

Male and Female Reproductive Strategies in the Polygynous Bobolink

Abstract

Most species of birds are socially monogamous, however approximately 8% of bird species are polygynous. By mating polygynously, females lose paternal care, but might gain access to a superior territory or male. We examined five factors that affect polygyny in bobolinks: territory size, perching sites, predation rate, insect abundance, and vegetation composition and structure. Our study site was located in the Pend Oreille River Valley in northeast Washington State. Artificial perching sites were placed in the field, male territories were mapped, nests located and monitored, and vegetation assessed from May to mid-July 2003. Approximately 55% of males were polygynous, and 45% were monogamous. Females arrived on the study site in three temporal waves that we categorized as: first - monogamous, second - primary, and third - secondary females. Monogamous territories had higher caterpillar densities, higher herbaceous coverage, and were smaller in size than polygynous territories, reflecting the patchy vegetation of the study site. The first wave of females selected small territories and were monogamous. The second wave of females selected remaining, large territories, the third wave of females mated polygynously on these larger territories. Monogamous females fledged the most young. In contrast, polygynous males fledged more young than monogamous males. Males defended large areas with perches in order to maximize chances of mating polygynously.

Introduction

Monogamy is observed in 90% and polygyny in only 8% of bird species (Faaborg 1988). It has been assumed that females mating polygynously pay a price for sharing a mate due to reduced male assistance (Verner 1964). Understanding why some females mate with an already mated male, instead of a bachelor male, gives insight into female reproductive strategies. The goal of our research was to compare male and female reproductive strategies of bobolinks (*Dolichonyx oryzivorus*) and relate them to the two hypotheses that address this topic: Polygyny Threshold Hypothesis and Random Female Settlement Hypothesis.

In polygynous breeding systems, males typically arrive before females on the breeding grounds to establish territories. Females arrive later in temporal waves. The first wave consists of older, more experienced females that are familiar with migration routes and nesting grounds. These older females select the best males and territories (Martin 1971, Wiens 1969). The first males selected usually become polygynous during the breeding season (Martin 1971). The Polygyny Threshold Hypothesis (Verner 1964, Verner and Willson 1966, Orians 1969) predicts that there is a selective advantage for the later-arriving female to mate polygynously

rather than monogamously, if she is able to gain access to a genetically superior male or superior habitat that the male occupies. Therefore, this hypothesis predicts that polygyny would be more prevalent in areas where male quality or habitat is heterogeneous. Studies involving bobolinks, a grassland bird species breeding in the northern United States and wintering on rice plantations in Argentina, have shown that polygyny is more common in habitats with heterogeneous distributions of grasshoppers, Lepidoptera and sawfly larvae, and herbaceous cover (Martin 1971, Wittenberger 1980). Differing spatial patterns of predation have also been associated with increased polygyny in populations of great reed warblers (*Acrocephalus arundinaceus*) (Hansson et al. 2000).

Assuming polygyny occurs under heterogeneous conditions, Emlen and Oring (1977) predicted that monogamy should occur in homogeneous habitats. However, Wootton et al. (1986) and Hartley and Shepherd (1995) documented some polygyny in homogeneous habitats, which could not be explained by the Polygyny Threshold Hypothesis. To account for the occurrence of polygyny in homogenous habitats, they proposed the Random Female Settlement Hypothesis. This hypothesis states that females are on a limited time budget upon arrival on the nesting grounds. Because of this limitation, females do not have the time or energy to assess every mating situation (i.e., habitat and male quality) that is available to

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them (Alatalo et al. 1988, Slagsvold et al. 1988). Therefore, polygyny arises due to lack of information by females (Wootton et al. 1986).

It has been suggested that a female might pair with the first male that she encounters due to time constraints (O’Donald 1980, Parker 1983). Therefore, males best able to signal their presence to females might attract more females (Dale and Slagsvold 1990). Males attract females by song (Eriksson and Wallin 1986), flight display (Mather and Robertson 1992), plumage color (Slagsvold and Lifjeld 1988), and defending large territories (Lightbody and Weatherhead 1987, Dale and Slagsvold 1990, Hartley and Shepherd 1995). Thus, the Random Female Settlement Hypothesis predicts that the most visible males with the largest territories should attract the most females.

Perching sites might increase a male’s visibility during song and before or after flight display. They also might allow males to see competitors easier, which would allow them to defend larger territories. Bobolinks and several other grassland bird species use both human-made structures and natural vegetation for perching (Wiens 1969, Harrison 1977, Knodel montz 1981, Vickery and Hunter 1995). Following the Random Female Settlement Hypothesis, males with perching sites on their territories should attract more females.

We manipulated the number of perch sites to examine the mating dynamics of a population of bobolinks, in order to understand the male and female reproductive strategies of this species. Our specific objectives were to examine how 1) territory size, 2) perching sites, 3) predation rate, 4) insect abundance, and 5) vegetation composition and structure affected the use of territories and reproductive success of bobolinks.

Methods

Field Methods

The study took place on a 35-ha field in the Pend Oreille River Valley of the Kalispel Indian Reservation in northeast Washington State (48° 22’ latitude, 117° 19’ longitude) during May-July of 2003. The field is bordered by the river, a railroad track, or stands of black cottonwood (*Populus trichocarpa*) or Douglas hawthorn (*Crataegus douglasii*) and is bisected by Trimble Creek (Figure 1). It is harvested annually in mid-July for timothy hay (*Phleum pratense*).

Male territories were mapped by the “flush” technique (Wiens 1969). Territory sizes of individual males were calculated by using a global position satellite unit and ArcView 3.2 (Environmental Systems Research Institute 1999).

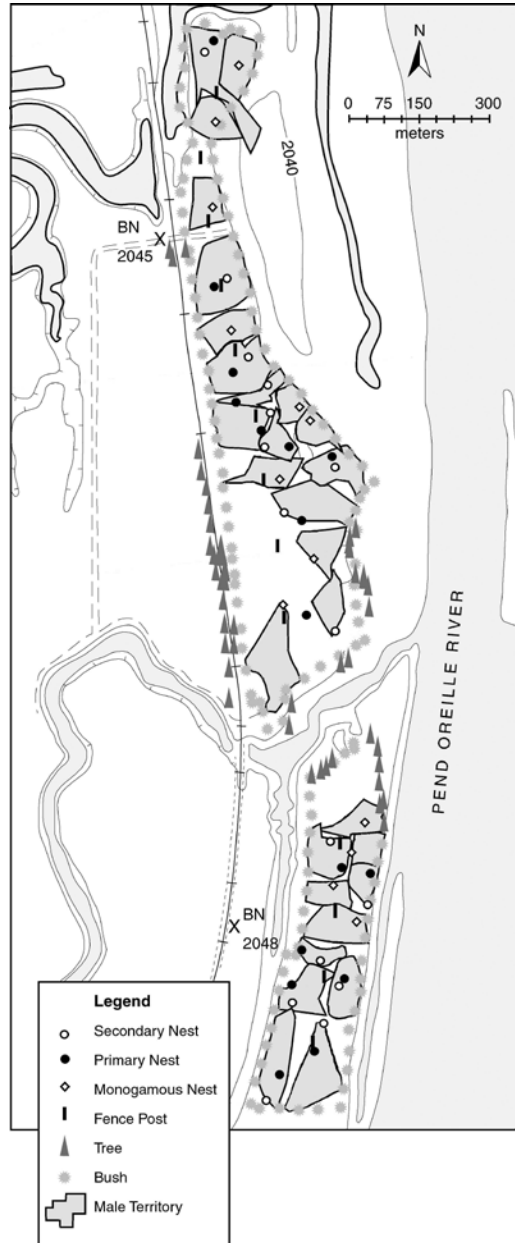


Figure 1. Bobolink male territories and nest locations on the study site in the Pend Oreille River Valley of northeast Washington State during May-July 2003. Base map taken from USGS DRG o48117d3 1:24000.

Before females arrived, 1.5 m fence posts were spaced 140 m apart in a row through the field to serve as artificial perches. A total of 13 posts was placed in the field (Figure 1). The top of each post was approximately 0.5 m above the grass, and the location of the first post was placed 140 m from the south edge of the field. Males have an average territory size of 0.72 hectares (Martin 1971, 1974; Wittenberger 1978); therefore, about half of the territories did not contain these artificial perches.

Nests were located by watching females return to them with nesting material or food items and by flushing females from nests. Once a nest was found, its location was plotted on a field map and recorded using a global position satellite unit. Distances from each nest to the edge of the field were calculated using Mapsource 3.02 (Garmin International 1999).

Each nest was monitored three times a week for predation and nestling development. Nestlings were categorized into four developmental stages: hatchling, nestling without feathers, nestling with feathers, and fledgling. Predation was defined by the loss of eggs, loss of nestlings before fledging, or destruction of the nest by predators. When a nest was predated, the number of eggs or nestlings lost was recorded.

Food sampling began during incubation (1 June) and continued until most of the nestlings fledged on the study site (2 July). Two non-overlapping transects were placed in each male's territory. Each transect was sampled four times during the nesting season, and a 38-cm sweep net was used to sample caterpillars, sawfly larvae, and grasshoppers. Fifty sweeps of the net were done along each transect (Wittenberger 1980). The total number of both larvae and grasshoppers caught in the net for each transect was recorded. The numbers of larvae and grasshoppers were summed for each territory during the season. To record what food items females and males were bringing to nestlings, a video camera was placed at five different nests for a period of one hour each.

Vegetation was sampled on the study site from 3 July to 17 July after most of the young had fledged, to minimize disturbance, and before hay harvest. Ten evenly spaced points, referred to as "territory" vegetation, were chosen in each male's territory for vegetation sampling. Vegetation was also measured and recorded at a sampling point immediately adjacent to each nest site, referred to

as "nest" vegetation. At each "nest" and "territory" sampling point, a 20 X 50-cm frame (Daubemire 1959) was used to estimate the percentage cover class of: sedge (*Carex sp.*), foxtail (*Alopecurus pratensis*), other grasses, and other herbaceous plants. Total cover, bare ground, and litter cover were similarly categorized. Three height measurements of the tallest vegetation were taken in each plot.

Statistical Analysis

We used two-tailed t-tests to compare the area, perimeter, amount of edge habitat, caterpillar numbers, and vegetation parameters between monogamous and polygynous territories. Females were categorized as monogamous, primary (first female to settle on a polygynous territory), or secondary (second female to settle on a polygynous territory). Nest initiation dates were back calculated using nestling hatching dates. Simple linear regression was used to examine the relationships between territory size and nest initiation date and between number of perching sites and nest initiation date.

We compared "nest" and "territory" vegetation characteristics using two-tailed t-tests and confirmed the results of the t-tests using logistic regression to differentiate between "nest" and "territory" vegetation. We used simple linear regression to examine the effect of "nest" vegetation characteristics on nest success.

Microsoft Excel 2000 (Microsoft Corporation 1999) and Statistical Analysis System (Statistical Analysis System Institute 2003) were used for statistical tests. The level of significance for all tests was $P = 0.05$.

Results

We located 29 territories and 48 nests on the study site (Figure 1). All nests (monogamous, primary, and secondary) were located at least 50 m away from the edge of the field. Of the 29 males, 16 were polygynous and 13 were monogamous. All 16 polygynous males attracted two females. Twenty-three males paired with a female before secondary females began settling. Therefore, six males had not attracted their first female before secondary females began settling. Four of these males were located near large stands of cottonwood trees. Three of the four males nesting near cottonwood trees only attracted one female. The

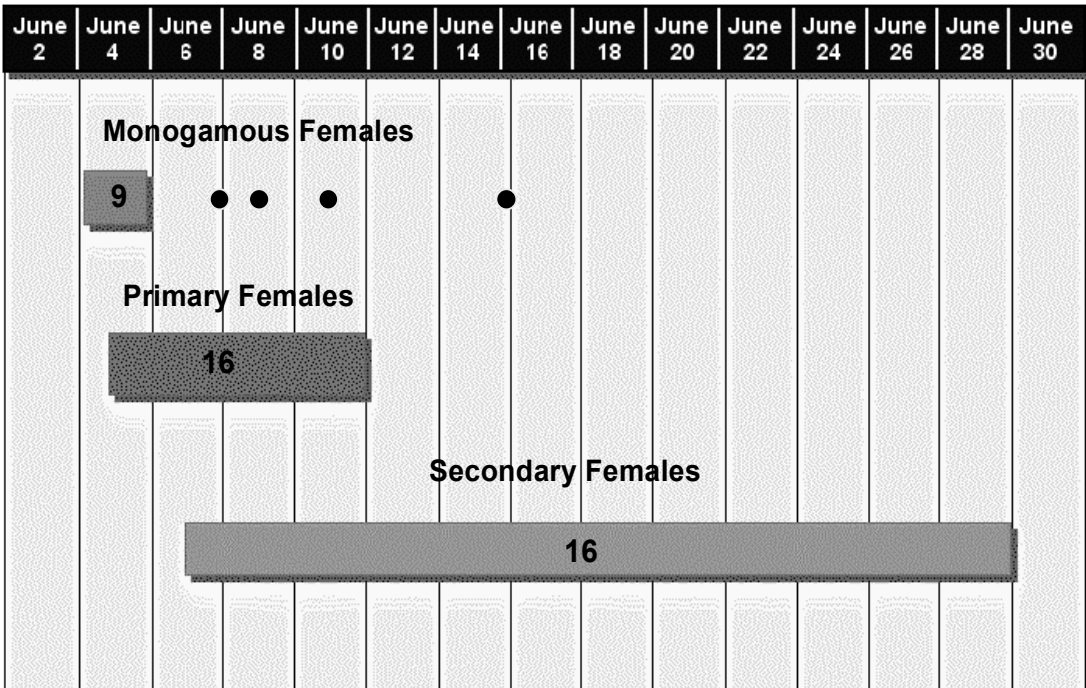


Figure 2. Nest initiation dates of monogamous, primary, and secondary female bobolinks located on the study site in the Pend Oreille River Valley of northeast Washington State during June 2003. Numbers within each block indicate the number of females nesting during the time period. Single dots represent one female.

fourth male was the last one on the study site to attract a secondary female. During the incubation period, we observed primary and secondary females following each other around the field. On several occasions, we saw secondary females follow primary females to their nests.

Nine of the 13 monogamous females initiated nests before 11 of the primary and all secondary females (Figure 2). Three of the four monogamous females that initiated nests later were on territories located next to large cottonwood stands. Nest initiation date was positively correlated with both the area of the territory ($P = 0.04$; $r = 0.34$) and the number of fence posts ($P = 0.008$; $r = 0.43$), indicating that a later arriving female settled these territories.

Although the area ($12,881 \pm 1,346 \text{ m}^2$) and perimeter ($428 \pm 32 \text{ m}$) of polygynous territories were larger than the area ($9,594 \pm 817 \text{ m}^2$) and perimeter ($346 \pm 18 \text{ m}$) of monogamous territories, the differences were not significant. Perching sites for males included Douglas hawthorn bushes that bordered the edges of the field and the fence posts we placed in the field. The territories of all

but one polygynous male abutted the edge of the field (Figure 1). Although the amount of edge of territories of polygynous males ($81.2 \pm 13.6 \text{ m}$) was greater than that of monogamous males ($68.8 \pm 11.8 \text{ m}$), the difference was not significant. Of the territories with fence posts, approximately 64% were held by polygynous males and 36% were held by monogamous males.

Eggs from only two of the 48 nests disappeared between nest surveys and no sign of predation, such as eggshells, was apparent at either nest. Both nests belonged to secondary females, and one of the females re-nested a week later on the same territory. Therefore, nest predation was not a factor at this site.

During the nesting season, we saw males and females bringing only caterpillars to nestlings. Video surveillance of six nests during breeding season showed that nestlings were exclusively fed caterpillars; therefore, we compared only caterpillar abundance between territories. Monogamous territories had significantly more caterpillars ($\bar{x} = 15.7 \pm 1.8/\text{sweep}$) than polygynous ones ($\bar{x} = 10.1 \pm 0.7/\text{sweep}$; $t = 2.34$; $df = 9$; $P = 0.02$).

Comparing the “territory” vegetation, the average percent herbaceous cover was greater and grass height was taller on monogamous than polygynous territories (Table 1). Compared to the vegetation across the entire territory, “nest” vegetation was characterized by higher herbaceous, total, and litter cover; less bare ground; and lower grass height (Table 2). Herbaceous cover was negatively correlated with grass height ($P = 0.001$; $r = -0.21$). Stepwise logistic regression ($P = 0.089$; total $r^2 = 0.12$) indicated that variance between “territory” and “nest” could best be explained by total coverage ($P < 0.001$; $r^2 = 0.05$), litter coverage ($P < 0.001$; $r^2 = 0.04$), and herbaceous coverage ($P < 0.001$; $r^2 = 0.03$).

On average, polygynous males fledged 7.5 ± 0.4 young, whereas monogamous males fledged 4.7 ± 0.3 young. Although the number of eggs laid was similar between females of different mating

TABLE 1. The average (\pm SE) percent coverage and grass height (cm) of “territory” vegetation on monogamous and polygynous bobolink territories located in the Pend Oreille River Valley of northeast Washington State in July 2003. NS denotes a non-significant resulting P -value. Degrees of freedom = 99.

	Monogamous	Polygynous	P -value
Sedge	0.05 ± 0.05	0.20 ± 0.14	NS
Foxtail	13.8 ± 2.3	12.2 ± 1.0	NS
Other Grass	61.3 ± 1.2	59.8 ± 0.8	NS
Herbaceous	17.4 ± 0.8	12.8 ± 0.5	0.05
Total	84.2 ± 0.5	80.6 ± 0.5	NS
Litter	83.2 ± 0.8	83.4 ± 0.8	NS
Bare Ground	29.8 ± 0.9	24.4 ± 1.1	NS
Grass Height	102.9 ± 2.6	99.6 ± 1.1	0.007

TABLE 2. The average (\pm SE) percent coverage and grass height (cm) of “territory” and “nest” vegetation located in the Pend Oreille River Valley of northeast Washington State in July 2003. NS denotes a non-significant resulting P -value. Degrees of freedom = 45.

	Territory	Nest	P -value
Sedge	0.15 ± 0.07	0.0 ± 0.0	NS
Foxtail	12.8 ± 1.1	16.8 ± 2.9	NS
Other Grass	60.5 ± 0.7	65.8 ± 2.2	NS
Herbaceous	14.6 ± 0.3	24.2 ± 1.7	0.003
Total	82.0 ± 0.3	92.2 ± 0.5	< 0.001
Litter	83.4 ± 0.6	95.7 ± 1.4	< 0.001
Bare Ground	26.5 ± 0.9	14.2 ± 2.0	0.009
Grass Height	101.0 ± 1.0	97.9 ± 2.3	0.04

TABLE 3. The average (\pm SE) nesting metrics of monogamous, primary, and secondary female bobolinks located in the Pend Oreille River Valley of northeast Washington State in 2003.

	Monogamous	Primary	Secondary
Nest Initiation Date	4 June	7 June	14 June
Number of Eggs	5.8 ± 0.2	5.9 ± 0.2	5.5 ± 0.2
Number Hatched	5.3 ± 0.3	5.3 ± 0.3	4.2 ± 0.5
Percent Hatched	92.8 ± 3.7	90.4 ± 4.1	76.8 ± 9.4
Number Fledged	4.7 ± 0.3	4.2 ± 0.5	3.2 ± 0.6
Percent Fledged of Eggs	83.5 ± 4.6	70.8 ± 8.2	63.1 ± 10.8
Percent Fledged of Hatched	90.1 ± 3.3	80.3 ± 8.8	80.5 ± 8.9

status, monogamous females successfully fledged more young than primary or secondary females (Table 3). The number of young fledged from a nest was positively correlated with herbaceous cover over the nest ($P = 0.05$; $r = 0.30$). No other “nest” vegetation characteristics were significantly correlated with number of fledglings.

Discussion

The differences between nest selection and fledgling success of the first-arriving, monogamous females and later-arriving, polygynous females suggest that neither the Polygyny Threshold nor the Random Female Settlement Hypothesis fully accounts for settlement patterns observed in these bobolinks. In addition, differences between nest success of monogamous and polygynous females and males suggest that these female and male bobolinks have different reproductive strategies.

Females arrived on the study site in three distinct waves with minimal overlap. The first wave consisted of females who became monogamous nesters, followed by primary and a few monogamous females, and then secondary females. The monogamous females that settled in the second wave nested on territories located next to dense stands of cottonwood trees. Stands of trees have been shown to inhibit bobolink settlement (Sample 1989, Helzer 1996), explaining why these three territories were settled later and did not attract secondary females. The Polygyny Threshold Hypothesis states that the settlement date of a territory is an important indicator of territory quality (Verner 1964, Verner and Willson 1966, Orians 1969). Indeed, the bobolink territories

that were settled first were of higher quality (i.e., high total, herbaceous, and litter coverage and high caterpillar numbers) than those settled later. However, in contrast with the Polygyny Threshold Hypothesis that predicts that first-settled territories should be polygynous (Martin 1971, Wittenberger 1980), we observed that these territories were monogamous.

Based on the differences in “nest” versus “territory” vegetation, it appeared that females selected high herbaceous, total, and litter coverage for nest sites. Herbaceous plants are associated with high densities of caterpillars (Jones 1963, Wittenberger 1980), which are the primary food of nestlings (Wittenberger 1978, 1980). Herbaceous plants also provide greater cover (Bollinger 1988, 1995), which might be critical for maintaining the temperature and concealment of nests (Pleszczynska 1978). Therefore, herbaceous coverage appeared to be a critical selection component of a territory in this study and other studies (Martin 1971, Wittenberger 1980). This type of nest habitat was distributed in patches throughout the field.

The first wave of females (monogamous females) might have selected habitat patches in small territories to minimize the likelihood that the male would mate polygynously. The second wave of females (primary females) nested with the remaining, unmated males on large territories. Finally, the last wave of females (secondary females) mated polygynously on large territories due to limited suitable nesting habitat.

Our observations of females following other females have not been noted in previous studies of bobolinks. Female interactions have been shown to contribute to polygyny in red-winged blackbirds (*Agelaius phoeniceus*), as Hurley and Robertson (1985) removed females from harems and found that more females settled on those territories. This suggests that females on a territory might prevent others from settling or that females looking for a territory assess the number of females on a territory before settling.

Bobolink males divide their time feeding nestlings at both the primary and secondary nests (Wittenberger 1978, 1980). This behavior could explain why monogamous females on our study site were more successful in fledging young than primary females. However, the earlier settling date of monogamous females could also account for the slight difference, because nest success

declines with later nest initiation (Alatalo et al. 1988, Slagsvold et al. 1988).

Polygynous females might be compensated for loss of exclusive paternal care by mating with a genetically superior male, thereby increasing the likelihood of their progeny’s survival and ability to produce offspring (Alatalo and Lundberg 1986). In pied flycatchers (*Ficedula hypoleuca*), polygynous males parented offspring who were more likely to survive into the next nesting season (Both 2002). According to the Polygyny Threshold Hypothesis, under heterogeneous male conditions, the genetically superior males should be selected first and become polygynous. In contrast, we observed that the first wave of females selected males that did not become polygynous.

It is possible that territory and male selection are separate choices for females. Bollinger and Gavin (1991) observed that 38% of nests contained at least one nestling that was sired from extra-pair fertilizations, suggesting that cheating is prevalent in bobolinks, and females are not restricted to mate with the male of the territory on which they settle. Thus, monogamous females could still mate with polygynous males and thereby gain the genetic advantage documented by Both (2002). Therefore, the best strategy for a female might be to nest on a monogamous male’s territory and cheat with a polygynous male.

To achieve this strategy, a female should arrive early on the nesting grounds. Early arrival allows the monogamous female to 1) select a male that defends a small, suitable territory and will contribute full paternal care, 2) monitor later-arriving females, and 3) maintain options to cheat with other males. Later-arriving primary females must select the remaining, large territories. Both the size of these territories and the later arrival date make it more difficult for primary females to monitor other females that might potentially nest on these large territories. Finally, secondary females arrive last and are limited by time and space. They resort to settling on the large territories with a highly visible male.

Mating polygynously maximized a male’s reproductive success. The best strategy for a male to become polygynous is to defend a large, albeit heterogeneous, territory with additional perches, from which to signal their presence to females and increase their chances of attracting more than one female. This enhanced visibility might also

provide polygynous males with more cheating opportunities with monogamous females.

Male and female bobolinks had very different reproductive strategies. In accordance with The Polygyny Threshold Hypothesis, 1) the first two waves of females (monogamous and primary females) either mated or attempted to mate monogamously, 2) the first wave of females (monogamous females) was the most reproductively successful, and 3) the overall highest quality territories were selected by the first wave of females. However, our results differ in that the first wave of females selected males that did not become polygynous. The Random Female Settlement Hypothesis appeared to explain the settlement of the third wave of females (secondary females). Thus, it appears that female settlement is very complex, and one hypothesis may not explain the settlement of each wave of females on the nesting grounds.

Literature Cited

- Alatalo, R. V., A. Carlson, and A. Lundberg. 1988. The search cost in mate choice of the pied flycatcher. *Animal Behaviour* 36:289-291.
- Alatalo, R. V., and A. Lundberg. 1986. The sexy son hypothesis: data from the pied flycatcher *Ficedula hypoleuca*. *Animal Behaviour* 34:1454-1462.
- Bollinger, E. K. 1988. Breeding dispersion and reproductive success of bobolinks in an agricultural landscape. Ph.D. Dissertation, Cornell University, Ithaca, New York.
- Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. *The Auk* 112:720-730.
- Bollinger, E. K., and T. A. Gavin. 1991. Patterns of extra-pair fertilizations in bobolinks. *Behavioral Ecology and Sociobiology* 29:1-7.
- Both, C. 2002. Fitness costs of polygyny in female Pied Flycatchers *Ficedula hypoleuca*. *Ardea* 90:129-138.
- Dale, S., and T. Slagsvold. 1990. Random settlement of female pied flycatchers, *Ficedula hypoleuca*: significance of male territory size. *Animal Behaviour* 39:231-243.
- Daubemire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Eriksson, D., and L. Wallin. 1986. Male bird songs attract females: a field experiment. *Behavioral Ecology and Sociobiology* 19:297-299.
- Environmental Systems Research Institute. 1999. ArcView geographic information systems (3.2). Environmental Systems Research Institute Incorporated, Redlands, California.
- Faaborg, J. 1988. *Ornithology: An Ecological Approach*. Prentice-Hall Incorporated, Englewood Cliffs, New Jersey.

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- Garmin International. 1999. MapSource (3.02). Garmin International Incorporated, Olathe, Kansas.
- Hansson, B., S. Bensch, and D. Hasselquist. 2000. Patterns of nest predation contribute to polygyny in the Great Reed Warbler. *Ecology* 81:319-328.
- Harrison, K. G. 1977. Perch height selection of grassland birds. *Wilson Bulletin* 89:486-487.
- Hartley, I. R., and M. Shepherd. 1995. A random female settlement model can explain polygyny in the corn bunting. *Animal Behaviour* 49:1111-1118.
- Helzer, C. J. 1996. The effects of wet meadow fragmentation on grassland birds. M.S. Thesis, University of Nebraska, Lincoln, Nebraska.
- Hurley, T. A., and R. J. Robertson. 1985. Do female Red-winged Blackbirds limit harem size? I. A removal experiment. *The Auk* 102:205-209.
- Jones, R. I. 1963. Identification and analysis of lesser and greater prairie chicken habitat. *Journal of Wildlife Management* 27:757-778.
- Knodel montz, J. J. 1981. Use of artificial perches on burned and unburned tallgrass prairie. *Wilson Bulletin* 93:547-548.
- Lightbody, J. P., and P. J. Weatherhead. 1987. Polygyny in the yellow-headed blackbird: female choice versus male competition. *Animal Behaviour* 35:1670-1684.
- Martin, S. G. 1971. Polygyny in the bobolink: habitat quality and the adaptive complex. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.
- Martin, S. G. 1974. Adaptations for polygynous breeding in the bobolink, *Dolichonyx oryzivorus*. *American Zoologist* 14:109-119.
- Mather, M. H., and R. J. Robertson. 1992. Honest advertisement in flight displays of bobolinks (*Dolichonyx oryzivorus*). *The Auk* 109:869-873.
- Microsoft Corporation. 1999. Microsoft excel 2000 (9.0). Microsoft Corporation, Redmond, Washington.

- O'Donald, P. 1980. Genetic Models of Sexual Selection. Cambridge University Press, Cambridge, Massachusetts.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589-603.
- Parker, G. A. 1983. Mate Quality and Mating Decisions. Cambridge University Press, Cambridge, Massachusetts.
- Pleszczyńska, W. K. 1978. Microgeographic prediction of polygyny in the lark bunting. *Science* 201:935-936.
- Sample, D. W. 1989. Grassland birds in southern Wisconsin: habitat preference, population trends, and response to land use changes. M.S. Thesis, University of Wisconsin, Madison, Wisconsin.
- Slagsvold, T., and J. T. Lifjeld. 1988. Plumage colour and sexual selection in the pied flycatcher *Ficedula hypoleuca*. *Animal Behaviour* 36:395-407.
- Slagsvold, T., J. T. Lifjeld, G. Stenmark, and T. Breiehagen. 1988. On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Animal Behaviour* 36:433-442.
- Statistical Analysis System Institute. 2003. Statistical analysis system (8.2). Statistical Analysis System Institute Incorporated, Cary, North Carolina.
- Verner, J. 1964. The evolution of polygamy in the long-billed marsh wren. *Evolution* 18:252-261.
- Verner, J., and M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-147.
- Vickery, P. D., and M. L. Hunter. 1995. Do artificial song-perches affect habitat use by grassland birds in Maine? *American Midland Naturalist* 133:164-169.
- Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological Monographs* 8:1-93.
- Wittenberger, J. F. 1978. The breeding biology of an isolated bobolink population in Oregon. *Condor* 80:126-137.
- Wittenberger, J. F. 1980. Vegetation structure, food supply, and polygyny in bobolinks (*Dolichonyx oryzivorus*). *Ecology* 6:140-150.
- Wootton, J. T., E. K. Bollinger, and C. J. Hibbard. 1986. Mating systems in homogeneous habitats: The effects of female uncertainty, knowledge costs, and random settlement. *The American Naturalist* 128:499-512.

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