Final Report to City of Boulder Open Space Department

Testing Female Restriction of Male Mating Success: The Suitability of Lark Sparrows

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1 Introduction

The number of females a male pairs with during a breeding season, male mating success, is closely linked to the structure of the male time budget (Maynard Smith 1977). The Female Restriction Model (FRM) makes predictions about the form of the male time-budget and the seasonal reproductive investment of males and females (Adamson 2000). To test these, an appropriate species must be found which meets the assumptions of the model.

Lark Sparrows *Chondestes grammacus* are medium sized emberizid sparrows, which nest monogamously, and occasionally polygynously (Byers et al. 1995). Female and male plumage is identical, and there are no significant differences in size between the sexes (Rising 1996). Lark Sparrows satisfy a number of the requirements for a study species to test the model, and on available study sites they are present in considerable numbers. Here I present the results of the 2000 field season and examine whether

the life history of Lark Sparrows satisfies the following assumptions of the Female Restriction Model:

- a finite breeding season
- males provide direct, material benefits to females
- males defend only a single territory
- young are more likely to survive if raised by two parents than one, and will not survive if deserted by both parents
- variance in parental care makes a more significant contribution to fitness than variance in female output
- female fitness is limited by material resources (food, nest sites, nest material and cover) on the breeding territory

The model also produces the following predictions in Lark Sparrows:

- females produce young conditioned upon male time investment (figure 1)
- a proportion of each sex abandons young, or lowers their level of parental care dependent upon their partner's investment during mating
- females will aggressively maintain a breeding sex ratio (BSR) of 1 (the ratio of number of females which breed to

the number of males which breed; Arnold and Duval 1994) (Table 1).

2 Methods

Study Sites

Two sites in the North Boulder Valley portion of City of Boulder Open Space Land were used in 2000. Boulder Valley Ranch was divided into northern and southern sections by Longhorn Road (N40°4′, W105°16′). The other site is approximately 2km east of Boulder Valley Ranch on land surrounding the Eagle Trail as it extends West from its trailhead on 51st street. These areas are semi-arid shortgrass prairie with a plant community typified by yucca (*Yucca* spp.), sage (*Artemisia* spp.), buffalo grass *Buchloe dactyloides* and scattered sumac (*Rhus aromatica*). Lark Sparrows prefer these habitats because they include large patches of bare ground and patchy cover (Dechant et al 1999; Carl Bock, personal communication).

Capture, Sexing, Marking and Measurements

Individuals were captured, marked, sexed and measured to accurately ascribe behaviors to particular individuals. All capture methods used 12mx3m Ecotone brand mist-nets. Three capture methods have been attempted, most with limited success. "Active mist-netting" uses a single panel

mist-net in an area where birds are currently active. "Passive mist-netting" is similar to mist-netting used in monitoring, where nets are set up in high traffic areas and little effort is made to lure the birds into the nets (Ralph et al. 1993). A playback scheme, suggested by Walker (personal communication) uses two speakers on either side of a single net so the researcher can move the source of the playback, adding to the capture subject's impression of a territorial rival.

I sexed individuals on the basis of a cloacal protuberance (male) or a brood patch (female), characteristics that develop when individuals enter reproductive condition (Pyle 1997). Wing chord and weight were also measured. I marked each individual with one numbered United States Geological Survey aluminum band and four colored leg bands. Females were marked with a black band and males with white on the left leg. Individuals were marked with a unique color combination of three bands on the right leg.

Behavioral Observations

I observed breeding behavior at 0600-0800 and 1700-1900 MST daily, at least 5 times weekly from 15 May to 28 July. I recorded the occurrence and frequency of behavior across multiple individuals, and also recorded time samples

for identifiable males. Often unmarked individuals were sexed by sex-specific behavior (e.g., copulations are only solicited by females) in the field.

Nest Finding and Territory Mapping

I located nests by observing the behavior of individuals. Hiding behind vegetation >20m from the focal birds and waiting for >5 min was often necessary for individuals to reveal a nest. Some nests were also found by following individuals carrying nest material. This method is unreliable, however, because male and female Lark Sparrows manipulate nest material in display, and do not always use it in nest building. All observations indicate that females build nests alone (personal observation; Rising 1996).

In order to keep track of nesting associations, I mapped territories for marked and unmarked individuals. Traditional spot-mapping techniques (Ralph et al 1993) are satisfactory in most cases, although owners often chased intruders well beyond the territorial boundary, making some boundaries less clear.

Roadside censuses assessed pre- and post-breeding population sizes. I counted birds on Longhorn Road at close to 0800 MST 25 April through 4 May and 21 July

through 28 July. This road is a common feeding site lined with fences often used for singing by male Lark Sparrows.

Results

Capture Results

Three birds (1 female, 2 males) were captured in 1999 with active mist-netting. The rest of that year's captures (4 males) were achieved by passive mist-netting. Passive methods captured all of the 2000 season's new birds (3 males, 1 female). One bird, originally captured in 1999, was re-captured with Walker's playback design.

Form and Timing of Breeding Behaviors

Observations reinforce Lark Sparrows' reputation as highly territorial birds (figure 2; Lambeth 1999). Territoriality began immediately after arrival on 5 May, and continued after birds began to flock together in late season (after 15 July). Two banded males (RYLB/WX and YRLB/WX) returned to the same territories that they occupied the previous year. Both failed to breed for a second year. Another banded male (RLGLB/WX) returned to a different part of the study site with different habitat characteristics from his successful breeding site the year before and also failed to breed. He arrived much later

than many other birds (5 June), and many territorial birds were spotted in his former breeding territory.

Pair formation occurred in week two, after 14 May, showing that males arrive first, possibly setting up territories before females arrive. Whether these pairs remained together throughout the season is unknown, since most birds were unmarked. All banded males displayed with nest-building females in multiple locations at different times in the season, but it cannot reliably be determined whether these were multiple females or simply the same pairs re-nesting in a different location. Birds began manipulating nest material after 13 June.

Lark Sparrows have three major types of complex song display in their repertoire: long song, short song and song flight. Long song is the typical Lark Sparrow song, produced by males, consisting of two or three whistles or downward slurs, a trill and a few low harsh notes. These can be reorganized many ways, and are often produced continuously for up to forty-five seconds. This song is often heard while the bird is perched atop a conspicuous shrub, stem, or tree. Males will also sing from the ground preceding display when a female is present, and in the presence of a predator (the researcher; personal

observation). Males produced long song throughout the season.

The short song consists only of the harsh notes and the "chip" note often heard while birds are foraging or traveling. Both males and females produce short song in aggressive contexts and males sing short song between bouts of long song. Short songs are much less common than long songs, shown by their small representation in figure 2.

Song flight (Baepler 1968)was first observed on the study site in 2000. This display consists of highly exaggerated ascending flight to a height of approximately 30m, from whence the bird begins singing long song in level flight. Then while still singing, the bird spirals downward toward the ground with highly exaggerated wingbeats. This is similar to song flight in Lark Buntings *Calamospiza melanocorys*. Song flight should be distinguished from flight song, which is a trill followed by harsh notes during directed, aggressive flight. Though it occurs in many other Emberizid species, the function of song flight is unclear (Wells and Vickery 1994). If song flight has a sexual function, it could be relevant to female manipulation of male behavior and time-budget.

The "Tail-Erect Bow Display", was fairly widespread throughout the season, accompanying most territorial

behavior. This behavior not only occurs in aggressive contexts, but also during predator defense. During this display a bird erects its tail, and most often fans the tail, exposing the white tail spots bordering the rectrices, raises its head exposing the dark spot in the center of the breast and repeatedly lowers and raises the head. Observation of individuals in the field shows that the size of the dot varies considerably in size between individuals. This may have an aggressive role as it does in other sparrows with similar plumage (e.g, Harris' Sparrow *Zonotrichia querula;* Rohwer 1982).

The occurrence of flocking, and along with it, agonistic behavior occurred at the close of the season (15-28 July). While some individuals remained unsuccessfully territorial (e.g., LBYLG/WX), counts indicated much higher abundance of foraging birds in flocks in previously occupied areas. Roadside censuses conducted 21-28 July indicated 30-50 birds on Longhorn Road, whereas during the breeding period similar counts showed only 8-10 individuals. Agonistic interactions in these flocks were common, with certain focal individuals repeatedly supplanting multiple birds.

Breeding Biology

No nest initiated before Day 30 (June 6) was successful. The causes of failure are various: nest abandonment by parents in the early stages of construction or incubation was common, accounting for 4 of 10 failures. Late-summer weather was responsible for one failure (2 nestlings). Predation accounts for all other nest failures (5). One nest was obviously destroyed by a large mammal, possibly a domestic dog, fox, raccoon, skunk or black bear. All other nests were intact beneath their cover when found predated. This allows for a variety of other predators to claim responsibility: bull snakes, mice, mule deer, jays (*Cyanocitta* spp.) and magpies (*Pica hudsonia*) in addition to those mentioned above. The results show that fledging success is significantly less than clutch size for all nests that initiated a clutch (t-test: $t=-5.9$, $p<0.001$, $n=10$, $df=8$; see table 2 for a summary of breeding biology variables). John Prather (personal communication) has reported similar predation rates for Lark Sparrows on other study sites (50%, 3 of 6 nests predated).

Conclusions and Discussion

An Evaluation of Capture Methods

Walker has reported high (>90%) success with this method used in Brewer's Sparrows *Spizella breweri*. Zach

Jones and Carl Bock (personal communication), working with similar methods, in similar habitat, have also reported high capture rates in Botteri's Sparrows *Aimophila botterii*. Out of approximately six hours using the two-speaker/single-net capture scheme in this study, one bird was captured. The method's low capture success can be attributed to two factors: (a) unavailability of local recordings and (b) the seasonal timing of the capture attempts. Timing of the capture attempts is critical (Carl Bock, personal communication), playback being most effective while territorial boundaries are still being contested. It is likely that this method failed due to improper seasonal timing.

The suitability of Lark Sparrows

Breeding success varies widely between attempts and presumably individuals. The breeding biology of Lark Sparrows fits the characteristic monogamous passerine model, allowing testing of the results of the female restriction model. The data show that individuals show the flexibility predicted by the model, which may cause a response to experimental perturbation. However, more data are needed to identify the best field methods before any experiments can be undertaken.

The breeding season is not only finite, but sharply limited as shown by the cut-off in breeding activity in late July. Seasonal weather patterns, for example in rainfall-level, may account for this pattern. Such time limitation increases the power of female restriction, due to the increased value of male time. Based on social associations, the breeding sex ratio is 1. Numerous studies have shown that social associations are not reliable indicators of parentage in many passerine species (Gowaty 1996), but no marked individuals were seen attending two nests simultaneously, and no territory appeared to have more than one nest.

There appear to be two different levels of female mating investment (clutch size): 2 eggs and 4 eggs. These are consistent with published reports of clutch size in Lark Sparrows (Byers et al 1995; Rising 1996). In this study it is difficult to conclude that these investment levels are significantly different due to small sample sizes. In addition to this possible variation in investment, one out of the two nests found with a brood size of two was only attended by a single adult (two adults were never seen defending or provisioning the nest simultaneously, which is normal for Lark Sparrows; personal observation). This could be conditional desertion, as

predicted by the model. Since clutch size is significantly different from fledging size, parental care plays a crucial role in determining fitness. This may verify the prediction that more variation in fitness is accounted for by parental care than female investment levels.

In accordance with the ecological assumptions and predictions of the female restriction model, suitable breeding habitat is limiting to male mating success (males cannot breed without a territory; Grigore 1999). Breeding adults occupy much larger territories on recently disturbed sites, and fledge fewer young (Grigore 1999) possibly satisfying the assumption that breeding resources are limiting to female fitness. Grigore's data were collected from a different subspecies of Lark Sparrow (*Chondestes grammacus grammacus*) than is present in Colorado (*Chondestes grammacus strigatus*), and at the edge of the species' range, so these data may not be accurate for Lark Sparrows in Colorado. However, Grigore (1999) provides much-needed vegetation data that may aid in design of experiments similar to those used by Plesczynska and Hansell (1980) in Lark Buntings.

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 sacoton 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

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Figures

Tables

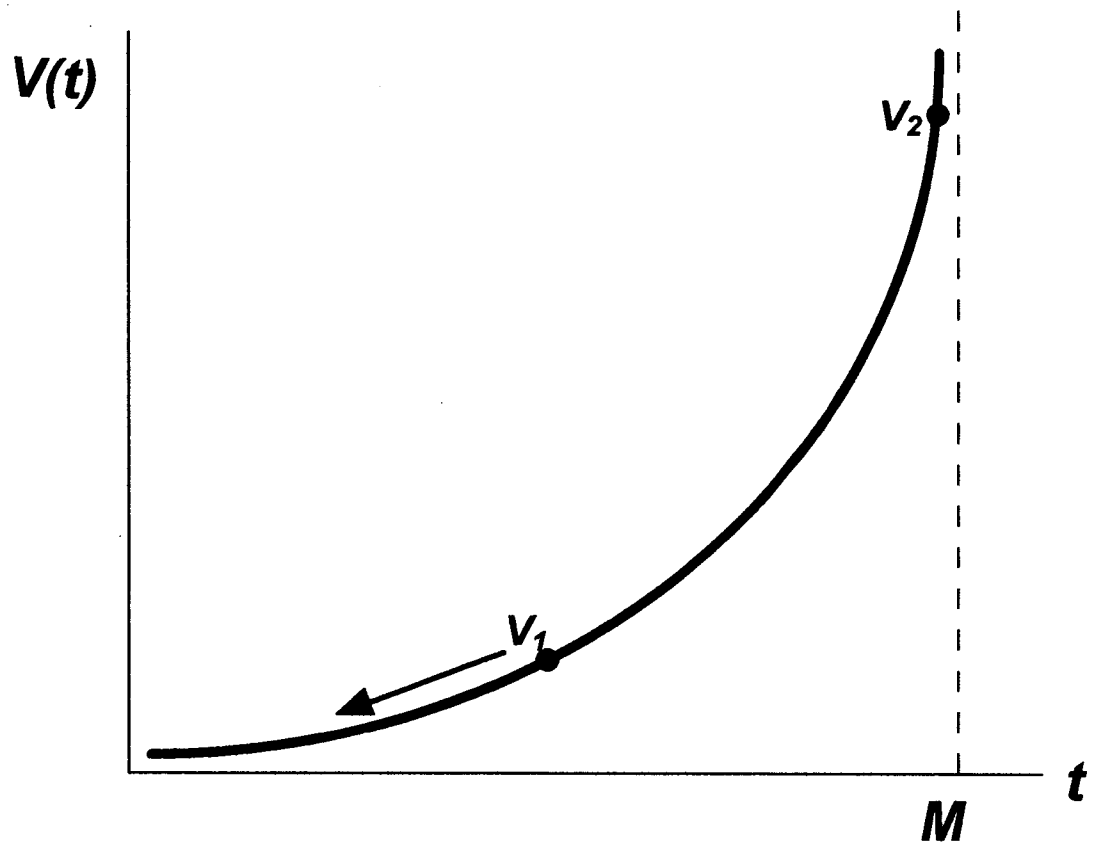

Figure 1

Tables

Model	*Experiment*	*Comparison*	*Strong Test*
General Model			
Greater Fitness Difference Caused by Variance in Parental Care	• Removal of one parent • Egg Transplantation	• Biparental vs. Uniparental care • Clutch size	• No: alternative: ▮ Male Care Essential▮ (Gowaty 1996)
Conditional Parental Behavior	Desertion or Lowered Parental Care induced by▮ • Repeated Male Removal to alter female perception of budgeting • Clutch size reduction	Correlation: • Within species: clutch size and male attentiveness • Within species: male time-budget and female attentiveness	• Weak for all tests: model does not guarantee existence of conditional strategies
Female Aggression Mechanism			
BSR=1	BSR=1 despite▮ • Male Removal • Male removal induces higher frequency of inter-female aggression	• Across species contradiction: Higher OSR=Higher BSR	Yes
Non-breeding female population	• Male removal induces non-breeding female population	• Across species: Higher incidence of non-breeding female population in monogamous species	No
Social Stimulation Mechanism			
▮Significantly different levels of output correlated with male investment	Female output lower with . . . • muted males Female output higher with . . . • ▮ enhanced▮ male	Correlational analysis of male investment and female investment (absolute and proportion of time/output)	Yes
Stimulatory behaviors have greatest value during fertile period	Higher male trait . . . • induced by onset of fertility • in presence of fertile female (laboratory)	• Correlational analysis across species	Yes

Table 1

Variable	Mean (x)=	Variance(s^2)=	N=	Range (max-min)=
Starting Date	30.7	120.4	13	35.0
Clutch Initiation Date	40.2	93.1	10	28.0
Clutch Size	3.6	0.70	10	2.0
Fledging Date	68.3	38.3	4	13.0
Fledging Success	0.90	2.4	13	4.0

Table 2