

BOBOLINK POLYGyny IN A HOMOGENEOUS HABITAT: A TEST OF THE ASYNCHRONOUS SETTLEMENT MODEL

The polygyny threshold model (Verner 1964; Verner and Willson 1966; Orians 1969) proposes that polygyny in territorial species of animals should occur under conditions in which the benefits of nesting in a high-quality breeding situation (territory quality, male quality, or both) outweigh the costs of sharing a mate with other females (e.g., reduced male parental care, competition for resources on the territory, increased predator attraction). Recently, Leonard (1990) proposed an alternative hypothesis (not mutually exclusive) concerning polygyny, the asynchronous settlement model. This hypothesis suggests that the costs of nesting polygynously can be reduced or avoided, which thereby increases the chances of polygyny, if females nest asynchronously within a territory. In the case of complete asynchrony (i.e., serial polygyny of Emlen and Oring 1977), females choosing territories late in the breeding season should assess both monogamous breeding situations and breeding situations in which other females have previously nested as equivalent, because the costs of polygyny are reduced or absent once previous females and their young have left the territory. In other words, although the territorial male mates polygynously, females nesting asynchronously on his territory breed monogamously from their point of view. Under these conditions, females may arbitrarily choose to nest on a territory with a bachelor or a previously mated male, particularly when territories have similar qualities. In long-billed marsh wrens (*Cistothorus palustris*), Leonard (1990) found an increase in fledging weight with increasing nest asynchrony, and Leonard and Picman (1987) found that the intervals between first-egg dates of sequentially nesting females were greater within territories than between territories.

In a previous article, we examined several potential hypotheses to explain the occurrence of polygyny in a bobolink (*Dolichonyx oryzivorus*) population nesting in a homogeneous hayfield in central New York (Wootton et al. 1986). We found no evidence that females followed the polygyny threshold model when choosing breeding situations, nor did we find any evidence supporting an alternate hypothesis that neutral female choice in conjunction with differential competitive abilities among males produces polygyny (Monahan 1977; Lightbody and Weatherhead 1987; Dale and Slagsvold 1990). We found instead that female nesting patterns closely followed distributions expected under a hypothesis that females settle randomly with respect to each other or a number of habitat characteristics. We suggested that under some circumstances polygyny might occur through random female settlement because of errors in territory assessment, unpredictable variation in reproductive success, limitations of rules of thumb that birds might use to choose territories, and costs of territory assessment.

The asynchronous settlement model provides an appealing alternative to the random settlement hypothesis in this bobolink population because it is consistent with many of the patterns we found (i.e., polygyny in an apparently homogeneous situation, no correlations between polygyny and breeding situation quality, and territory choices apparently made to some extent independently of what other females do). For this reason, we tested whether bobolinks in this population followed the asynchronous settlement model by testing several predictions that distinguish the asynchronous settlement model from a model of random female settlement. First, the asynchronous settlement model predicts a selective advantage to those females that nest asynchronously, whereas the random settlement model does not. Therefore, the degree of nest asynchrony within a territory should enhance the mean reproductive success on that territory, especially in a homogeneous field. Second, the asynchronous settlement model predicts that females choose territories that increase nest asynchrony, whereas the random model does not. Therefore, pairs of females within territories should nest more asynchronously than expected for pairs of females randomly chosen from the population as a whole.

METHODS

We conducted the study on a 19-ha upland hayfield 6.4 km south of the Cornell University Biological Field Station near Bridgeport, New York, during all of the 1984 and 1986 nesting seasons and a portion of the 1985 nesting season (prior to field mowing). We captured 51 of 53 (96%) territorial males in 1984, 44 of 47 (94%) in 1985, and all 30 (100%) in 1986. Fifty-four of 56 (96%) nesting females were marked in 1984, 54 of 59 (92%) in 1985, and 39 of 41 (95%) in 1986. We marked individual birds with unique combinations of colored leg bands and painted tail stripes. Nests were found and mapped with the aid of poles placed in 50 × 50-m grids throughout the field. Nesting dates, clutch sizes, fledging success, and fledgling weights (1984 only) were recorded. Because the high percentage of marked individuals in the population allowed us to identify birds with undiscovered nests, we believe that we found all or nearly all of the nests in the population. Male territory boundaries were mapped using a combination of Wiens's (1969) "flush" technique and passive observation. A description of the study site and methods is presented in more detail elsewhere (Wootton et al. 1986; Bollinger 1988). Females were assigned mates based on which male fed at the nest or which territory contained the nest if we did not observe male feeding. However, this assignment did not perfectly reflect male reproductive success, because some bobolink nests contain young of multiple paternity (Gavin and Bollinger 1985; Bollinger and Gavin 1991).

The degree of asynchrony was defined simply as the number of days between first-egg dates (i.e., the date on which the first egg of a clutch was laid) of pairs of nests. First-egg dates are appropriate measures to use here because they can be determined objectively for all nests that we observed and because they directly reflect nesting asynchrony. (See Stutchbury and Robertson 1987 and Teather et al. 1988 for a discussion of the reliability of different measures of temporal patterns of female territory choice and nest initiation.)

TABLE 1
RESULTS OF REGRESSIONS OF NEST ASYNCHRONY ON FLEDGING SUCCESS

Regression Model and Population Used	Slope*	SE	P
Simple regression:			
All females ($n = 53$)	-.07	.04	>.5
Early females ($n = 27$)	-.08	.06	>.5
Late females ($n = 26$)	-.08	.07	>.5
Multiple regression with seasonal effects:			
All nests:			
All females ($n = 53$)	-.06	.04	>.5
Early females ($n = 27$)	-.08	.06	>.5
Late females ($n = 26$)	-.02	.08	>.5
Nests fledging ≥ 1 young:			
All females ($n = 39$)	-.02	.03	>.5
Early females ($n = 21$)	-.06	.03	>.5
Late females ($n = 18$)	-.04	.03	>.5

* All slopes are of signs opposite to those predicted by the asynchronous settlement model.

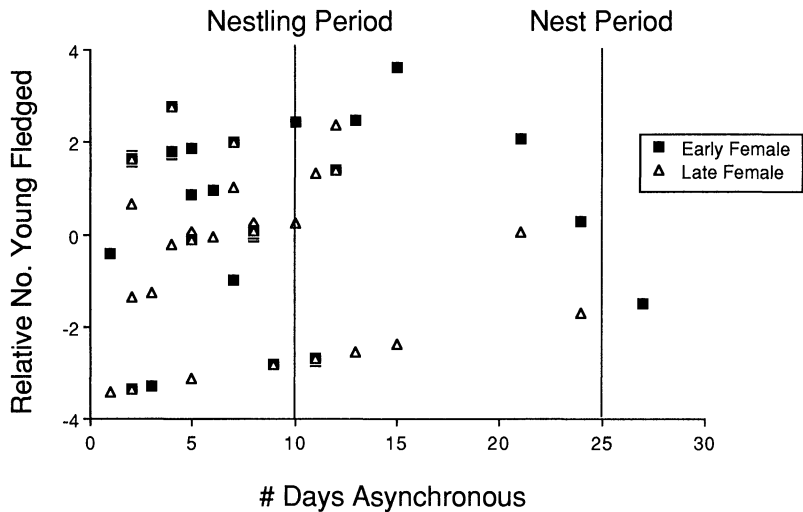


FIG. 1.—Fledging success adjusted for seasonal effects as a function of the difference in nest initiation date (e.g., first-egg date) between pairs of female bobolinks on polygynous territories. Data are from the 1984–1986 nesting seasons and include complete nest failures resulting from predation. *Solid squares* and *open triangles* represent the earlier- and later-nesting female of a pair, respectively. Multiple observations at a point are represented by *bars* or *partial triangles*. The average length of time taken from hatching to fledging and from the first egg laid to fledging is designated by *vertical lines*.

To test whether nesting asynchronously conferred a reproductive advantage, we related the number of young fledged from each nest in polygynous territories to the degree of nesting asynchrony using linear regression. Because fledging success declines seasonally in our population (Wootton et al. 1986), we also used multiple regression to determine the relationship between fledging success and nest asynchrony independent of time during the breeding season. Nests lost as mowing casualties in 1985 were excluded from the analysis. We also used linear regression to look for a positive relationship between mean fledgling weight and nest asynchrony, because fledgling weight can correlate with fledgling survival in some species (Perrins 1965; Howe 1976; Garnett 1981; Drent 1984; Nur 1984; Brown and Brown 1986). Significance for all regressions was assessed using one-tailed tests because the asynchronous settlement model predicts a specific (positive) relationship between nest asynchrony and measures of fledging success.

To determine whether birds on the same territory nested more asynchronously than expected in a random hypothesis, we compared nesting asynchrony between pairs of females in polygynous territories (i.e., territories containing more than one nesting female during the breeding season) relative to that expected between randomly chosen pairs of females using Monte Carlo techniques. To derive the distribution of asynchrony expected at random between a pair of females, we first assigned individual females in the population a number. We then randomly chose numbers corresponding to females from each nesting population using a uniform distribution to form 200 female pairs. Females paired with themselves were excluded. Then, using the observed first-egg dates for each individual female, we obtained a distribution of differences in observed first-egg dates between randomly drawn pairs to use as the expected distribution of nest asynchrony if females had settled at random. This distribution was then compared to the distribution of differences in first-egg dates between pairs of polygynous females on the same territory using a Kolmogorov-Smirnov two-sample test between cumulative frequency distributions (Sokal and Rohlf 1981). Two such tests were performed: one for the 1984 season and another for the 1986 season. We did not test for asynchrony in the 1985 population because of the potential confounding effects of field mowing before the breeding season was completed. If the differences between distributions were deemed significant, the asynchronous settlement model, rather than a random settlement model, was supported.

RESULTS

Fledging success did not increase with increasing time between nest initiation on polygynous territories, whether early females, later females, or all females were considered (table 1) (all $P > .5$). Fledging success was, if anything, negatively associated with increasing nest asynchrony (table 1; fig. 1), regardless of whether or not we used a regression model that accounted for the effects of first-egg date on fledging success and whether or not we included nests that had completely failed as a result of predation. Fledgling weight also did not increase with increasing time between nest initiation on polygynous territories (slope =

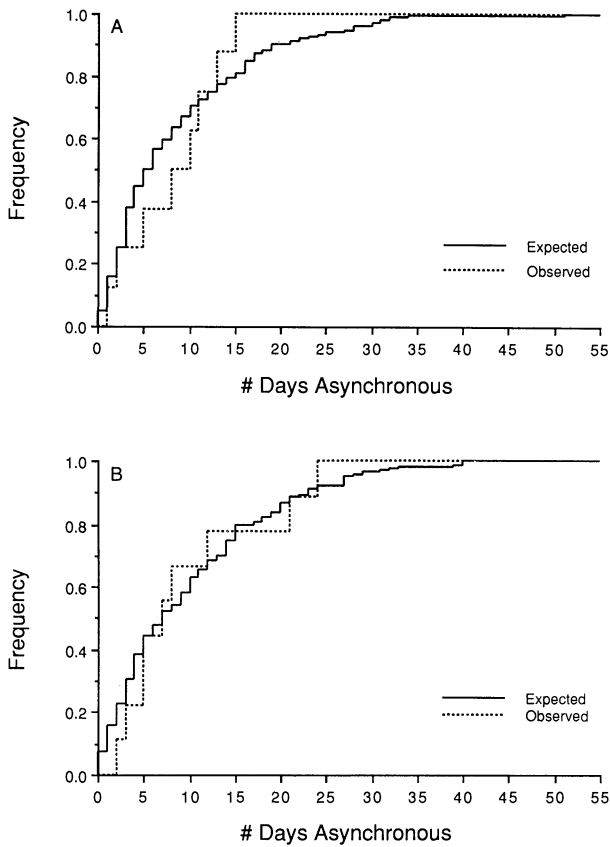


FIG. 2.—Cumulative frequency distribution of the number of days between initiation of pairs of nests. *Solid line*, expected distribution from a sample of 200 randomly chosen female pairs. *Dashed line*, observed distribution of female pairs from polygynous territories. A, 1984 nesting season; B, 1986 nesting season. The observed distributions do not differ significantly from random (Kolmogorov-Smirnov tests, $P > .4$).

0.38, SE = 0.28, $P > .1$), nor did relative fledgling weight increase with nesting date held constant (slope = 0.06, SE = 0.24, $P > .4$).

The distribution of differences between nest initiation dates of female pairs within polygynous territories (1984, $\bar{X} = 8.12 \pm 5.08$ d, $n = 8$; 1986, $\bar{X} = 9.7 \pm 7.87$ d, $n = 9$) did not deviate significantly from that expected under a random hypothesis (fig. 2) (random pairs of females: 1984, $\bar{X} = 8.52 \pm 8.53$, $D = 0.22$, $P > .4$; 1986, $\bar{X} = 9.84 \pm 9.12$, $D = 0.16$, $P > .4$). Indeed, the observed means were slightly smaller than expected at random, which indicated that our failure to find a wider spread of nest initiation dates within territories compared to randomly chosen female pairs was not simply the result of low statistical power.

DISCUSSION

Available evidence does not support the hypothesis that polygyny in our bobolink population was facilitated by asynchronous nesting. Females in polygynous situations neither nested more asynchronously than expected nor showed any increased reproductive success with increasing nest asynchrony. Furthermore, the asynchronous settlement model predicts increased polygyny in the territories with the earliest-nesting females because they provide the greatest opportunity for asynchronous nesting, but this pattern does not occur within our bobolink population (Wootton et al. 1986). Hence, females showed no evidence of preferentially choosing the territory that provided the greatest asynchrony at the time of settlement. Finally, if the observed levels of polygyny were purely the result of nest asynchrony, polygyny would not be expected until all territories were filled. However, 7%–12% of the territorial males remained bachelors throughout a breeding season, and when the first polygynous nest was initiated, 20%–72% of the territorial males were not mated. We therefore fail to find support for the asynchronous settlement model in our population. At this time, random settlement independent of other females still provides the most consistent explanation of polygyny in this population. As noted previously, only site fidelity both within this population (Wootton et al. 1986) and between populations (Bollinger 1988; Gavin and Bollinger 1988; Bollinger and Gavin 1989) appears to affect female settlement patterns in a nonrandom manner. However, this fidelity appears to be independent of the settling patterns of other females within a breeding season.

Nesting asynchronously may be of little value to individuals in this population. First, costs of being polygynous appear to be low (Wootton et al. 1986), whereas benefits of nesting asynchronously have not been detected. Additionally, the seasonal decline in nesting success (typical of many species of birds) reduces the chances that nesting delays, which might promote asynchrony, would be beneficial.

Although the asynchronous settlement model does not appear to hold in this population, the development of definitive tests is difficult (Altmann et al. 1977; Vehrencamp and Bradbury 1984; Davies 1989). For example, appropriate tests may be more complicated than those described above in many situations because differences in habitat quality may interact with the period between nest initiation to determine the breeding patterns in a population. In these situations, a stronger test might require comparing reproductive success and degree of polygyny in populations in which either settlement asynchrony is experimentally induced or habitat variation is controlled for statistically. In our population, which occurred in a very homogeneous field, we have found no evidence that the degree of polygyny or nesting success is affected by either our measures of habitat quality (Wootton et al. 1986) or the interval between nesting starts (see above). It seems unlikely that either factor plays an important role in promoting polygyny in our bobolink population without some evidence that mating patterns are nonrandomly associated with habitat characteristics and/or nesting asynchrony.

The recent development of alternate hypotheses to the polygyny threshold

model, such as the asynchronous settlement model, the neutral female choice/male competition model (Monahan 1977; Lightbody and Weatherhead 1987; Dale and Slagsvold 1990), and the site-fidelity hypothesis (Wootton et al. 1986; Yasukawa and Searcy 1986) suggest the likely possibility that breeding systems, such as polygyny, may have evolved for different reasons in different species. In fact, for some species, our understanding of the evolution of polygyny may be further promoted by separating the selective factors impacting components of breeding systems (e.g., nest site selection vs. mate choice by females). In any event, we feel that alternative hypotheses allow a more powerful investigation of breeding systems by providing explicit predictions that differentiate them from each other (see Searcy and Yasukawa 1989). We believe that their application to different populations will allow faster progress in assessing the factors affecting the evolution of breeding patterns.

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