlings with a saline solution with measurements of the injection site occurring both prior to injection and 25 hours post-injection. In addition, nestling tarsus length and body mass were measured at 12-days old. The data were then statistically analyzed to determine helper influence on nestling fitness. From this, they found that the presence of helpers at a nest had a significant influence on the nestling's immune response. Nestlings that had helpers assisting in their care saw increased levels of immune response relative to those nestlings without helpers. In addition, they determined that tarsus length had a positive correlation with helper number, while body mass was not correlated with helper number. These results were significant as they determined a possible health factor that could have influenced helping

behaviour in a corvid species, even if that factor only had a subtle effect on nestling fitness. Future studies are needed to determine the actual factors leading to the results observed in the study. Research should focus on determining whether decreased food stress, or even the quality of the food brought by helpers itself would be a factor that would lead to the observations and results presented in the study.

Contribution: This article was chosen because it showed how helper presence has high associations with reproductive success in this species. It also advanced the understanding of why cooperative breeding occurred in this species of corvid through the investigation of helper influence on immune response. The research supported previous studies that looked at how helper provisioning could bolster nestling immunity via increased food access. The work also posits future areas of exploration, including the exact role that helpers may have in the increased fitness of chicks, as well as long-term studies to determine long-term benefits from helping behaviour.