Avian Altruism and Conservation Conundrums: The Mockingbirds of Galapagos

Figure 1: Galapagos mockingbird perched on an Opuntia cactus pod on Santa Fe Island. (Author)

Michael Zhu Chen

Professor Bill Durham – Sophomore College: Darwin, Evolution, and Galapagos

Stanford University

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ABSTRACT

The mockingbirds of the Galapagos Islands have played an important role historically and biologically. Charles Darwin was originally inspired by the different physical characteristics of the mockingbirds on the various islands of the archipelago. More than two hundred years later, biologists are studying their history of speciation and their unique social behaviors. This report investigates the evolutionary origins of the cooperative breeding behavior of the mockingbirds of Galapagos, in which non-breeding birds become “helpers-at-the-nest” and assist pairs of breeding birds in raising offspring. Such “altruistic” behavior must have some benefit to the helper by nature of having been selected for, but studies have found that there are no direct fitness benefits to the helper. This raises the question: What are the benefits to helpers in the absence of direct fitness benefits? Two hypotheses are proposed: Hypothesis 1 is that helpers are closely related to breeders and hypothesis 2 is that offspring raised by helpers reciprocate help. Data from case studies of Galapagos mockingbirds on Genovesa Island appear to support both hypotheses. Lastly, this report examines the current status of mockingbirds of the Galapagos and the conservation challenges facing the critically endangered Floreana mockingbird.
INTRODUCTION

When Charles Darwin first set foot in the Galapagos Islands, he was immediately captivated by the incredible diversity of flora and fauna on the archipelago. The mockingbirds of Galapagos fascinated Darwin as an example of species divergence on the different islands. In the *Voyage of the Beagle*, Darwin writes: “my attention was first thoroughly aroused by comparing together the various specimens … of the mockingthrush” (Darwin 1839). Indeed, his inspiration for the theory of natural selection may be partially attributed to his observations of the diverse morphology of the mockingbirds of Galapagos.

There are four species of endemic mockingbirds that occupy four different regions of the archipelago (figure 3), which suggests that the ancestor radiated via allopatric speciation.
(Arbogast et al. 2006; Curry & Grant 1990). A phylogeny based on mitochondrial and nuclear DNA sequence markers is shown in figure 4. The Hood (Espanola) mockingbird, *Mimus macdonaldi*, is found only on Espanola Island. Similarly, the San Cristobal (Charles) mockingbird, *Mimus melanotis*, is found only on San Cristobal Island. The Floreana mockingbird, *Mimus trifasciatus*, is now extinct on its home island of Floreana, but small populations remain on the islands of Champion and Gardner near Floreana (Grant et al. 2000). The Galapagos mockingbird, *Mimus parvulus* (a specific species of mockingbird, not to be confused with mockingbirds of Galapagos in general), is the most common species of mockingbird in the Galapagos. It has a range that spreads across the northwest corner of the archipelago that includes Santa Cruz, Santiago, Isabela, and Fernandina (Curry & Grant 1990).

![Figure 3: Map of Galapagos Islands showing the distribution of mockingbird species. (Curry 2010)](image)

![Figure 4: Phylogeny of the mockingbirds of the Galapagos based on mitochondrial and nuclear DNA sequence markers. (Lovette et al. 2012)](image)
Despite their classification as distinct species, the various mockingbirds of Galapagos share many features including a long slim beak, long legs, and a long tail. They differ primarily in their size, wingspan, beak, and plumage (Arbogast et al. 2006). For instance, the Galapagos mockingbird has two horizontal white stripes on its wing whereas the Floreana mockingbird has three—hence, the name *trifasciatus* (Durham, personal communication). The Espanola mockingbird is the largest of the four species and has a long curved beak, followed by the slightly smaller Floreana mockingbird and the moderately smaller San Cristobal and Galapagos mockingbirds (Curry & Grant 1990).

Three out of the four species of mockingbird in Galapagos (all except the San Cristobal mockingbird1) participate in cooperative breeding, in which so-called “helpers-at-the-nest” assist pairs of breeding birds (Curry 1989). Helpers tend to be young adult mockingbirds that have not yet acquired their own mate and/or territory on which to breed (Grant & Grant 1979). These birds have been found to help pairs of monogamous breeders for up to 3 years, assisting in various aspects of breeding including foraging and territory defense (Curry & Grant 1990). Such behavior is quite unusual in the animal kingdom and may be described as “altruistic,” but not in the traditional sense of the term. Since the underlying intent of animal behavior generally cannot be determined, altruism in evolutionary biology is simply defined as an action that increases the reproductive fitness of another individual, with no consideration of the intentions.
with which the action was performed (Okasha 2003). This definition stands in contrast to human altruism, in which intentions determine the altruistic nature of actions.

The altruistic helping behavior observed in the mockingbirds of the Galapagos is probably an adaptation that arose through natural selection. Natural selection promotes behaviors that enhance the survival and reproduction of individuals and their genes (Mayr 2001). For helping behavior to be maintained in the mockingbird population, the benefits to the breeders and helpers must exceed the costs of the behavior. Studies have shown that as expected, helping behavior benefits the breeders by reducing the workload on the parents, especially the father (Grant 1983; Kinnaird & Grant 1982). Helpers ease the burden of raising young on the breeders by providing food and defense for the offspring.

Helping behavior must also benefit the helper bird in order to be evolutionarily favorable. Mockingbirds are intensely territorial, and it is possible that territorial constraints limit the number of birds that can breed in a given year, prompting the non-breeding birds to become helpers (Curry 1989). However, this does not explain why non-breeding birds would actively engage in helping behavior. By engaging in helping behavior, the helper bird may receive direct benefits (such as higher survival rates in groups) and indirect benefits (such as improving the
transmission of its own genes by helping closely related breeders). If there were no benefits to the helpers, the behavior would not be observed since it would not have been naturally selected for. Studies have found that the direct fitness and survival benefits of helping are negligible (Curry & Grant 1990; Robert L Curry 1988). A study has also found that the offspring of breeders with past breeding experience do not have increased survival rates compared to novice breeders, suggesting that helper birds do not gain parenting skills and become better parents in the future from their experience as a helper-at-the-nest (Kinnaird & Grant 1982). This raises the question: What are the indirect benefits to helpers? Two hypotheses pertaining to this question will be explored in the remainder of the report: Hypothesis 1 is that helpers are closely related to breeders and hypothesis 2 is that offspring raised by helpers reciprocate help.

The remainder of the report will focus on the conservation challenges faced by the mockingbirds of the Galapagos. Similar to other species on the archipelago, the mockingbirds of the Galapagos are vulnerable to environmental changes due to their small populations and their uniquely adapted behaviors such as helpers-at-the-nest (Curry & Grant 1990). These behaviors and their unique adaptations to the isolated environment of the Galapagos Islands may hinder their ability to respond to human influences. Protecting the four endemic mockingbird species of Galapagos is a priority because of their rarity and because they comprise a substantial portion of the seventeen species of mockingbirds worldwide (Lovette et al. 2012). Galapagos mockingbirds are prevalent across the major islands of the archipelago and have been assigned a “least concern” conservation status (BirdLife International 2012). On the other hand, the Hood mockingbird and San Cristobal mockingbirds have been assigned “vulnerable” and “endangered” statuses and the Floreana mockingbird is “critically endangered” (BirdLife International 2015). This section of the
report will focus on the current status and conservation of the critically endangered Floreana mockingbird.

Figure 7: Galapagos mockingbirds are fairly common on the northwest and central islands of the archipelago. (Author)

METHODS

A case study of Galapagos mockingbirds on Genovesa Island will be referenced in this report since there is a significant dataset on mockingbird behavior from Genovesa Island. Similar behaviors have been observed in mockingbirds on other islands, but were monitored less thoroughly (Curry & Grant 1990). It is interesting to note that many of the scientific studies on this topic would

Figure 8: Map of Genovesa Island. (Robert L. Curry 1988)
have been difficult to conduct in a continental environment. The naiveté of the Galapagos mockingbirds allows researchers to closely monitor its natural breeding behaviors. Lastly, information on the current status and conservation of the Floreana mockingbird was obtained from studies of the remaining population on Champion Island.

**RESEARCH QUESTION:** What are the indirect benefits to helpers?

- **HYPOTHESIS 1:** Helpers are closely related to breeders.

Although helpers may not benefit directly from helping at the nest, helpers may receive benefits in the form of increased propagation of shared genes if they are closely related to the breeders. By helping breeders that are closely related, helpers would be helping offspring with which they share genetic material. Thus, helping would benefit the helper by vicariously transferring a portion of its genes through the success of the offspring. In this way, helping may be a form of kin selection, in which an individual vicariously passes on some portion of its own genes by enhancing the reproductive success and survival of close relatives (Okasha 2003). Kin selection is a mechanism of natural selection that is also observed in other species including Arabian babblers (*Turidoides squamiceps*) (Clutton-Brock 2002). Individuals of these species risk their own survival to guard others in their family group from predators.

Figure 9 shows a correlation between the genetic relatedness of helpers to the breeders they are helping and the percentage of birds that actively engage in that type of helping relationship. The percentage of helping observed for breeder birds that are closely related (e.g. helpers helping their parents or a parent and a sibling) is 28%. The percentage of helping is greatly reduced to 11% and 16% for breeders that are not as closely related. The difference
between the 11% and 16% figures is not significant since a difference of 5% is equivalent to a difference of only 3 birds. These data support the notion that helpers are more likely to help breeders that are closely related.

<table>
<thead>
<tr>
<th>Relatedness category</th>
<th>Relationship of breeders to helper</th>
<th>% helping</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r \geq 0.5$</td>
<td>parent x parent, parent x sibling</td>
<td>28</td>
<td>94</td>
</tr>
<tr>
<td>$0.38 \geq r \geq 0.12$</td>
<td>parent x half-sibling, parent x non-relative, full sibling x non-relative, offspring x non-relative</td>
<td>11</td>
<td>53</td>
</tr>
<tr>
<td>$r \approx 0$</td>
<td>Both non-relatives</td>
<td>16</td>
<td>145</td>
</tr>
<tr>
<td>$P^d$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ After Curry (1988a).
$^b$ Includes birds of unknown sex.
$^c$ Estimated minimum relatedness between potential helper and nestlings.
$^d$ $\chi^2$ tests of independence; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

Figure 9: Chart showing the correlation between relatedness and helping rate. Birds are more likely to help birds that are closely related. (Curry & Grant 1990)

Not only do helpers tend to help breeders that are closely related, but helpers also improve the survival of the offspring that they help to raise. As shown in figure 10, the average number of offspring that fledge is increased by about 0.75 fledglings with one helper-at-the-nest. This is a substantial increase in survival rate and supports the kin selection hypothesis. By helping closely related breeders, helpers improve the survival of the offspring with which they share a significantly percentage of genetic material. Thus, the hypothesis that helpers tend to help closely related breeders is supported and helpers do benefit indirectly by enhancing the transmission of their genes vicariously through closely related offspring.
HYPOTHESIS 2: Offspring raised by helpers reciprocate help.

Helpers may imprint upon the offspring and increase the likelihood that the offspring will reciprocate help when they become mature. The likelihood of reciprocation may be enhanced further since the offspring raised by helpers are more likely to survive to adulthood as shown in hypothesis 1. Reciprocation would benefit the helper in the same way that breeders benefit from helpers.

Figure 11 shows the relationship between the number of currently breeding birds that previously helped to feed offspring in the nest and the percentage of the surviving offspring that reciprocated help when they became adults. The authors control for the differences in the survival rate of offspring due to differences in feeding by only considering the offspring that
survive to adulthood when calculating the percentage of birds that are helping. When both of the current breeders had previously fed the offspring as helpers-at-the-nest, the percentage of the offspring that return to help them in return is 30%. This percentage decreases to 15% and 7% as the number of breeders that had previously helped to raise the offspring decreases to one and zero, respectively.

<table>
<thead>
<tr>
<th>Number of breeders</th>
<th>% helped</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both</td>
<td>30</td>
<td>96</td>
</tr>
<tr>
<td>One</td>
<td>15</td>
<td>33</td>
</tr>
<tr>
<td>Neither</td>
<td>7</td>
<td>104</td>
</tr>
</tbody>
</table>

This percentage decreases to 15% and 7% as the number of breeders that had previously helped to raise the offspring decreases to one and zero, respectively.

Figure 11: Chart showing the correlation between the number of current breeders that previously fed another breeding pair's offspring and the rate at which those same offspring help the current breeders in return. The helping rate increases as the number of past helpers increases. (Curry & Grant 1990)

These data show a clear correlation between previous helping of offspring and future reciprocation of help from the mature offspring, suggesting that offspring raised by helpers do indeed reciprocate help. The authors state that on average, “15% of [helpers] that bred after they had helped…received help from the birds that they had helped to raise” (Curry & Grant 1990). However, one could argue that the reciprocation is simply due to kinship–since helpers tend to help closely related breeders (as seen in hypothesis 1), the offspring may simply be reciprocating help due to the same mechanism of kin selection rather than a true mechanism of reciprocation.
that expected from a mechanism based on association than from kinship alone” (Curry & Grant 1990). In fact, “56% of potential helpers fed unrelated nestlings whose parents had fed the potential helpers but none fed related nestlings whose parents had not fed the potential helper in the nest” (Curry & Grant 1990). This evidence is significant because it shows that helpers who fed unrelated offspring still received help in return despite not being genetically related, as kin selection would predict. However, none of the offspring went out of their way to help related breeders if the breeders had not previously fed the offspring in the nest. This serves as a negative control and suggests that reciprocation is not simply due to kin selection, supporting hypothesis 2.

Combining hypotheses 1 and 2 suggests that associative learning may be the mechanism underlying both kin selection and reciprocation. Associative learning in the nest may allow breeders and helpers to imprint on the offspring during feeding and can act as a heuristic mechanism for offspring to learn genetic relationships in the absence of other cues. This form of learning is beneficial for offspring so that they can identify birds that are closely related and help them in the future (kin selection). However, associative learning is not a foolproof mechanism. When an unrelated bird acts as a helper, the offspring will also learn to reciprocate help towards the unrelated bird (reciprocation). Thus, the kin selection process of hypothesis 1 and the reciprocation process of hypothesis 2 may occur as a result of the same underlying mechanism of associative learning.
STATUS AND CONSERVATION OF THE FLOREANA MOCKINGBIRD

The Floreana mockingbird has been decimated by invasive species ranging from the invasive botfly to black rats and feral cats, dogs, and goats (Curry 1986; Grant et al. 2000). The presence of invasive species on the main island of Floreana extirpated the species from the island—only two small populations remain on the nearby islets of Champion and Gardner, shown in figure 13 (Grant et al. 2000).

![Figure 13: Left: Map showing Floreana Island, Champion Island, and Gardner Island. (Grant, Curry, Grant 2000) Right: A view of Champion Island at sunset from Floreana Island. (Author)](image)

Only a small population of about 50 birds currently remains on Champion Island (Antonio-Galapagos National Park guide, personal communication), and a single natural or human caused event could wipe out the entire population. The population of Floreana mockingbirds on Champion Island is shown in figure 14, shaded based on whether the bird is a breeder or a non-breeder. In this figure, the Floreana mockingbird’s vulnerability becomes clear. Since the remaining population is so small, there are relatively few non-breeding birds that are capable of helping-at-the-nest. As discussed earlier in the report, helpers are important for the reproductive success of breeders. Low numbers of helpers interfere with the natural cooperative
breeding behavior of the mockingbirds, reducing their ability to endure natural and human-induced environmental changes.

The small population of mockingbirds creates another challenge: genetic drift and inbreeding. Before they were extirpated from Floreana, Floreana mockingbirds could immigrate between Floreana and the small islets of Champion and Gardner, allowing for genetic variation and a larger gene pool. With only two small populations remaining on two distant islands, the mockingbirds suffer from inbreeding and genetic drift, which weakens their immune systems among other problems. The genetic heterozygosity of the Champion population is estimated to be half of its original value (Grant et al. 2000), indicating that the genetic diversity of the population has declined significantly. The Floreana mockingbird may be more susceptible to diseases such as the avian pox as a result.
In order to protect the Floreana mockingbird, steps have been taken to initiate a captive breeding program, with the eventual goal of reintroducing the birds to Floreana Island. The captive breeding program crosses birds from Champion Island with birds from Gardner Island to generate more formidable hybrids by increasing their genetic diversity (Karl Campbell, personal communication). Additionally, steps have been taken to plan the eradication of the invasive black rats on Floreana Island to restore the habitat to its natural state before the hybrids are reintroduced. Karl Campbell and his team at Island Conservation, a non-governmental organization, are working to plan the eradication, which is one of the largest scale eradications of small rodents ever performed on an island (Hanson & Campbell 2013). Finally, local and global education may help to inform people about their own environmental footprint and about the delicate state of these endemic species.

CONCLUSIONS

This report has explored the indirect benefits to helpers-at-the-nest. Two hypotheses were investigated: hypothesis 1 is that helpers are closely related to breeders and hypothesis 2 is that offspring raised by helpers reciprocate help. Both hypotheses were supported by a case study of a representative population of Galapagos mockingbirds on Genovesa Island. The possibility that a heuristic mechanism of associative learning underlies both kin selection and reciprocation was also discussed, and it seems plausible that this mechanism would lead to the observed behavioral phenomena. Lastly, the current status and conservation challenges of the Floreana mockingbird were discussed with respect to the Champion Island population. Current projects to breed Floreana mockingbirds in captivity and reintroduce the species to Floreana Island were also discussed.
The San Cristobal mockingbird has never been reported to participate in cooperative breeding behavior. This may be due to several reasons, one being that the habitats of San Cristobal Island are exceptionally diverse, which results in an abundance of breeding territory (Curry & Grant 1989). The plentiful breeding territory is reflected in the formation of smaller groups of mockingbirds on San Cristobal Island and a reduction in the number of non-breeding birds. Another possible reason is that the population of the San Cristobal mockingbird has been reduced by predation from invasive land mammals, contributing to an even larger surplus of breeding territory. As the proportion of non-breeding birds decreases due to these two combined effects, the number of helpers is substantially reduced to the point where helping has not been reported.
ACKNOWLEDGEMENTS

I would like to thank Professor Bill Durham, Annette Esquibel, Mari Jaeger, and my classmates for making this expedition such an incredibly life-changing experience. You all are my favorite charismatic & endemic species!

Figure 15: The diverse endemic specimens of Galapagos SoCo! (Wallace)
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