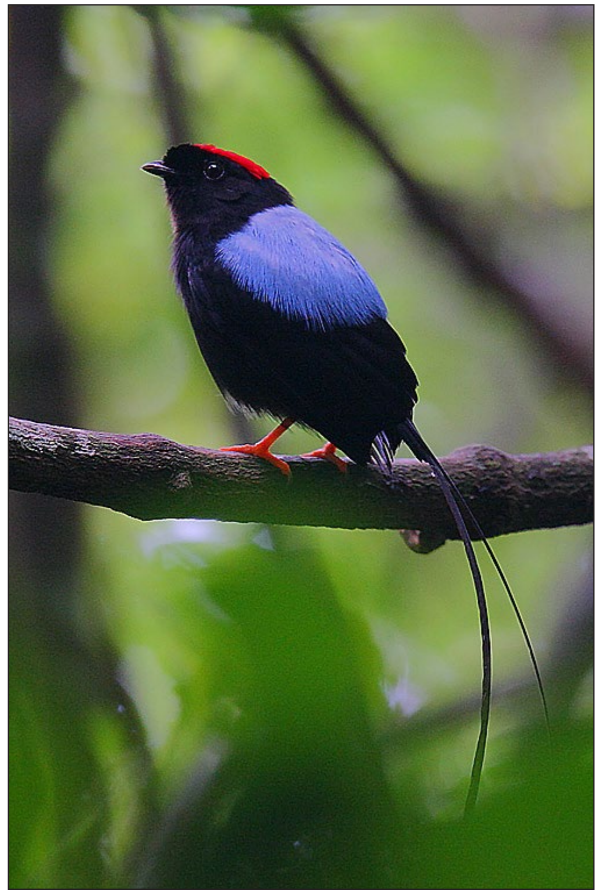
The Waiting Game: A Case Study on the Behavioral Ecology of Long-Tailed Manakins



by
Susan Bandoni Muench
Department of Biology
SUNY Geneseo, Geneseo, NY

Part I – Courtship

The long-tailed manakin is a perching bird from Central America with very unusual courtship behavior. Males of the long-tailed manakin form leks. Leks are gatherings in which males display either communally or competitively to attract females. In the long-tailed manakin, leks consist of two males, an alpha and a beta male. In addition, there can be as many as 11 other males that take part in the lek. The alpha and beta males perform a leapfrogging dance and butterfly flights for visiting females, accompanied by synchronous vocalizations called toledo calls. After the two males dance and call together in a display for females, only one male will actually mate. The leks persist over multiple years. Female long-tailed manakins visit multiple leks over the breeding season, but mate at a single lek each season.

Questions

1. Propose a list of questions that an evolutionary biologist might ask about this system in order to design an experiment.
2. What possible explanations can you propose for cooperative displays in the long-tailed manakin? Are there some possibilities you can rule out easily with just a little more information? What information do you need?
3. Choose one question and formulate a testable hypothesis.

Part II – Kinship

Charles Darwin (1859) was the first biologist to raise the question of why individuals might forego their own reproduction and assist others. He raised the question in reference to non-reproductive workers among the social insects. Darwin concluded that the workers might derive a benefit from contributing to the reproductive success of their relatives. Later, Hamilton (1964a, 1964b) coined the term *inclusive fitness* to describe the sum of direct and indirect reproductive contributions. Indirect reproductive contributions are those of close relatives who share genes with an individual and therefore are able to pass these genes on. Through the concept of inclusive fitness, it is possible to explain some otherwise puzzling behaviors as increasing an individual's indirect fitness. According to Hamilton, altruistic behaviors should occur when the cost to the actor's direct fitness is offset by gains in indirect fitness.

David McDonald and Wayne Potts (1994) decided to test the hypothesis that pairs of cooperating males in the long-tailed manakin are closely related. They collected tissue samples from 33 pairs of birds, and examined variation in microsatellite loci. Four polymorphic loci were identified, each with two to four alleles. Using the microsatellite data, they calculated relatedness coefficients (see Textbox below). Their data are shown in Table 1.

Table 1. Relatedness coefficients.

Pairs of cooperating males with R > 0	16
Pairs of cooperating males with R < 0	17
Mean relatedness coefficient (with confidence limits)	–0.014 (–0.35, 0.7)

Questions

1. What do these data suggest?
2. The kin selection hypothesis can be reformulated in at least one other way given the data above. What is another way that kinship could show an effect, and how would you test for this?

Textbox: Relatedness Coefficients

In studies of the long-tailed manakin, two measures of relatedness are used. Although these measures are somewhat similar, they are calculated in different ways and used for different purposes.

The first, Wright's coefficient of relatedness, is a measure of how many genes relatives should share on average, given relationships that are known. Wright's coefficient of relatedness, r, is calculated as $.5^n$, where n is the number of links in the genealogy, summed for the number of shared ancestors. Thus, full siblings are separated by two steps in the genealogy and share two ancestors, resulting in an r value of 0.5. Half-siblings are separated by the same number of steps in the genealogy, but share only one ancestor, and so are related by only 0.25. First cousins are separated by four steps, but share two ancestors, for a relatedness coefficient of 0.125.

The second, the relatedness coefficient of Queller and Goodnight (1989), is used to estimate relatedness when the exact relationships among individuals are unknown. Individuals may share an allele either by descent or because that allele is common in the population. This relatedness coefficient, R, is calculated by comparing an allele frequency for one individual (1, .5 or 0 in a diploid species) to that of a reference individual, as well as in comparison to the population, summed over many alleles. Thus, $R = \sum (p_y - p)/\sum (p_x - p)$. Values of this relatedness coefficient can vary from –1 to 1, with full siblings expected to have values of 0.5. Negative values result when two individuals share fewer alleles than the expected based on the frequencies of those alleles in the population.

Part III – Cooperation

An alternative way of exploring the role of kin selection is to investigate whether cooperating relatives might be more successful than cooperating unrelated males. In this case, unrelated males might still form pairs if relatives were unavailable.

McDonald and Pott's data are shown in the table below.

Table 2. Coefficients of relatedness for pairs of cooperating males.

Comparison	$R < 0$	$R > 0$
Pairs mating during the field season	7	4
Pairs displaying more than 10 times	6	3

Questions

1. What do these data indicate?
2. What other possible explanations can you propose to explain the association between the alpha and beta males?
3. Formulate a hypothesis to test one of your proposed explanations.

Part IV – Benefits

McDonald and Potts next considered whether there might be other possible benefits to the beta male cooperating with the alpha male in the lek. One possibility that they considered was whether the beta male may sometimes copulate. A second possibility was that the beta male may play the alpha role at a later date, perhaps after the death of the alpha male. In that case, beta males would benefit more if females show site fidelity. This might happen if the new display closely resembles the old. Also, under these conditions, McDonald and Potts predicted that the beta male's later success would be correlated with the success of the earlier alpha male. Their data from each of these comparisons are shown in Tables 3 and 4.

Questions

1. For each of the benefits listed in Table 3, identify what form of selection is at work. Are these possibilities mutually exclusive?
2. Based on these data, why do long-tailed manakins cooperate in lek displays?

Table 3. Benefits of cooperation for the beta male.

Benefit	*Selection*	*Evidence*
Copulations during beta tenure		4 of 263 from 1983–1992
Succession to alpha role		11 of 11 documented turnovers
Female site fidelity		16 of 27 site-faithful 10 of 16 mated with replacement alpha
Mating success correlated with predecessor's success		Spearman rank correlation r_s = 0.71 for visits, r_s = 0.83 for copulations

Table 4. Mating success of beta males after ascension to alpha status, in comparison with their predecessors. All are based on at least 50 hours of observation. Female visits were measured in seconds present during the 2-hour observation period.

Bands Beta/Predecessor	*Turnover from Beta to Alpha*	*Female visits Beta*	*Female visits Predecessor*	*Copulations Beta*	*Copulations Predecessor*
3596/4790	1989–1990	7.34	6.02	0.000	0.000
2120/1965	1991–1992	83.29	120.24	0.086	0.087
1935/3570	1992–1993	89.34	98.84	0.014	0.045
3570/3315	1991–1992	98.84	173.28	0.045	0.111
1805/4685	1990–1991	290.45	420.64	0.136	0.327
4990/1805	1991	157.69	290.45	0.143	.0136
1820/4990	1991–1992	304.22	157.69	0.217	0.143
1585/4690	1984–1985	324	260.30	0.350	0.290

References

Darwin, C. 1909, c1859. *The Origin of Species*. Vol. 11. New York: P F Collier and Son. <http://books.google.com/books?id=YY4EAAAAYAAJ&pg=PP7#v>

Goodnight K. F., and D.C. Queller. 1989. Estimating relatedness using genetic markers. *Evolution* 43(2): 258–275. Also available online: <http://www.jstor.org/stable/2409206?origin=crossref>

Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7(1): 1–16.

Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7(1): 17–52.

McDonald, D. B. University of Wyoming, Department of Zoology and Physiology. Long-tailed manakin dance video clip [Video, 10 sec.]. Laramie, WY. <http://www.uwyo.edu/dbmcd/lab/LTMvideo.htm>

McDonald, D. B., and W. K. Potts. 1994. Cooperative display and relatedness among males in a lek-mating bird. *Science* 266(5187): 1030–1032. Also available online: <http://www.jstor.org/stable/pdfplus/2885492.pdf>

Mennill, D. Bird Songs of Santa Rosa National Park. Long-tailed manakin calls: Toledo; [Audio, 7 sec.]. Windsor, ON, Canada. <http://web2.uwindsor.ca/courses/biology/dmennill/CostaRica/LTMA/CRLTMA.html>

Internet references accessible as of March 26, 2021.