Evolution of Cooperative Breeding in the Galapagos
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Abstract: This paper explores the environmental pressures that select for cooperative breeding in the Galapagos mockingbird, Mimus. parvulus and the Galapagos hawk, Parabuteo unicintus. Both species possess an evolutionary lineage that predisposes them to cooperative breeding. The two environmental pressures that will be discussed are food scarcity and a variable, unpredictable climate. Food scarcity drives the selection for helping behavior in cooperative mockingbird groups because dominant pairs within territories may sabotage breeding attempts of subordinate pairs, which increase their inclusive fitness by demonstrating helping behavior toward the dominant pair’s hatchlings. Food scarcity drives cooperative polyandry in Galapagos hawks because high levels of competition between females result in one female per territory, and increased survivorship for cooperative group members gives cooperative breeders a long-term reproductive advantage. Cooperative breeding as a selected response to a variable, unpredictable climate allows for reproduction rates and helping behaviors rates that allocate resources sustainably.
INTRODUCTION

Cooperative breeding is a mating system in which three or more individuals behave like parents toward a single brood (Carrete et al. 2006). Roughly three percent of birds worldwide are cooperative breeders. This breeding strategy usually occurs in areas of limited land and resources (Koenig and Dickinson 2004). In the Galapagos, the four species of mockingbird, *Mimus parvulus*, *Mimus trifasciatus*, *Mimus macdonaldi*, and *Mimus melanotis* are all cooperative breeders (Curry and Grant 1989), as is the Galapagos hawk, *Buteo galapagoensis* (Faaborg 1985). This paper will focus on the evolution of cooperative breeding in *Mimus parvulus* and *Buteo galapagoensis*.

There are two general conditions that tend to promote the evolution of cooperative breeding. The first is an evolutionary lineage that is predisposed to cooperative breeding (Arnold and Owens 1998). According to the phylogeny of the *M. parvulus*, it has close relatives, *Mimus longicaudatus* and *Mimus gilvus*, which are cooperative breeders (see figure 1). However, their closest relative on the

![Figure 1 Phylogenetic tree that shows relationship between M. parvulus and M. gilvus, cooperative breeders, and M. gundlachii, a non-cooperative breeder. (Lovette et. al 2012)
mainland, *Mimus gundlachii*, does not breed cooperatively (Lovette et al. 2012). Similarly, a relative of the Galapagos hawk, *Parabuteo unicinctus* breeds cooperatively, but its closest relative, *Buteo swainsoni* does not (Faaborg and Bednarz 1985). Both the Galapagos mockingbird and Galapagos hawk have a lineage predisposed to cooperative breeding, yet since both species display a breeding strategy distinct from that of their closest relatives on the mainland, there must be an environmental pressure that promotes cooperative breeding in the Galapagos.

Indeed, ecological facilitation is the second condition required for the evolution of cooperative breeding (Arnold and Owens 1998). This paper is centered on the environmental factors in the Galapagos that drive the selection for cooperative breeding.

**HYPOTHESES**

- Food scarcity in the Galapagos promotes the evolution of cooperative breeding.
- The unpredictable, variable climate in the Galapagos promotes the evolution of cooperative breeding.

This paper will explore if and how each of these environmental factors – food scarcity and an unpredictable, variable climate – affect the evolution of cooperative breeding in both Galapagos mockingbirds and Galapagos hawks.
RESULTS

Food scarcity and cooperative breeding in *M. parvulus*

Galapagos mockingbirds live in territorial groups. The dominant pair within the group, which is typically composed of the oldest members, breeds regularly. Many of the subordinate group members help take care of the dominant pair's chicks. A study on Genovesa demonstrated that the entirety of the land area was divided into mockingbird territories (Curry 1988).

This extreme territoriality can be explained from the perspective of food scarcity. Mockingbirds are omnivores, and their food supply is relatively immobile throughout the year. Unlike finches on the Galapagos, which are not cooperative
breeders and which often move around to follow their food source throughout the year, mockingbirds spend energy defending a piece of land (Curry and Grant 1989).

Within the territorial groups, there is strong competition for resources on the limited land. The dominant pair is a formidable competitor for the scarce resources of the limited territory. They sabotage the breeding attempts of subordinate members, harassing them as they attempt to copulate, or destroying their nests. This leaves more available resources for the young of the dominant pair (Brown et. al 1997). Many of the subordinate members help care for the dominant pair’s young (Kinnaird and Grant, 1982), and are more likely to help if they do not have young of their own. This helping behavior can be explained by kinship selection. The helpers and recipients of the help are usually related, which means that helping behavior increases inclusive fitness (Kinnaird and Grant, 1982). From their research on cooperatively breeding mockingbirds on Genovesa, Grant and Kinnaird concluded “helping enhanced the indirect component of the fitness of the helper (1982).” Hatchlings that receive help are 19% more likely to fledge, so the subordinate members, by increasing the likelihood that their relatives survive, pass on their genes indirectly (Curry 1988).

Mockingbird territories on Genovesa are saturated (Grant and Kinnaird, 1982), meaning that it is nearly impossible for individuals to survive if they are not members of a territorial group. The competition for food can be severe. Subordinate members that are part of groups have the benefit of surviving on the resources that belong to the group, and of passing on genes indirectly. Furthermore, if they live long enough, they may
inherit the territory and become dominant; usually the oldest members are dominant (Curry and Grant, 1990).

Food scarcity promotes territoriality, and food scarcity within the territories promotes selection for dominant pairs that will sabotage other pairs, decreasing competition, and increasing the amount of help they receive.

**Climate Unpredictability and Cooperative Breeding in M. parvulus**

The unpredictable climate of the Galapagos means that the changes in food supply can come as a surprise. In rainy periods, more mockingbirds breed (see figure 2). When there is more rain, the dominant pair does not sabotage as many subordinate pairs. The dominant pair still receives help, though usually less than when they sabotage more birds. Other pairs sometimes receive help as well (Curry and Grant 1989).

During rainy seasons, subordinate pairs have a chance to pass on their genes directly. If this never happened, it is unlikely that natural selection would have favored this system, since most of the population would have little direct reproductive fitness.

The unpredictability, not just the variability, of the climate is important in the evolution of cooperative breeding. Whenever it starts raining, it is in the subordinate pairs’ interests to breed. If it continues to rain, the dominant pair will typically allow the
nesting to proceed. However, if a drought ensues, the dominant pair will likely sabotage at least some of the subordinate pairs. This happens with minimal energy drains on the subordinate pairs. In a drought, it is unlikely that a subordinate pair would be able to successfully compete for resources, so no energy is wasted attempting to raise young (Curry and Grant, 1989). The subordinate member can then help pass on its genes indirectly by allocating resources to other hatchlings.

Cooperative breeding is a strategy that allows for the allocation of scarce resources of a limited territory to be distributed in a climatically responsive manner; when it is wet, more hatchlings are permitted, and when it is dry, there is more helping behavior to support fewer hatchlings.

**Food Scarcity and Cooperative Breeding in**

**B. Galapagoensis**

Not all Galapagos hawks are cooperative breeders. On Fernandina, they breed monogamously. On Santa Fe, 33% of territories belonged to cooperatively breeding groups, and on Santiago, 87% of the territories were occupied by cooperative groups. Cooperative breeding tends to be more common on islands with less food supply, and where all of the land is divided into territories; only on some islands does polyandry have the selective advantage (see figure 4) (Faaborg and Bednarz 1985).
correlation alone speaks strongly in favor of the hypothesis that food scarcity promotes the evolution of cooperative breeding.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mating system</th>
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<th>No. of males</th>
<th>No. of young</th>
<th>No. young per nest</th>
<th>No. young per male</th>
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<td></td>
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<td>23</td>
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<td>0.1</td>
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<tr>
<td></td>
<td>Polyandry</td>
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<td>48</td>
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<td>71</td>
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<td>0.89</td>
<td>0.34</td>
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</tbody>
</table>

Figure 2 Data from a three-year study. On Santa Fe, monogamy yields more young per nest. On Santiago, polyandry yields more young per nest. Males in monogamous pairs had more young in during the year of this study. (Faaborg and Bednarz 1985)

Hawks are highly territorial hunters, and they often catch prey in groups. Food scarcity helps explain the formation of territorial groups, since it is beneficial to have protected hunting ground and other individuals to hunt with. Because the females are extremely competitive for the scarce food resources, there is typically only one female per territory. All of the males, typically 2-5 per female, must mate with the same female if they want to remain a member of the territorial group and mate at all. There is a disproportionate number of males because when the hawks are too young to form a breeding group, they wander around the island, hunting by themselves or in transient groups. Females are less skillful hunters, and are much more likely to die before reaching breeding age (DeLay et. al, 1996).
In any given year, a male member of a monogamous pair will have more fledglings than a male member of a polyandrous cooperative group. However, hawks that live in groups tend to live longer; group members have a survivorship of 85% over two years, compared with 40% survivorship of non-cooperative group members (see figure 4). Therefore, over the course of a lifetime, the males in cooperative groups have the reproductive advantage, since even with fewer fledglings per year, on average, they have more fledglings per lifetime (Faaborg 1985).

Also, as male members of a group die off, they are not replaced. Therefore, the longest-surviving male can pass down his genes regularly for the remainder of his life (DeLay et. al, 1996). Natural selection favors long-lived cooperative breeders, since they have the greatest reproductive advantage.

Food scarcity promotes territorial groups, and because the females are hyper-competitive, there is typically only one female per territory, promoting cooperative polyandry. Members of cooperative groups, even though they pass on their genes less frequently, have the overall reproductive advantage.
Climate Unpredictability and Cooperative Breeding of *B. Galapagoensis*

The relationship between climate unpredictability and cooperative breeding in Galapagos hawks is not well studied. However, Faaborg’s 1980 study of Galapagos hawks suggests that during dry years, monogamous hawks produced 0.2 more fledglings per nest than the cooperatively breeding hawks. In the wettest year of the study, however, cooperative groups produced twice as many fledglings per nest.

*B. galapagoensis*

This pattern indicates that when the climate is such that food resources are relatively abundant, the cooperative groups are more able to capitalize on the resources than the monogamous pairs are. In the drier years, it appears that the cooperative groups are more likely to conserve their energy rather than to struggle
to support many young when resources are scarce. Perhaps this is because cooperative breeders live longer, and so can afford to wait for a wet year.

However, the data from this study is limited, and consists of only a few years. More research is needed, but from the preliminary observations, the adaptation of cooperative breeding appears to allow Galapagos hawks to better take advantage of the variable climate.

**CONCLUSION**

Both food scarcity and an unpredictable climate appear to affect the evolution of cooperative breeding in both *M. parvulus* and *B. galapagoensis*. In both cases, food and land scarcity promotes the formation of territorial groups. In the case of the mockingbirds, the dominant pairs encourage helping behavior within the territories in order to allocate the scarce resources to their own young. In the case of the Galapagos hawks, the strong competition for resources amongst the females leads to a system conducive to cooperative polyandry, since there is typically only one female per territory.

Both cooperative breeders are able to take advantage of the wetter years. In both species, the number of fledglings increases during wet periods. In mockingbird groups, helping behavior decreases during the wet years while breeding increases. In the dry years, there is more helping behavior, and all of the resources are allocated to fewer offspring. In contrast, the hawks appear to increase the amount of helping behavior during the wet season, since they are able to take advantage of the extra resources during rainy periods. That extra food is brought to the chicks by the helpers. Cooperative breeding as a selected response to an unpredictable
climate allows for sustainable reproduction, because there are fewer offspring
during the dry years, and during the wet years, the extra resources are utilized – in
the mockingbirds, they are utilized by the subordinate members which are
permitted to breed, and in the hawk groups, they are utilized by the extra chicks
which the group is able to raise.

Both climate and resources scarcity appear to promote the evolution of
cooperative breeding in the Galapagos.


Curry, R. L. and Grant, P. R., “Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment,” Cooperative Breeding in Birds: Cambridge University Press.


