Carina Liebmann October 17, 2012
Midterm Paper

Manakins are small birds where the male members participate in lekking, something many organisms do but manakins do a little differently then most. [3] Lekking is a place where a group of males display to females in an attempt to attract and mate with them. This is an example of sexual selection, where one sex, in this case the females, has a choice of males and picks which to mate with based off of their displays and characteristics. Because of the competitive nature among males wanting the females' attention, most often males compete against each other in leks.[10] In the case of manakins, however, cooperation instead of competition can be seen between males during lekking displays. [3]

Manakin males form groups of about 13 in territories used for lekking. An alpha male and a beta male play the main roles in the display, working together to sing duets and dance for the females. [7] Singing in unison is an important first step for the males, as this is what will initially attract the female.[9] The dancing ritual then consists of the alpha and beta males dancing, jumping, and flying over one another, occasionally with the other males in the territory jumping up at down separately nearby.[5] The main cooperative dance between the alpha and beta, often referred to as the "leap frog dance" takes place on a display branch. Closer to the female, the alpha males jumps up, hovers and the beta males slides forward. The alpha then lands behind the beta and the beta jumps up, and the alpha slides forward, creating a continuous circular dance.[6] Manakin males displaying the "leap frog" can be seen in Appendix A. The alpha also participates in some dance moves alone.[2] In total the pair, or individuals, may perform up to eleven different moves, "the pip flight, paired slow flight, up-and-down, leapfrog dance, back-and-forth, eek displays, slow solo flight, quick-turn, swoop, bounce, and bow."[4] Over several years the same pairs work together, both maintaining their respective role of alpha or beta.[1] The beta male is dedicated, participating in "more than 3 million toledo calls" and engaging in "more than 1000 hours of dual-male leapfrog hops and labored butterfly flight" over the course of many years. [5] Still, despite the beta males efforts in the mating ritual and attracting females, the alpha is the only one to mate with the females. [5] Since manakin parental care is entirely maternal, the alpha male's only role to have offspring is to mate with the female, spreading his genes. After mating the male is able to right away seek out another female, again displaying with the beta male. [4] As the beta male dedicates most of its time to attract females, only the alpha males mates with her, so why does the beta male help the alpha male?

Two different hypotheses that try to answer this question are shown in Table A. The predictions based on each hypothesis can also be seen. The first hypothesis deals with kin selection. This suggests that the beta male is a relative of the alpha male, sharing some genes. By helping the alpha male some of the beta's genes, the ones shared with the alpha male, will get passed on. [7] If the beta's main goal is to get as much of its genes spread by helping a relative, the beta should choose the alpha it will help based on which alpha in the area is their closest relative available.

Another hypothesis is that the beta male benefits long term from helping the alpha, rather than receiving immediate reproductive benefits. Helping the alpha could lead to the beta male taking over when the alpha male leaves the territory or dies. [1] The beta may also be learning to

improve it's dance and song to maximize its reproductive success when it becomes an alpha. [9]

To test the first hypothesis, whether the beta is helping the alpha due to kin selection, DNA tests were performed to see whether the beta and alpha males are closely related. [3] In addition to testing and comparing individual pairs, multiple pairs of manakins in neighboring territories were tested for relatedness. Relatedness between individual manakins throughout the area where compared to their the relatedness of parterns. This was to determine whether the pairs where as closely related as possible or whether there were other pairings that could have happened that could have been more closely related. [7]

Out of the pairs of manakin males tested for relatedness only 16 of 33 tested pairs were positively related. This means kin selection does not apply to manakins, as the majority of the betas are not helping out relatives, therefore not having their genes spread through the alpha successfully reproducing. [7] The argument that perhaps no close relatives were available to the betas is dismissed with the test where relatedness relative to only the other possible options of pairing was studied. The DNA results from pairs across multiple territories found that the beta and alpha males were the closest related pair possible for only 1 of 13 pairs studied, concluding that most manakin males were not with their closest relative even if they could be. [7] Appendix B shows the relatedness of pairs as compared to other relatedness in manakins, as well as relatedness of pairs made at random, showing the existing pairs are no more related then if they were made at random. [1] Betas and alphas do not pair based off how related they are, proving relatedness and kin selection is not the reason that cooperation occurs between male manakins. [3]

The second hypothesis, whether there is a long term benefit for the beta, becoming an alpha, was tested through examining the manakin male behavior. In multiple tests the observed alpha was removed from multiple territories and the behavior of the beta was observed. Test were done where the alphas were removed naturally, it died or moved to another territory, and tests were done where the alpha was relocated by people. [1] Another test further explored the longterm benefit of helping the alpha, the possibility the beta learns from the alpha to become a successful alpha later. This was tested by recording and tracking the singing of the beta and alpha over years. The consistency of the song and the betas ability to match the alphas frequency was tracked. [9]

Through observing manakins throughout multiple mating seasons it was discovered that beta males were more likely to become alphas over non beta males, 10 out of 67 betas became alphas the following year while 6 of 164 non betas males became alphas. However, when the alphas were removed, either naturally or by people performing the tests, the betas did not take on the role of alphas, or if they did they did not last long as an alpha male. Even if the beta males initially displayed more alpha like behavior, most did not hold their position. They often became betas to new males. [1] This find suggests the beta does learn from the alpha, and they help the alpha to learn, not just to wait to eventually take over the role of alpha. The results from the test with the removed alphas suggest the betas in those experiments where generally not yet skilled enough to take the alpha position. [8] It was observed that some betas who briefly held and then lost alpha positions did not seem to perform as well as other alphas yet, suggesting they needed more practice first. Whether more time with an alpha is what helps the beta improve is explored.

The test of beta males' singing skill suggested further that the role of beta is a time of

practice. As age increased, so did the betas singing skill. Their singing was more consistent and they matched the alpha's frequency with more accuracy the longer they were a beta. [9] Beta males were also generally younger than the alpha male, suggesting growth in skill and learning that leads to becoming an alpha. With such a complex dance, with about 11 moves and singing, the practice helps the beta become better both at singing and dancing. [1] This is important since better frequency matching in song, as with better cooperation in dance, attracts more females. [9] Not only does the improvements mean the beta will later be more successful at attracting females as an alpha, but betas having skill when still a beta helps their lek display area become popular among females. Females often return to territories they were impressed with in following years. This means if a manakin male works harder as a beta, when it becomes an alpha male it will have more females coming to mate. [7]

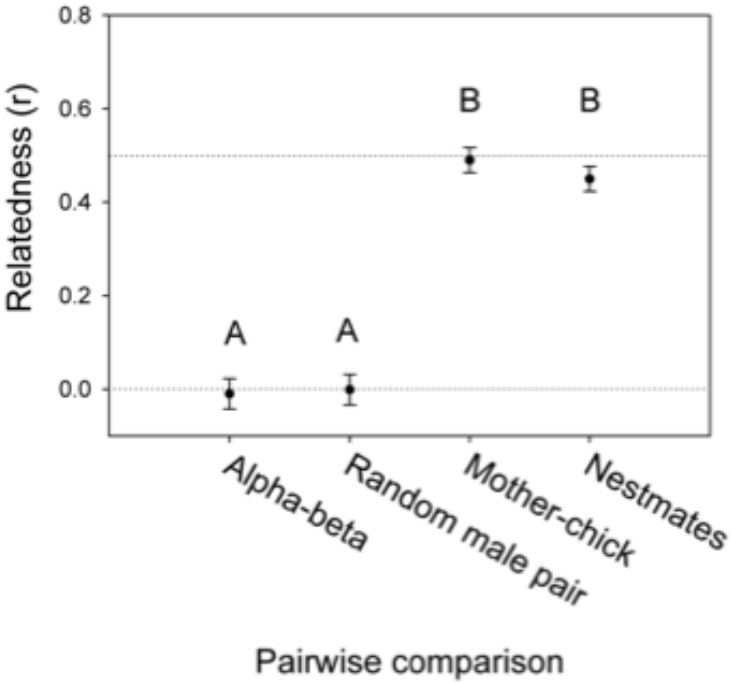
In lekking, male competition is common as males compete for female attention. A manakin beta male however, helps an alpha male even though only the alpha gets to mate. This is not because the beta male is related to the alpha and helps spread its own genes by helping the alpha, but rather helping has a long term benefit. Once ready the beta is most likely to become the alpha if the current alpha leaves or dies, but it first must develop its skill through the experience of helping, otherwise it is not ready to take over the alpha role. [6]

Appendix

Hypotheses	Predictions		
	Beta and Alpha Relation	Reproductive Benefits	Role of Female Selection
Betas help alphas due to Kin Selection (indirectly passing on some genes by helping a relative mate)	When choosing a partner betas will choose the alpha most closely related to them to get the most genes possible passed on through the reproduction of the alpha.	Benefit is immediate, during the time of the beta helping the beta's genes are getting passed on.	Individuals cannot impress the female, so it is more beneficial for the beta to help out an alpha relative and get some genes passed on. Females attracted to cooperative dance and singing, encouraging cooperation in lekking.
Betas help alphas to later become an alpha and to develop skills necessary to be an alpha.	The alpha acts as a temporary leader for the beta. The beta will be younger, having less experience and therefore requiring guidance.	Benefit is long term and not immediate. The beta will become an alpha because it is "next in line" and uses skills learnt from helping.	Individuals cannot impress the female, better for beta to help out and learn to increase chances of becoming a successful alpha. Female attracted to cooperative dance and singing, encouraging cooperation in lekking.

Table A. *Hypotheses and Predictions*

Appendix A. *Two males, an alpha and beta, participate in leapfrog dance infront of female [2]*



Appendix B. *Chart shows relateness of alpha-betas as compared to other relationships of manakins. [1]*

Bibliography

1 Duval, Emily H., "Adaptive Advantages of Cooperative Courtship for Subordinate Male Lance-Tailed Manakins", *The American Naturalist,* Vol. 169.4, April 2007. Pg 423-432.

2 Duval, Emily H., "Ongoing Research Projects", http://bio.fsu.edu/duvalResearch.html#cooperation, Accessed 12-Oct-2012.

3 Dybas, Cheryl., "Manakins, Birds of Tropical Forests, Cooperate for Common Goal", http://www.nsf.gov/discoveries/disc_summ.jsp?cntn_id=119853, Accessed 13-Oct-2012.

4 Flannagan, Karen, Kevin Schmidt, and Wendy Tori, "Chiroxiphia lanceolata", http://neotropical.birds.cornell.edu/portal/species/lifehistory?p_p_spp=502956 Accessed 13-Oct-2012.

5 Freeman, Scott and Jon Herron., "Why do Male Long-Tailed Manakins Cooperate during Courtship?", http://wps.prenhall.com/esm_freeman_evol_3/12/3318/849564.cw/index.html Accessed 6-Oct-2012.

6 Greij, Eldon., "Dance club: male manakins help each other attract mates, but there's not always a girl for every guy", *Birder's World,* Vol. 21.6, December 2007. Pg 48.

7 McDonald, David B., and Wayne K. Potts., "Cooperative display and relatedness among males in a lek-mating bird." *Science,* Vol. 266.5187, November 1994. Pg 1030.

8 Milius, S., "Why does a buddy help another male flirt?", *Science News,* Vol. 166.1, July 3, 2004. Pg 14.

9 Trainer, Jill M., David B. McDonald and William A. Learn., "The development of coordinated singing in cooperatively displaying long-tailed manakins", *Behavioral Ecology,* Vol. 13.1, February 2001. Pg 65-69.

10 Zimmer, Carl., *Evolution : The Triumph of an Idea*. New York: HarperCollins, 2001. (Pratt)