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Female Restriction of Male Mating Success
OSMP Studies 4131

Study



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**Female Restriction of
Male Mating Success in
Lark Sparrows
Chondestes grammacus
with Suggestions for
Management**

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Introduction

The mating systems of mammals tend towards a pattern predicted from the relative size of gametes produced by male and female individuals (Parker, Baker and Smith 1972). Females produce large gametes rich in nutrients, while males produce small gametes consisting only of a flagellum and genetic information. This difference, referred to as anisogamy, reflects a difference in the inherent levels of investment by males and females. Males, due to the minimal investment involved in a single breeding attempt, are often free to desert and inseminate more females, increasing their reproductive success without caring for offspring (Trivers 1972). In many groups of animals, this pattern leads to minimal male involvement in the breeding cycle, and desertion of the female after copulation.

However, in birds over ninety percent of species tend to show social monogamy and biparental care (Lack 1968). The common situation in birds is for one male and one female to collaborate on care of young. What stops a male from deserting, or more generally, what are the determinants of male mating success (number of mates)? This classical question of avian mating systems questions the costs and benefits of alternative male breeding strategies (Ketterson and Nolan 1994). Two hypotheses have been proposed for this pattern in birds. (1) Facultative polygyny: a male's mating success is determined by his ability to partition time between two separate nests (Alatalo et al 1981). (2) Resource Defense Polygyny: a male's mating success is determined by his ability to defend breeding resources (Orlans 1969). Resource defense polygyny is referred to as "failed polygyny" by Gowaty (1996) and Birkhead and Møller (1996).

A third hypothesis was tested by this study, (3) female restriction: male mating success is determined by the female's ability to restrict his time (Maynard Smith 1977). This proposes that there has been selection on the female to restrict the male, in order to gain the maximal amount of material benefits (nest defense, food, parental care). Gaining these material benefits allows females to conserve resources for future reproduction, thus increasing lifetime

reproductive success (Gwynne 1984). Such selection on the female would produce a situation for males where maximum reproductive success would be achieved with a single female (Maynard Smith 1977).

Female restriction can occur by a number of mechanisms. Slagsvold and Lifjeld (1994) proposed a modification of the Polygyny Threshold Model (Orians 1969) based on female restriction of male mating success through aggression. Although selection on the female may have produced the male breeding strategy in this situation, it will be indistinguishable from resource defense polygyny. In this situation, selection on the female may be difficult to detect.

Alternative to a strict aggression model of restriction, female reproductive output can be enhanced by social conditioning, such as hearing a singing male, or taking part in displays, or copulating (Catchpole 1986; Cheng et al 1998). This corresponds to the 'long courtship' indicated by Maynard Smith (1977). If a female will only mate with a male after he has invested a certain amount of non-promiscuous mating effort (Gwynne 1984), then he will not have time to nest with another female simultaneously. The Female Restriction Hypothesis therefore proposes an inverse relationship between mating success and non-promiscuous mating effort. This yields the prediction that males who spend a larger amount of time singing at off-peak hours, as well as displaying and copulating are more likely to be successful nesters.

Methods

Study Species

This hypothesis was tested on Lark Sparrows *Chondestes grammacus* in the Summer of 1999. The Lark Sparrow is a medium-sized member of the Emberizidae that nests monogamously and rarely polygynously (Verner and Willson 1969). Lark Sparrows are the ideal species for this study because males are strongly territorial during pair-formation, making them easy to capture for banding. Also, males sing throughout the breeding season, making them especially useful for studying this particular variable. They are highly visible and sing loudly from conspicuous perches, making color bands easily distinguishable. Though the sexes are similar in plumage and size, birds were sexed from identification of a brood patch (females) or a cloacal protuberance (males). Birds were captured in mist-nets in late May through the first week of June and banded with unique color combinations on the right leg along with a sex specific band and a numbered United States Geological Survey band on the left leg. Males were banded with white and females with black leg bands for ease of sex identification.

Study Site

The study was conducted on the Boulder Valley Ranch Open Space (N40°4', W105°16') North of Boulder, Colorado. The study area is semi-arid shrubland, typified by sage (*Artemisia* spp.), sumac (*Rhus aromatica*) and yucca (*Yucca*) vegetation. Both major study areas within the site included extensive stands of cottonwoods (*Populus sargentii*). The area is typical of habitat occupied by Lark Sparrows in other geographical areas (Dechant et al. 1999).

Determination of Male Time Partitioning

Males were observed within two off-peak singing periods, between 0700-0900 and 1400-1600 MST. Each male was observed individually for 10 minutes at a time. Verbal notes of changes in behavior were made on a hand held tape recorder, then later timed with a stopwatch and transcribed. The total number of seconds spent on foraging, vigilance, predator defense, aggression, maintenance (preening), travel, feeding the female, feeding young, calling, display, singing and copulation, was then recorded in a table along with the time of day and date. Males which had not been observed recently were given priority over more recently observed males.

Results

Six males and one female Lark Sparrow were captured and banded in early June. All were completely color-banded along with aluminum USGS leg bands. As expected, birds were easily sexed from identification of a brood patch or cloacal protuberance.

Behavioral observations sampled these six males a median of four times each with a total of 260 sample minutes (Table 1). One male (RLGLB/WX) was successful (was observed feeding fledglings). Another male (YLGLB/WX), disappeared from the study site after two observations. Male YLBR/WX was found to be nesting with the single banded female (YLGR/WX), but that nest was destroyed by an unidentified mammal. One nest of an unbanded pair was abandoned after significant persistent disturbance by public visitors to the study site. The remaining two males were seen intermittently consorting with unbanded birds, and their level of singing varied throughout the season. As singing level declines in other sparrows after pair-formation (Searcy 1981), this leads me to believe pair bonds were not stable and/or nests failed. These males were not seen accompanying fledglings at any time during the season, as was RLGLB/WX and many pairs of unbanded birds on the site.

Overall, RLGLB/WX spent a larger proportion of his time singing than did other males. Table 1 shows mean total seconds for successful versus unsuccessful males. Since the successful category had a sample size of one, a statistical analysis of these results is impossible. However of the sampled time, RLGLB/WX spent a larger proportion of his time on singing. Despite this result, the pattern does not carry over to the other relevant activities, displaying and copulating (Figure 1). Unsuccessful males spent a larger proportion of time on both displaying and copulating (Figure 2).

Suggestions for Management

Dechant et al. (1999) synthesized the habitat requirements of and the effects of management on Lark Sparrows in North America. An overwhelming number of studies concluded that burning and grazing are both beneficial to Lark Sparrows (e.g. Bock and Bock 1992). The strongest effects of burning were found in grasslands dominated by native vegetation. For example, in Arizona, Lark Sparrow abundance increased dramatically two years post-burn in native vegetation, whereas no difference was observed between burned and unburned areas dominated by sacaton grass (*Sporobolus wrightii*; Bock and Bock 1988).

Lark Sparrows tend to prefer shortgrass and mixed-grass uplands to tallgrass remnants (Bock et al 1995). Many studies have found Lark Sparrows preferring grazed fields over ungrazed pastures (Baepler 1968; Newman 1970; Walley 1985). These Lark Sparrow preferences toward burned and grazed areas may have to do with food preferences and foraging practices, which often includes walking extensive areas of bare ground and either pouncing on large insects or gleaning smaller insects off of overhanging twigs (personal observation).

The Dechant et al. (1999) summary provides these suggestions for management:

- 1) Preserve native pasture and rangeland
- 2) Avoid disturbances during nesting such as haying, burning or grazing. Burns should be conducted before March, before Lark Sparrows arrive on their breeding grounds (Renwald 1977).

- 3) Leave approximately 10% brush cover for use by Lark Sparrows during brush removal. Lark Sparrows need some woody vegetation for nesting.
- 4) Burns should be conducted at five- to eight-year intervals to increase open foraging areas

Discussion

One male Lark Sparrow was successful. He spent a larger amount of his time singing, yet less time displaying and copulating. The results qualitatively validate the female restriction hypothesis for the prediction of disproportionate song investment, but are merely preliminary. Sample sizes are insufficient to provide meaningful results. More data on successful males are required before a valid conclusion can be made. The distribution of individually marked birds across the study site made it difficult to maximize observation time and include time for nest-searching. Future efforts would be wise to concentrate mist-netting in a single locality, so that time searching for banded birds will be minimized. This may also increase interactions between banded birds, thereby making social interactions tractable.

There are also complications with the structure of the female restriction model. As mentioned above, female restriction can occur by a number of mechanisms, therefore the predictions of the model will vary with the active mechanism. The predictions resulting from one mechanism's formulation of the model may not be borne out due to variation in the function of particular male behaviors. For example, if song form and function varies with context, as in the Great Reed-Warbler *Acrocephalus arundinaceus* (Catchpole 1983), then the prediction of disproportionate song investment would only hold for certain forms of the song. Therefore, the failure of all the successful male's relevant activities to fit the pattern is not a refutation of the Female Restriction hypothesis. The function of male behaviors must be clearly established before their relevance to female reproductive output can be determined.

Problems arise when the structure of the breeding cycle is taken into account. Continuous acoustic stimulation cannot account for all male time during the breeding cycle. Once a clutch is laid male song cannot enhance female reproductive output. Until the next clutch (a second brood) is initiated, the female will either have to resort to aggression (which would cost incubation time) or heightening the costs of desertion by conditional parental investment, resulting in a lowered reproductive success for both male and female.

This leads to the simpler formulation of the Female Restriction hypothesis given by Maynard Smith's (1977) model 1, which relies on a long courtship and a significantly low probability of re-mating after copulation. Similar models were explored by Dawkins (1976), Grafen and Sibly (1978), and Schuster and Sigmund (1981). This produces key predictions for other variables; breeding synchrony and level of extra-pair fertilization should be negatively correlated. If a male has time available post-laying, then he will have to resort to covert extra-pair copulations. However, since many of these females will be paired and the male will be busy protecting his previous investment (feeding his social mate on the nest), the male will not re-nest.

Summary

The preliminary results from this field season qualitatively validate the prediction of disproportionate song investment. The results cannot be trusted, since small sample sizes prevent a robust statistical analysis. Future studies of these variables must consider variation in the function of particular forms of display and song. Also, the structure of the breeding cycle leaves the disproportionate song investment prediction for the pair-formation to pre-laying period only. This produces the added prediction of a negative correlation between breeding synchrony and frequency of extra-pair fertilization.

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Tables and Figures

Legend for Band Colors

R=red

Y=yellow

B=black

W=white

X=numbered aluminum United States Fish and Wildlife Service leg band

LB=light blue

LG=light green

Table 1. Mean total seconds per observation period for successful versus unsuccessful males.

Male	Singing	Displaying	Copulation	n
RLGLB/WX	321.5	0	0	2
YLBLG/WX	0	10	0	2
YLBR/WX	112.8	11.5	0	6
RYLB/WX	60.2	9.5	0	6
YRLB/WX	123.5	11.7	2	6
LBRLB/WX	127.3	37.5	1.5	4

Time Spent Singing by Male Sparrows

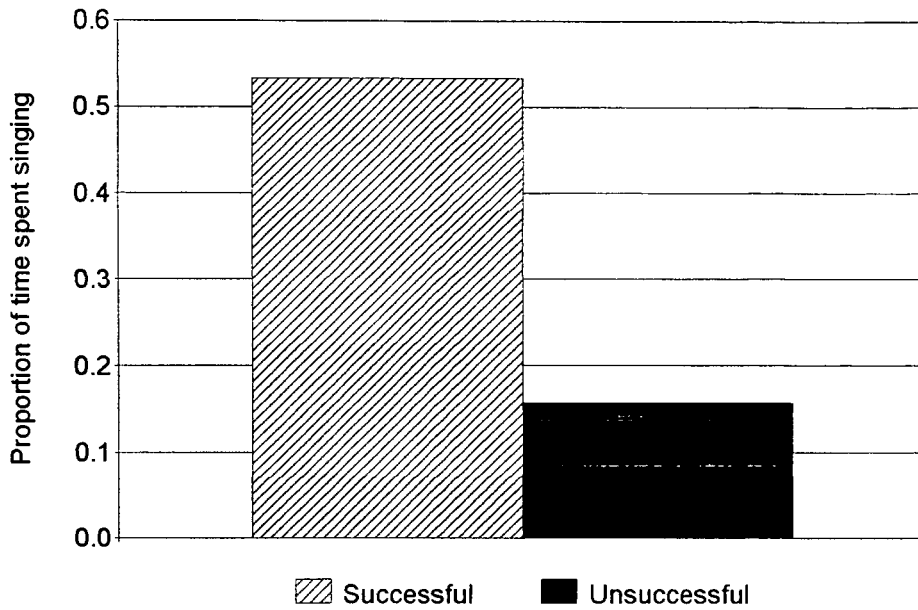


Figure 1. Proportion of time spent singing by successful and unsuccessful male Lark Sparrows.

Time Spent on Display and Copulation

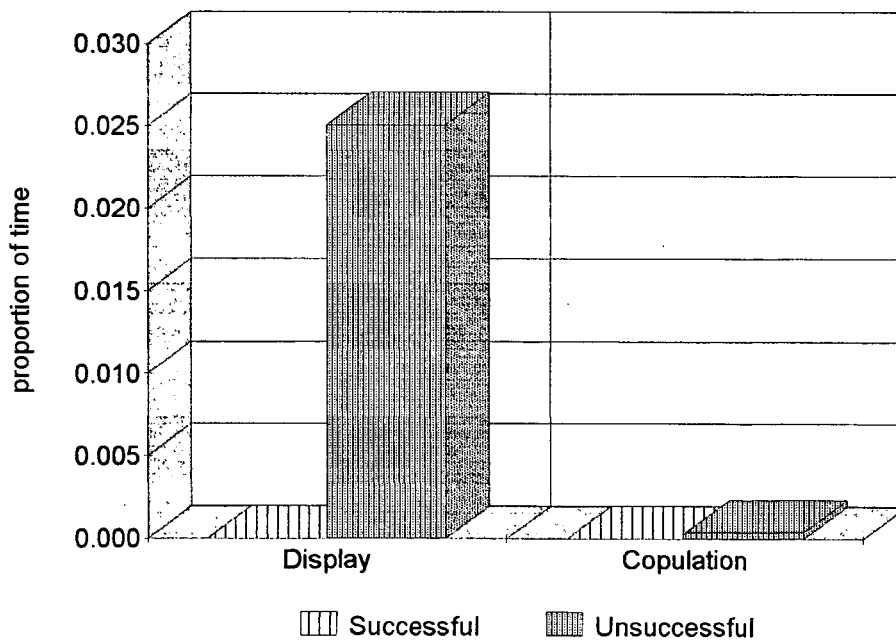


Figure 2. Proportion of time spent by successful and unsuccessful males on display and copulation.