lower halves were isolated, and many large fish were present. Unknown factors had led to different numbers of adult males in the two halves, which then caused a significant difference in the mean size of transforming males (25.18 mm for the lower pool, 21.91 for the upper pool [$t(31) = 2.80$, $P = .005$]).

The evolution of the social inhibition system can be understood in terms of individual fitness advantage. The courtship displays of these and other poeciliid males are highly conspicuous, and adult males are likely to be in greater danger of predation than juveniles are (*4, 9*). Since large poeciliid males are dominant over smaller ones (*5, 10, 11*) and enjoy a mating advantage (*11, 12*), it is probably a better strategy to delay maturation in the presence of adult males until reaching a size sufficient for dominance or until competing adults are removed by predation, rather than to mature at a small size in their presence.

These relationships may have secondary, but important, demographic consequences. The most obvious is that the system ensures a steady supply of adult males and tends to buffer the population against losses by predation. While populations suffering from heavy predation would have fewer adult males than predation-free populations, the differences would be less than expected in the absence of social inhibition. In addition, as Sohn has suggested for *Gambusia* populations (*13*), predation would lead to small adult males because of the reduction in the number of adult males present. Fewer and smaller males would leave more food available for reproduction by females, further buffering the population against the effects of predation.

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## Microgeographic Prediction of Polygyny in the Lark Bunting

Abstract. *Field experiments on breeding populations of lark buntings (*Calamospiza melanocorys*) in South Dakota support the hypothesis that polygyny is promoted by a high variance in quality among male territories. Among these birds protection of the nest site from solar radiation is the major indicator of quality: nestling survival was significantly correlated with nest-site cover, and experimental increase of shading resulted in higher reproductive success. Males with superior territories attracted two mates, whereas those with poor territories failed to attract any. Secondary females had fledging success at least equal to that of contemporaneous monogamous pairs. On the sole basis of a shading score for each territory, the mating status of males (polygynous, monogamous, or bachelor) was predicted accurately in new areas of Colorado and North Dakota before females arrived.*

Polygyny, the simultaneous bonding of one male with more than one female, is relatively rare in animal populations, having been reported only for various taxa of mammals and birds (*1*). The factors favoring the selection of this particular mating system are largely a matter of speculation. Most hypotheses suggested have been derived from avian systems that offer the best documented examples of this phenomenon (*2*). A currently favored hypothesis is that of Verner (*3*), later extended by Orians (*4*), which proposes that polygyny is selected over monogamy when the differences among male territories are such that females are better off mating with an already mated male on a good territory rather than with a bachelor on a poor one. I now report evidence from field experiments that supports this hypothesis.

Previous data collected on avian and mammalian polygynous mating systems appear contradictory and have been taken to either support (*5*) or refute (*6*) the Verner-Orians hypothesis. Those studies contrasted the reproductive success of females of different mating status throughout the entire reproductive season, hence the confusion. I focused on the comparison crucial to the hypothesis: contrasting the reproductive success of monogamous and secondary females mating synchronously.

To this end I studied breeding populations of lark buntings (*Calamospiza melanocorys*) among which I predicted polygyny (*7*). This was simply inferred from the heterogeneity of the habitat, the extreme color dimorphism, and the elaborate vocal displays, all well-known characteristics of this grassland finch.

The pair structure and reproductive success of lark buntings were studied from 1974 to 1976 in Hughes County, South Dakota, on a 4-hectare field of unevenly distributed alfalfa (*Medicago sativa*) and sparse grasses (*Stipa spartia, Agropiran smithii*). As males arrived on the breeding grounds, I determined both configuration and size of territories (Fig. 1) (*8*). Females arrived over a 9-day period, starting 1 week after the arrival of males. All breeding birds were color-banded to allow individual identification.

The first females to arrive mated monogamously with males holding territories. Among those arriving on days 5 and 6, some became secondary females of already mated males (*9*). The others mated monogamously, and so did all females arriving thereafter. About 20 percent of territorial males did not acquire any females throughout the season.

Female reproductive success is measured by the number of fledglings (Table 1). The results support the Verner-Orians hypothesis: among contemporaneous monogamous and secondary nests, in 23 of 35 possible comparisons (*10*) secondary females fledged as many as or more young than monogamous females (one-tailed sign test, $P < 0.05$).

In order to identify the factors determining the female's mating choice, features of both males and territories were tested for heterogeneity. I found no statistical differences (*11*) among bachelors, monogamists, and bigamists with respect to visual and acoustic characters such as body size, surface of the white wing patch (flashed during song-flight displays), and time spent singing. Thus the stimuli probably stem from the territories themselves. Most food for nestlings is obtained outside the territory;


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thus variation in the food available among territories should be of no importance to females. The major factors responsible for nestling mortality were heavy precipitation, extreme temperatures, and predation from garter snakes, blue racers, and ground squirrels. Therefore, the degree of cover at the nest site is likely to control female reproductive success. I thus predicted that the crucial factors favoring the occurrence of polygyny pertained to characteristics of cover.

I tested this hypothesis by measuring (*12*) (i) distance to the nearest alfalfa plant (on this field nests were always placed on the ground under this particular species), (ii) vertical density of foliage, and (iii) intensity of light (*13*) at 10 cm above the ground.

In a discriminant analysis with canonical variates, the first variate separated the sample points into three groups (*14*)—bigamous, monogamous, and bachelor territories. The single best discriminating variable was light (*15*). Light contours (*16*) over the field were superimposed on a map of male territories (Fig. 1). For each territory, light values, recorded randomly over the entire range, were correlated with those of the respective nest sites ($r = .85$, $P < .01$). The territories with two nesting females coincided with the lowest light contour values; that is, they offered the best protection from solar radiation. In contrast, territories that never acquired any females had the highest contour values. Consequently I hypothesized that female reproductive success would be determined by the intensity of solar radiation reaching the nest.

I measured illuminance at 36 nests on days of laying and recorded the number of young fledged per nest. As expected, there was a high correlation ($r = -.82$, $P < .01$) between the two variables. Moreover, since the illuminance at the ground level increases with the season as a result of drying and wilting vegetation, early nests must favor survival more than late nests. A multiple correlation analysis was performed on 44 nests among (i) daily illuminance at each nest; (ii) mortality of young measured daily; (iii) food availability (number of grasshoppers sampled randomly by sweeping method); (iv) day, starting with day 1; (v) daily average of the earliness of initiation index for all nests; and (vi) predation (number of snakes and ground squirrels found randomly within each territory). All partial correlation coefficients were significant ($P < .01$) with $r$ ranging from .76 to .94, except for the combinations including the food or predation variable. Thus, early nests did better because of better shading provided by nest cover rather than because of depleted food or increased predator pressure (*17*).

Table 1. Reproductive success (total number of young fledged from total number of eggs laid) of all nests initiated synchronously with secondary nests and that of secondary nests. There were no significant differences between groups within each year ($t$-test, $P > .05$).

| Year | Monogamous | | | Secondary | | |
|---|---|---|---|---|---|---|
| | Ratio | Proportion | Nests (No.) | Ratio | Proportion | Nests (No.) |
| 1974 | 11:21 | .5 | 5 | 6:12 | .5 | 3 |
| 1975 | 13:21 | .6 | 6 | 9:15 | .6 | 4 |
| 1976 | 18:29 | .6 | 7 | 10:16 | .6 | 4 |

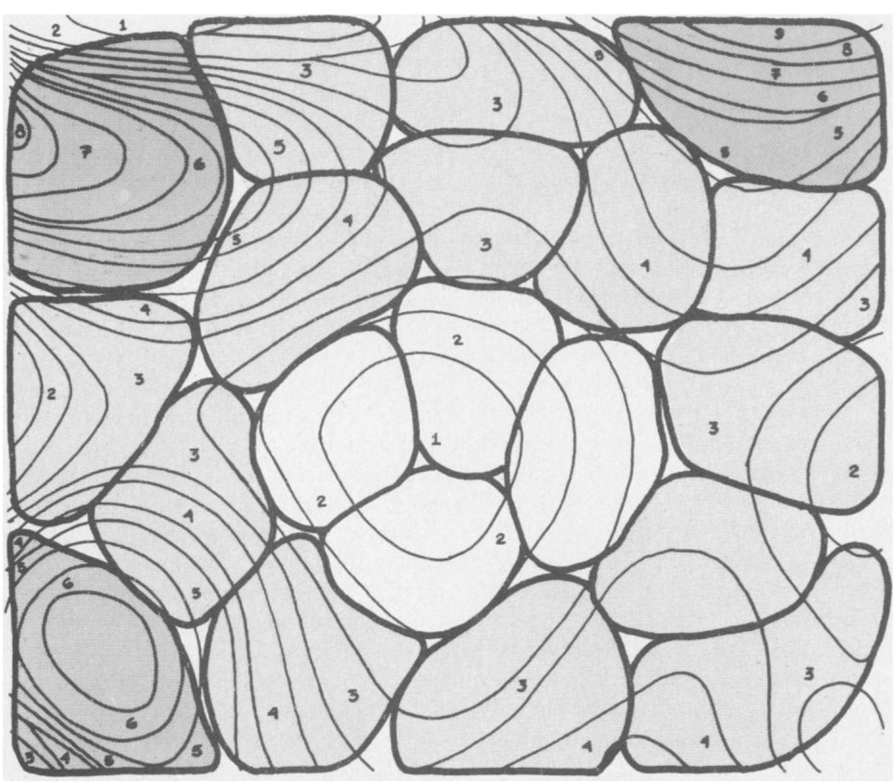

Fig. 1. Map of patchy alfalfa field showing territories belonging to males that were bigamous (no shading), monogamous (light shading), and bachelor (dark shading) superimposed over contoured sixth-degree surface of the light variable. Increasing numbers indicate increasing light intensity.

One should be able to increase reproductive success by decreasing the intensity of sunlight at the nest. On a different study area, crowns of plastic leaves were fixed on top of alfalfa plants above 43 of 85 nests. Control nests fledged 49, 52, and 42 percent of eggs hatched in 1974, 1975, and 1976, respectively; manipulated nests fledged 76, 74, and 65 percent of eggs. The difference was significant for each year ($t = 2.39$, $P < .02$; $t = 2.50$, $P < .02$; $t = 2.29$, $P < .05$).

Finally, if light values indicate attraction of territories to females, one should also be able to predict the future mating status of each territorial male on this basis alone. Means of illuminance values pertaining to bigamous, monogamous, and bachelor territories in central South Dakota were used to predict the number (0, 1, or 2) of females a territorial male would acquire in both northern Colorado and North Dakota. In Colorado, 28 out of 31 predictions pertaining to specific territories were correct (binomial test, $P < .0001$), and in North Dakota, 24 out of 27 ($P < .001$), thus supporting the hypothesis that light is the determining factor of polygyny in the lark bunting.

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**References and Notes**

1. For a recent synthesis of mating systems, see S. T. Emlen and L. W. Oring, *Science* **197**, 215 (1977).
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8. Territorial boundaries were determined by plotting the sites of aggressive encounters between neighboring males, by a multiple flush procedure [J. A. Wiens, Ornithol. Monogr. 8, 1 (1969)] and by plotting the points where playbacks of conspecific songs elicited a response from a given territorial male.
9. Secondary females do not receive any assistance from the males.
10. I compared over the three seasons the number of fledglings from each nest of a secondary female with that from each of the monogamous nests initiated on the same day. I hypothesized that the secondary nests would fledge as many or more young than the monogamous nests.
11. An analysis of variance was carried out on the daily time spent singing for bachelors, monogamists, and bigamists. For morphological attributes, correlations were calculated ($r$ = .12 for body length; $r$ = .35 for wing patch surface).
12. The variables were measured according to the following procedure. Numbered stakes were placed in a square grid system at 25-m intervals over the entire field. Sampling positions were located by a stratified random design, which ensures random placement of samples as well as equal sampling intensities over all sections of the field. Grid lines served as transects, and a sample location determined randomly was positioned between every pair of points along each grid line [J. A. Wiens, Ornithol. Monogr. 9, 1 (1969)]. At each sampling location, two crossed stakes delineated horizontally four 90-degree sectors. The distance from the intersection of the stakes to the nearest alfalfa plant in each quadrant was measu→ [R. L. Dix, J. Range Manage. 14, 63 (1961)]. At each of the four ends of the stakes, vertical foliage density was measured by inserting a rod vertically through the vegetation to the ground. Counts were made of the number of stems and leaves of all vegetative types intercepting the rod in 10-cm intervals above the ground. To evaluate the shading properties of the vegetation at the sample points, penetration of light (in lux) through the vegetation was measured with a photometer (Lunasix 3) 10 cm above the ground. Light readings were made on a clear day between 1130 and 1330 C.D.T.
13. The biological rationale behind the use of this variable is the following. Organisms may be said to generally select nesting sites with the least variation of daily temperature, and light provides a rapid and accurate covariant of temperature ($r$ = .94) [W. K. Pleszczynska, thesis, University of Toronto (1977)].
14. The first eigenvector of a principal component analysis had already segregated the sample points into three groups pertaining to territories of bachelors, monogamists, and bigamists. A discriminant function was constructed.
15. The F value to enter or remove, 246, associated with light was much larger than the next largest F, 36.
16. Sixth-degree polynomials were calculated for light by a trend surface analysis.
17. Predation pressure is not the cause of the increasing nestling mortality with the advancement of the season, because an increasing proportion of this mortality is due to desiccated young. This proportion is furthermore underestimated because dead nestlings are removed by the parents whenever at least one live nestling remains in the nest.
18. I thank R. I. C. Hansell and S. T. Emlen for helpful discussions, encouragement, and constructive criticism. I also thank F. Briand and J. D. Rising for critically reading the manuscript. Many people provided valuable assistance in the field, in particular S. Pleszczynski, C. Anders, and R. Hunter. Supported by Canada Council grant 3-654-120-60 to J. D. Rising.

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# Bone Marrow Origin of Hepatic Macrophages (Kupffer Cells) in Humans

Abstract. *Hepatic macrophages (Kupffer cells) from two male recipients of bone marrow transplants from females were studied for fluorescent Y body staining and sex chromatin (Barr body). After the transplant, macrophages had the sex karyotype of the donor, indicating that human hepatic macrophages originate in bone marrow.*

Transplantation studies in rodents have suggested that hepatic macrophages (Kupffer cells) are derived from a bone marrow precursor. For example, mice that received high-dose radiation and bone marrow transfusion from T6/T6 chromosome–marked donors possessed dividing hepatic macrophages of donor origin (*1*). However, other investigators have demonstrated a low but measurable proliferative capacity in hepatic macrophages, a finding that lends support to the concept of a self-sustaining population (*2*). Thus, there are two potential mechanisms for hepatic macrophage renewal, development from a bone marrow precursor and local self-replication.

To evaluate the mechanism of hepatic macrophage reconstitution in humans, we studied two male patients who had received bone marrow grafts from HLA-identical female donors. Patient 051 was

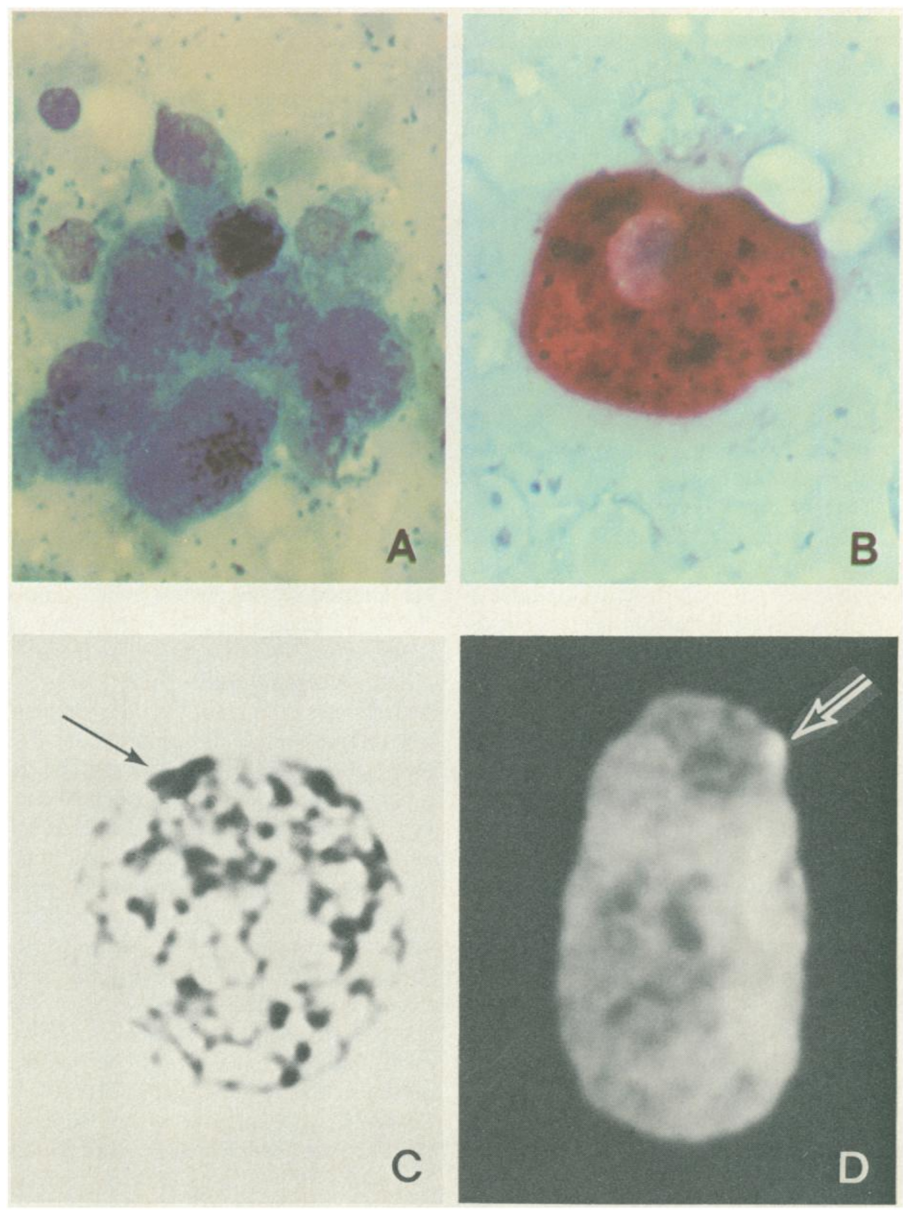


Fig. 1. Morphological studies of hepatic macrophages. (A) Giemsa stain of Kupffer cells with ingested bile pigment and hemosiderin. (B) $\alpha$-Naphthyl butyrate esterase stain of a hepatic macrophage. (C) Sex chromatin in hepatic macrophage (patient 051). (D) Fluorescent Y body in normal male hepatic macrophage.


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