NESTING AND MATING DECISIONS AND THEIR CONSEQUENCES IN THE BAYA WEAVERBIRD *Ploceus philippinus*

By

SUHEL QUADER

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA
2003

To my parents and my brother for their support; and to the BSAP for starting it all.

ACKNOWLEDGMENTS

My advisor, Jane Brockmann, allowed me the freedom and independence to pursue my own research ideas. Without her intellectual contribution this project would have been impossible to complete. She shared advice and editorial comments freely; and her broad perspective on the field of animal behavior has enriched my education.

Rich Kiltie, Doug Levey, Colette St. Mary, and Katie Sieving were wonderful committee members—their suggestions greatly improved my research, and their patience and understanding helped me through a busy last semester. I also thank Rebecca Kimball and Ginger Clark for comments on one of my chapters.

Various agencies funded my research, including the University of Florida, the American Museum of Natural History, the American Ornithologists' Union, and Sigma Xi. I am grateful to them. In India, V. C. Ambedkar, Lalitha Raj, and U. N. Ravi Kumar, helped me search for a suitable field site. I am very grateful to the Birdwatchers' Society of Andhra Pradesh, and in particular Siraj Taher and Aasheesh Pittie, for facilitating and encouraging my research. Tom Hash and Fran Bidinger made my work at ICRISAT possible. Prashant Bhardwaj, Lydia Flynn, Cecile Grenier, Radha Ranganathan, A. Giridhar Rao, K. Hanumanth Rao, and many others made my stay a pleasure. I thank the Andhra Pradesh Forest Department for granting me permission to study baya weaverbirds.

For advice and help in collecting and analyzing genetic material, I thank Dan Brazeau and Ginger Clark at the University of Florida and Jonathan Crouch, Hutokshi

Crouch, Santosh Gurtu, Abdul Gafoor, Bryan Moss, and G. Soma Raju at ICRISAT. T.L. Prasad let me use his vehicle in 2000; without it, field work would have been very difficult, indeed. For help in the field, I thank Irfan Quader, Jane Brockmann, and especially Kavita Isvaran.

The graduate students in Zoology have been a source of stimulating discussion and pleasant companionship. My intellectual development has been much advanced by my interactions with Becca Hale, Billy Gunnels, Ben Miner, Toshi Okuyama, April Randle, Sarah Schaack, Nat Seavy, Laura Sirot, Markus Tellkamp, Manjula Tiwari, Manuel Vélez, and Amy Zanne. I thank the staff of the Department of Zoology, and especially Karen Pallone, for all manner of help and advice over the years. Skye White helped draw some of the figures in this dissertation.

Ben Bolker and Craig Osenberg teach challenging and inspiring courses in the Department of Zoology. Ben Bolker's ecological models course helped me develop confidence in using various quantitative methods. I am grateful to them both.

My parents and brother have always supported me in everything I have done. Their love and encouragement and interest in what I do have made my tenure as a graduate student all the more enjoyable and fulfilling.

The person who has had the greatest influence on me over most of my adult life is Kavita Isvaran. I have learnt from her, and have attempted to follow her example in both professional and personal spheres of life. She is my closest colleague and companion; this dissertation is as much hers as it is mine.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

NESTING AND MATING DECISIONS AND THEIR CONSEQUENCES IN THE BAYA WEAVERBIRD *Ploceus philippinus*

By

Suhel Quader

August 2003

Chair: H. Jane Brockmann
Major Department: Zoology

The evolution and persistence of elaborate traits can often be explained by sexual selection, the evolutionary process associated with acquiring mates. When these traits are complex behavioral patterns, changes in neural structure and learning ability may be involved. One such behavior is nest building, which is done with particularly impressive skill by male weaverbirds. In most weaverbirds, males build nests without any female assistance, and females are thought to choose mates by evaluating their nests. Although there are some data on mate choice in weaverbirds from aviaries, information on nesting and mating patterns and their consequences is lacking from the wild. Here, I describe results from a field study of baya weaverbirds, *Ploceus philippinus*, in India. I examine male and female nesting decisions in relation to an important abiotic factor, wind. I also ask whether nest structure is an important cue to females while choosing mates, and evaluate the possibility that females use male phenotype and nest location instead. To understand why females pay attention to particular characters, I investigate the benefits of female choice by examining which factors best explain variation in nesting success. I also use microsatellite DNA tools to test the assumption that outward patterns of pairing and egg laying reflect actual mating and nesting decisions. I find little evidence linking female choice to nest structure. Instead, nest location seems to play a larger role. Appropriate nest location is also important in male settlement, and males cluster their nests in leeward locations, where nests are protected from strong winds. Also, nests placed high above ground are both preferred by females and safer from predators than are lower nests. Thus, nest location is a particularly good predictor of nesting success, which may explain why females pay little attention to nest structure. Molecular analyses indicate that most clutches are fertilized by the builder of the nest in which they are laid, and show that the level of intraspecific brood parasitism is low. Although I found little evidence of female choice for nest structure in the baya weaverbird, past choice may have led to the current distribution of trait values.

CHAPTER 1
GENERAL INTRODUCTION

Sexual selection is a powerful force shaping evolutionary patterns (Andersson 1994; Darwin 1897). Intrasexual competition and intersexual mate choice have given rise to various elaborate traits of males and females. Some of the most spectacular of these traits are morphological exaggerations, including weapons used in battle over mates and elaborate ornaments used in mate choice. But apart from influencing the evolution of external morphology, sexual selection has also played a role in the evolution of behavioral traits like territoriality (Davies 1978), song (Catchpole and Slater 1995; Searcy and Andersson 1986), and mate guarding (Birkhead 1998; Birkhead and Møller 1992). The development and performance of some of these behavioral traits may be quite complex, and may require both modification of neural structure and function and a substantial learning component. Both of these features are essential for the development and production of bird song, which is used to acquire and defend territories, and to attract mates (Catchpole and Slater 1995; Konishi 1994; Searcy and Andersson 1986). Similarly, female choice for well-built bowers (Borgia 1985, 1995a) may explain the correlation between male brain size and bower complexity in bowerbirds (Madden 2001). This means that sexual selection may lead to the evolution of skills as varied as song production and bower construction, and also the underlying neural structure and learning mechanisms.

Weaverbirds (Passeridae: Ploceinae) are an ideal system in which to study the role of sexual selection in the evolution of a learned skill. Ploceine weaverbirds form a large and diverse group containing 117 species (Sibley and Monroe 1990) that are well-known for the diversity and complexity of the nests they build. In the genus *Ploceus* (63 spp.), males do much of the nest building, and most female *Ploceus* take no part in building nests at all (Collias and Collias 1964b; Crook 1963). Males in these species weave together plant fibers to form roughly globular nests, which are placed in a fork in a tree, suspended from the tip of a branch, or woven into the tips of reeds close to water (Collias and Collias 1964b; Crook 1963). After males have built their nests, females arrive and visit several nests before pairing. Female choice of mates has been presumed to be based largely on the quality of the available nests (Collias and Collias 1964b, 1984; Crook 1960). Some evidence of this comes from a species that has been intensively studied, the village weaverbird *Ploceus cucullatus* (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al. 1978). Males of this species require substantial experience and learning to assemble a normal-looking nest (Collias and Collias 1964a, 1973), which implies that female choice may well influence the evolution of the ability of males to develop appropriate skills. Although sexual dimorphism and among-species variation in neural structure has not been investigated in weaverbirds, one would expect male brain morphology to differ from that of females, and for this sexual dimorphism to be greatest in those species in which females play no part in nest building.

Despite strong indications that female choice is involved in the evolution of male nest-building ability in weaverbirds, the few studies done have had mixed results. N.E. Collias and co-workers manipulated nest traits in a series of aviary experiments with village weaverbirds. They present some evidence that females are influenced by color, material, and quality of nests (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al.

1978). However, they also show that some of their results could be explained by changes in male behavior resulting from their experimental treatments. Their manipulations were substantial, often producing nests far beyond the range of normal variation, so it is difficult to determine the degree to which these results can be generalized to natural conditions. Finally, the reasons for which females show preferences are not known because data on the benefits to female village weaverbirds of choosing one nest over another are not available.

In this dissertation, I extend our understanding of nesting and mating decisions in weaverbirds by studying a common Indian ploceine, the baya weaverbird (*Ploceus philippinus*). Baya weaverbirds are well-suited for the study of female choice for male skill. Females take no part in nest building, and males build nests that are exceptionally finely woven (Ali 1931; Crook 1964a). Nests are placed prominently in colonies, making them easy to study. Manipulations to nests can be made in the field, and males reject altered nests only if drastic changes are made (Crook 1964a). In addition, various attributes of nests have been proposed to affect their safety from predation and weather (Crook 1963, 1964a, Davis 1971). If the structure of a nest influences how safe it is, one would strongly expect females to use nest structure in making mate-choice decisions.

In Chapter 2, I address an important abiotic cause of nest failure (wind), and ask whether males appear to be sensitive to this factor when establishing territories and building nests. I also quantify the degree to which these territorial and nesting decisions influence nest safety using experiments and observations, and I ask whether females pay attention to the bearing and orientation of nests in relation to wind. In Chapter 3, I combine experimental and correlational approaches to identify possible cues used by females while choosing mates. To assess the degree to which different nest attributes predict reproductive success, I explore the correlates of fledging success and daily probability of survival of nests (Chapter 4). Finally, I used molecular tools to test the implicit assumption that outward patterns of pairing and egg laying reflect actual mating and nesting decisions (Chapter 5). Such a test is necessary given the widespread occurrence of extra-pair paternity and intraspecific brood parasitism in birds. This study contributes detailed information on nesting and mating decisions for a representative of an important and diverse group of birds, and provides new insights into our understanding of the process of sexual selection for behavioral skills.

CHAPTER 2
SEQUENTIAL SETTLEMENT BY NESTING MALE AND FEMALE WEAVERBIRDS: THE ROLE OF MONSOON WINDS

Introduction

How do animals make decisions about where to reproduce? A classical model is that in order to maximize fitness, females should track factors associated with reproductive success, and males should distribute themselves according to female location (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). Factors influencing female settlement may be both abiotic and biotic, and can have strong effects on reproductive success (Clark and Shutler 1999; Martin 2001). Female settlement may be related to microclimate (Sedgeley 2001; Walsberg 1981), food quality (Shelly et al. 1987), and predation risk (Martin and Roper 1988), among other factors. However, males and females may settle sequentially rather than simultaneously, with males often preceding females. If females are absent when males settle, there should be selection on males to use cues associated with locations preferred by females.

Clearly, an overall understanding of settlement patterns requires an examination of the decisions made by individuals of both sexes (Meek and Barclay 1996; Mitchell 2001). What is the nature of these sequential decisions when males settle before females, and what are the fitness consequences? I investigate the relationship between a highly consistent abiotic factor (wind) and nesting decisions of males and females in a system in which males settle first. I also explore how these decisions can be understood in terms of the influence of wind on reproductive success. If wind is a strong selective force, then both males and females should choose maximally protected nesting locations from among those available.

In the baya weaverbird *Ploceus philippinus* (Passeridae: Ploceinae), as in many polygynous weavers, males establish small territories in trees. There are often many territories in a single tree. Within their territories, males build elaborate hanging nests to which they attract females (Ali 1931; Ambedkar 1964). If a female accepts a nest, she mates with the male who built it, lays her clutch in the nest, and takes care of the young largely on her own. Because no food resources are associated with a particular nest and because males rarely feed nestlings (Ambedkar 1964; S. Quader pers. obs.), the main direct (i.e., nongenetic) benefits that females receive are the nest and its attributes (location and structure). This means that both male and female settlement decisions can be studied in relation to selection of nests and nest sites, and in the absence of confounding benefits from other resources within a territory, such as food.

The baya weaverbird breeds during the rainy season (monsoon) in the Indian subcontinent (Ali and Ripley 1987). The main monsoon is driven by large low-pressure systems in Central Asia causing moisture-laden air over the Indian Ocean to move northeastward. In peninsular India, these winds blow strongly and consistently from the southwest. Several authors have commented on the clustering of nests on the eastern (leeward) side of colony trees (Ali 1931, Davis 1971), and have suggested that this is because leeward nests are protected from strong winds. In addition, Davis (1971) proposed that eggs in improperly oriented nests (with nest entrances facing the wind) are more likely to fall out of the nest than are eggs in nests with entrances oriented away from the wind (Figure 2-1). The hypothesis that wind direction and velocity influences optimal nest placement and orientation (and thus affects male and female nesting decisions) is as yet untested.

In this chapter, I present experimental and observational data that address two questions: (1) is wind a selective force on nest placement and orientation, and (2) are the nesting decisions made by male and female baya weaverbirds consistent with such a selective pressure? I collected data on wind direction and velocity, and manipulated the placement and orientation of nests containing artificial eggs. I also recorded male and female settlement, and the success of nests in different locations. Using these data, I discuss observed patterns of male and female behavior in terms of their fitness consequences.

Methods

Study Species

The baya weaverbird is distributed throughout South Asia in savanna-like habitats and around agricultural fields (Ali and Ripley 1987). Nests are constructed exclusively by males within small, contiguous territories among the outermost branches of colony trees. I refer to the compass bearing of a nest from the center of its tree as its nest bearing. Nests are built with grass and palm fiber, and construction passes through several distinct stages, including an intermediate helmet-shaped structure. Completed nests are closed, with a vertical entrance tube of varying length (Ali 1931; Crook 1964a). The rotation of a nest around its vertical axis is variable, and the entrance tube may face any direction. Nest-entrance orientation describes this rotation, and is the compass bearing from the center of a nest to its entrance. Nest-entrance orientation is determined early on in nest construction, well before the helmet stage (Davis 1971). I recorded all compass bearings to the nearest degree using a Suunto MCA-D compass. Females visit a male's nest partway through construction, during the helmet stage. If a female chooses a helmet, the male completes the structure by weaving the floor of the brood chamber and constructing the entrance tube on the opposite side. Further paternal investment is largely restricted to occasionally adding fresh fiber, repairing any damage that may occur to the nest, and guarding the nest from intruders. The male often goes on to construct a new nest nearby and may attract additional females as the season progresses. At any given time, however, males usually do not have more than one nest at the helmet stage (Ali 1931).

Study Area and Weather

I studied a population of baya weaverbirds from June to October 1998–2000 at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Patancheru, Andhra Pradesh, India (17.53°N, 78.27°E; 545 m above sea level). Peak breeding activity occurred during these months, which coincide with the southwesterly monsoon. Data on mean daily wind direction and velocity for the period 1992–2000 were obtained from the ICRISAT agrometeorology division. Using meteorological convention, compass bearings (measured with respect to magnetic North) for wind directions refer to the direction from which winds blow. All baya colonies studied were located less than 3 km from the ICRISAT weather station. To explore seasonal variation in weather and settlement patterns, I divided the breeding season into two halves: early (June, July) and late (August, September).

Field Experiment

Between 13 July and 16 September 2000, I carried out a field experiment to evaluate the effect of nest bearing and nest-entrance orientation on the probability of egg loss. I fashioned modeling clay into artificial eggs similar in dimensions and mass to real baya eggs. Artificial eggs were, on average, 4.2% and 10.7% smaller in length and width, and 12% heavier than real eggs. Clutches of three artificial eggs (the modal clutch size) were placed in abandoned complete nests collected from baya colonies. These nests were then affixed using thin wire to trees commonly used by bayas for nesting (*Acacia nilotica*, *Prosopis juliflora*, and *Leucaena leucocephala*).

Preliminary observations suggested that immature male bayas entered experimental nests and tossed out artificial eggs. To prevent this, I tied shut the entrance tube of each nest with twine. Each experimental replicate consisted of four nests in different combinations of nest bearing ($\overline{X}$ [range]; windward 260º [224–320º], $n = 26$ or leeward 88º [64–126º], $n = 26$) and nest-entrance orientation (facing wind 262º [212–324º], $n = 26$ or facing away 92º [30–152º], $n = 26$). Other aspects of nest location (height above ground, diameter of supporting branch, etc.) were similar among treatments within a replicate, and closely matched characteristics of natural nests. All four nests in each replicate were run simultaneously until at least one nest lost eggs, for a maximum of 5 days. I also recorded the identity of any nests snagged on thorns (for trials on *A. nilotica* and *P. juliflora* only; *L. leucocephala* is thornless) because this may make access to the nest easier for predators. Replicates in which one or more nests were damaged (e.g., by the arboreal mouse *Vandaleuria oleracea*) were discarded from analyses of egg loss, but were used to investigate snagging patterns.

Male Settlement and Nest Construction

Nesting colonies were found in a variety of situations. Some colony trees were situated in open woodland. Others were located on the edges of open ponds or on the steep embankments of stormwater ditches or irrigation canals. Davis (1971) proposed that in such cases nests are clustered on the side of the tree that overhangs water (or the downward slope) to protect from predation rather than from wind, so I classified these colonies as directional. If all sides of the tree were equal with respect to slope and the presence of water, I classified the colony as nondirectional. To investigate the settlement patterns of males, I measured the bearing and orientation of the entrance of nests in 1998 (13 colonies), 1999 (20 colonies), and 2000 (32 colonies). In all, I measured 1445 nests, including nests at the helmet stage.

Female Choice and Nesting Success

To examine the relationships among nest characters, female choice, and nesting success, I regularly monitored marked nests in a subset of colonies. Of nests marked at the helmet stage, I recorded the identity of those that received eggs (indicating that they were chosen by a female). For each completed nest in which a full clutch was laid, I recorded whether eggs persisted until hatching or whether the entire clutch disappeared. Nestling presence until fledging was similarly recorded. Nests that failed for causes other than strong winds (e.g., from predation by rodents), were not used in the main analysis because there is no reason to expect such predation to be correlated with nest bearing or nest-entrance orientation. It should be noted that egg and nestling disappearance could be caused either by nest contents falling out of the nest because of wind or, for example, by predation by snakes. However, of 27 cases of egg disappearance after which the area below the nest was searched thoroughly, egg remains were found on the ground in 21 cases. This suggests that snake predation is not a major cause of nest failure, because snakes usually eat prey items whole (Cundall and Greene 2000).

Analysis

I present summary statistics for circular data (rounded to the nearest degree) as $\overline{X}$ ± 95%CI (indicating the magnitude of the 95% confidence interval) and *r* (the length of the mean vector). The statistic *r* is a measure of how clumped a circular distribution is (Zar 1996), and can range from 0 (no mean angle can be described) to 1 (all the data are concentrated in the same direction). I used the Rayleigh test to evaluate whether nest measures were significantly clumped. All *F* statistics reported were calculated from the Watson-Williams test (Zar 1996), which is used to evaluate the null hypothesis that two circular distributions have the same mean. Circular variables did not differ significantly from a von Mises distribution (required for the Watson-Williams test). Because multivariate and ANOVA-like statistical methods for circular variables are not well developed, I used simple comparisons throughout. Circular statistics were computed in the statistical language R 1.3.0 (Ihaka and Gentleman 1996) using either code that I wrote or the CircStats package for R (written by Ulric Lund and Claudio Agostinelli). Summary statistics for linear variables are presented as $\overline{X}$ ± SE. All statistical tests are two-tailed, with $\alpha = 0.05$.

Results

Wind Direction and Velocity

Weather data from 1992–2000 show that during the breeding season, winds blew consistently from the southwest (mean of yearly means 235° ± 13°, $r = 0.954$, $n = 9$ y), and that this did not vary substantially over the season (early 243° ± 12°, $r = 0.959$; late 228° ± 16°, $r = 0.934$; Watson-Williams test: $F_{1,16} = 2.57$, $P = 0.128$; Figure 2-2). Mean wind direction, however, did not reflect the direction from which the strongest winds blow. Over the entire season, on days that experienced the highest 10% of wind velocities, winds blew from a mean direction of 249° ± 25° ($r = 0.890$, $n = 9$ y). Mean wind velocity over the season was 12.35 ± 0.40 kmh^{-1} ($n = 9$ y) and velocity declined sharply from June to September (early 14.94 ± 0.50 kmh^{-1}; late 9.76 ± 0.37 kmh^{-1}; paired *t*-test: $t_8 = 14.3$, $P < 0.001$; Figure 2-2).

Field Experiment

Eighteen replicate quartets of nests were run, five of which could not be used in egg-loss analyses (see Methods). Of the 13 usable replicates, eggs were lost from one nest in a quartet in 5 replicates. In all 5 of these replicates, the entire clutch of three eggs was lost from the windward nest with entrance facing the wind. Thus, nests with this combination of bearing and entrance orientation were significantly more likely to lose eggs than were nests in any other treatment (Cochran's *Q* test: $\chi^2 = 15$, d.f. = 3, $P = 0.002$). The frequency of egg loss did not vary with time in the season (early vs. late; 2 × 2 Fisher exact test: $P = 0.217$). Nests were snagged in 5 of 15 replicates placed on thorny trees. Of the 8 nests snagged, all but one was windward (windward vs. leeward; binomial test, $P = 0.070$). More nests tended to be snagged early than late in the season, but this trend was not significant (2 × 2 Fisher exact test, $P = 0.130$).

Male Settlement and Nest Construction

Nests were significantly clumped in bearing and entrance orientation. Over all years, mean location of nests was at a bearing of 113º ± 3º ($r = 0.706$, Rayleigh test, $P < 0.001$, $n = 1445$ nests, Figure 2-3A) and mean entrance orientation was 112º ± 3º ($r = 0.617$, Rayleigh test, $P < 0.001$, $n = 1445$ nests, Figure 2-3B). There was a significant positive angular-angular correlation (r_{aa}, Zar 1996) between the compass bearing of a nest and its entrance orientation ($r_{aa} = 0.33$, $n = 1445$, $P < 0.001$). Nests in nondirectional and directional colonies showed differing patterns of bearing and orientation. Nests in nondirectional colonies were located significantly more leeward than those in directional colonies (nondirectional: 93º ± 3º, $r = 0.848$, $n = 581$; directional:

129° ± 4°, $r = 0.671$, $n = 864$; $F_{1,1443} = 233.32$, $P < 0.001$). A similar pattern existed for nest-entrance orientation (nondirectional: 100° ± 4°, $r = 0.703$, $n = 581$; directional: 122° ± 4°, $r = 0.579$, $n = 864$; $F_{1,1443} = 54.13$, $P < 0.001$). For directional colonies, the average direction of maximum safety from predation (i.e., the direction of water or a downward slope) was 125° ± 4° ($r = 0.625$, $n = 864$). For nests in these colonies, nest bearing was positively correlated with direction of maximum safety ($r_{aa} = 0.416$, $P < 0.001$, $n = 864$), and so was nest-entrance orientation ($r_{aa} = 0.164$, $P < 0.001$, $n = 864$).

Because wind velocity declined over the season, one might expect corresponding changes in nest construction. To investigate changes in nest bearing and nest-entrance orientation over the season I used measurements on helmets only, because unlike completed nests, the helmet stage is transient (and thus helmets represent recent settling decisions). Helmets in nondirectional colonies that were built early in the breeding season were placed significantly more leeward than those built late in the season (early: 90° ± 8°, $r = 0.823$, $n = 100$ helmets; late: 107° ± 12°, $r = 0.827$, $n = 44$ helmets; $F_{1,142} = 6.77$, $P = 0.010$, Figure 2-4A). Similarly, nest-entrance orientation was more leeward early (97° ± 9°, $r = 0.769$, $n = 100$) than late in the season (115° ± 14°, $r = 0.751$, $n = 44$; $F_{1,142} = 5.57$, $P = 0.019$; Figure 2-4B).

Female Choice

Female choice of site may be influenced by both wind direction and safety from predation, so I restrict analyses of female choice to nests in nondirectional colonies. Helmets that were chosen (indicated by being completed and by receiving a full clutch) did not differ from those not chosen (nest never completed) either in nest bearing or in nest-entrance orientation (Table 2-1).

Nesting Success

Here, I compare successful nests with those that failed because of wind. Data from both directional and nondirectional colonies are combined, because nests that failed for causes other than wind are excluded. Early in the season, nests that retained eggs until hatching were located significantly more leeward than those whose eggs were tossed out by wind (eggs retained 89º ± 7º, $r = 0.908$, $n = 52$; eggs lost 110º ± 26º, $r = 0.872$, $n = 9$; $F_{1,59} = 4.69$, $P = 0.034$; Figure 2-5A), but this difference disappeared late in the season (eggs retained 98º ± 11º, $r = 0.758$, $n = 62$; eggs lost 95º ± 39º, $r = 0.679$, $n = 9$; $F_{1,69} = 0.04$, $P = 0.842$; Figure 2-5B). When nestling loss was compared, the difference was in the same direction but was not significant. As a result, fledging (which requires both egg and nestling retention) was only marginally associated with nest bearing (early: eggs and nestlings retained 87º ± 11º, $r = 0.919$, $n = 22$; eggs or nestlings lost 103º ± 17º, $r = 0.896$, $n = 18$; $F_{1,38} = 3.826$, $P = 0.058$; late: retained 98º ± 17º, $r = 0.767$, $n = 29$; lost 103º ± 17º, $r = 0.817$, $n = 23$; $F_{1,50} = 0.175$, $P = 0.677$). Nest orientation was unrelated to egg or nestling retention, either early or late in the season, or overall (all comparisons NS). Causes of nest failure other than wind were common—these showed no relationship with either nest bearing or nest-entrance orientation. When all failed nests in nondirectional colonies were included in the analysis, the bearing and nest-entrance orientation of successful nests were indistinguishable from those of unsuccessful nests (bearing: successful nests, 96º ± 11º unsuccessful nests 100º ± 11º; orientation: successful nests 91º ± 15º, unsuccessful nests 100º ± 13º; both comparisons NS).

Discussion

Strong monsoon winds impose an important selective pressure on the location of baya weaverbird nests. Male decisions about where to defend territories and build nests in a tree appear to reflect selection in relation to wind direction. However, females do not seem to discriminate among the narrow range of available nests.

Results from the field experiment show that nest bearing and nest-entrance orientation can influence the retention of eggs in the nest. Experimental nests placed on the windward side of trees and oriented with nest-entrance facing the wind were more likely to lose their clutch of artificial eggs than were nests with other combinations of bearing and orientation. Whole clutches were lost in 5 of 13 such nests, indicating that wind may cause complete nest failure. Baya nests also snagged on the thorny branches to which they were attached—an additional cost for nests on the windward side of colony trees. These results suggest that males should strongly avoid building nests in windward locations, and indicate that both nest bearing and nest-entrance orientation can influence reproductive success in baya weaverbirds, as previously supposed (Ambedkar 1964; Davis 1971). Similar variation in nest-site quality in relation to wind has been found in other species. For example, in the white-browed sparrow-weaver, *Plocepasser mahali*, roost nests constructed on the windward side of trees suffer more damage than do leeward nests (Ferguson and Siegfried 1989).

Male baya weaverbirds built nests in the location and orientation predicted by the results from the field experiment. Nests were strongly clustered on the leeward side of colony trees, especially in nondirectional colonies. Nests in directional colonies, on the other hand, were clustered over water or a downward slope, suggesting that safety from predation is another factor affecting nest placement. Mean nest-entrance orientation was generally opposite to wind direction, as predicted by Davis (1971). Wind direction does not, however, fully explain the bearing or orientation of baya nests (Figure 2-3). This may be because wind is only one of many causes of nest failure (see below).

There were striking seasonal changes in the location of new helmets and in patterns of nest failure. Late in the season, males built their helmets more toward the wind than they did earlier (Figure 2-4), and the early-season difference in bearing between nests retaining eggs and those losing eggs due to strong wind disappeared (Figure 2-5). Why might this be? The drag force on a nest, causing it to be displaced from its normal vertical position, should vary as wind velocity raised to the power of 1.5 to 2 (Vogel 1984). This means that the 35% reduction in wind velocity over the season translates into a reduction in drag of between 48% and 58%. Such a disproportionate reduction in drag with decreased wind velocity may partly explain the marked seasonal change in nest bearing and nest-entrance orientation.

Do females show the same strong preference for leeward locations as do males? I found no evidence that female choice is related to nest attributes within the range of helmets that males build (Table 2-1). Mean compass bearing and orientation of chosen nests at the helmet stage were not significantly different from the bearing and orientation of nonchosen helmets. This lack of choice may occur because available nests are already strongly clustered in leeward locations. However, even within the highly restricted natural variation in nests, those that lost eggs for wind-related causes early in the season were located significantly more windward than nests that retained eggs. Why, then, do females appear to ignore nest bearing while making decisions about where to settle? The answer appears to be that, precisely because males cluster their nests in leeward locations, wind is a minor cause of nest failure in the baya. If all causes of nest failure are included in the analysis, successful and unsuccessful nests do not differ in nest bearing or nest-entrance orientation. Similarly, in the cliff swallow *Hirundo pyrrhonota*, males nest in a clumped manner while females settle at random among the clumped males (Meek and Barclay 1996), presumably because the available nests offer a roughly equal probability of success.

These results point to an interesting problem: when options available to females are constrained by preceding decisions made by males, it may be difficult to detect female preferences, even if strong preferences exist. For example, if male bayas cluster their nests in leeward locations because of strong female choice for such locations, it might not pay females to choose from among the resulting restricted variation among nests. To test for preferences, then, it may not be sufficient to look for correlates of female choice from within the observed variation in male phenotype (regardless of whether such variation is natural or is experimentally produced). Instead, females must be experimentally presented with male phenotypes (including extended phenotypes, such as nests) beyond the range of current natural variation. A similar argument applies to identifying natural selection on a trait. In this study, natural selection on nest bearing and orientation would have been severely underestimated had the treatments in the field experiment been based solely on observed variation in these traits. Behavioral ecologists and evolutionary biologists are often hesitant to carry out extreme manipulations. Nevertheless, such manipulations are necessary to reveal certain natural and sexual selection pressures that would otherwise be hidden from scrutiny.

In conclusion, wind does indeed appear to exert selection on nest placement and orientation in baya weaverbirds. Monsoon winds are strongly directional and consistent, and may cause complete nest failure in inappropriately constructed nests. Males built nests on the leeward sides of colony trees, with nest-entrances facing away from the prevailing wind. Females did not appear to choose from among the nests available to them based on these characters. This is perhaps because the marked clustering of nests results in only a weak relationship between nest bearing and orientation and the retention of eggs and nestlings. Causes of nest failure other than wind removed this pattern entirely. Although not detected in this study, female preferences may nonetheless exist. Experimental manipulations of nests to produce variation outside the natural range may be necessary to detect unexpressed female preferences.

Table 2-1. Nest bearing and nest-entrance orientation of helmet-stage nests chosen and not chosen by females.

	Chosen			Not chosen			Watson-Williams test	
Nest	$\overline{X}$ ± CI (°)	r	n	$\overline{X}$ ± CI (°)	r	n	F_{1,n_1+n_2-2}	P
Bearing								
Early	96 ± 8	0.890	71	93 ± 11	0.807	56	0.363	0.548
Late	96 ± 18	0.602	46	112 ± 8	0.813	21	1.370	0.246
Combined	97 ± 8	0.777	119	98 ± 9	0.800	77	0.026	0.872
Entrance orientation								
Early	95 ± 10	0.809	71	98 ± 11	0.802	56	0.288	0.592
Late	95 ± 23	0.491	46	117 ± 19	0.802	21	2.151	0.145
Combined	95 ± 10	0.675	119	104 ± 10	0.794	77	1.793	0.183

Note: summary statistics are means ± 95% confidence limits; r is the length of the mean vector.

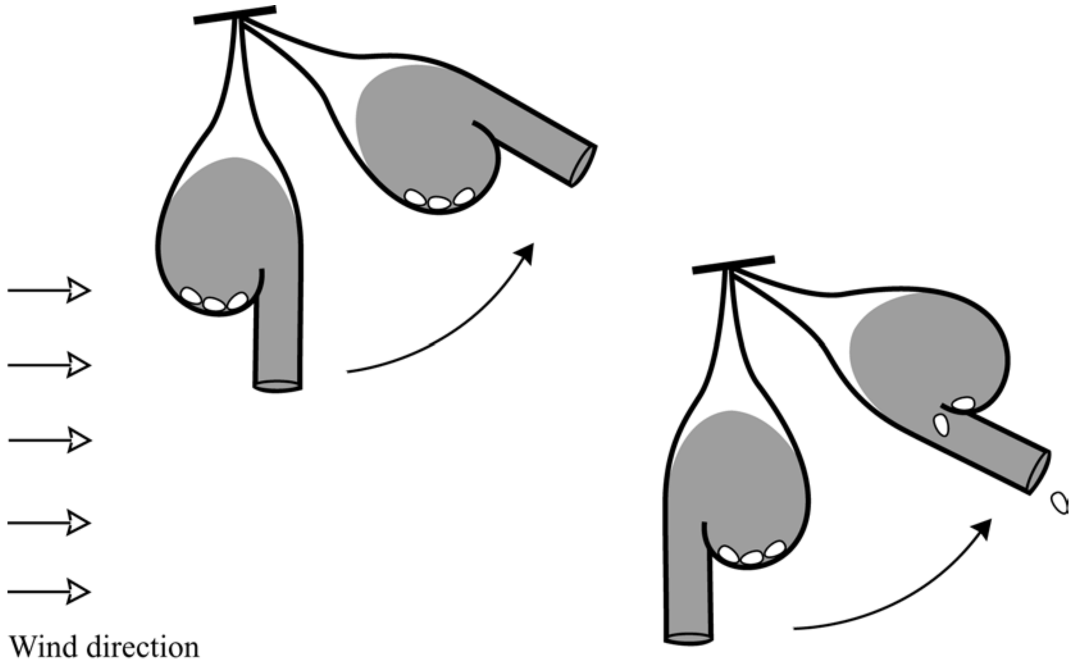

Figure 2-1. Hypothesized effect of nest-entrance orientation on the probability of losing eggs during strong winds (modified from Davis 1971, Forma et Functio 4:225–239). Nests with entrance tubes facing the wind are predicted to run a higher risk of losing eggs than are nests with entrance tubes facing away from the wind.

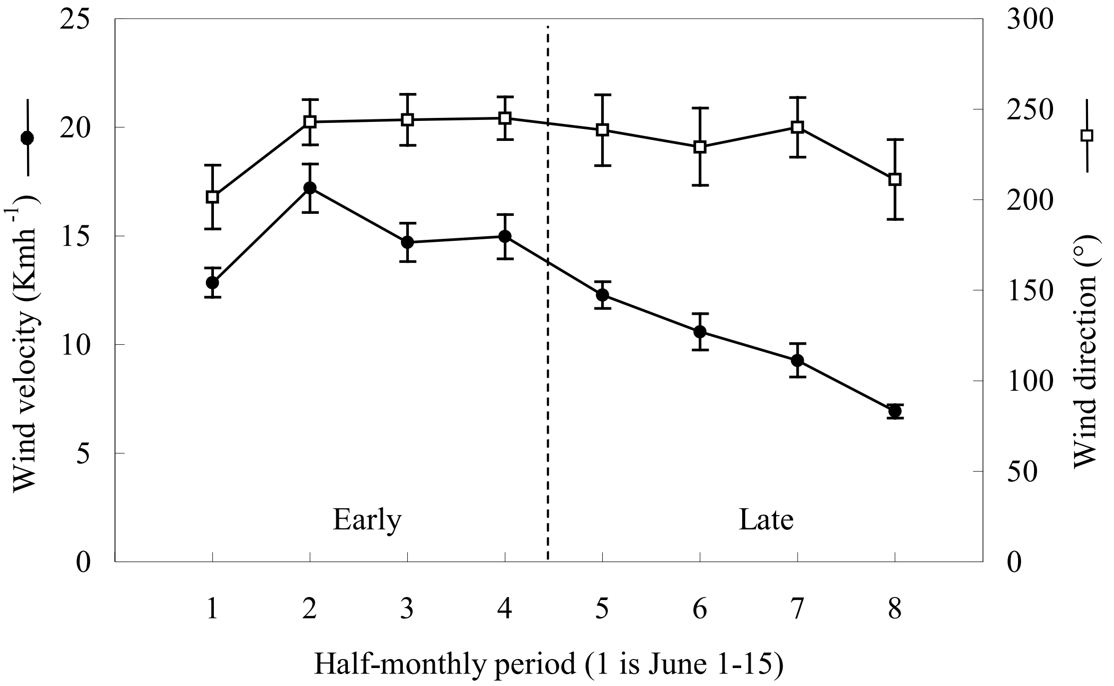

Figure 2-2. Mean wind velocity (●) and direction (□) from June to September, 1992-2000, at Patancheru, India. Error bars represent ± 1 SE for velocity and 95% confidence limits for direction (*n* = 9 years for each half-monthly period).

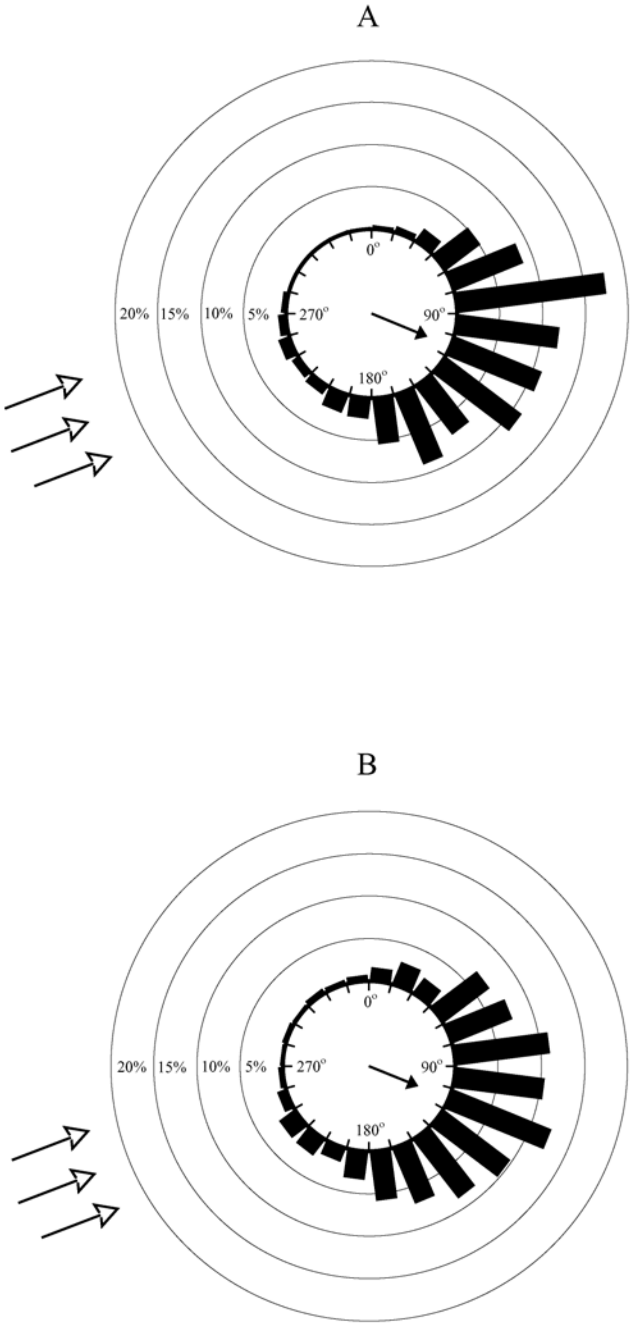

Figure 2-3. Circular frequency distributions of nest bearing and nest-entrance orientation. A) nest bearing; B) nest-entrance orientation (*n* = 1145 nests; bin width 15°). Arrows inside the circles indicate the direction and length (*r*) of the mean vector (radius of the inner circle is 1). Outer, light circles indicate scale (as a percentage of the sample size). Arrows pointing inward represent the direction of the strongest 10% of winds.

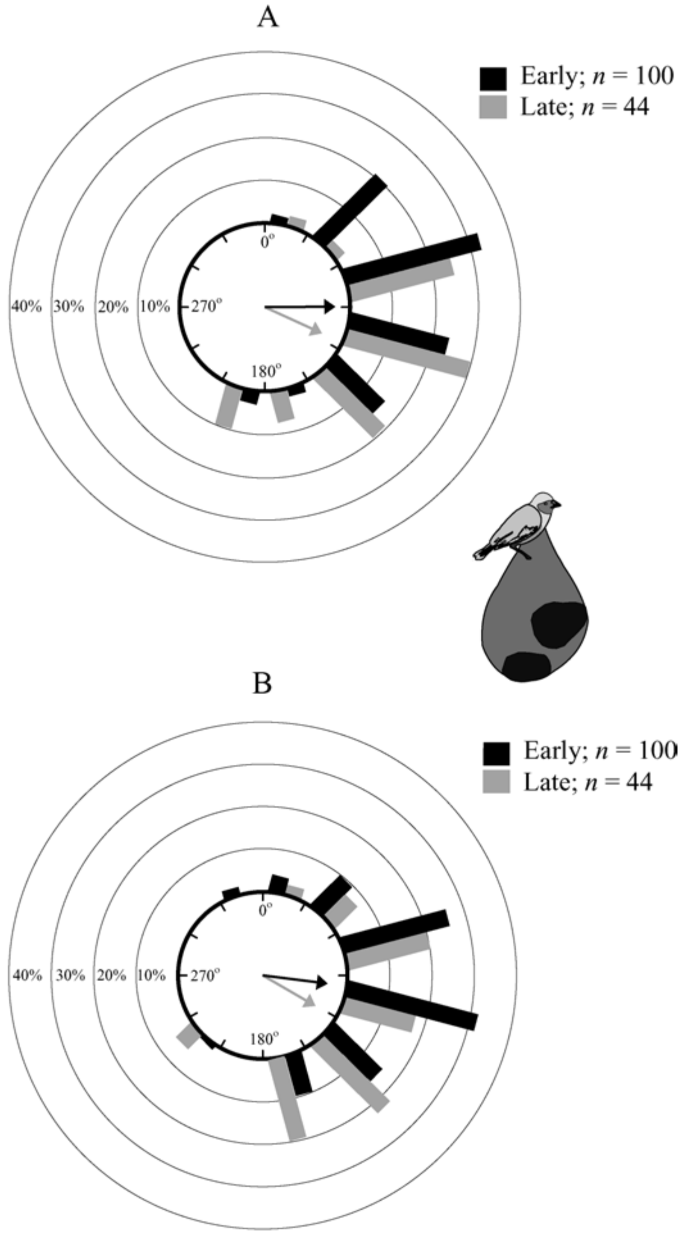

Figure 2-4. Circular frequency distributions comparing early and late helmet nests in terms of nest bearing and nest-entrance orientation. A) nest bearing; B) nest-entrance orientation (bin width 30°). Arrows indicate direction and length of mean vectors as in Figure 2-3. Late nests are significantly different from early nests in both bearing and entrance orientation.

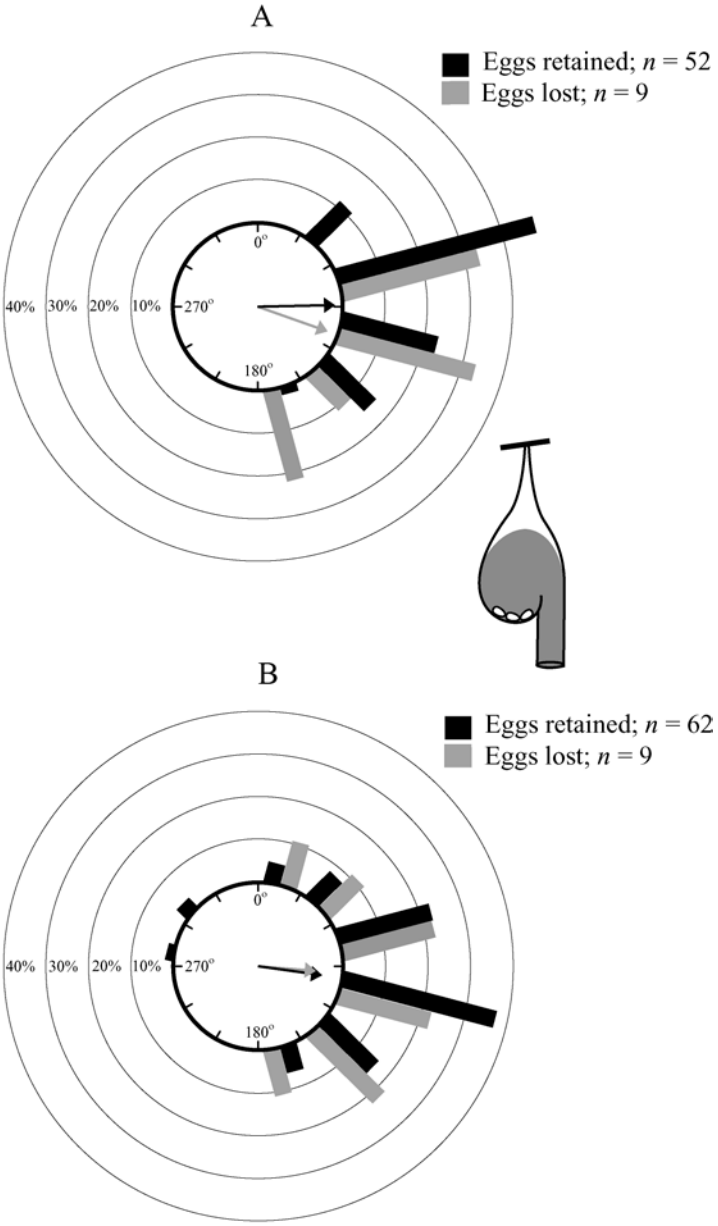

Figure 2-5. Circular frequency distributions comparing nest bearing of nests that retained eggs with nests that lost eggs due to strong wind early and late in the breeding season. A) early and B) late nests. Arrows indicate direction and length of mean vectors as in Figure 2-3. Early in the season, the bearing of nests that retained eggs was significantly different from those that lost eggs, but this difference disappeared late in the season.

CHAPTER 3
DO FEMALE BAYA WEAVERBIRDS PREFER ELABORATE NESTS? EXPERIMENTAL AND CORRELATIONAL EVIDENCE

Introduction

Studies of mate choice have typically focused on preference by females for male morphological or behavioral traits. Such studies provide a detailed picture of the role that female choice can play in influencing the evolution and maintenance of elaborate and exaggerated male morphology and behavior, including bright coloration (Houde 1997), eyes on stalks (Wilkinson and Reillo 1994), elongated tail feathers (Andersson 1982), and many other traits (reviewed by Andersson 1994).

In a variety of species, however, males also build structures that are thought to be used by females in making mating decisions. These structures range from the mud balls of fiddler crabs (Christy et al. 2002) and stone piles of wheatears (Moreno et al. 1994), to the elaborate bowers of bowerbirds (Borgia 1985, 1995a; Uy and Borgia 2000) and the nests and nest-like structures of several species of fishes (Kellogg et al. 2000; Lindström 1992; Nelson 1995; Oliveira et al. 2000) and birds (Collias and Victoria 1978; Evans and Burn 1996; Friedl and Klump 1999; Hoi et al. 1994; Jacobs et al. 1978). Nest-building may also be involved in post-mating sexual selection if females adjust their investment into offspring according to expected male parental care levels (Soler et al. 1998a, b). So, female choice may select for extended phenotypes (Dawkins 1982) of males, and therefore, their associated mechanical and engineering skills. These skills, like bird song, may in turn depend on underlying neural and learning mechanisms (Catchpole and Slater 1995; Konishi 1994; Madden 2001; Searcy and Andersson 1986).

Female choice for structures built by males should be particularly common when strong direct benefits are involved, such as when the structures are nests in which females lay their eggs. In many species of weaverbird (Passeridae: Ploceinae), nest building is carried out exclusively by males. Males display on their nests to visiting females, who subsequently lay their eggs in the nests (Collias and Collias 1964b). In these species, nests are thought to play an important role in female choice of mates, but there have been few tests of this presumption (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al. 1978). In the village weaverbird (*Ploceus cucullatus*), evidence for the role of nests in pair formation is mixed. In aviary studies, females prefer fresh (green) nests to old (brown) nests, but males also display at higher rates at fresh nests (Collias and Victoria 1978). Thus the effects of the nests on female choice may be confounded with effects of male behavior. Several lines of evidence suggest that females may pay more attention to the males or to the males' territories than to the nest structures they construct (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al. 1978). Little is known about female choice from among natural variation in nests in the field.

I tested the hypothesis that nests are a primary mate-choice cue in the baya weaverbird (*Ploceus philippinus*) using a combination of observations and experimental manipulations in the field. Male baya weavers construct particularly elaborate nests and display on them during female visits. I measured male morphology and behavior, and nest location and architecture to assess which has the strongest influence on female choice. To uncouple the effects of nest structure from the potentially confounding effects of male phenotype and nest location on female choice, I exchanged nests between males and measured the response of visiting females. If female visitation is determined by nest structure, the pattern of female visits should be altered by the manipulation. The absence of such a response would indicate that females use male phenotype or nest location, and not the nest itself, while making mate choice decisions.

Methods

Study Species

The baya weaverbird is common in agricultural and savanna-like landscapes throughout peninsular India. In the breeding season (May to October, coinciding with the southwestern monsoon rains), there is clear sexual dichromatism; males molt into a striking yellow and brown nuptial plumage, while females remain pale brown. Males weave nests out of grass and palm fiber, and females take no part in the nest-building process apart from lining the brood chamber with feathers. Nests are suspended from the tips of twigs of trees (frequently *Acacia, Prosopis*, or palms), often, but not always, over water. Many males may construct their nests on the same tree, and thus form colonies of variable size.

Males defend a small three-dimensional territory in a tree in which their nest is constructed. Nest construction passes through several stages. First, a vertical ring of fiber is constructed, woven to a twig. Males continue to weave until the nest reaches a partially complete stage. Nests at this stage resemble a helmet, complete with chinstrap (Figure 3-1A) (Ali 1931; Ambedkar 1964; Crook 1964a). Males display to visiting females by quivering their wings and uttering a high-pitched screeching song while perched on or near their helmet nests. Extreme forms of this display consist of males hanging upside down from the helmets, wings flapping. A visiting female perches on the chinstrap of the helmet, pulls at nest fibers with her bill, and pushes at the walls with her wings. Sometimes the pair mates while perched on the chinstrap (Ambedkar 1964; S. Quader, pers. obs.). Before eggs are laid, the male must complete the nest by weaving the floor of the brood chamber. He also builds a vertical entrance tube (Figure 3-1C) of variable length. Work on the entrance tube may continue until well after the eggs are laid and the chicks hatch. Egg laying may commence at any time after the completion of the floor of the brood chamber. Females incubate eggs and feed nestlings. On rare occasions (and especially toward the end of the season), males may bring food to the nestlings (Ali 1931; Ambedkar 1964; S. Quader, pers. obs.). After eggs are laid, males continue to weave small amounts of fresh fiber into their completed nests, especially if repair is needed. Often, the male will commence to build another helmet close by, and may attract another female. If a helmet is not accepted by any female, the male tears it down, and may build a new one in its place.

Study Site

I carried out fieldwork on farmland belonging to the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (17.53°N, 78.27°E; 545 m asl). The habitat consisted of active and fallow cropland with scattered trees, ponds, and streams. Mean annual rainfall is 942 mm (92% of which falls during May-October), and average annual minimum and maximum temperatures are 19.3°C and 31.8°C (1990–2000 data from ICRISAT agrometeorology service). I studied 13, 20, and 32 colonies from May to October of 1998, 1999, and 2000 respectively. Distances between colonies varied from 30 m to 2 km. When nests were situated on neighboring trees, separated by less than 5 m, I classified them as a single colony. I monitored helmet nests by tagging and numbering them as they were built. Nests were situated between 2 and 5 m off the ground, so I used a stepladder to reach them. During regular censuses (usually every other day), I recorded nest stage (helmet or complete). I considered all nests with a closed brood chamber complete, because such nests are ready to receive eggs. Contents of complete nests were examined directly if the entrance tube was short; otherwise I pushed an otoscope through the wall of the nest to inspect the interior.

Measuring Nests

I measured various potential correlates of female choice of helmet nests. I calculated the date on which each helmet was constructed (later converted to number of days past May 31). To account for differences among colony trees, I measured several aspects of each colony. It has been suggested that, for reasons of safety, bayas prefer to nest in thorny trees overhanging water (Ambedkar 1964; Collias and Collias 1964b; Crook 1963; Davis 1974). Thus, I classified colony trees according to whether or not they were armed with thorns and overhung water. I also counted the number of helmet nests and complete nests in the colony on the day that each new helmet was constructed.

Characters of the nests themselves can be separated into those relating to nest location (e.g., height and position in relation to other nests) and those describing nest architecture (e.g., nest dimensions and quality of weave). I measured location and architecture variables of helmet nests before nest completion; many of these variables are illustrated in Figure 3-1. Location variables included the vertical distance between the ground or water and the point of attachment of the nest to the branch (nest height), the diameter of the branch at the point of nest attachment, the horizontal distance of the nest from the trunk of the colony tree, and the number of neighboring nests within 1 m of the nest being measured. Among architectural variables, I derived an index of nest volume, calculated as the product of nest length, maximum external width, and maximum external depth. I measured the length of the woven suspension from the point of attachment to the branch to the point at which the nest surface broadens to form the roof of the structure (Figure 3-1B). I calculated an index of the area of the entrance opening by multiplying the length of the longest axis of the opening with the length of the axis perpendicular to this. An index of the area of the brood chamber opening was calculated in the same way.

I evaluated the overall quality of construction by examining three aspects of weaving: the fineness of the material used (based on the thickness of the fiber), the neatness of the weave (based on the number of free ends protruding from the surface of the helmet), and bilateral symmetry (around a vertical plane bisecting the chinstrap and nape of the helmet). The fineness of the material used was assessed by inspecting the entire lateral surface of the nest, excluding the suspension. Fibers were classified as thin (< 0.5 mm in diameter), medium (0.5–1 mm), or thick (> 1mm), and the overall fineness of the material was classified as fine if > 60% of the surface was woven with thin fibers, or coarse otherwise. I counted the number of fibers protruding by > 1 cm from c. 15 cm^2 of the lateral surface of each helmet. The neatness of the weave was classified as high if I found < 5 such loose ends and as low if there were ≥ 6 loose ends. Finally, nests with no or slight departures from bilateral symmetry were considered symmetrical, and those with large departures from symmetry were classified as asymmetrical. Summary statistics for continuous measures of helmet location and architecture are shown in Table 3-1.

Behavioral Observations

I carried out hour-long continuous focal observations on between one and five helmets at a time. During these observations, I recorded male attendance time (time spent in contact with the nest or within a 1 m radius of it) and time spent weaving. I defined a bout of weaving as a period of time during which males either wove freshly gathered fiber into their nests or modified the weave of existing fiber. I measured the number of display bouts; any fluttering of wings was considered display and because I was unable to measure their duration accurately I treat display bouts as events. I set 30 s as the minimum interval between separate display bouts. During focal observations I also measured the number of times males stole fiber from other nests in the same colony, and the number of times males were stolen from. A female visit to a helmet was recorded whenever a female was in physical contact with the nest. The identities of visiting females were unknown because I was unable to band most females until after they started incubating eggs.

I used mist nets to capture males and females throughout the season. Each individual was given a unique color combination of leg bands. I did not use bands colored yellow because leg bands of the same color as secondary sexual characters are known to influence mate choice and other behaviors in some birds (e.g., Burley 1982, Burley et al. 1996; Johnsen et al. 1997; Metz and Weatherhead 1993), and sexual dichromatism in the baya stems mostly from the bright yellow crown and breast that males acquire during the breeding season. The following morphometric variables were recorded: wing chord (flattened), tail length (from uropygial gland to tip of longest retrix), tarsus length, bill length (from anterior edge of nostril), bill depth and width (both at anterior edge of nostril), and mass. Each of these measures shows significant sexual dimorphism (Table 3-2), with males being larger in all linear measures, but females being heavier than males.

Nest Exchange Experiment

To evaluate the hypothesis that nest structure at the helmet stage is a primary determinant of female choice, I exchanged nests between pairs of males. This experiment was conducted in 1998 (between 25 July and 26 September; 13 replicates) and 1999 (between 8 July and 22 July; 3 replicates) during the morning. Using hour-long continuous observations, I identified pairs of males in the same colony such that one male was highly visited by females (popular male) relative to the other (unpopular male). After finding such a pair, I removed the helmets belonging to each male by cutting the twigs to which they were attached. I measured the helmets (as described above) and then exchanged them between the two males, affixing them in their new locations with thin wire. A 1 h focal sampling session was conducted immediately after the exchange (within 30 min) to measure the response of female visitors and male owners to the manipulation. Males continued to remain within their original territories after the exchange.

This manipulation uncouples the effect of nest structure on female visitation rate from the effects of nest location and male phenotype. If nest structure is the chief determinant of female visitation then, following the exchange, the pattern of female visits to each male should track the change in helmets such that the erstwhile unpopular male of the pair should become highly visited, while female visits to the previously popular male should decline. On the other hand, if nest structure is less important than nest location or male phenotype, female visits should continue as before the manipulation. Female responses were measured immediately after the manipulation so that there was insufficient time for males to make significant alterations to the structure of their new nests.

Analysis

To determine whether chosen nests differed from nonchosen nests, I used a multivariate generalization of the *t*-test, Hotelling's T^2 test (Manly 1986). I carried out separate Hotelling's tests using attributes of nest structure, and attributes of nest location.

These tests serve as a general guide to whether structure or location, or both suites of attributes are different in chosen and non chosen nests.

To identify the degree to which individual male and nest variables predict female choice, I used generalized linear models (GLM). The dependent variable (whether a helmet is chosen or not) is binary, so I used binomial GLMs with a logit link function (Agresti 1996). A potential problem with simple GLM analyses is that clustering of data may increase Type I error (Krackow and Tkadlec 2001). For example, nests are grouped in colonies, and colonies may differ in their average probability of having a helmet chosen. If this is so, then the problem is essentially one of nonindependence of data points; the probability that any given nest is chosen is not independent of that of every other nest in the population. This means that error (deviations from the prediction) can be divided into two sources—that attributable to among-colony variation, and that attributable to differences among nests within a colony. To take into account possible among-colony variation, one can use mixed-effects models (Krackow and Tkadlec 2001; Pinheiro and Bates 2000), in which the explanatory variables of interest are specified as fixed effects and the grouping factor (here, colony identity) is a random effect. I used generalized linear mixed models (GLMM) using a penalized quasi-likelihood method (glmmPQL; Venables and Ripley 2002) to estimate parameters describing the influence of hypothesized predictors on the probability that a helmet is chosen. For models with multiple fixed effects, I did not attempt to use model selection techniques to reduce the number of independent variables. Instead, hypothesis tests are based on *t*-statistics derived from the marginal parameter estimates and associated standard errors calculated from the full model (Pinheiro and Bates 2000). I conducted all analyses in the statistical and programming language R (Ihaka and Gentleman 1996).

Statistical power of GLMM analysis

One potential problem with GLMMs is that they may not perform well with unbalanced designs (i.e., when colony sizes vary widely). Because the number of helmets in the baya colonies I studied varied between one and 56, the data are highly unbalanced. I conducted computer simulations to investigate the performance of the glmmPQL function (Venables and Ripley 2002) in analyzing binomial responses when colony sizes are variable. The basic model was of the form $g(prob) = i + b_1x_1 + b_2x_2$, where *prob* is the probability of success, $g(prob)$ is the logit transformation (= log [$prob/(1-prob)$]), and x_1 and x_2 are fixed effects whose values were drawn from a uniform distribution with minimum = 0 and maximum = 3. The parameters b_1 and b_2 were assigned values of −1 and 0 respectively, and were used to estimate statistical power and the Type I error rate, respectively. To simulate a random effect, *i* (the intercept) for each colony was drawn from a normal distribution with a mean of 0.5 and standard deviation (SD) of one. Colony sizes (for each of 30 colonies) were assigned by adding one to values drawn from a Poisson distribution with a mean of 4. Estimates of b_1 were statistically significant in 98% of 1000 simulation runs, demonstrating that the method has high statistical power. Estimates of b_2 were statistically significant in 6% of runs, indicating that the Type I error rate is close to that expected. These results suggest that glmmPQL performs well for binary outcomes even when colony sizes are highly variable. Because different sets of data were available for male morphology, male behavior, and nest traits, the relationship between female choice and each of these groups of traits was examined separately.

The estimated coefficients from binomial GLMs represent the change in the log odds of a helmet being chosen, and so these numbers are difficult to interpret. To present a readily understandable metric of the influence of each fixed effect, I calculated the change in the probability of being chosen that is accompanied by a 1 SD increase in each fixed effect from its mean, keeping all other fixed effects at their means (or mode, in the case of categorical variables). I estimated the degree of nonindependence of nests within a colony by calculating the expected correlation in probability of success between nests as $s_b^2/(s_b^2 + s^2)$, where s_b^2 and s^2 are the estimated between-colony and within-colony variances respectively (Pinheiro and Bates 2000). This correlation was 0.5, indicating that nests within colonies are not independent, and that mixed modeling is justified.

Problems in analyzing linear models may arise if, for example, independent variables are correlated (Sokal and Rohlf 1995). To check whether the overall conclusions were robust, I analyzed correlates of helmet choice in two alternative ways. I conducted discriminant function analysis to differentiate chosen from nonchosen helmets using architecture and location variables separately. I also carried out principal components analysis on architecture and location measures separately, and conducted GLMM analyses on the resulting reduced set of uncorrelated axes. There were no qualitative differences in the results from these different analyses, so I present the outcome of GLMM analyses of the original variables. Data are presented for all years combined, and summary statistics are means ± 1 standard error (SE).

Results

Most helmets were never made into completed nests (63.1% of 388 helmets); they were either torn down or abandoned. Female visits to helmets were good predictors of whether a helmet would be completed: helmets visited by females during hour-long focal sessions were much more likely to be completed than those not visited (2 × 2 Fisher exact test, odds ratio = 10.17, $P < 0.001$, $n = 133$ helmets). While 79.1% of 43 visited nests were completed, only 26.7% of 90 non-visited nests were completed. Females laid one or more eggs in most completed nests (85.3% of 116 completed nests for which a complete history is available). This is likely to be an underestimate because nests depredated at an early stage would be scored as having no eggs. Taken together, these results suggest that nest completion is a good indicator of female choice, and that female visits to a nest predict how likely a nest is to be chosen. In the following analyses I take nest completion to be a sign that a helmet was accepted by a female. The few completed nests that received no eggs were either torn down or abandoned.

Correlational Results

Seasonal patterns in the number of reproductive females were examined by testing a model with linear and quadratic date terms, both of which explained significant variation in the probability of nest completion (linear and quadratic coefficients 0.054 and −0.0006, $P = 0.05$ and 0.01 respectively, $n = 324$ helmets; Figure 3-2). The number of available females (measured by the probability of a helmet being chosen) is thus highest shortly after the season starts, and declines steadily thereafter. To take this seasonality into account, I included linear and quadratic date terms in all subsequent models.

I evaluated the influence of seven morphological traits on the probability that a helmet would be accepted. Because each individual male contributed between 1 and 7 helmets to the analysis, male identity was included in the GLMM as a random effect. The morphological traits were not highly intercorrelated (highest Pearson correlation 0.34, $n = 68$). Of the seven traits, only bill width was marginally significantly related to the probability that a helmet was completed (Table 3-3). Males with narrower bills tended to be more likely to have their helmet nests chosen by a female.

To evaluate the relationship between female choice and male behavior, I used a GLMM with colony identity as random effect. None of the five behavioral variables measured was a significant predictor of nest completion (Table 3-4).

Hotelling's tests showed that chosen nests were significantly different from nonchosen nests in location attributes (9 variables, $n_{\text{chosen}} = 36$, $n_{\text{nonchosen}} = 97$, Wilks' lambda = 0.851, $P = 0.016$) but not in architecture attributes (9 variables, $n_{\text{chosen}} = 36$, $n_{\text{nonchosen}} = 97$, Wilks' lambda = 0.901, $P = 0.15$). Nest traits were also analyzed using GLMMs with colony as a random effect. A strength of using a linear modeling approach is that the explanatory power of continuous and categorical predictor variables can be evaluated simultaneously. I found four significant predictors of helmet choice: three location attributes, and one architecture attribute (Table 3-5). Chosen helmets were significantly higher than non-chosen helmets; an increase in height of 1 SD from its mean was associated with a 0.34 increase in the probability of being chosen. Nests attached to thick branches were less likely to be chosen: chosen and non-chosen helmets were attached to branches of diameter 3.84 ± 0.21 mm ($n = 39$) and 4.09 ± 0.19 mm ($n = 104$) respectively. Surprisingly, nests in colonies over water were significantly less likely to be chosen than those over dry ground (difference in probability of being chosen, −0.39). Finally, weave neatness was also a significant predictor of helmet choice (Table 3-5), with 38.6% ($n = 101$) of helmets with neat weave chosen compared with 25.0% ($n = 64$) of helmets with untidy weave chosen.

Nest Exchange Experiment

The helmet nests of paired popular and unpopular males used in the exchange experiment did not differ from one another in any consistent manner (Wilcoxon paired tests, $n = 12–16$ pairs, $P > 0.05$ for all 15 variables). Male attendance, time spent weaving, and frequency of display was also similar between highly and poorly visited males (Wilcoxon paired tests, $n = 16$, $P > 0.05$). After the exchange, all but two males accepted their new nests without a drastic change in behavior. Both these males were poorly visited before the exchange, and rejected a highly visited male’s helmet by tearing it down. These two trials were excluded from further analyses. Wilcoxon paired tests show that in the remaining 14 trials, the manipulation did not change either female behavior (number of visits; popular $W = 48.5$, $P = 0.48$; unpopular $W = 7.5$, $P = 0.59$) nor male behavior (attendance; popular $W = 41$, $P = 0.91$; unpopular $W = 48$, $P = 0.80$). After the exchange of helmets, female visitation continued to be significantly higher at the same location (and thus at the same male) as before the exchange (Figure 3-3; Wilcoxon paired test on post-exchange visitation, $W = 87$, $n = 14$ pairs, $P = 0.029$).

Discussion

In general, when only males build nests, one would expect females to discriminate among nests either for reasons of male assessment or to choose those nests well-suited to the local environment (physical conditions, predators). Evidence for both these effects exists. For example, Hoi et al. (1994) found that female penduline tits (*Remiz pendulinus*) prefer larger, more insulated nests. Similarly, mate choice in several fishes is thought to be influenced by nest site quality related to safety from predation (e.g., Östlund-Nilsson 2000). In magpies, *Pica pica*, and barn swallows, *Hirundo rustica*, on the other hand, it has been argued that nests serve the same function as a conventional “ornament” (Soler et al. 1998a, b). In many species of weaverbird, males display their nests to females, suggesting that females may use nests for mate choice (Collias and Collias 1964b, 1984). In addition to there being potential direct benefits to choosing good nests, males require learning and skill to be able to weave the nests (Collias and Collias 1964a), and this may enable nests to function as signals of male quality.

However, my results from baya weaverbirds do not support this prediction. Data on unmanipulated nests and the results from the nest exchange experiment suggest that nest architecture is not the most important cue used in female choice. Using generalized linear mixed models, I found that nest completion (a sign of female acceptance) was significantly related to nest location (diameter of branch, nest height, and location of colony relative to water). The probability that a helmet was chosen also tended to decline with one attribute of the male, bill width.

One measure of nest architecture was significantly related to the probability of a helmet being chosen. Neatly woven helmets with few fibers protruding from the surface were more likely to be chosen than poorly woven helmets. Thus, it is possible that females may use helmet architecture as a cue in mate choice. Note that when testing the significance of fixed effects in GLMMs, I present statistics based on the full model, that is, when all possible predictor variables are included. This means that nest site (in relation to water), branch diameter, nest height, and neatness of weave explain separate portions of variation in the probability that a helmet is chosen, and the patterns seen cannot be explained by correlations between the various predictor variables. Given this, nesting location is a better overall predictor of choice because three location variables are independently associated with helmet choice, while only one architectural feature is significantly related to helmet completion. This conclusion is also supported by results from the Hotelling's test, which revealed overall differences between chosen and nonchosen nests in location but not in structure.

The secondary role of male phenotype and nest structure when compared with nest location is reinforced by the results from the helmet exchange experiment. Contrary to my initial prediction, the experiment provided little support for the hypothesis that nest structure at the helmet stage plays an important role in female choice. When popular males were given nests from unpopular males, and vice versa, the pattern of female visits remained largely unchanged. Females continued to visit formerly popular males and to avoid formerly unpopular males after the exchange of helmets. Popular and unpopular males used in the exchange experiment were not measurably different in male phenotype, helmet location, or helmet architecture, so there was no clearly discernable reason why females should prefer some experimental males over others. Note that, because most visiting females were not banded, I was unable to tell whether there were multiple visits by different females, or whether I simply recorded the same females on repeated visits. If the same females were visiting these nests multiple times then the single hour-long observation immediately post-manipulation may not have been sufficient to detect longer-term changes in female visits in response to the exchange. However, I used this protocol because inferences drawn from possible later changes in female visits would have been complicated by the changes that males made to the architecture of their newly assigned nests.

Why do females not use nest structure when there may be direct benefits to do so? A possible explanation is that past female choice has indeed influenced the evolution of nest architecture through male weaving skill, but that females do not currently choose because most males have the requisite skill to make a good nest. All males do in fact seem to be capable of manufacturing an acceptable nest, because nest structure is not a good predictor of safety from predation or weather (Chapter 4). An alternative to the sexual selection scenario is that male nest-building has evolved solely through natural selection because a male's fitness is directly influenced by nest quality, independent of any preference that females may have. There may be a way to separate these hypotheses. If strong past female choice has occurred then it is possible that females retain a preference for good nests. Since all current nests are good, the preference is hidden, but it should be revealed if nest structure is manipulated to beyond the range of natural variation. If, on the other hand, nests have evolved solely through natural selection, there should be no hidden preference to uncover. The sexual selection and natural selection hypotheses are, of course, not mutually exclusive, but the results of nest manipulations may indicate which is most important.

Thus, in principle, performing extreme manipulations of traits suspected to play a role in mate choice can give us important information on past selection, even when choice does not currently occur. Collias and co-workers (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al. 1978) have, in effect, done precisely this when they manipulated nest color and nest composition in village weaverbirds. Unfortunately males are not passive recipients of these experimental treatments, and even though they appear to accept natural nests readily (this study), more dramatic manipulations of their nests can lead to nest rejection or a change in their behavior such as a reduction in display rate (Collias and Victoria 1978; Collias et al. 1979; Jacobs et al. 1978). As a consequence, patterns of female choice in relation to nest manipulation in the village weaverbird are difficult to interpret.

Although I found little evidence that females choose males on the basis of nests they build, nest location seems to play a larger role. Helmets attached to thin branches were more likely to be chosen than helmets attached to thick branches, although this pattern was only marginally significant. A possible reason that thin branches may be attractive to females is that nests on these branches may be safer from predation. Baya weavers tend to build their nests on the very tips of the outer branches of colony trees, and this has been proposed to be an adaptation against egg-eating snakes, which must coil around a branch and then loop around and into the entrance tube of a complete nest to reach the eggs (Ambedkar 1964). Safety from predation may also explain why females prefer nests high in colony trees. Data on nesting success collected in this population support the hypothesis of Ambedkar (1964) and Crook (1964a) that high nests are safer from predation than are low nests. By monitoring the fate of individual nests I found that both the probability of fledging and survival time (time to failure) increased with nest height (Chapter 4). Why females should prefer helmets over dry ground is less clear. It is commonly believed that bayas (and other species of weaverbird) often nest in trees with branches overhanging water because these are particularly safe locations (Ali 1931; Ambedkar 1964; Crook 1964a; Davis 1974), but I have found no evidence that fledging success or nest survival varied with position of nests relative to water (Chapter 4).

In summary, I have found that female choice of helmets in the baya weaverbird is better explained by nest location than by nest architecture or male phenotype. The results of the helmet exchange experiment argue against the hypothesis that nest architecture plays a primary role. While correlational analyses indicate that weave neatness may influence female choice, it appears that location is a better overall predictor of helmet acceptance by females. The reason for this seems to be that females gain direct benefits in the form of nest safety by choosing nests in suitable locations.

Table 3-1. Summary statistics of attributes of helmet location and architecture. Number of helmets and completed nests in the colony were measured at the time of helmet construction.

Attribute	Mean ±	sd	(range)	CV%	*n*
No. helmets in colony	5.80 ±	3.44	(1–17)	59.37	165
No. complete nests in colony	4.59 ±	4.84	(0–20)	105.44	165
Diameter of branch (mm)	4.02 ±	1.58	(1.9–9.6)	39.34	143
Distance to trunk (m)	2.79 ±	0.81	(80–490)	28.81	165
Distance to nearest neighbor (cm)	65.09 ±	37.12	(20–220)	57.03	164
Number of nests in 1 m radius	1.91 ±	1.26	(0–6)	66.16	165
Height from ground (m)	3.52 ±	0.60	(2.2–5.3)	18.59	160
Length of suspension (cm)	9.75 ±	5.77	(0–29)	59.18	164
Helmet volume (cm^3)	1648.32 ±	782.15	(418–6734)	47.45	165
Area of entrance (cm^2)	58.45 ±	10.18	(31.5–94.5)	17.42	165
Area of brood chamber opening (cm^2)	46.68 ±	11.84	(0–72)	25.38	165

Table 3-2. Morphometrical measurements on male and female baya weaverbirds. Males are significantly larger than females in all linear measures, while females are significantly heavier than males.

	Males		Females			
	mean ± 1SE	*n*	mean ± 1SE	*n*	*t*	*P*
Wing length (mm)	70.80 ± 0.006	223	67.73 ± 0.008	148	22.01	< 0.0001
Tail length (mm)	49.16 ± 0.007	222	46.71 ± 0.010	147	15.09	< 0.0001
Tarsus length (mm)	23.77 ± 0.004	155	23.38 ± 0.004	138	5.82	< 0.0001
Bill length (mm)	12.69 ± 0.002	222	12.60 ± 0.003	148	2.21	0.0277
Bill width (mm)	7.13 ± 0.001	222	7.00 ± 0.002	148	4.48	< 0.0001
Bill depth (mm)	8.61 ± 0.001	222	8.44 ± 0.002	148	5.54	< 0.0001
Mass (gm)	24.16 ± 0.006	214	24.53 ± 0.012	144	−2.21	0.0282

Table 3-3. Male morphological correlates of female choice, from GLMM analyses with male identity as random effect. A linear and a quadratic date term were also forced into the model (estimated coefficients were 0.121 and −0.001, respectively). $n = 34$ males.

	Partial coefficients ± SE	DF	*t*	*P*
Intercept	30.165 ± 33.030			
Wing length	−0.132 ± 0.485	20	−0.271	0.789
Tail length	0.365 ± 0.331	20	1.104	0.282
Tarsus length	0.120 ± 0.303	20	0.396	0.696
Bill length	−0.910 ± 1.559	20	−0.584	0.566
Bill width	−3.698 ± 2.015	20	−1.835	0.081
Bill depth	0.555 ± 1.286	20	0.431	0.671
Mass	−0.503 ± 0.403	20	−1.246	0.227

Table 3-4. Female choice in relation to male behavior at the helmet from GLMM analyses with colony identity as random effect. Data are frequencies per hour or proportion of time per hour of observation. *n* = 87 helmets observed.

	Partial coefficients ± SE	DF	*t*	*P*
Intercept	0.128 ± 2.069			
Date	0.043 ± 0.076	62	0.558	0.579
Date^2	−0.0003 ± 0.0006	62	−0.424	0.673
Display frequency	−0.047 ± 0.060	62	−0.787	0.434
Frequency of being stolen from	−0.039 ± 0.226	62	−0.172	0.864
Frequency of stealing	−0.062 ± 0.299	62	−0.209	0.835
Attendance	−0.0005 ± 0.0005	62	−1.031	0.307
Time spent weaving	0.001 ± 0.001	62	1.105	0.273

Table 3-5. Female choice in relation to nest structure and nest location based on GLMM with colony as random effect. Significant and near-significant *P*-values are marked with an asterisk; *n* = 140 helmet-stage nests.

	Partial coefficients ± SE	DF	*t*	*P*
Intercept	−6.042 ± 3.807			
Date	0.057 ± 0.067	97	0.85	0.398
Date^2	−0.0003 ± 0.0004	97	−0.69	0.492
No. helmets in colony	0.219 ± 0.139	97	1.58	0.116
No. complete nests in colony	0.047 ± 0.083	97	0.56	0.573
Colony tree thorny?	0.188 ± 0.966	25	0.19	0.848
Colony tree over water?	−3.346 ± 1.331	25	−2.51	0.019*
Diameter of branch (mm)	−0.309 ± 0.168	97	−1.84	0.069*
Distance to trunk (m)	−0.001 ± 0.004	97	−0.36	0.716
Number of nests < 1 m	0.365 ± 0.225	97	1.62	0.108
Height from ground (m)	0.944 ± 0.445	97	2.12	0.036*
Length of suspension (cm)	−0.035 ± 0.047	97	−0.74	0.462
Helmet volume (cm^3)	0.0000 ± 0.0005	97	0.07	0.944
Area of entrance (cm^2)	−0.014 ± 0.034	97	−0.42	0.677
Area of brood chamber opening (cm^2)	−0.005 ± 0.023	97	−0.24	0.813
Fiber thickness (0/1)	−0.009 ± 0.541	97	−0.02	0.985
Neatness of weave (0/1)	1.218 ± 0.552	97	2.20	0.030*
Helmet symmetry (0/1)	0.259 ± 0.503	97	0.51	0.608

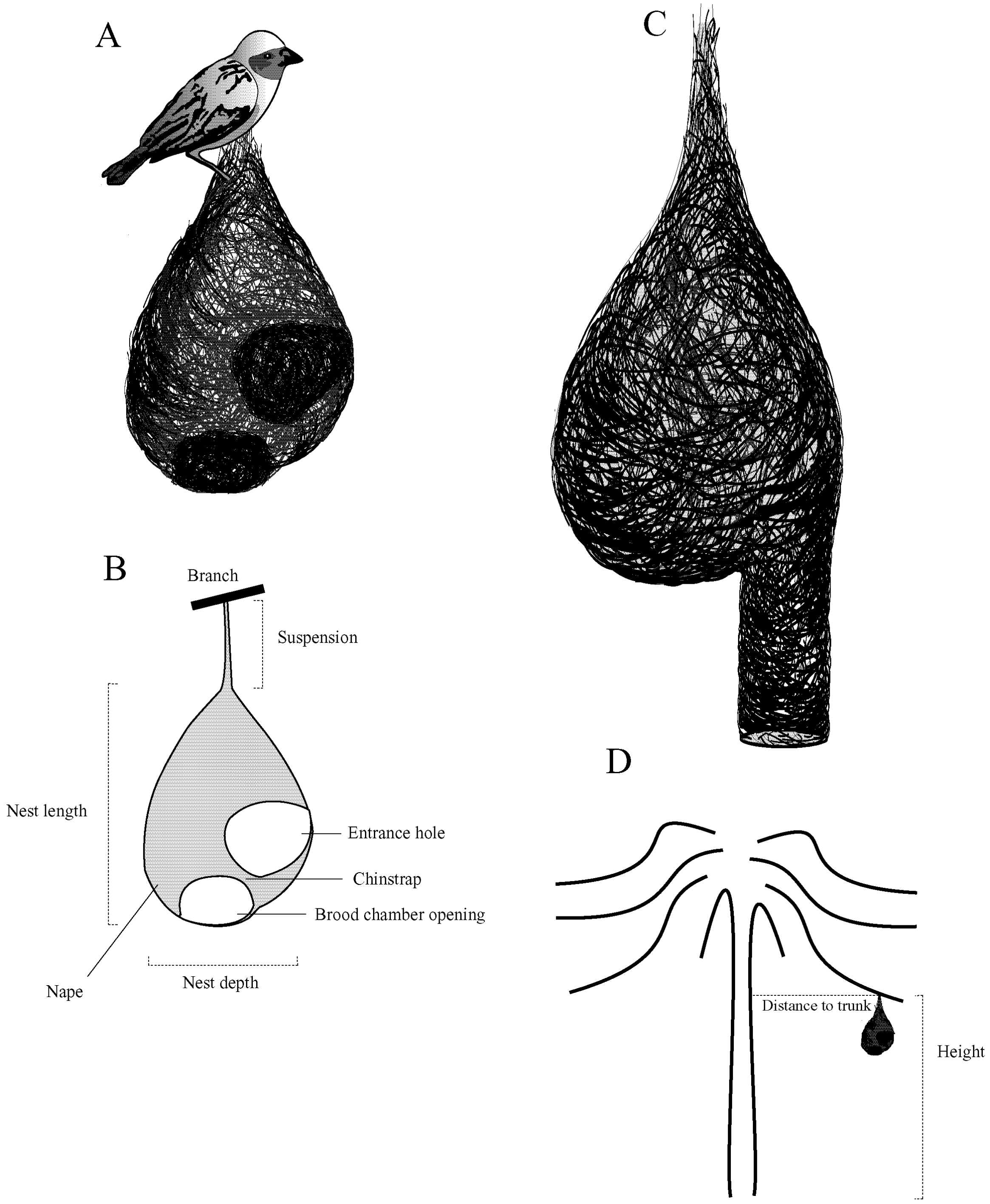

Figure 3-1. Stages in the construction of baya weaver nests. Males build their nests to an incomplete, helmet, stage (A). If the helmet is chosen by a female, the male completes the nest by closing the brood chamber and constructing an entrance tube (C). Schematics of baya nests show some of the measured architectural (B) and location (D) attributes.

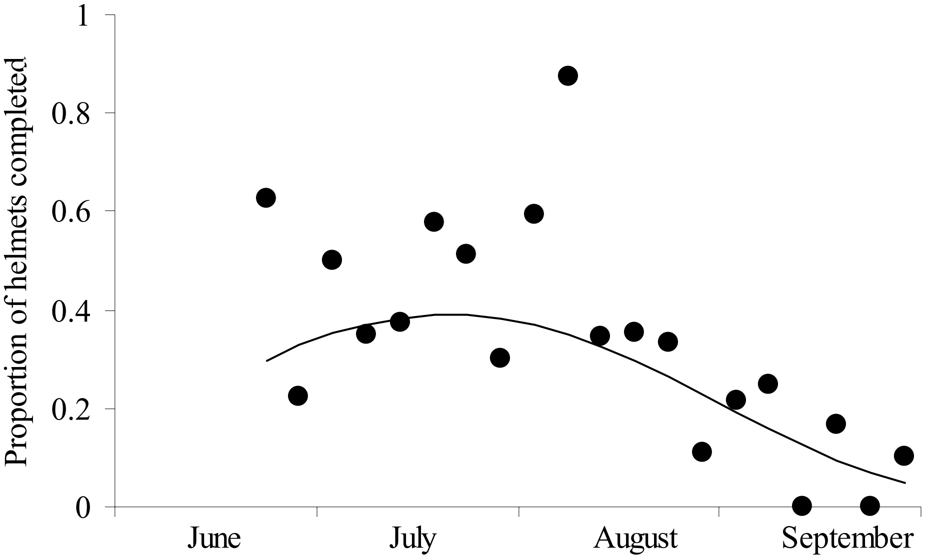

Figure 3-2. Proportion of helmets completed (accepted by females) in relation to date of construction. Proportions are calculated from between 4 and 37 helmets. The best fit line was obtained from a GLMM with colony identity as random effect (log odds of completion = $-1.8 + 0.054\text{Date} - 0.00055\text{Date}^2$), where day 1 is June 1.

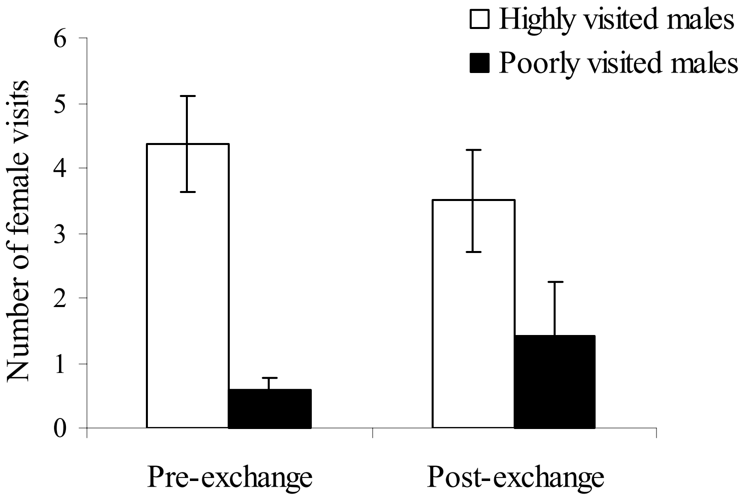

Figure 3-3. Female visits before and after helmets were exchanged between highly and poorly visited males. Pattern of female visits remained similar after the exchange. Highly visited males remained well-visited, and poorly visited males received few visits by females. The apparent interaction between male category and nest exchange is largely driven by two males in each category. $n = 14$ pairs of males.

CHAPTER 4
CONSEQUENCES OF NEST CHOICE: REPRODUCTIVE BENEFITS ASSOCIATED WITH NEST LOCATION AND STRUCTURE IN THE BAYA WEAVERBIRD

Introduction

What benefits do females gain from making decisions about where to nest? In many species, females appear to benefit from specialized structures that males build. At their simplest, these structures may alert females to the presence of a male, and allow them to orient towards him (e.g., the mud pillars of the fiddler crab *Uca musica*; Christy et al. 2002). Nests may also signal male quality, such as in sticklebacks *Gasterosteus aculeatus* (Barber et al. 2001). In bowerbirds (*Ptilonorhynchus* and *Chlamydera* spp.), females appear to choose owners of well-built structures (Borgia 1985, 1995a) and in doing so, acquire mates with high competitive ability and low parasite load (Borgia and Collis 1989, 1990). Other benefits of mating at bowers may include avoidance of male aggression during courtship (Borgia 1995b; Borgia and Presgraves 1998).

Nests or nest-like structures may also be associated with other direct (i.e., nongenetic) benefits to females. For example, female penduline tits *Remiz pendulinus* prefer large nests, apparently because these are better insulated than small nests (Grubbauer and Hoi 1996; Hoi et al. 1994). Female winter wrens *Troglodytes troglodytes* prefer males with multiple nests on their territories, and the number of nests on a territory indicates the relative safety of the territory from predation (Evans 1997; Evans and Burn 1996). In the red bishop *Euplectes orix*, females appear to settle at random at nests, so a male who builds many nests may attract multiple females to his territory (Friedl and

Klump 1999, 2000). In this situation it is not known whether females gain direct benefits by choosing from among available nests.

Weaverbirds provide a good model system in which to study female choice for nests and the benefits associated with such choice. In many weaverbird species only the male takes part in nest building, and females choose among available males and their nests (Crook 1963). In the village weaverbird *Ploceus cucullatus*, manipulations of nest color and materials provide some evidence for mate choice based on nests (Collias and Victoria 1978; Jacobs et al. 1978; but see Garson 1979), although the benefits of these choices remain unknown. In the baya weaverbird *Ploceus philippinus*, I have found little evidence that females choose mates based on nest structure. Instead, nest location seems to play a major role in female choice (Chapter 3). Is this because nest location has a greater influence on nest quality than does nest structure?

Several aspects of weaverbird nest structure and location have been hypothesized to contribute to nest quality. The most frequently discussed is the entrance tube, which may serve to reduce predation by hindering the entry of snakes into the nest (Crook 1963). However, it has not been conclusively demonstrated that long entrance tubes protect against snakes, and we do not know whether snakes are indeed the largest source of nest failure in these birds (but see Pitman 1958). Entrance tubes may not deter other predators, and rodents appear to be able to enter nests regardless of the length of the entrance tube (S. Quader, unpublished data). In some African species, the entrance tube may function to restrict the entry of the brood parasitic diederick cuckoo (*Chrysococcyx caprius*), although comparative data do not provide strong support for this hypothesis (Freeman

1988). In India, however, weaverbirds are not parasitized by cuckoos, but entrance tubes can still be extremely long (up to about 1 m, Ali and Ripley 1987).

Predation is thought to also select for situating nests in thorny trees, and in trees overhanging water (Ambedkar 1964; Collias and Collias 1964b; Crook 1963; Davis 1974). If predation is an important cause of nest failure, there may be benefits to nesting in large colony through a dilution effect (Hamilton 1971). Within a colony tree, increasing height from the ground should enhance safety from terrestrial predators. Also, baya nests are typically built on the outermost branches of a tree and it is possible that the further toward the outer tips of the branches a nest is, the safer it is. Finally, the thickness of the branch a nest is attached to may play a role. Thick branches may give a snake easy access to a nest (Crook 1963). Conversely, thick branches are probably less likely to break in strong monsoon winds than are thin branches. Nest concealment plays an important role in escaping predation in many species of small passerine birds, but this is unlikely to be the case in baya weaverbirds, whose nests are large and prominent and clustered in colonies on the outermost branches of colony trees. Strong winds sometimes cause eggs and nestlings to fall out of the nest, and Collias and Collias (1964b) suggest that deep egg chambers prevent this from occurring. Collias and Collias also suggest that that strong weave makes it difficult for a predator to gain access to the brood by pushing through the nest walls. Here I use data on fledging success and the survival time of nests to examine whether nest location or nest structure provides benefits to females in the baya weaverbird.

Methods

Study Species and Field Site

The baya weaverbird is distributed throughout South Asia in savanna-like habitats, and especially near cultivation. It breeds primarily during the seasonal monsoon rains (June to September), in colonies of variable size. Females play no part in nest building (Ali 1931, personal observations). A male builds a partial nest structure (called a helmet) suspended from a branch within a small three-dimensional territory in a tree (Chapter 3). He then displays on the helmet to visiting females (Ali 1931; Crook 1960; Chapter 3). If a female accepts a helmet, the male completes the nest, and egg laying may commence immediately after the floor of the brood chamber has been woven. Completed nests resemble a closed basket and the male extends the nest opening into a vertical entrance tube of varying length (Figure 4-1). I investigated the nesting success of baya weaverbirds on farmland belonging to the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT–Asia), Patancheru, India (17.53°N, 78.27°E; 545 m above sea level).

Monitoring and Measuring Nests

I monitored nesting colonies from May through October, 1998–2000. Distances between colonies varied from 30 m to 2 km. When nests were located on neighboring trees, separated by less than 5 m, I classified them as belonging to a single colony. Because nests are highly visible, most nests were detected and tagged before egg-laying was complete. Colonies were visited every 1–4 days. During each visit I examined nest contents by pushing an otoscope through the side of the nest. I assumed that nests were found before clutch completion if I found no additional eggs in subsequent visits (n = 128 nests). Clutches were considered complete once I recorded no change in the number of eggs on successive visits. Seventy-eight nests were found after clutch completion.

Signs of nest failure included broken eggs with contents partially or completely missing, eggs or nestlings on the ground under the nest, nestlings missing and blood smears in the nest, and dead nestlings in the nest, sometimes partially eaten by ants or rodents. When all eggs or nestlings were missing and could not be found under the nest, nest failure was attributed to predation by snakes. Nests sway violently under windy conditions, so if I found cracked, but otherwise intact eggs, or if part of the clutch or brood had fallen to the ground under the nest, I assumed that strong winds were the likely cause. When eggs were broken and eaten in the nest, or when nestlings were killed and partly eaten (often with blood smeared inside the nest), I attributed failure to rodent predation. Like Ali and Ambedkar (1956), I sometimes found a long-tailed tree mouse (*Vandaleuria oleracea*) established in the nest on the day I detected nest failure. Failure here was attributed to the mouse, and I occasionally found a newborn mouse brood in such nests on a subsequent visit. Ten nests that seemed abandoned by the parents (eggs present, but cold and not incubated) were excluded from analysis.

Once a nest is chosen by a female, the male completes the brood chamber and elongates the entrance tube. I measured attributes of nest location and structure once per nest, after the brood chamber was completed and the entrance tube extended to below the floor of the brood chamber. After this stage nest dimensions did not change substantially, apart from the entrance tube, which males often continued to elongate until well after hatching. Entrance tube length changed over time, and in these analyses I use the distance (in cm) from the bottom of the brood chamber to the lowermost edge of the entrance tube at clutch completion (Figure 4-1). I measured other attributes of nest structure as follows. The length (cm) of the woven suspension was defined as the distance between the point of attachment of the nest to the branch and the point at which the woven fabric broadened to form the roof of the nest (Figure 4-1). I multiplied nest length (distance from roof to bottom of brood chamber), maximum external width (lateral width at the widest part of the brood chamber), and maximum external depth (distance between anterior and posterior edges of the nest, Figure 4-1) to give an index of nest volume (cm^3). The entrance tube ends in a roughly circular opening; I calculated an index of the area of this opening (cm^2) by multiplying its diameter at the widest point with the length of the axis perpendicular to this. Eggs are prevented from falling out of the nest by a threshold, which projects upwards anterior to the brood chamber (Figure 4-1). I measured the height of the topmost point of this threshold from the bottom of the brood chamber. I also assigned binary scores to nests according to three aspects of weave quality: weave neatness, fineness of fiber, and nest symmetry. I scored neatness of weave based on the number of loose fibers projecting > 1 cm from the exterior of the nest. This measure as well as fiber fineness was based on an examination of c. 15 cm^2 of the surface of the nest lateral to the brood chamber. Weave neatness was classified as high if I found < 5 fibers protruding from the surface of the nest or low if there were ≥ 6 such loose ends. The overall fineness of the fibers used was classified as high if > 60% of the surface was covered in fine (< 1 mm in diameter) fibers or low if > 40% of the surface was covered in fibers > 1 mm in diameter. I scored nest bilateral symmetry according to symmetry around a vertical plane passing antero-posteriorly through the center of the suspension, threshold, and entrance tube. Nests were classified as showing high symmetry if they were perfectly symmetric or slightly asymmetric. I classified highly asymmetric nests as possessing low symmetry.

I also measured five attributes of nest location. These were the horizontal distance (m) from each nest to the main trunk of the colony tree; the height (m) of the nest from the ground (or water) to the point of attachment of the nest to its branch (Figure 4-1); the distance (cm) between a nest and its nearest neighbor in the colony was measured from this point of attachment; and the diameter (mm) of the branch at the point of nest attachment. I also counted the number of neighboring nests in a 1 m radius of the center of the nest being measured. In addition, I measured three aspects of the colony tree, including the type of tree (armed with thorns or thornless) and whether the branches used for nesting overhung water or dry ground. A further colony attribute that may influence nest success is colony size (number of nests). In order to calculate a meaningful measure of colony size for each nest, I counted the number of active nests (nests with eggs and/or nestlings) in a colony on the day that the clutch of the focal nest was completed.

Analyses

To determine whether there was an overall difference between nests that fledged young (successful nests) and those that did not (unsuccessful nests), I used a multivariate generalization of the *t*-test, Hotelling's T^2 test (Manly 1986). I carried out separate Hotelling's tests using attributes of nest structure, and attributes of nest location. These tests serve as a general guide to whether structure or location or both suites of attributes are different in successful and unsuccessful nests.

I used two different statistical approaches to identify specific factors correlated with nest success: generalized linear mixed models and survival analyses. As in the analysis of the correlates of helmet choice (Chapter 3), I confirmed the qualitative results of these analyses using discriminant function analysis and principal components analysis.

Generalized linear mixed modeling

I classified nests into those that failed and those that succeeded by labeling as successful any nest that fledged one or more young. To explore the influence of a combination of potential predictor variables on this binary outcome (fledging successful or unsuccessful), I used generalized linear modeling with a binomial response and a logit link function (Agresti 1996). In this approach, the log odds of success ($\log(p/(1-p))$, where p is the probability of success) is modeled as a linear combination of explanatory variables. A potential problem is that each nest cannot be assumed to form an independent observation. Rather, nests within colonies may share different baseline probabilities of success. If this is so, then treating nests as if they were independent will inflate Type I error rates (Krackow and Tkadlec 2001). By treating colony identity as a random effect, however, differences between colony means are taken into account and pseudoreplication can be avoided. A model with one or more random effects is called a mixed model, and the explanatory variables of interest are called the fixed effects. I used generalized linear mixed models (GLMMs) to explore factors related to nest success using the glmmPQL function of Venables and Ripley (2002) in the statistical and programming language R (Ihaka and Gentleman 1996). One potential concern with these analyses arises from the extremely unbalanced nature of the data because the number of nests available per colony varied widely. However, I have shown using simulations (Chapter 3) that glmmPQL with a binomial outcome performs well even with highly unbalanced data. In these simulations statistical power was high and Type I error was close to the nominal 0.05 level. In the results of GLMM analyses on nest success I do not attempt to follow a likelihood-based model selection procedure because the use of likelihood ratio tests to prune the number of fixed effects in a mixed model is not valid (Pinheiro and Bates 2000). Instead, I present estimated partial coefficients for each explanatory variable, as well as the associated *P*-values based on conditional *t*-statistics as recommended by Pinheiro and Bates (2000). Thus, when there are multiple significant predictor variables, each explains a separate portion of the variation in fledging success. When describing significant predictors of fledging success, I present the increase in the probability of survival associated with a unit increase in the predictor from its average, when holding all other variables constant at their average value (or mode for binary variables). To estimate the degree of nonindependence of nests within a colony, I calculated the expected correlation in probability of success between nests as $s_b^2/(s_b^2 + s^2)$, where s_b^2 and s^2 are the estimated between-colony and within-colony variances respectively (Pinheiro and Bates 2000).

Survival analysis

One methodological limitation of classifying nests into those successful and those unsuccessful is that the outcome of a nesting attempt is often ambiguous, especially for nests close to fledging young. For example, if a nest is active on the 28th day after the clutch was completed but is empty on the 31st day (when mean fledging time is 30 days), then one must use some arbitrary decision rule to assign success or failure. Such an approach can be subjective and inconsistent (Manolis et al. 2000). One possible alternative is to discard nests with ambiguous outcomes, but this can be wasteful, especially because such nests may form a large proportion of the data. Instead, time-to-failure data such as are available here can be examined using survival analyses (Manolis et al. 2000). In these analyses, successful nests and nests with ambiguous fates are treated as censored—one can be confident that they survived at least t days, but their true lifetime is unknown. The lifetimes of nests known to have failed, on the other hand, are known and these are not censored. An additional advantage of using survival analyses is that nests that were not monitored from the very beginning can be included in the analysis, provided that the time elapsed until the nest entered the study can be calculated.

I used Cox proportional hazards regression (Venables and Ripley 2002) to identify factors correlated with nest survival time. This is a semi-parametric method for conducting survival analyses in which no assumption about the distribution of survival times need be made. However, one must assume that hazards are proportional. The hazard is the risk of failure in a short time period $t + \Delta t$, given that the nest has survived to time t. The proportional hazards method makes the assumption that the proportional change in hazard associated with a given factor is constant over time. For example, if at the beginning of incubation, nests overhanging water experience a 10% reduction in hazard relative to nests overhanging dry ground, this proportionate reduction in hazard must remain constant until fledging regardless of the change in absolute hazard.

I used the R function coxph (Venables and Ripley 2002) to explore correlates of nest survival time. I censored the survival times of successful nests and those with uncertain fates at the last day on which nestlings were observed. For the subset of nests that I found only after egg-laying was complete, I estimated date of clutch completion by subtracting the median incubation time of 12 days (range 10–14, n = 70 nests with known incubation times) from the known date of hatching. The estimated date of failure was calculated as the midpoint between the date that the nest was last seen active and the date that failure was first observed. Note that, on average, this date is likely to be slightly later than the true date of failure (Miller and Johnson 1978). I also took into account possible nonindependence of survival times of nests within colonies by declaring colonies as strata. This procedure allows different colonies to have different baseline hazards and is analogous to treating colony identity as a random effect in a mixed-effects model (Venables and Ripley 2002). To examine the assumption that hazards are proportional, I used the function cox.zph (Venables and Ripley 2002), which tests the null hypothesis that the estimated hazard ratio is unrelated to time.

Fledging success (whether a nest fledges young or not) and nest survival (time until nest failure) are different ways of looking at the same problem. Most studies of the correlates of nest success divide nests into two categories—successful and unsuccessful (e.g., Li and Martin 1991, Hanski et al. 1996). Although one might consider the survival time of a nest to be irrelevant if it eventually failed, this time to failure provides additional information on how likely the nest was to fledge young. In addition, delayed entry and uncertain fates of nests can be incorporated into survival analysis. In this paper, rather than choose one method (GLMM) over another (survival analysis), I identify correlates of nest success that show congruent patterns across both approaches.

Results

Colony and Nest Characters

I monitored 43 colonies over the three years of the study, four of which were followed in multiple years. Six of these 43 colonies were situated overhanging water, and 29 colonies were in trees armed with thorns. Thorny colony trees were either *Acacia nilotica* or *Prosopis juliflora*. Unarmed colony trees were predominantly *Leucaena leucocephala*. Measures of nest location for individual nests were typically highly variable (Table 4-1). Coefficients of variation (CV) for location traits ranged from 21.3%

(nest height) to 82.0% (number of neighboring nests). Nest structure, in contrast, had some highly conserved traits and some very variable traits. External dimensions of nests tended to be uniform (CV: external width 13.7%, external depth 7.1%, height of threshold 17.5%). Other aspects of architecture showed substantial variation (length of suspension 60.7%, length of entrance tube at clutch completion 93.7%).

Hatching and Fledging Duration

For all nests for which a complete record is available (i.e., monitored from clutch completion), the number of days from clutch completion to hatching was 12.35 ± 0.12 (mean ± SE, $n = 70$). Based on nests found before hatching, the nestling period was 17.48 ± 0.27 days ($n = 54$). Overall nesting time (from clutch completion to fledging) was 30.26 ± 0.36 days ($n = 26$).

Fledging Success

Estimates of the proportion of nests that survived until hatching and fledging depended on which nests were included. Fewer nests that were monitored from clutch completion fledged young (23.4% of 111 nests with unambiguous fates) than all nests combined (35.2% of 176 nests; Table 4-2). Thus, the probability of fledging young was lower for nests monitored from the start than for nests found after clutch completion (Fisher exact test, odds ratio 0.56, $P = 0.036$). This is as one would expect because the latter category does not include those nests that failed early (Mayfield 1961, 1975). Similar patterns were obtained for hatching success (Table 4-2). However, fledging rates based on nests with unambiguous outcomes may be an underestimate because they exclude 13 nests whose fates were uncertain. Eight of these nests survived at least 25 days; if they are counted as having fledged young, then the proportion of successful nests is 28.6%.

The number of nests surviving declined at a roughly constant rate over the nesting period (Figure 4-2). Rates of nest failure were slightly higher than average at the very beginning of nesting and again around hatching or just after. The survival curve shows that the proportion of nests that survived for at least 27 days is 36.8%. All nests that survived longer were either successful (42 nests) or had uncertain fates (4 nests). One can predict the average proportion of nests expected to survive until fledging by assuming that the daily survival of nests after 27 days is the average of daily survival between days 24 and 27. Then, given that mean nesting time is approximately 30 days, one would expect 32.6% (95% confidence interval 28.7%–37.1%) of nests to survive until fledging. Causes of nest failure varied, and appeared to be primarily related to strong winds (23.8%), snake predation (26.1%), and rodent predation (38.1%; n = 84 failed nests). I estimated the correlation in probability of fledging between nests in the same colony by conducting a GLMM analysis with only an intercept, and colony as random effect. Variance estimates for between-colony and within-colony variation yielded an expected within-colony correlation of 0.82.

Correlates of Success

Hotelling's tests showed that successful nests were significantly different from unsuccessful nests in location (including colony attributes: 9 variables, $n_{\text{fledged}} = 24$, $n_{\text{failed}} = 32$, Wilks' lambda = 0.49, $P < 0.001$) but were only marginally different in architecture attributes (10 variables, $n_{\text{fledged}} = 24$, $n_{\text{failed}} = 32$, Wilks' lambda = 0.71, $P = 0.07$). To identify individual correlates of nest success, I used GLMMs and Cox regression.

Nest success in relation to date

I first investigated whether success was related to date of clutch completion by fitting models with both a linear and a quadratic date term. Both terms were marginally significant predictors of hazard in survival analyses (hazard ratios 0.82, $P = 0.07$ for Date, and 1.004, $P = 0.07$ for Date^2). The hazard ratios can be interpreted as the proportionate change in hazard for a unit increase in the explanatory variable. Here, for a one-day increase in Date, the hazard decreases by 18%, while a unit increase in Date^2 is associated with an increase in hazard of 0.4%. Date of clutch completion was a strong predictor of fledging success in GLMM analyses (coefficients of Date and Date^2, 0.17, $P = 0.014$, and −0.001, $P = 0.031$ respectively, $n = 172$ nests). Here, the coefficients describe the change in the log odds of success associated with a unit increase in the explanatory variables. Note that these results mirror those from the Cox regression—for example, Date is associated with a decrease in hazard and an increase in the log odds of fledging. Thus, nest success is low at the beginning, increases to a peak towards the middle, and declines at the end of the season (Figure 4-3). Because date of clutch completion was a consistent predictor of nest success, I included linear and quadratic date terms in all subsequent survival and GLMM analyses.

Colony attributes

To investigate whether nest colony attributes explain variation in nesting success, I explored the influence of colony location (over water or dry ground) and type of colony tree (armed with thorns or bare). Neither of these variables explained significant amounts of variation in nest survival (Cox regression) or fledging success (GLMM), and they are not considered further. However, both linear and quadratic terms of the number of active nests in a colony were significant predictors of nest survival (hazard ratios 1.48, $P = 0.02$

for linear, and 0.97, *P* = 0.03 for quadratic), and both terms are included in subsequent analyses of nest survival (Cox regression, see below). Number of active nests did not explain significant variation in fledging success, so this variable is not included in subsequent GLMM analyses.

Nest attributes

Neither nest survival nor fledging success was correlated with length of the entrance tube at clutch completion, and this variable is not considered further. While statistically controlling for date of clutch completion, nest survival was nonlinearly related to the number of active nests in the colony at clutch completion (Table 4-3). The hazard ratios for the linear (13.1) and quadratic (0.78) terms indicate that an increase in the number of active nests is associated with first increase and then a decrease in the hazard. This means that nest survival is longest in small and large colonies and is shortest in colonies of intermediate size. Nest survival also decreased with the length of the nest suspension and increased with height from the ground, although the latter relationship is only marginally significant (Table 4-3). The estimated hazard ratios for these two variables show that a 1 cm elongation of the suspension is associated with a 15.6% increase in hazard and that an increase in nest height of 1 m predicts a 94.7% decrease in hazard. Other variables, including nest volume, number of neighbors in 1 m, and height of the threshold, were not significant predictors of nest survival.

GLMM analysis (Table 4-4) indicated that the probability of fledging was significantly related to date of clutch completion (as described earlier; Figure 4-3). In addition, the probability of fledging increased with branch diameter and height from the ground. Holding other variables at their average (or mode), the increase in fledging probability was 6% and 10% for a 1 mm increase in branch diameter and a 1 m increase in height, respectively. One architectural variable was also a significant predictor: fledging success of nests woven with relatively fine fiber was higher (48% of 25 nests) than that of nests woven with thicker fiber (29.5% of 43 nests); a decrease in fiber thickness from relatively thick to relatively thin was associated with an increase in the probability of fledging of 18%. Overall, two factors showed congruent patterns across survival analyses and GLMM analyses. Hazard changed as a quadratic function of date and decreased with the height of the nest in survival analyses. Similarly, the probability of fledging was quadratically related to date and increased with nest height.

Cox regression and GLMM analyses gave somewhat different results. Cox regression showed that nest survival was related to the number of active nests in a colony and the length of the nest suspension. These variables were not significant predictors of fledging success in GLMM analyses, in which the diameter of the branch was significantly related to fledging. A possible explanation for these differences is that the GLMM analyses use only a subset of the nests in the Cox regression (specifically, those nests for which complete records are available, and whose fate was unambiguous). This cannot explain the differences entirely, because when I carried out Cox regression on the subset of nests used in GLMM analyses, the number of active nests and the length of the suspension remained significant predictors of nest survival. Regardless of the origin of the differences, certain patterns are consistent across both analyses. Nesting date was a strong predictor of nest outcome in both analysis, and nest height is significant in GLMM analysis and marginally significant in Cox regression.

Discussion

What are the benefits to female baya weaverbirds of choosing from among available nests? Among potential benefits, the most obvious is finding a nest that is well-constructed and is safe from predators and harsh weather. Direct benefits to females include nests with better insulation qualities (Grubbauer and Hoi 1996; Hoi et al. 1994) and territories with greater concealment from predators (Evans 1997; Evans and Burn 1996). Are there attributes of baya nests that are good predictors of nest safety? By measuring the correlates of nest outcome (nest survival and fledging success), I show that nest location (colony size, nest height, diameter of branch) is a better predictor of direct benefits to females than is nest architecture (length of suspension, fiber thickness) when nesting date is statistically controlled. These results may explain why female baya weaverbirds appear to pay more attention to nest location than to nest architecture while making mate choice decisions (Chapter 3).

Overall fledging success in baya weaverbirds was low, suggesting that there should be strong benefits to males of making appropriate decisions about where to build a nest and how to construct it. Similarly for females it should be important to choose a well constructed nest in a safe location. What is the relative importance of nest location and nest architecture? Generalized mixed modeling and survival analyses suggested that nest location plays a larger role in influencing safety than nest architecture.

The time of nesting appears to be an important correlate of nest outcome. Linear and quadratic terms of the date on which the last egg of a clutch was laid were significant predictors of both fledging success (GLMM) and nest survival (Cox regression). This pattern strongly suggests that the probability of nest success is highest towards the middle of the nesting season (Figure 4-2). If mid-season peaks in nest success are a general phenomenon in the baya, it would pay females to decide when to breed accordingly. This does, in fact, appear to be what females do: clutch initiation, measured by the proportion of nests accepted by females, also peaks at the middle of the season (Chapter 3).

Do colony characteristics influence nest success? Contrary to popular hypotheses (Collias and Collias 1964b; Crook 1963) I found no evidence that nests in colonies overhanging water or those in thorny trees were more successful than nests in trees over dry land or those in unarmed trees. While colony placement did not explain variation in nest success, other attributes of colonies did. Nest survival was strongly correlated with the number of active nests in a colony at clutch completion. Survival time was high at small colony sizes (0–3 additional active nests), decreased at intermediate colony sizes (4–7 nests), and increased thereafter (8–9 nests). Fledging success, however, was not significantly related to colony size as estimated by GLMM.

I have shown elsewhere (Chapter 3) that female choice of partly built (helmet stage) nests is more closely associated with nest location than with nest architecture. If the reason that females choose is to obtain safe nests, then one would predict that nest success should be primarily related to nest location and not to nest architecture. Controlling for nesting date, three variables were correlated with nest survival. Nest survival was highest at small and large colonies, for nests with short woven suspensions, and for those situated high in the colony tree. Colony size is known to correlate with reproductive success in some species (Brown et al. 1990), but not in others (Brown and Brown 1996; Davis and Brown 1999). Theoretical treatments of optimal colony size usually assume that intermediate sizes are optimal, while empirical studies show that reproductive success may increase, decrease, or show no trend with colony size (Brown et al. 1990). A disruptive trend, with intermediate colony sizes being worse than small or large sizes, is rarely observed (but see Brunton 1999). In the baya, longest nest survival occurred in colonies with 0–3 and 8–9 active nests in addition to the focal nest (mean minimum survival time 19.3 d, n = 120). Nests in colonies with 4–7 additional active nests had a mean minimum survival time of 14.7 d (n = 52). A possible reason why nest survival is low in colonies of intermediate size is that such colonies are large enough to attract predators, yet are too small for nests to enjoy a significant dilution effect. However, the data do not support this interpretation. The proportion of nest failure that could be attributed to snake or rodent predation was similar for small (70% of 48 nests), intermediate (63% of 39 nests) and large (66% of 12 nests) colonies. The reason for variation in nest survival with colony size is thus unclear. Note that baya colonies may frequently be much larger than in my study, and I cannot generalize beyond the range I observed (0–9 active nests besides the focal nest). One other attribute of nest location appeared to be correlated with nest survival. The hazard of a nest tended to decline with its height above the ground, although this trend was only marginally significant.

A single architectural variable was correlated with nest survival. Nests with short suspensions had a lower hazard than those with long suspensions, possibly because short suspensions prevent nests from being tossed about violently in strong winds (Ali 1931) and thereby losing their eggs or nestlings. Interestingly, if snakes are major predators then one would expect nests with longer suspensions to fare better than those with short suspensions. Rodent predation, on the other hand, is unlikely to be affected by suspension length. However, major sources of nest failure did not differ appreciably between nests with long and short suspensions. Suspension length was the most variable of architectural measures after the length of the entrance tube at egg-laying (CV 60.7% and 93.3%

respectively). This could mean either that suspension length is not under strong selection or that optimal suspension length is closely tied with variation in other nesting conditions.

Fledging success was highest in nests attached to thick branches, situated high in colony trees, and woven with relatively fine fibers. Again, predation by snakes should select for placing nests on the thinnest branches, the opposite pattern to that observed. Thick branches, on the other hand, may stabilize nests during strong winds, and may also be less likely to break. Some support for the hypothesis that thick branches help nests stay stable in strong winds comes from a comparison of causes of failure of nests attached to branches grouped into two categories: thick (≥ 5 mm) and thin (< 5 mm). Of 29 failed nests on thin branches, failure could be attributed to eggs and/or nestlings falling out of the nest in 34.5% of cases. The corresponding figure for the 10 failed nests on thick branches is 20.0%.

Nest height is thought to be an important influence on nesting success in birds (Martin 1993). Although ground-nesting species experience lower average nest-predation rates than off-ground nesters (Martin 1993), within tree-nesting species, predation tends to decrease with height (Creswell 1997; Schmidt and Whelan 1999). Nest height was clearly related to fledging success in the baya. This is what one would predict if predators (snakes and/or rodents) were wary of ascending high in trees, although the range in the height of nests studied was rather small (2.0–5.3 m, CV 21.3%). The proportion of high nests (> 3 m) that failed from rodent or snake predation was 48.1% ($n = 27$), substantially smaller than the corresponding figure (88.2%, $n = 27$) for low nests (≤ 3 m). This supports the hypothesis that an increase nest height is associated with an increase in fledging success primarily through a reduction in predation. As in analyses of nest survival, only one architectural attribute was significantly associated with fledging success: nests constructed out of fine fibers had higher fledging success than those with coarse fibers. The reasons for this are not immediately clear, unless fine fibers are associated with a tighter weave and better insulation against wind and rain (Collias and Collias 1964b).

Given that nest predation appears to be the major cause of nest failure in the baya weaverbirds, accounting for an estimated 65% of nest failures, can females distinguish nests that are likely to escape predation from vulnerable nests? In the great reed warbler, *Acrocephalus arundinaceus*, females preferentially settle on territories with low predation rates (Hansson et al. 2000), and a similar pattern is seen in the winter wren (Evans 1997; Evans and Burn 1996). Using only information on the height of a nest and the diameter of the branch to which it is attached, female baya weaverbirds may be able to make reasonably good predictions about the risk of failure. A GLMM with only these two variables (and date) predicted 75.8% (n = 64) of nest outcomes correctly. Nest location may thus provide the best cues to females searching for nesting situations that provide the greatest direct benefits.

Table 4-1. Attributes of nest location and nest architecture. Number of active nests and entrance tube length are as measured on the date of clutch completion.

Attribute	Mean ±	SD	(range)	CV%	*n*
No. active nests in colony	3.28 ±	2.83	(0–12)	86.36	185
Distance to tree trunk (cm)	242.60 ±	74.95	(80–570)	30.90	154
No. nests in 1 m radius	2.04 ±	1.67	(0–6)	82.01	154
Diameter of branch (mm)	5.07 ±	1.92	(1.8–11.9)	37.81	147
Height from ground (m)	3.18 ±	0.68	(2–5.3)	21.29	154
Length of suspension (cm)	14.80 ±	8.98	(0–54)	60.70	154
Nest length, L (cm)	20.67 ±	4.09	(14–40)	19.78	142
Nest width, W (cm)	8.91 ±	1.22	(6.5–14.5)	13.70	154
Nest depth, D (cm)	13.39 ±	0.95	(10–15)	7.13	147
Nest volume index, L×W×D (cm^3)	2400.25 ±	528.03	(1368.5–4977)	22.00	135
Entrance tube length (cm)	3.75 ±	3.50	(0–14)	93.28	99
Entrance tube area (cm^2)	41.98 ±	19.25	(16–200)	45.86	154
Height of threshold (cm)	5.05 ±	0.88	(2–7)	17.51	142

Table 4-2. Numbers of nests that survived until hatching and fledging, numbers that failed before hatching and fledging, and number whose fates were unknown. Data are presented for all nests monitored, as well as for the subset of nests for which a complete record was available (those monitored from the date of clutch completion).

	Hatching		Fledging	
	All nests	Complete record only	All nests	Complete record only
Survived	135	69	62	26
Failed	63	53	114	85
Unknown	4	2	25	13
Total	202	124	201	124

Table 4-3. Correlates of nest survival based on Cox proportional hazards regression. Hazard ratio refers to the relative change in hazard associated with a unit increase in the predictor variable. A hazard ratio of 1 would imply that hazard does not change with the putative predictor. Significant and near-significant *P*-values are marked with an asterisk; $n = 104$ nests.

Predictor	Hazard ratio (95% C.I.)	*z*	*P*
Date	0.678 (0.500–0.920)	−2.46	0.014*
Date^2	1.003 (1.001–1.010)	2.44	0.015*
No. active nests in colony	13.145 (3.180–54.343)	3.56	0.0004*
No. active nests in colony^2	0.775 (0.667–0.901)	−3.32	0.0009*
Distance to tree trunk (m)	1.723 (0.469–6.334)	0.82	0.41
No. nests in 1m radius	1.193 (0.732–1.943)	0.71	0.48
Diameter of branch (mm)	1.413 (0.907–2.204)	1.53	0.13
Length of suspension (cm)	1.156 (1.033–1.295)	2.52	0.012*
Nest volume (cm^3)	1.000 (0.998–1.001)	−0.48	0.63
Entrance tube area (cm^2)	0.983 (0.939–1.029)	−0.73	0.47
Height of threshold (cm)	1.503 (0.841–2.686)	1.38	0.17
Height from ground (m)	0.053 (0.002–1.400)	−1.76	0.079*
Fiber thickness (0/1)	0.848 (0.151–4.759)	−0.19	0.85
Weave neatness (0/1)	0.663 (0.174–2.528)	−0.60	0.55
Symmetry of nest (0/1)	1.160 (0.351–3.832)	0.24	0.81

Table 4-4. Results of GLMM analysis of predictors of fledging success, with colony identity as the random effect. Coefficients are parameters of the linear combination of variables describing the log odds of success. Significant and near-significant *P*-values are marked with an asterisk; *n* = 63 nests.

Predictor	Coefficient	S.E.	DF	*t*	*P*
Intercept	−24.010	7.720			
Date	0.297	0.108	35	2.72	0.009*
Date^2	−0.002	0.001	35	−2.48	0.018*
Distance to tree trunk (m)	1.326	0.785	35	1.69	0.100
No. nests in 1 m radius	−0.071	0.276	35	−0.26	0.799
Diameter of branch (mm)	0.707	0.304	35	2.32	0.026*
Height from ground (m)	1.518	0.621	35	2.44	0.020*
Length of suspension (cm)	−0.043	0.051	35	−0.83	0.409
Fiber thickness (0/1)	2.119	1.017	35	2.08	0.045*

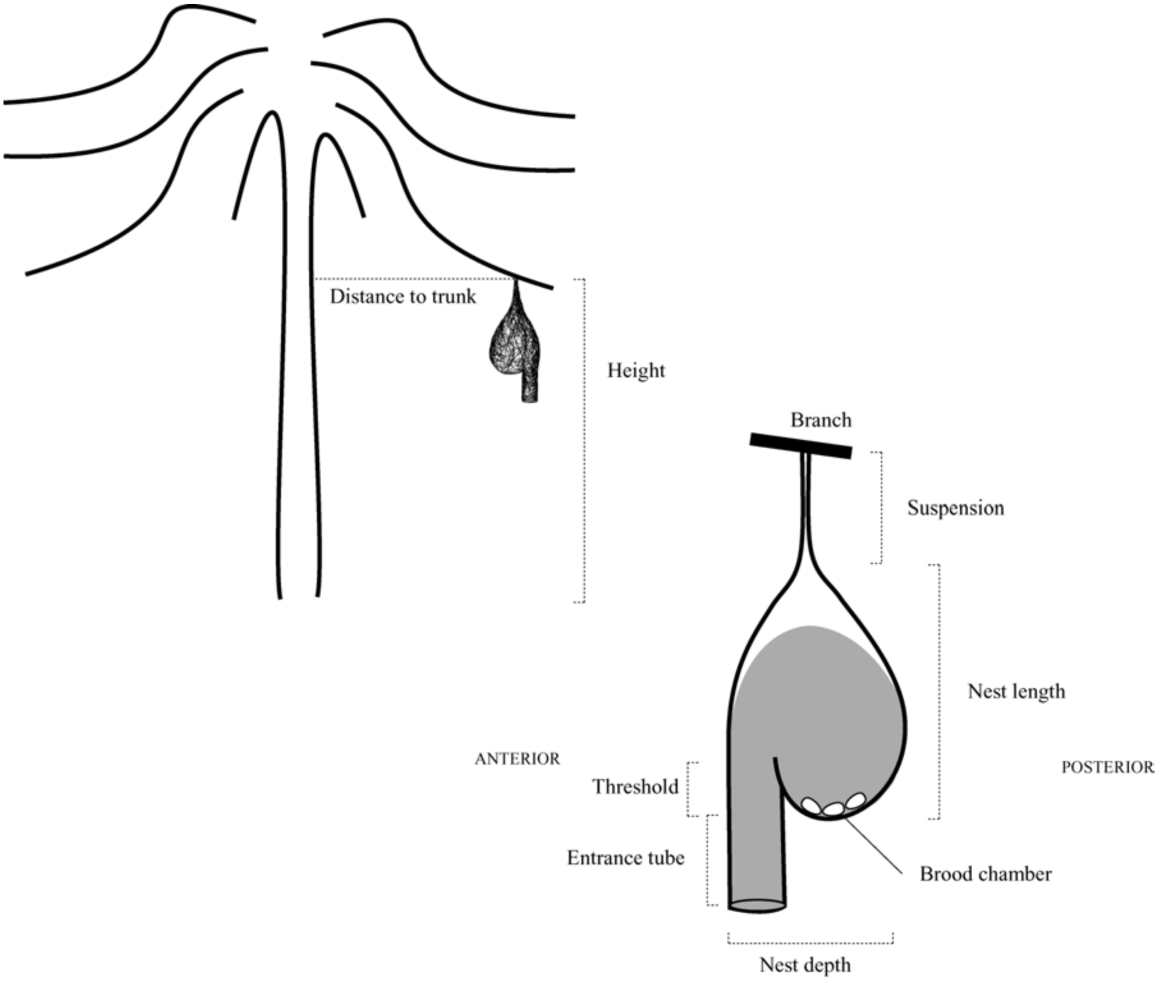

Figure 4-1. Some attributes of the structure and location of baya weaverbird nests. For descriptive purposes, I consider the entrance to be anterior to the threshold and the brood chamber posterior to the threshold.

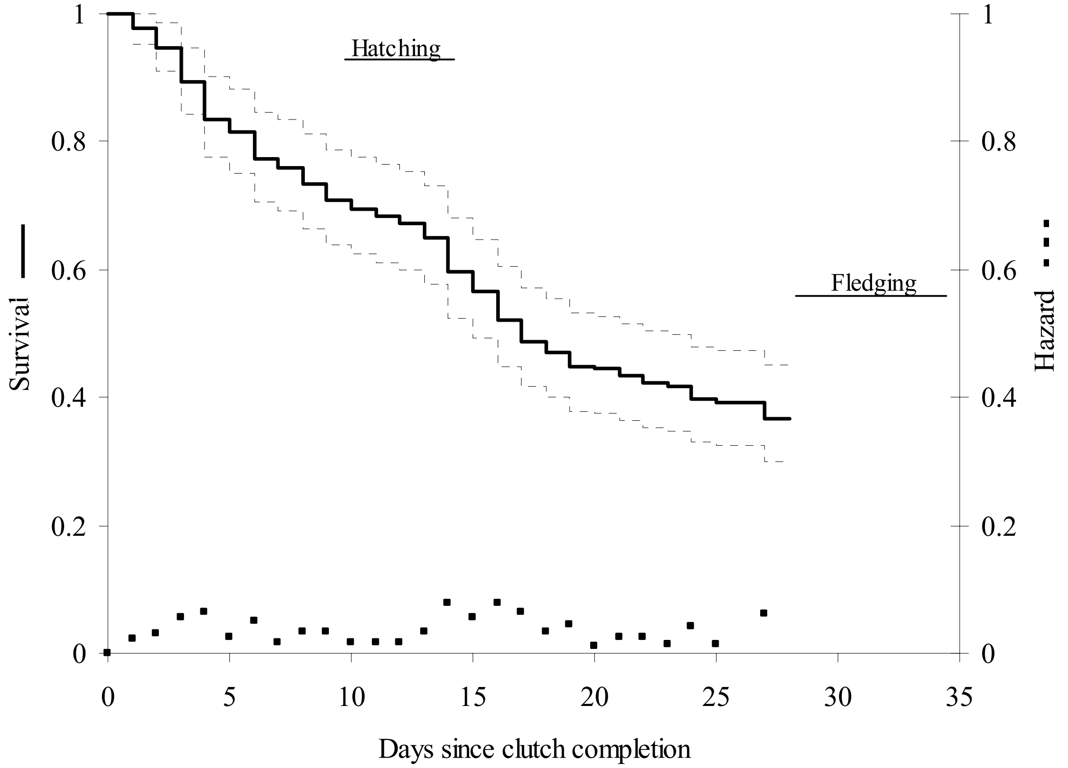

Figure 4-2. Kaplan-Meier survival curve (solid line) of baya weaverbird nests, starting from the date of clutch completion. Dashed lines are 95% confidence intervals. The curve is based on a starting sample of 131 nests. The hazard (solid squares) is not constant through the nesting period, and there is higher risk immediately following clutch completion and around and following hatching, than at other times. The curve does not extend beyond day 27 because all nests that survived until this point either fledged young or had ambiguous fates and were therefore censored.

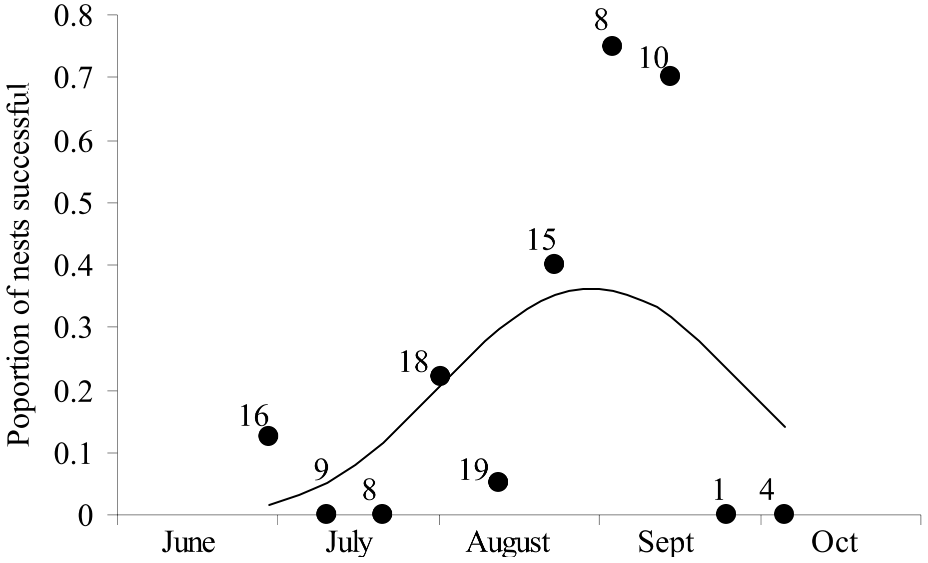

Figure 4-3. Proportion of successful nests (those that fledged ≥ 1 young) in relation to date of clutch completion (number of days since May 31). The number above each data point is the number of nests used to calculate the proportion. The curve describes the best-fit equation, $\log_e$ (odds of success) = −8.1 + 0.17Date − 0.00096Date^2, which was obtained by GLMM analysis with colony identity as a random effect.

CHAPTER 5
RATES OF EXTRA-PAIR PATERNITY AND INTRASPECIFIC BROOD PARASITISM IN THE BAYA WEAVERBIRD

Introduction

Field studies of nesting and mating decisions in birds are complicated by the discovery that social pairing between males and females does not necessarily reflect the underlying genetic mating system (Birkhead and Møller 1992; Gowaty 1996; Westneat et al. 1990). Molecular genetic estimates of the frequency of extra-pair paternity (EPP) are now available for over 150 species. Across these species, EPP rates vary from 0% to over 70% of young (Arnold and Owens 2002; Griffith et al. 2002). Even in socially monogamous birds, long thought to epitomize sexual fidelity (Lack 1968), EPP rates can be surprisingly high (an average of 23% of young in temperate passerines; Hasselquist and Sherman 2001). In addition to mating with males outside the pair, females may lay their eggs in the nests of other females, parasitizing the parental efforts of others (Yom-Tov 1980, 2001). The proportion of broods affected by intraspecific brood parasitism (IBP) varies among species from 0% to 47% (Arnold and Owens 2002). Thus, recent work on EPP and IBP cautions against assuming that all eggs in a nest are fertilized by the territorial male, or even that all eggs belong to the female who incubates them.

These findings carry important implications for field studies of birds. If many offspring are fathered outside the pair, then mate choice cannot be assessed by simply identifying which male a female associates with or which male's territory she nests in.

For example, genetic information can substantially increase (Whittingham and Lifjeld 1995) or decrease (Jones et al. 2001; Lanctot et al. 1997) measures of the variance in male reproductive success relative to those calculated without this information. Similarly, outward patterns and consequences of nesting decisions may be misleading if females lay a significant fraction of their eggs in others' nests. Finally, variation in parental care within and among species may be related to the certainty of parentage of both males and females (Mulder et al. 1994; Sorenson 1992). For these reasons, it is essential to measure the rates of EPP and IBP in the population under study when investigating reproductive behavior. If these rates are low, basing inferences on outward patterns of mating and nesting is justified. On the other hand, if EPP, IBP, or both are common, intensive genetic sampling of the population may be necessary to assess confidence in apparent patterns in mate choice and nesting decisions.

I have shown that female choice in the baya weaverbird, *Ploceus philippinus*, appears to be best explained by direct benefits associated with choosing safe nesting locations (Chapters 3 and 4). However, these conclusions are based on the assumption that females mate with the male whose nest they lay eggs in, and that females do not distribute a large proportion of their eggs in other nests. In the absence of direct evidence about the mating and egg-laying decisions of females, the conclusions reached in Chapters 3 and 4 are tentative. In addition, information on EPP and IBP can be used to investigate additional factors that females pay attention to. For example, if nest location is causally associated with nest success, then females who are forced to nest in poor locations might be expected to distribute some of their eggs into nests in safer locations. Under these circumstances, IBP rates should be high.

The ecology of baya reproduction appears to provide ample opportunity for EPP and IBP. Opportunities for extra-pair copulations are likely to increase with breeding density and synchrony (Møller and Birkhead 1993; Stutchbury and Morton 1995), and the same should be true for IBP. Bayas show both high density and synchrony. They typically nest in colonies, which are variable in size (Ambedkar 1964, Davis 1974). In large colonies territories can be tightly clustered and distances between nests of neighboring males are often less than 1 m (S. Quader pers. obs.). Because resource abundance is dependent on rainfall, which is strongly seasonal, breeding can be highly synchronous, with many females being fertile simultaneously. Thus, it is likely that frequent opportunities for extra-pair copulations and IBP arise.

In this paper I use behavioral observations to assess the opportunity for IBP and extra-pair copulations, and the frequency of within-pair copulations. I then investigate the frequency of EPP and IBP using microsatellite DNA markers. Microsatellite markers are short segments of DNA consisting of a variable number of simple repeat sequences. They have many advantages over other molecular methods (e.g., allozymes and multilocus fingerprinting) for studying parentage (Ellegren 1992; Queller et al. 1993). Microsatellites are co-dominant markers, inherited in a Mendelian fashion. Hence, the genotype of each individual can be unambiguously determined, and offspring must possess one paternal and one maternal allele at each locus. Microsatellites are typically highly variable, with this polymorphism being produced by differences in the number of repeats of a base motif. As a result, a relatively small number of loci can provide sufficient resolution to exclude non-parents with confidence, and even to assign parentage to one of many candidates (Bernatchez and Duchesne 2000). Finally, a tiny amount of tissue is all that is needed to amplify microsatellite loci using the polymerase chain reaction (PCR).

Methods

Study Species and Field Methods

Baya weaverbirds are common in savanna-like habitats throughout South Asia (Ali and Ripley 1987). In much of peninsular India the main breeding season is during the southwesterly monsoon rains, between June and October. Males defend small three-dimensional territories in colony trees, where they weave nests made of grass and palm fiber. Between July and October 1998–2000, I carried out field work on breeding bayas on land belonging to the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT–Asia) at Patancheru, Andhra Pradesh, India (17.53°N, 78.27°E; 545 m above sea level). I trapped adult males and females using mistnets erected around colony trees. Each individual was given a numbered metal band, as well as a unique color combination of plastic leg bands. In some species leg bands influence mate choice and other reproductive decisions, especially when band colors match those of secondary sexual ornaments (e.g., Burley 1982; Burley et al. 1996; Johnsen et al. 1997; Metz and Weatherhead 1993). Because the most striking sexual difference between breeding bayas is the bright yellow plumage on the crown and breast of males (Ali and Ripley 1987), I did not use yellow color bands. I was able to trap and band only 40–70% of all individuals in the colonies I monitored because the birds seemed to quickly detect and avoid the nets.

Each nest was tagged and numbered, and was monitored through egg laying until chicks fledged or the nest failed (Chapters 2 and 4). I assigned ownership of nests by conducting focal watches on colonies and observing the building behavior of males—

these males were the putative fathers of nestlings raised in their nests. The identity of females settling at nests was also assigned by watching nests. The female observed to fly into a nest to incubate eggs or feed nestlings was considered the putative mother of the nestlings in that nest. I monitored the presence and number of eggs and nestlings by pushing an otoscope through the side of the nest. In 1999 and 2000, I made an incision in the side of a subset of nests to remove and measure nestlings ≥ 7 days old (after hatching) and to take tissue samples (see Molecular Methods below). Nestlings were replaced in the nest within 10 minutes of removal, after which I sewed the incision shut with transparent plastic fishing line. Males typically returned soon after I left, and used fresh grass fiber to repair the damage I had done. Note that, because I only sampled nestlings ≥ 7 days old, and because only about 44–49% of complete broods survive until this stage (Chapter 4), these data do not necessarily reflect patterns of EPP and IBP at egg-laying.

Male bayas sometimes follow females as they fly to and from colonies, suggesting that mate guarding may occur in this species. In order to assess the degree to which males guarded fertile females, I conducted 30–60 min continuous focal observations on nests at various stages. Because nests in a colony were situated close together, I was able to watch up to five nests simultaneously. During these observations, I recorded the total length of time that the male was present at the nest, the female was present at the nest, both were present together, or both were absent. An individual was considered present when it was either perched on its nest or within 1 m of it. Due to the thickness of the foliage of many colony trees, I could not say for certain that an individual was not elsewhere in the colony when it was not within a 1 m radius of the nest. However, when males and females left a nest, they either hopped onto a nearby branch or flew clearly away from the colony, so the criterion applied is likely to represent time away from the colony.

I estimated the opportunity for IBP as the proportion of time during which neither male nor female was present at the nest. This was calculated for nests observed between the date the first egg was laid and 8 days after clutch completion. Opportunities for extra-pair copulations arise when males and females are apart. To calculate the proportion of time during which extra-pair copulations could occur, I summed the time the male (but not the female) was present at the nest with the time that the female (but not the male) was present. Because I was unable to follow individuals when they left the colony, this measure represents the minimum, not the absolute time during which the male and female were separated and extra-pair copulations could potentially occur. I assumed that the fertile period of a female extended from 5 days before she laid her first egg to the day on which she laid the last egg of the clutch (Birkhead 1998). I also compared the behavior (time at the nest) of males and females during the fertile period with their behavior during a non-fertile period, between the first and twelfth day after the last egg was laid. I calculated the opportunity for extra-pair copulations and IBP based only on observations carried out between 0630 and 1130 Indian Standard Time, because female birds are thought to be most fertile in the morning and eggs are typically laid before noon (Birkhead 1998). During these, and other focal nest observations, I also counted any within-pair or extra-pair copulations that occurred on or near the nest under observation. These observations were carried out both in the morning (mostly) and evening.

Molecular Methods

I drew 30–60 µL of blood from trapped adults by brachial venipuncture; this blood was stored in c. 800 µL of Queen's lysis buffer (Seutin et al. 1991). To obtain tissue from nestlings I plucked 1–3 feathers from each individual. The base of growing ("blood") feathers contained sufficient blood for subsequent molecular analyses. Feathers were air-dried and stored in paper pouches until they could be processed. Eleven nestlings from five nests were found freshly dead in their nests. These nestlings were dissected, and approximately 200 mm^3 of internal organs (mostly liver) was placed in lysis buffer. I isolated DNA from tissue stored in buffer using standard phenol-chloroform extraction. DNA pellets were air-dried and resuspended in 100 µL of TE (10 mM Tris, 0.1 mM EDTA). DNA from feather samples was extracted using a DNeasy Tissue Kit (QIAGEN Inc., Valencia, CA).

I screened DNA samples with 8 sets of microsatellite primers developed from closely related species. These were WBSW1, 2, 4, 7, 9, and 11 from the white-browed sparrow weaver *Plocepasser mahali* (McRae and Amos 1999); *Pdo*µ3 from the house sparrow *Passer domesticus* (Neumann and Wetton 1996); and ESC4 from the reed bunting *Emberiza schoeniclus* (Hannotte et al. 1994). The six WBSW primers have been shown to amplify polymorphic markers in the Southern masked weaver *Ploceus taeniopterus* (McRae and Amos 1999), and all eight primer sets I investigated successfully amplified polymorphic microsatellite markers in the redbilled quelea *Quelea quelea* (Dallimer 1999). Of these eight primer sets, I found that WBSW1, WBSW11, and *Pdo*µ3 gave a polymorphic product in the baya weaverbird, and I subsequently used these three loci in parentage analyses. WBSW1 is a dinucleotide (TG) repeat that yields a product of length 172–190 bp in the species from which it was isolated. WBSW11 is a complex dinucleotide $(AC)_{15}\ldots(GT)_6$ repeat with product length 183–213 bp (McRae and Amos 1999). *Pdo*µ3, on the other hand, is a tetranucleotide (TCCA) repeat of smaller product length (112–172 bp) in the house sparrow (Neumann and Wetton 1996).

I carried out PCR reactions in a 10 µL volume containing 0.5 µM of each primer, 100 µM of each dNTP, 0.25 units of Taq polymerase (Promega Corporation), and 1.5-2.0 mM of $MgCl_2$ (Table 5-1) in 50 mM KCl and 10 mM Tris-HCl. This mixture was subjected to 35 cycles of 93°C for 30 s, *X*°C for 60 s, and 72°C for 30s, followed by 72°C for 3 min. The annealing temperature (*X*) varied with the primer used (Table 5-1). PCR products were size-sorted using electrophoresis in 9% denaturing polyacrylamide (19:1 acrylamide to bisacrylamide) gels. As a size reference, I ran a 50 bp ladder in 1 to 4 lanes of each 49-lane gel. Bands were visualized by silver staining. Molecular analyses were carried out in the Applied Genomics Lab at ICRISAT, India.

Marker Analysis and Parentage

I scored the sizes of PCR fragments using UVIdoc software (UVItec, Cambridge, UK), by comparing each band with the 50 bp reference marker. Allele frequencies, observed and expected heterozygosities, and exclusion probabilities were calculated using the software program CERVUS (Marshall et al. 1999). These metrics were very similar regardless of whether all genotyped individuals were used or whether only (putatively unrelated) adults were used, so I present data based on all individuals. I searched for evidence of null, or nonamplifying, alleles (Pemberton et al. 1995) by comparing the number of observed and expected heterozygotes (assuming Hardy-Weinberg equilibrium) using χ^2 goodness-of-fit tests. An overabundance of apparent homozygotes is a diagnostic feature of the existence of one or more null alleles

(Pemberton et al. 1995). An excess of apparent homozygotes may occur in the heterogametic sex (here females) if the locus is sex-linked.

Because IBP rates are typically lower than EPP rates in passerines (Arnold and Owens 2002), I followed previous workers (e.g., Johnson et al. 2002) in first determining whether there was any evidence for IBP by comparing the genotypes of nestlings with their putative mothers. The putative mother was considered to be the genetic mother of a nestling if, at each locus, at least one of her alleles matched at least one of the nestling's alleles. Once maternity was confirmed in this manner, the putative father's genotype was compared with the non-maternal alleles of the nestling. If the male possessed the non-maternal allele at each locus, he was considered to be the genetic father; if he did not, I concluded that the nestling was the result of an extra-pair fertilization. At some nests the putative mother was not sampled. In such cases, paternity of the putative father was evaluated in the absence of any information on the mother. Confidence limits on proportions of young and broods affected by EPP and IBP were calculated following Zar (1996, p. 524).

To estimate the degree of confidence that can be placed in the results, I calculated the average probability of parental exclusion for each microsatellite locus (Marshall et al. 1998). This is the probability that the genotype of a randomly chosen non-parent will not match that of an offspring. This exclusion probability depends on whether or not the other parent is known with certainty. Because I proceeded in a stepwise fashion, first evaluating maternity and then paternity, the probability for maternal exclusion is lower than that for paternal exclusion. This procedure was carried out for all clutches at which both putative parents were sampled (n = 6 clutches). For those clutches in which only the putative mother was sampled (*n* = 16), the probability of maternal exclusion is based on neither parent being known with certainty. A similar procedure was adopted for clutches at which only the putative male but not the female was sampled (*n* = 5). Nestlings and adults from other nests were also genotyped to increase the sample size for the calculation of allele frequencies and, thus, exclusion probabilities. The average probability of exclusion at each locus was then pooled to obtain an overall exclusion probability. Of the 140 total individuals sampled, 131 were genotyped at all three loci, and 9 were genotyped at two loci.

Results

The microsatellites used in this study showed substantial variation, with 11 to 16 alleles per locus. Observed heterozygosities were high, and were similar to those expected based on Hardy-Weinberg equilibrium (Table 5-1), suggesting that null alleles are rare or absent and that none of the loci is sex-linked (χ^2 tests, all $P > 0.05$). Overall exclusion probabilities across all three loci combined were 0.868 for the first parent and 0.961 for the second parent given that the other parent is known. Figure 5-1 illustrates that microsatellite bands on a polyacrylamide gel can be used to exclude non-parents.

The putative mother's genotype matched that of all the nestlings in 20 of the 22 nests for which the female was sampled. In one nest, one of three nestlings did not share any alleles with the mother at the *Pdo*µ3 locus (allele lengths, in number of base pairs, of mother and nestling [140, 132] and [128, 128] respectively). In the other nest, one of two nestlings did not share any alleles with the mother at the WBSW1 locus (allele lengths of mother and nestling [203, 203] and [207, 207] respectively). Thus, evidence for intraspecific brood parasitism was detected in 9.1% of 22 nests (95%CI, 11.2–28.7%) and 3.5% of 57 nestlings (95%CI, 0.4–12.1%). Because putative mothers and nestlings at two nests were only genotyped at two loci, the operational exclusion probability is 0.859, marginally lower than that if all individuals were genotyped at all loci.

Offspring matched the genotype of the putative father in all but one nest of the 11 for which the male was sampled. In this nest, all three nestlings appeared to have been sired by one or more extra-pair males. One of the offspring matched the male at the WBSW1 locus, two at the WBSW11 locus, and none at the *Pdo*µ3 locus. The putative female at this nest was sampled, and matched all offspring. The genotypes of all three offspring perfectly matched one male from a neighboring territory in the same colony tree. This male built his own nest at the same time as the first male, and eggs were laid in both nests simultaneously. This male also sired all nestlings in his own nest. Thus, extra-pair young were found in 9.1% of 11 nests (95%CI, 0.2–40.3%) and 11.1% of 27 nestlings (95%CI, 2.3–28.7%) were fathered by a non-pair male. The operational exclusion probability for a random male in the population was 0.919.

Focal observations of nests indicated that between clutch initiation and 8 days after clutch completion, when IBP is likely to occur, neither male nor female was present at or near the nest for 74.5% (SE = 9.2%, $n = 12$ nests) of the duration of focal observations. During a female's fertile period, opportunities for extra-pair copulations occurred, at minimum, 17.8% (SE = 4.6%) of the time. The minimum time that males and females spent apart increased to 33.7% (SE = 10.7%) after the fertile period, but this change was not significant (Mann-Whitney test, $U = 85$, $n_1 = 20$, $n_2 = 11$, $P = 0.31$; Figure 5-2). The minimum time both male and female were together (at the nest) also did not change substantially from the fertile period (1.4% ± 0.7%) to after the fertile period (2.1% ± 1.5%, Mann-Whitney test, $U = 133$, $n_1 = 20$, $n_2 = 11$, $P = 0.35$; Figure 5-2).

I observed a total of 26 copulations. Three pairs of birds contributed 3, 2, and 5 copulations to this total. Twenty-one copulations involved a female mating with a male on or in his nest. The remainder took place on the colony tree, away from other nests, following which the female flew into the nest of the male she copulated with. An additional mating was attempted by a neighboring male while the female was perched on another male's nest. This attempt was unsuccessful because the female flew away. Copulations were observed between one and three days before the first egg was laid. Of the 10 nests for which the dates of egg-laying were known, copulations were observed a mean of 1.98 days before the first egg was laid (SE = 0.29 d).

Discussion

Baya weavers seem like prime candidates for having high rates of EPP. Extra-pair paternity rates have been proposed to increase with breeding density (Gowaty and Bridges 1991) and breeding synchrony (Stutchbury and Morton 1995), and decrease with the degree of paternal care (Mulder et al. 1994). As a colonial species, the baya breeds at medium-to-high, and sometimes extremely high local densities. For example, it is fairly common for 20 males to defend territories in a space of dimensions 10 m × 10 m × 10 m. Such densities should provide ample opportunities for extra-pair copulations. Nesting synchrony is typically high because the breeding is constrained by the highly seasonal monsoon rains (Ambedkar 1964). Lastly, the level of paternal care is difficult to assess. Males do not incubate eggs, and rarely feed nestlings (Ali 1931; Ambedkar 1964). Males do, of course, construct the entire nest; they continue to add to it during incubation and later, and they may also defend it against intruding adult and juvenile males.

My results suggest that bayas show moderate levels of EPP (11.1% of nestlings), near the average of all species for which reliable estimates are available (10.46%, *n* = 129 species, calculated from Appendix 1 in Griffith et al. 2002). Compared with other passerines, bayas show a rate that is slightly lower than average (14.98%, *n* = 80 passerine species). Among colonially nesting passerines, however, bayas seem to have unusually low EPP rates. For example, in the redwinged blackbird, *Agelaius phoeniceus*, an average of 28.1% of offspring are extra-pair (Griffith et al. 2002). In the two closest relatives of the genus *Ploceus* for which comparable data are available, EPP rates are estimated as 17.6% in the red bishop (*Euplectes orix*, Friedl and Klump 1999) and 10.1% in the house sparrow (*Passer domesticus*, Griffith et al. 2002). Broad confidence intervals around estimates are a common problem in studies of EPP (Griffith et al. 2002), and the low sample size in my study means that the statistical confidence in the estimated frequency of EPP is also low. Confidence limits around the estimate are 6.4–18.1% and 2.3–28.7% at the 50% and 95% levels respectively. Still, it seems safe to conclude that the majority of nestling bayas are fathered by the owner of the nest in which they are raised.

What might explain this moderate EPP rate even though the social behavior of bayas would seem to favor extra-pair copulations? From a male’s point of view, two strategies of maximizing the number of genetic offspring are mate guarding and frequent copulation. Males in many birds show one or the other of these strategies (Birkhead 1998). Although male bayas may follow females occasionally, there are multiple constraints on a male’s time. During a female’s fertile period, her mate must complete his nest in preparation for her clutch and, in addition, males cannot leave their territories for long periods of time because their nests are then vulnerable to being damaged or even destroyed by other colony males. A consequence of these constraints is that males are unable to follow females continuously. I found that males spent a minimum of 17% of their time apart from their mates, certainly sufficient time for extra-pair copulations to occur. I have not found much evidence for the other male strategy, frequent within-pair copulations. Based on 127 h of observations of nests during the fertile period of females, the rate of within-pair copulations at or near the nest was 0.118 matings per nest-hour. Taken together, the relatively low EPP rate despite incomplete mate guarding and low within-pair copulation rate, suggests that female bayas do not regularly seek extra-pair copulations. Why should this be? Nesting success is typically low in this population; only about 30% of nests fledge any young. If nest success is largely driven by nest location (Chapter 4) then it would pay females to seek safe nesting sites because these represent direct benefits (Andersson 1994). Any incremental benefits from mating with extra-pair males may then be negligible given the low survival rate of broods and stochastic mortality. Costs of extra-pair matings (Petrie and Kempenaers 1998) may then eliminate any small genetic benefit that a female might accrue for her offspring by mating with a high-quality male. The main costs to females of seeking extra-pair copulations is thought to be the loss or reduction of male parental investment (Birkhead and Møller 1992), but this loss may not always be important (Westneat and Sargent 1993).

Both male and female were absent from the nest for long periods of time (mean = 74.5%) during and after egg-laying. These absences provide ample opportunity for IBP by other females. Using microsatellite markers I found that approximately one in ten broods were parasitized by conspecific females. This is considerably higher than the average for all birds (2.76% of broods, n = 89 species), as well as for passerines alone (1.8%, n = 57; calculated from Appendix in Arnold and Owens 2002). In terms of the proportion of nestlings, however, the number is low (3.5%). If nest location is of paramount importance to nest survival, one might expect those females forced to settle in poor locations to make the best of a bad situation by distributing their eggs in nests in favorable locations. The data indicate that this does not occur frequently. One possibility is that I have underestimated the frequency of IBP in this study. If IBP tends to increase clutch size, and if large clutches are associated with lower nestling survival, then clutches suffering from IBP may be less likely to survive to being sampled. However, there is no evidence that clutch size is associated with fledging success in baya weaverbirds. The proportion of nests that fledged young was similar for clutch sizes ≤ 3 (32.9% of 97 nests) and clutches > 3 (35.2% of 88 nests). In two other populations of baya weaverbirds, the existence of IBP has been inferred from the presence of extraordinarily large clutches, or from an unusual sequence of egg laying (Ambedkar 1964, Dhindsa 1990). Ambedkar (1964) found two clutches of seven eggs and one of eight eggs among the 140 nests he studied. These clutches are more than twice the median size of three eggs for this species. In two additional nests, eggs appeared in a non-normal sequence (multiple eggs on the same day or new eggs appearing several days after clutch completion). Dhindsa (1990) inferred IBP from egg-laying sequence in two of 45 nests in a separate population. Thus, previous estimates of the proportion of brood parasitized nests are 2.8% (Ambedkar 1964) and 4.4% (Dhindsa 1990), and it seems a general conclusion that IBP is uncommon in baya weaverbirds.

My estimates of EPP and IBP in baya weaverbirds are close to the average found in those birds for which these data are available. What does this mean for conclusions based on outward patterns of mate choice and nesting success in this species? IBP seems to be sufficiently rare (3.5% of nestlings) that one can safely ignore it while calculating reproductive success of females. The effect of EPP (11.1% of nestlings) will depend on the distribution of extra-pair fertilizations among males in the population. If EPP is distributed highly nonrandomly, it is possible that male traits may also be under strong sexual selection through female choice. I do not have data to test this possibility. Still, patterns of female settlement suggest that nest location is of primary importance to females when mating nesting decisions, and while separate benefits to mating with high quality males may exist, these are likely secondary in value.

Table 5-1. Polymerase chain reaction conditions for the three microsatellite loci used in parentage analysis, and measures of the variability of the loci. These measures are based on genotyping 140 individuals. Expected heterozygosity is calculated assuming Hardy-Weinberg equilibrium. Exclusion probabilities for (1) the first parent, and (2) the second parent given that the first parent is known are calculated from Jamieson (1994) and Marshall et al. (1998).

Locus	PCR conditions		No. of alleles	Size range (bp)	Heterozygosity		Exclusion probability	
	T (X °C)	$MgCl_2$ (mM)			Obs	Exp	1	2
WBSW1	54	1.5	11	197–217	0.786	0.787	0.526	0.607
WBSW11	50	2.0	16	179–211	0.868	0.807	0.457	0.632
*Pdo*µ3	52	1.5	14	92–172	0.807	0.872	0.576	0.733

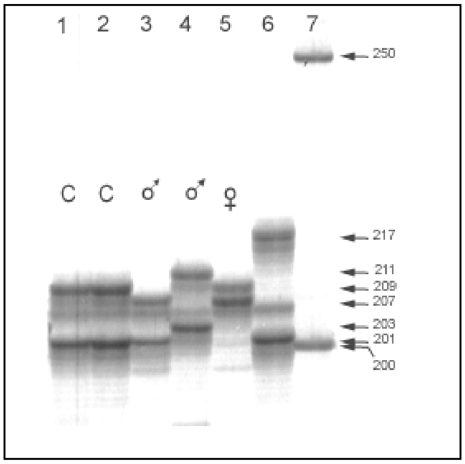

Figure 5-1. An example of the results of polyacrylamide gel electrophoresis using PCR amplification of the WBSW1 locus. Two chicks from a single nest are in lanes 1 and 2. Lane 3 is the putative father, lane 4 another male from the same colony, and lane 5 the putative mother. Lane 6 is a chick from another nest. Lane 7 shows two fragments from a 50 bp ladder. Arrows indicate the locations of different alleles, and the associated numbers are the sizes (bp) of amplified alleles. Note that neither allele of the non-parent male matches any of the chicks' alleles, while the genotype of both chicks is consistent with that of the putative father and the putative mother.

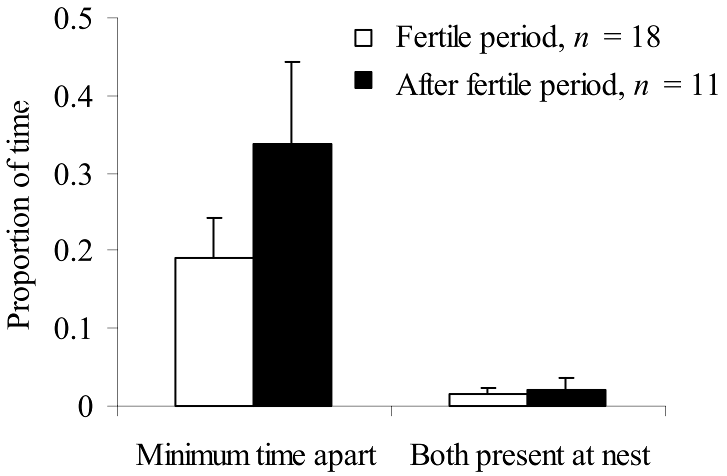

Figure 5-2. Focal observations on nests at different stages. Minimum time apart is the minimum length of time the members of a pair spend apart (i.e., when one or the other is present at the nest, but not both). During the female's fertile period, this measure is a minimum estimate of the time during which extra-pair copulations may occur. The time that both male and female spend at the nest is a minimum estimate of time spent mate guarding.

CHAPTER 6
GENERAL CONCLUSIONS

Nesting and Mating Decisions in Weaverbirds

Is there any evidence that female baya weaverbirds (*Ploceus philippinus*) choose their mates based on the structure of the nests that males build, and do females gain direct benefits from doing so? Given that males must learn how to weave nests, female choice for nest structure would imply that male weaving skill has evolved, at least in part, through sexual selection. One might imagine that nest structure should be an important determinant of a female's reproductive success, because she lays all her eggs in the nest (Chapter 5), and 30 days must elapse after egg-laying before the young are able to leave the nest (Chapter 4). If the safety of a nest is related to its structure, then it would pay females to base mate choice decisions on variation in nest structure.

Surprisingly, I have not found compelling evidence linking female choice to nest structure. Unlike penduline tits *Remiz pendulinus* (Hoi et al. 1994), and possibly village weavers *Ploceus cucullatus* (Collias and Victoria 1978; Jacobs et al. 1978), female bayas do not seem to base their choice of mates on naturally-available variation in nest structure. This conclusion is supported by data from an experiment in which I switched nests between males as well as by results from a larger, correlational dataset (Chapter 3). The correlational data indicate that nest location may play a larger role than nest structure in influencing female choice. Appropriate nest location seems, in fact, to be a particularly important factor in baya reproduction. Strongly directional monsoon winds select for nests being located on the leeward side of colony trees, and this is where males concentrate their nest-building activity (Chapter 2). Similarly, other attributes of nest location (chiefly nest height above the ground) are better predictors of nest success than are attributes of nest structure (Chapter 4), and this provides a possible reason why females seem not to place primary importance on structure when choosing where to nest.

These conclusions are based on the assumption that outward patterns of female mating and nesting decisions are reliable. However, a female's offspring need not necessarily be fathered by the builder of the nest she lays her eggs in, and a female may also not lay all her eggs in a single nest. In fact, extra-pair paternity and intraspecific brood parasitism is widespread in birds (Arnold and Owens 2002; Griffith et al. 2002). I used molecular methods to test the assumption that outward patterns of mating and nesting truly indicate whom female baya weaverbirds mate with and where they lay their eggs (Chapter 5). Results from these analyses indicate that most clutches are fertilized by the builder of the nest in which they were laid, and that the level of intraspecific brood parasitism is low.

Female Choice and Nest Attributes

Do the findings described in this dissertation imply that sexual selection has played no role in the evolution of nest structure and thus male skill in weaverbirds? Unfortunately, the data do not provide a definitive answer. It is possible that past female choice has, to a large degree, shaped the evolution of male nest building. Based on the behavior of estrildid finches, a closely-related outgroup to the Ploceinae, the ancestral ploceine pattern was likely one in which either the female built a nest alone, or both sexes shared in nest-building (Collias and Collias 1964b; Sibley and Ahlquist 1990). As males started to take on a larger and larger role, any male who was able to build a better nest, and at an earlier age, would be favored. Strong sexual selection, then, would rapidly lead to a stage when all breeding-age males were able to build an acceptable nest. According to this scenario, the result of this process is what we see today. Once nests are sufficiently good at retaining eggs and young, any correlation between nest structure and nest quality (e.g., safety from predation) would break down. Any further increment in, for example, weave quality, would be selected against because of production costs to males or evaluation costs to females. That is, the trait would be in that part of phenotypic space in which stabilizing selection occurs (Endler 1986; Wade 1987). In this way, if a trait is designed to solve an ecological problem, once that problem has been solved, the trait no longer evolves.

Why, then, have I not found stabilizing female preference functions? One possibility is that there is variation in female preference (Wagner 1998), such that there is not a peak, but a plateau of female preference with respect to nest structure (Figure 6-1A). Possible reasons for between-female variation in preference include variation in female quality or mate-sampling strategies (Wagner 1998). Another possibility is that the variation in structure is insufficient to detect stabilizing selection (Figure 6-1B; Endler 1986; Wade 1987). What should we do if we suspect this to be the case? If the trait were under natural selection or intrasexual selection, then it may be possible to manipulate it to create the variation required to detect selection (as implied by Wade 1987). Under female choice, however, this approach will only work if females retain ancestral mate choice rules (Ryan 1997; Ryan and Wagner 1987). It seems reasonable to expect them to do so, because otherwise trait values should not be maintained over time. Although manipulations of weaverbird nests can be done, extreme changes result in changes in male behavior as well, including nest attendance, display rates, and even nest rejection

(Collias and Victoria 1978; Collias et al. 1979; Crook 1964a; Jacobs et al. 1978). Hence, it may be difficult to separate the influence of nest structure on mate choice from other confounding effects.

In contrast to my findings on female choice in relation to nest structure, I found strong directional selection on nest location. Why should this be? More generally, why do we see directional selection for any trait in any species (Arnold 1992; Endler 1986)? Models of adaptive landscapes typically imagine a single peak in fitness in relation to the value of a trait (Arnold 1992) and, in such situations, trait means tend to evolve toward the peak and equilibrate there (Lande 1979). However, a recent review of linear (i.e., directional) and quadratic (i.e., stabilizing) selection coefficients across a large range of taxa and phenotypes concluded that stabilizing selection was typically rarer and weaker than directional selection (Kingsolver et al. 2001). Frequency-dependent selection is one mechanism that may maintain trait means below the fitness peak (Lande 1976, 1980). Other reasons why the mean of a trait may not reach the peak of the female preference function over evolutionary time include costs of trait production and the distribution of limited resources. In weaverbirds, nest location may well be limited by the distribution of appropriate nesting sites. Nests must be built on the leeward side of trees, as high as possible, suspended from branches of the appropriate diameter, and so on (Chapter 4). Here, a male’s ability to acquire a good nesting location depends on other males in the population and if predation pressure favors high nesting density (Chapter 4), competition for safe locations may be particularly intense. This means that even if there is nothing in principle that prevents a male from building a perfect nest, other males interfere with his quest for a perfect location. Thus, directional female choice for nest location may continue as a consequence of the persistence of a directional relationship between nest survival and attributes of nest location, like nest height.

Comparative Studies—the Next Step?

The results described in this dissertation suggest that weaverbirds may not, in fact, be such good subjects in which to study sexual selection for skill as previously supposed. The possible reasons why I detected no current female choice for nest structure are expected to apply broadly to all species in the subfamily. Weaverbirds do, however, remain well-suited for the study of the ontogeny of weaving ability and for comparative studies of nest attributes. Weaverbirds show wide variation in sexual dichromatism, coloniality, habitat, mating system, nest structure, and quality of weave (Collias and Collias 1964b; Crook 1964a). In fact, Crook (1964b) used this variation to conduct one of the first systematic comparative analyses of behavior (Krebs and Davies 1987). Crook showed that mating system in weaverbirds is correlated with diet and habitat—monogamous species are insectivorous forest-dwellers, while polygynous species are granivorous colonial-nesters living in savanna habitats. He argued that these patterns are largely driven by differences in food availability. The food of insectivorous species is dispersed, favoring the evolution of resource territories, biparental care, and monogamy, while the superabundance of grass seeds during seasonal rains in savanna habitats leads to flocking, colonial nesting, uniparental care, and thus polygyny. Crook did not, however, relate these differences to variation in nest characteristics. If sexual selection is, in part, responsible for variation in nest structure and quality, then one would predict a correlation between degree of polygyny and quality of weave across species. Unfortunately, this comparison cannot yet be made because reliable data on these two characters are not available, and neither is a recent phylogeny of the group.

Conclusion

Some behavioral skills, like song and nest-building, may be under strong sexual selection. In baya weaverbirds, however, I have found limited evidence for current female choice for attributes of nest architecture. Architectural traits may need to be manipulated beyond the range of current variation to better evaluate female preferences. In addition, historical questions about the selective factors associated with the evolution of nest architecture may be best answered using a comparative approach. Current female choice in baya weaverbirds appears to be more closely related to nest location than to nest architecture. Constraints imposed by the availability of suitable nesting sites provide a general reason why directional female choice for nest location persists to the current day.

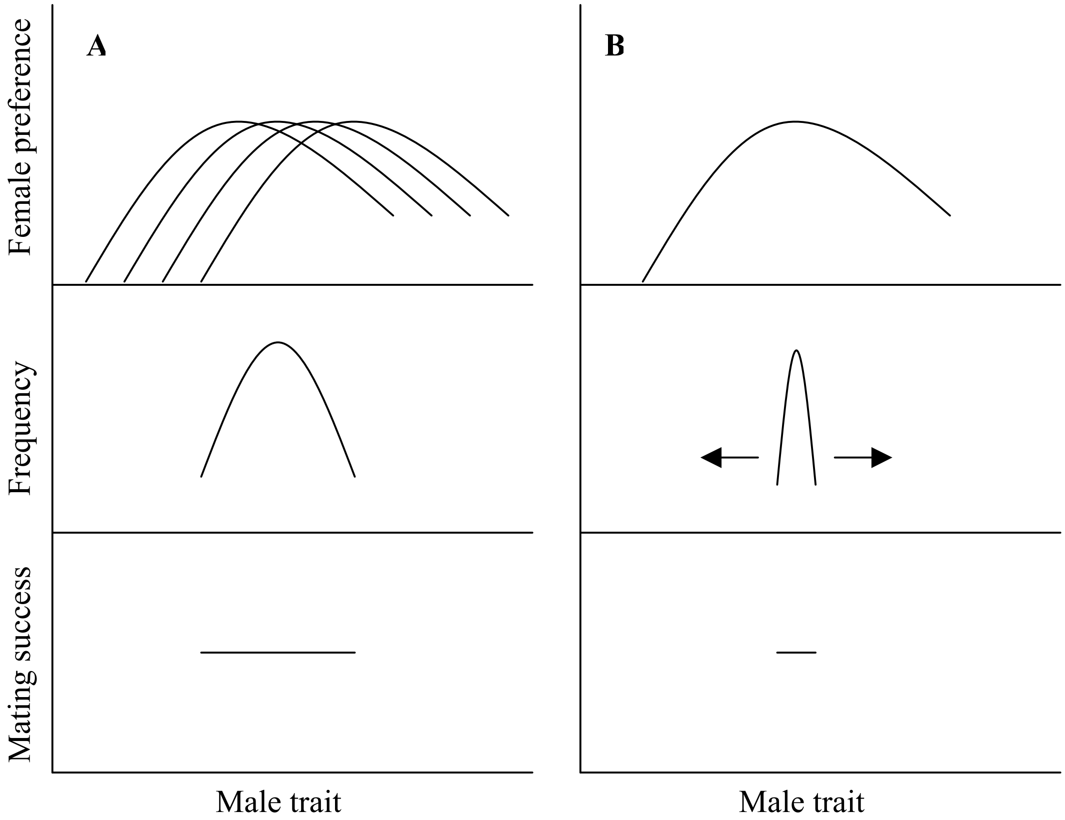

Figure 6-1. Conditions under which one would expect to find no relationship between male mating success and the degree of elaboration of a male trait. The top panels show a unimodal female preference, with intermediate trait values being preferred. The middle panels show the frequency distribution of male trait values, and the bottom panels show male mating success in relation to male trait. A) the effect of between-female variation in preference function on the population-level pattern. If the maximally preferred male trait value differes slightly between females, a plateau of female preference results at the level of the population. B) if there is little variation in trait values, then female preferences may only be detected if male traits are manipulated to extreme values, beyond the range of current variation.

LIST OF REFERENCES

Agresti A, 1996. An introduction to categorical data analysis. New York: John Wiley and Sons.

Ali S, 1931. The nesting habits of the baya (*Ploceus philippinus*): a new interpretation of their domestic relations. J Bombay Nat Hist Soc 34:947–964.

Ali S, Ambedkar VC, 1956. Notes on the baya weaver bird, *Ploceus philippinus* Linn. J Bombay Nat Hist Soc 53:381–389.

Ali S, Ripley SD, 1987. Compact handbook of the birds of India and Pakistan together with those of Bangladesh, Nepal, Bhutan and Sri Lanka, 2nd ed. Delhi: Oxford University Press.

Ambedkar VC, 1964. Some Indian weaver birds: a contribution to their breeding biology. Bombay: University of Bombay.

Andersson M, 1982. Female choice selects for extreme tail length in a widowbird. Nature 299:818–820.

Andersson M, 1994. Sexual selection. Princeton: Princeton University Press.

Arnold KE, Owens I PF, 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. Proc R Soc Lond B, 269:1263–1269.

Arnold SJ, 1992. Constraints on phenotypic evolution. Am Nat 140:S85–S107.

Barber I, Nairn D, Huntingford FA, 2001. Nests as ornaments: Revealing construction by male sticklebacks. Behav Ecol 12:390–396.

Bernatchez L, Duchesne P, 2000. Individual-based genotype analysis in studies of parentage and population assignment: how many loci, how many alleles? Can J Fish Aq Sci 57:1–12.

Birkhead TR, 1998. Sperm competition in birds: mechanisms and function. In: Sperm competition and sexual selection (Birkhead TR, Møller AP, eds). San Diego: Academic Press; 579-622.

Birkhead TR, Møller AP, 1992. Sperm competition in birds: evolutionary causes and consequences. London: Academic Press.

Borgia G, 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): An experimental analysis. Anim Behav 33:266–271.

Borgia G, 1995a. Complex male display and female choice in the Spotted Bowerbird—specialized functions for different bower decorations. Anim Behav 49:1291–1301.

Borgia G, 1995b. Threat reduction as a cause of differences in bower architecture, bower decoration and male display in 2 closely-related bowerbirds *Chlamydera nuchalis* and *C. maculata*. Emu 95:1–12.

Borgia G, Collis K, 1989. Female choice for parasite-free male Satin Bowerbirds and the evolution of bright male plumage. Behav Ecol Sociobiol 25:445–454.

Borgia G, Collis K, 1990. Parasites and bright male plumage in the Satin Bowerbird *Ptilonorhynchus violaceus*. Am Zool 30:279–286.

Borgia G, Presgraves DC, 1998. Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis. Anim Behav 56:1121–1128.

Bradbury JW, Vehrencamp SL, 1977. Social organization and foraging in emballonurid bats, III: mating system. Behav Ecol Sociobiol 2:1–17.

Brown CR, Brown MB, 1996. Coloniality and the cliff swallow: the effect of group size on social behavior. Chicago: University of Chicago Press.

Brown CR, Stutchbury BJ, Walsh PD, 1990. Choice of colony size in birds. Trends Ecol Evol 5:398–403.

Brunton D, 1999. "Optimal" colony size for Least Terns: An inter-colony study of opposing selective pressures by predators. Condor 101:607–615.

Burley NT, 1982. Reputed band attractiveness and sex manipulation in zebra finches. Science 215:423–424.

Burley NT, Parker PG, Lundy K, 1996. Sexual selection and extrapair fertilization in a socially monogamous passerine, the zebra finch (*Taeniopygia guttata*). Behav Ecol 7:218–226.

Catchpole CK, Slater PJB, 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.

Christy JH, Backwell PRY, Goshima S, Kreuter T, 2002. Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms. Behav Ecol 13:366–374.

Clark RW, Shutler D, 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80:272–287.

Collias EC, Collias NE, 1964a. The development of nest-building behavior in a weaverbird. Auk 81:42–52.

Collias EC, Collias NE, 1973. Further studies on development of nest-building behavior in a weaverbird. Auk 81:42–52.

Collias EC, Collias NE, Jacobs CH, McAlary F, Fujimoto JT, 1979. Experimental evidence for facilitation of pair formation by bright color in weaverbirds. Condor 81:91–93.

Collias NE, Collias EC, 1964b. Evolution of nest-building in the weaverbirds. Univ Cal Publ Zool 73:1–162.

Collias NE, Collias EC, 1984. Nest building and bird behavior. Princeton, NJ: Princeton University Press.

Collias NE, Victoria JK, 1978. Nest and mate selection in the village weaverbird (*Ploceus cucullatus*). Anim Behav 26:470–479.

Cresswell W, 1997. Nest predation: The relative effects of nest characteristics, clutch size and parental behaviour. Anim Behav 53:93–103.

Crook JH, 1960. Studies on the reproductive behaviour of the Baya Weaver [*Ploceus philippinus* (L.)]. J Bombay Nat Hist Soc 57:1–44.

Crook JH, 1963. A comparative analysis of nest structure in the weaver birds (Ploceinae). Ibis 105:238–262.

Crook JH, 1964a. Field experiments on the nest construction and repair behavior of certain weaver birds. Proc Zool Soc Lond 142:217–255.

Crook JH, 1964b. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour, Supplement X, 1–178.

Cundall D, Greene HW, 2000. Feeding in snakes. In: Feeding: form, function and evolution in tetrapod vertebrates (Schwenk K, ed). San Diego: Academic Press; 293–333.

Dallimer M, 1999. Cross-species amplification success of avian microsatellites in the redbilled quelea *Quelea quelea*. Mol Ecol 8:695–698.

Darwin C, 1897. The descent of man and selection in relation to sex, 2nd ed. New York: D Appleton and Co.

Davies NB, 1978. Ecological questions about territorial behaviour. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific; 317–350.

Davis JA, Brown CR, 1999. Costs of coloniality and the effect of colony size on reproductive success in purple martins. Condor 101:737–745

Davis TA, 1971. Variation in nest-structure of the common weaverbird *Ploceus philippinus* (L.) of India. Forma et Functio 4:225–239.

Davis TA, 1974. Selection of nesting trees and the frequency of nest visits by baya weaverbird. J Bombay Nat Hist Soc 71:356–366.

Dawkins R, 1982. The extended phenotype. Oxford: Oxford University Press.

Dhindsa MS, 1990. Intraspecific brood parasitism in the baya weaverbird *Ploceus philippinus*. Bird Behav 8:111–113.

Ellegren H, 1992. Polymerase-chain-reaction (PCR) analysis of microsatellites—a new approach to studies of genetic relationships in birds. Auk 109:886–895.

Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Endler JA. 1986. Natural selection in the wild. Princeton, NJ: Princeton University Press.

Evans MR, 1997. The influence of habitat and male morphology on a mate-choice cue: The display nests of wrens. Anim Behav 54:485–491.

Evans MR, Burn JL, 1996. An experimental analysis of mate choice in the wren: A monomorphic, polygynous passerine. Behav Ecol 7:101–108.

Ferguson JWH, Siegfried WR, 1989. Environmental factors influencing nest-site preference in white-browed sparrow-weavers (*Plocepasser mahali*). Condor 91:100–107.

Freeman S, 1988. Egg variability and conspecific nest parasitism in the *Ploceus* weaverbirds. Ostrich 59:49–53.

Friedl TWP, Klump GM, 1999. Determinants of male mating success in the red bishop (*Euplectes orix*). Behav Ecol Sociobiol 46:387–399.

Friedl TWP, Klump GM, 2000. Nest and mate choice in the red bishop (*Euplectes orix*): Female settlement rules. Behav Ecol 11:378–386.

Garson PJ, 1979. Female choice in village weaverbirds. Anim Behav 27:309–310.

Gowaty PA, 1996. Field studies on parental care in birds: new data focus questions on variation among females. Adv Stud Behav 25:477–531.

Gowaty PA, Bridges WC, 1991. Nestbox availability affects extra-pair fertilizations and conspecific nest parasitism in eastern bluebirds, *Sialia sialis*. Anim Behav 41:661–675.

Griffith SC, Owens IPF, Thuman KA, 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol 11:2195–2212.

Grubbauer P, Hoi H, 1996. Female penduline tits (*Remiz pendulinus*) choosing high quality nests benefit by decreased incubation effort and increased hatching success. Ecoscience 3:274–279.

Hamilton WD, 1971. Geometry for the selfish herd. J Theor Biol 31:295–311.

Hanotte O, Zanon C, Pugh A, Greig C, Dixon A, Burke T, 1994. Isolation and characterization of microsatellite loci in a passerine bird - the reed bunting *Emberiza schoeniclus*. Mol Ecol 3:529–530.

Hanski IK, Fenske TJ, Neimi GJ, 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk 113:578–585.

Hansson B, Bensch S, Hasselquist D, 2000. Patterns of nest predation contribute to polygyny in the Great Reed Warbler. Ecology 81:319–328.

Hasselquist D, Sherman PW, 2001. Social mating systems and extrapair fertilizations in passerine birds. Behav Ecol 12:457–466.

Hoi H, Schleicher B, Valera F, 1994. Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: the importance of nest quality. Anim Behav 48:743–746.

Houde AE, 1997. Sex, color, and mate choice in guppies. Princeton, NJ: Princeton University Press.

Ihaka R, Gentleman R, 1996. R: a language for data analysis and graphics. J Comp Graph Stat 5:299–314.

Jacobs CH, Collias NE, Fujimoto JT, 1978. Nest color as a factor in nest selection by female village weaverbirds. Anim Behav 26:463–469.

Jamieson A, 1994. The effectiveness of using co-domimant polymorphic allelic series for (1) checking pedigrees and (2) distinguishing full-sib pair members. Anim Genet 25:37–44.

Johnsen A, Fiske P, Amundsen T, Lifjeld JT, Rohde PA, 1997. Colour bands, mate choice and paternity in the bluethroat. Anim Behav 59:111–119.

Johnson LS, Hicks BG, Masters BS, 2002. Increased cuckoldry as a cost of breeding late for male house wrens (*Troglodytes aedon*). Behav Ecol 13:670–675.

Jones AG, Walker D, Kvarnemo C, Lindstrom K, Avise JC, 2001. How cuckoldry can decrease the opportunity for sexual selection: Data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. Proc Nat Acad Sci USA 98:9151–9156.

Kellogg KA, Stauffer JR Jr., McKaye KR, 2000. Characteristics that influence male reproductive success on a lek of *Lethrinops* c.f. *parvidens* (Teleostei: Cichlidae). Behav Ecol Sociobiol 47:164–170.

Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P, 2001. The strength of phenotypic selection in natural populations. Am Nat 157:245–261.

Konishi M, 1994. An outline of recent advances in birdsong neurobiology. Brain Behav Evol 44:279–285.

Krackow S, Tkadlek E, 2001. Analysis of brood sex ratios: implications of offspring clustering. Behav Ecol Sociobiol 50:293–301.

Krebs JR, Davies NB, 1987. An introduction to behavioural ecology, 2nd ed. Oxford: Blackwell Scientific.

Lack D, 1968. Ecological adaptations for breeding in birds. London: Methuen Ltd.

Lanctot RB, Scribner KT, Kempenaers B, Weatherhead PJ, 1997. Lekking without a paradox in the buff-breasted sandpiper. Am Nat 149:1051–1070.

Lande R, 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lande R, 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution 33:402–416.

Lande R, 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

Li P, Martin TE, 1991. Nest site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

Lindström K, 1992. Female spawning patterns and male mating success in the snad goby *Pomatoschistus minutus*. Mar Biol 113:475–480.

Madden J, 2001. Sex, bowers and brains. Proc R Soc Lond B 268:833–838.

Manly BFJ, 1986. Multivariate statistical methods: a primer. London: Chapman and Hall.

Manolis JC, Andersen DE, Cuthbert FJ, 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117:615–626.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM, 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655.

Martin TE, 1993. Nest predation among vegetation layers and habitat types—revising the dogmas. Am Nat 141:897–913.

Martin TE, 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? Ecology 82:175–188.

Martin TE, Roper JJ, 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51–57.

Mayfield HF, 1961. Nesting success calculated from exposure. Wilson Bull 73:255–261.

Mayfield HF, 1975. Suggestions for calculating nest success. Wilson Bull 87:456–466.

McRae SB, Amos W, 1999. Characterization of hypervariable microsatellites in the cooperatively breeding white-browed sparrow weaver *Plocepasser mahali*. Mol Ecol 8:903–904.

Meek SB, Barclay RMR, 1996. Settlement patterns and nest-site selection of cliff swallows, *Hirundo pyrrhonota*: males prefer to clump but female settle randomly. Can J Zool 74:1394–1401.

Metz KJ, Weatherhead PJ, 1993. An experimental test of the contrasting-color hypothesis of red-band effects in red-winged blackbirds. Condor 95:395–400.

Miller HW, Johnson DH, 1978. Interpreting the results of nesting studies. J Wildl Manage 42:471–476.

Mitchell NJ, 2001. Males call more from wetter nests: effects of substrate water potential on reproductive behaviours of terrestrial toadlets. Proc R Soc Lond B 268: 87–93.

Møller AP, Birkhead TR, 1993. Cuckoldry and sociality: a comparative study of birds. Am Nat 142:118–140.

Moreno J, Soler M, Møller AP, Linden M, 1994. The function of stone carrying in the black wheatear, *Oenanthe leucura*. Anim Behav 47:1297–1309.

Mulder RA, Dunn PO, Cockburn A, Lazenbycohen KA, Howell MJ, 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proc R Soc Lond B 255:223–229.

Nelson CM, 1995. Male size, spawning pit size and female mate choice in a lekking cichlid fish. Anim Behav 50:1587–1599.

Neumann K, Wetton JH, 1996. Highly polymorphic microsatellites in the house sparrow *Passer domesticus*. Mol Ecol 5:307–309.

Oliveira RF, Miranda JA, Carvalho N, Gonçalves EJ, Grober MS, Santos RS, 2000. Male mating success in the Azorean rock-pool blenny: the effects of body size, male behaviour and nest characteristics. J Fish Biol 57:1416–1428.

Östlund-Nilsson S, 2000. Are nest characters of importance when choosing a male in the fifteen-spined stickleback (*Spinachia spinachia*)? Behav Ecol Sociobiol 48:229–235.

Pemberton JM, Slate J, Bancroft DR, Barrett JA, 1995. Nonamplifying alleles at microsatellite loci—a caution for parentage and population studies. Mol Ecol 4:249–252.

Petrie M, Kempenaers B, 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol 13:52–58.

Pinheiro JC, Bates DM, 2000. Mixed-effects Models in S and S-PLUS. New York: Springer.

Pitman CRS, 1958. Snake and lizard predators of birds. Bull Brit Ornithol Club 78:82–86, 99–104, 120–124.

Ryan MJ, 1997. Sexual selection and mate choice. In: Behavioural ecology: an evolutionary approach, 4th ed (Krebs JR, Davies NB, eds); 179-202.

Ryan MJ, Wagner WE Jr, 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific mates. Science 236:595-597.

Queller DC, Strassmann JE, Hughes CR, 1993. Microsatellites and kinship. Trends Ecol Evol 8:285–288.

Schmidt KA, Whelan CJ, 1999. Effects of exotic *Lonicera* and Rhamnus on songbird nest predation. Conserv Biol 13:1502–1506.

Searcy WA, Andersson M, 1986. Sexual selection and the evolution of song. Ann Rev Ecol Syst 17:507-533.

Sedgeley JA, 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. J Appl Ecol 38: 425–438.

Seutin G, White BN, Boag PT, 1991. Preservation of avian blood and tissue samples for DNA analyses. Can J Zool 69:82–90.

Shelly TE, Greenfield MD, Downum KR, 1987. Variation in host plant quality: influences on the mating system of a desert grasshopper. Anim Behav 35:1200–1209.

Sibley CG, Ahlquist JE, 1990. Phylogeny and classification of birds: a study in molecular evolution. New Haven, CT: Yale University Press.

Sibley CG, Monroe BL, 1990. Distribution and taxonomy of birds of the world. New Haven, CT: Yale University Press

Sokal RR, Rohlf FJ, 1995. Biometry, 3rd ed. New York: W. H. Freeman.

Soler JJ, Cuervo JJ, Møller AP, De LF, 1998a. Nest building is a sexually selected behaviour in the barn swallow. Anim Behav 56:1435–1442.

Soler JJ, Møller AP, Soler M, 1998b. Nest building, sexual selection and parental investment. Evol Ecol 12:427–441.

Sorenson MD, 1992. Comment: why is conspecific nest parasitism more frequent in wildfowl than in other birds? Can J Zool 70:1856–1858.

Stutchbury BJ, Morton ES, 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour 132:675–690.

Uy JAC, Borgia G, 2000. Sexual selection drives rapid divergence in bowerbird display traits. Evolution 54:272–278.

Venables WN, Ripley BD, 2002. Modern applied statistics with R. New York, Springer.

Vogel S, 1984. Drag and flexibility in sessile organisms. Am Zool 24:37–44.

Wade MJ, 1987. Measuring sexual selection. In: Sexual selection: testing the alternatives (Bradbury JW, Andersson MB, eds). Chichester: John Wiley and Sons; 197–207.

Walsberg GE, 1981. Nest-site selection and the radiative environment of the warbling vireo. Condor 83:86–88.

Westneat DF, Sargent RC, 1993. Sex and parenting—the effects of sexual conflict and parentage on parental strategies. Trends Ecol Evol 11:87–91.

Westneat DF, Sherman PW, Morton ML, 1990. The ecology and evolution of extrapair fertilizations in birds. Curr Ornith 7:331–369.

Whittingham LA, Lifjeld JT, 1995. Extra-pair fertilizations increase the opportunity for sexual selection in the monogamous House Martin *Delichon urbica*. J Avian Biol 26:283–288.

Wilkinson GS, Reillo PR, 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. Proc R Soc Lond B 255:1–6.

Wagner WE Jr, 1998. Measuring female mating preferences. Anim Behav 55:1029-1042.

Yom-Tov Y, 1980. Intraspecific nest parasitism in birds. Biol Rev 55:93–108.

Yom-Tov Y, 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143:133–143.

Zar J, 1996. Biostatistical analysis, 3rd ed. London: Prentice-Hall.

BIOGRAPHICAL SKETCH

Suhel Quader studied Zoology at Ramnarain Ruia College of the University of Bombay, where he received his B.Sc. degree in 1993. He then studied Wildlife Science at the Wildlife Institute of India, Dehradun (Saurashtra University), and received his M.Sc. degree in 1995. In his Master's thesis, he studied the nonbreeding social organization of great tits (*Parus major*). He joined the Department of Zoology at the University of Florida in August 1996, where he received a Ph.D. in August 2003 for his work on reproductive behavior of baya weaverbirds (*Ploceus philippinus*).