

within the retina. A clinical implication of this study is that in contrast to some normally pigmented children with congenital strabismus, where early corrective surgery achieves a moderate degree of binocularity of vision (23), infants with ocular albinism would not benefit from surgery to achieve binocular vision, as they lack the neuronal substrate for cortical binocularity.

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References and Notes

- C. L. Sheridan, *J. Comp. Physiol. Psychol.* **59**, 292 (1965).
- R. D. Lund, *Science* **149**, 1506 (1965).
- R. A. Giolli and M. D. Guthrie, *J. Comp. Neurol.* **136**, 99 (1969); *ibid.* **142**, 351 (1971).
- R. W. Guillery, *Brain Res.* **14**, 739 (1969).
- D. J. Creel, *Nature (London)* **231**, 465 (1971); *J. Comp. Physiol. Psychol.* **77**, 161 (1971). The Siamese cat and other Himalayan strains of mammalian species have a special type of albinism in which a temperature-labile tyrosinase system allows pigment to form only on the cold parts of the body, such as the face, ears, tail, and feet.
- R. A. Giolli and D. J. Creel, *Brain Res.* **55**, 25 (1973); R. W. Guillery, *ibid.* **33**, 482 (1971); and J. H. Kaas, *Science* **180**, 1287 (1973); R. W. Guillery, G. L. Scott, B. M. Cattanch, M. S. Deol, *ibid.* **179**, 1014 (1973); K. J. Sanderson, R. W. Guillery, R. M. Shackelford, *J. Comp. Neurol.* **154**, 225 (1974).
- D. Creel, C. J. Witkop, Jr., R. A. King, *Invest. Ophthalmol.* **13**, 430 (1974).
- R. W. Guillery, A. N. Okoro, C. J. Witkop, Jr., *Brain Res.* **96**, 373 (1975). This has since been verified in several other human albino brains (R. W. Guillery, personal communication).
- D. Creel and R. A. Giolli, *J. Comp. Neurol.* **166**, 445 (1976).
- D. J. Creel, R. E. Dustman, E. C. Beck, *Exp. Neurol.* **29**, 298 (1970); D. J. Creel and R. A. Giolli, *ibid.* **36**, 411 (1972).
- E. Nettleship, *Trans. Ophthalmol. Soc. U.K.* **29**, 57 (1909).
- F. E. O'Donnell, Jr., R. A. King, W. R. Green, C. J. Witkop, Jr., *Arch. Ophthalmol.*, in press.
- R. E. Dustman and E. C. Beck, *Electroencephalogr. Clin. Neurophysiol.* **26**, 2 (1969); T. Harmony, J. Ricardo, G. Otero, G. Fernandez, S. Llorente, P. Valdes, *ibid.* **35**, 237 (1973).
- D. J. Creel, R. E. Dustman, E. C. Beck, *Exp. Neurol.* **40**, 351 (1973).
- C. J. Witkop, Jr., *Adv. Hum. Genet.* **2**, 61 (1971); C. J. Witkop, Jr., J. G. White, R. A. King, in *Heritable Disorders of Amino Acid Metabolism*, W. L. Nyman, Ed. (Wiley, New York, 1974), p. 171.
- H. Spekreijse, O. Estevez, D. Reits, in *Visual Evoked Potentials in Man: New Developments*, J. E. Desmedt, Ed. (Clarendon, Oxford, 1977), p. 16; A. M. Halliday, G. Barrett, E. Halliday, W. F. Michael, in *ibid.*, p. 121; D. A. Jeffreys, in *ibid.*, p. 134.
- G. F. A. Harding, in *ibid.*, p. 500.
- F. E. O'Donnell, G. W. Hambrick, W. R. Green, W. J. Iliff, D. L. Stone, *Arch. Ophthalmol.* **94**, 1883 (1976); F. E. O'Donnell, W. R. Green, J. A. Fleishman, G. W. Hambrick, *ibid.* **96**, 1189 (1978); B. A. Walker, L. Martin, T. Coffman, in *Birth Defects: Original Article Series*, D. Bergsma, Ed. (Williams & Wilkins, Baltimore, 1971), vol. 9, No. 3, p. 200.

- H. H. Jasper, *Electroencephalogr. Clin. Neurophysiol.* **10**, 371 (1958).
- R. W. Guillery, *Sci. Am.* **230**, 44 (May 1974); D. H. Hubel and T. N. Wiesel, *J. Physiol. (London)* **278**, 33 (1971).
- D. Creel, R. A. King, C. J. Witkop, Jr., A. N. Okoro, in *Pigment Cell*, T. B. Fitzpatrick, Ed. (Karger, Basel, in press), vol. 4.
- S. S. Stensaas, D. K. Eddington, W. H. Dobbelle, *J. Neurosurg.* **40**, 747 (1974).
- M. Ing *et al.*, *Am. J. Ophthalmol.* **61**, 1419 (1966); O. Kleinfeld, H. Fink, E. Schubach-Erz, *Albrecht von Graefes Arch. Klin. Exp. Ophthalmol.* **189**, 165 (1974); D. M. Taylor, *J. Pediatr. Ophthalmol.* **11**, 3 (1974); M. S. Banks, R. N. Aslin, R. D. Letson, *Science* **190**, 675 (1975).
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Social Inhibition of Maturation in Natural Populations of *Xiphophorus variatus* (Pisces: Poeciliidae)

Abstract. According to analyses of field samples, social inhibition of maturation is at work in natural populations of the variable platyfish, *Xiphophorus variatus*. In the laboratory, adult males inhibit the maturation of juveniles; the inhibition is overcome as the juveniles increase in size. The proportion of maturing males in any field collection is related to the number of adult males present and the size of the juveniles. The more adults, the fewer maturing males are present; the larger the average juvenile, the greater the number of males maturing. The evolution of this system is best understood in terms of individual selection, but consequences of the system buffer the population against the effects of predation.

Social interactions can affect the structure of vertebrate populations. Systems in which social inhibitions affect demographic variables such as fecundity (1), sex ratios (2), and probability of sexual maturation (3) have been described. These systems are of interest because they exemplify homeostatic control of demography through behavioral intervention and illustrate the phenomenon of social control over phenotype (4).

Laboratory studies have shown that adult size and the timing of maturation in male fishes of the genus *Xiphophorus* are under social control (3). A larger juvenile inhibits a smaller one from maturing, but is not inhibited in turn. The inhibiting fish matures early and stops growing, whereas the inhibited fish continues to grow until reaching a size sufficient to overcome the inhibition. At that point it matures and stops growing, us-

Table 1. Some characteristics of *X. variatus* populations. These characteristics change from year to year and are related. The table lists mean size ($\bar{X}$) of and relative size difference between juvenile (j) and transforming (t) males [$(X_t - X_j)/\bar{X}$] (for samples with more than five of each), the relative proportion of adult males [$P_a/(1 - P_a)$], and the proportion of transforming males (P_t) for 15 different samples of two populations taken over a 10-year period. The proportion of adults is the number of adult males divided by the total number of males. The number of transforming males divided by the total number of nonadult males is P_t .

Sample	Sample size	$\bar{X}$ (mm)	$(X_t - X_j)/\bar{X}$	$P_a/(1 - P_a)$	P_t
<i>Encino</i>					
Big pool					
1970	59	24.30	0.146	1.681	0.273
1973	101	19.86	0.148	1.294	0.182
1974	31	26.43	0.052	1.066	0.400
Upper pool					
1973	30	21.48		1.500	0.333
1975	50	20.16	0.124	0.667	0.300
Lower pool					
1975	31	19.28		1.584	0.333
<i>Sarco</i>					
Pool 1					
1973	87	24.43	0.131	1.174	0.550
1975	124	23.99	0.156	1.584	0.479
1977	67	27.07	0.129	1.793	0.667
Pool 3					
1977	30	20.58		1.309	0.154
Pool 6					
1967	92	19.95	0.056	0.261	0.342
1973	33	21.02	0.020	0.138	0.793
1977 (upper)	74	21.13	0.078	0.848	0.525
1977 (lower)	71	23.71	0.105	1.451	0.414
Pool 9					
1967	23	20.49		1.083	0.364

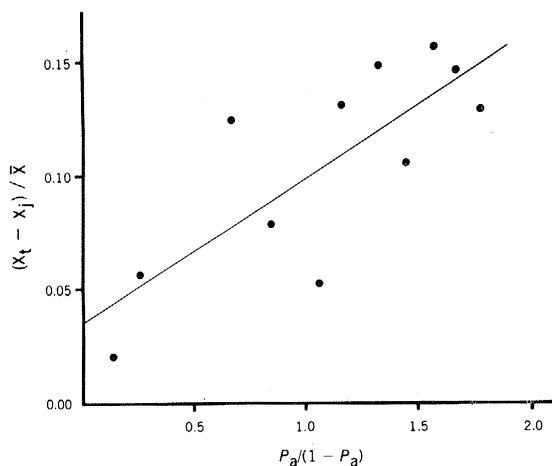


Fig. 1. The effect of adult inhibition on the size of transforming males. The difference in size between transforming and juvenile males expressed as a proportion of mean size is plotted against the ratio of adult to nonadult males. In collections with a high proportion of adult males, transforming males are significantly larger than juveniles ($r = .78$, $P = .0025$).

usually at a size larger than that of the first.

Mature males also inhibit juveniles. The effect is mediated by social dominance and may be general in the Poeciliidae (5). The poeciliid fishes are a major element of the Middle-American freshwater ichthyofauna and are characterized by ovoviviparity—internal development of young (6). The anal fin differentiates into a sperm transfer organ, the gonopodium, as males mature.

Because all of the studies cited were conducted under controlled laboratory conditions, the question can be raised whether the phenomenon occurs under natural conditions. Is social inhibition of maturation important in natural populations, and if so, how does it affect their demography? Table 1 lists the characteristics of 15 independent samples of two populations from southern Tamaulipas, Mexico, sampled over a 10-year period (7). Males were classified as mature, maturing, or juvenile (8). The proportion of adults is that with respect to all three classes, and the proportion of transforming males is that with respect to nonadult males. The population characteristics are related in ways that demonstrate the importance of social inhibition of maturation as a natural phenomenon.

In some samples, juvenile and maturing males were similar in size, but in others, the juveniles were significantly smaller than maturing males. Size is correlated with the proportion of adults in the sample ($r = .78$, $t(9) = 3.79$, $P = .0025$) (Fig. 1). In samples having many adults, transforming males were considerably larger than juveniles; in samples having few adults, differences were minor. My interpretation is that juveniles in samples with a high proportion of adults were highly inhibited and only the largest could begin to mature, whereas in samples with few adult males, inhibition was slight.

This interpretation suggests that the proportion of transforming males in any population is controlled by the strength of the inhibition and the ability of juveniles to break through it. If the inhibition is exerted through dominance, the ratio of the number of adults to the number of nonadults should be a good measure of this effect. If the inhibition is overcome by attaining large size, the mean size of nonadults should be a good measure of the ability of the juveniles to mature in the presence of adults. Neither of these

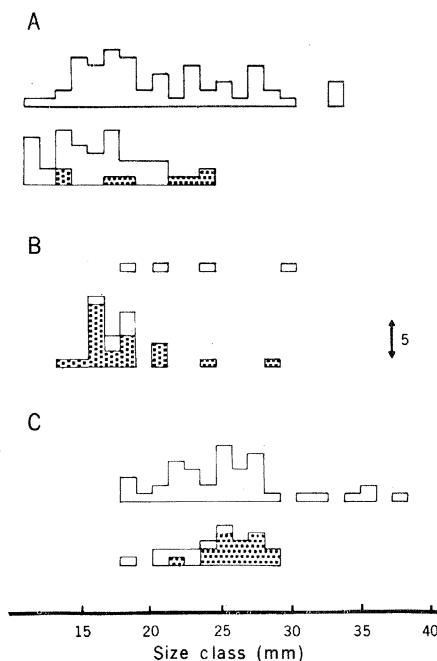


Fig. 2. The size distribution of adult (upper histogram), transforming (filled portion of lower histogram), and juvenile males (remainder) for three collections. (A) Sample from Big Pool, 1973; (B) pool 6, 1973; and (C) pool 1, 1977. Juveniles in samples A and C were strongly inhibited from maturing, but in sample C were large enough to overcome it. Sizes of juveniles and transforming males differ significantly in samples A and C ($t \geq 2.85$, $P \leq .005$).

measures alone is significantly correlated with proportion of transforming males, but together they account for a significant portion of its variation. Partial correlation coefficients, measuring the effect of either factor on proportion of transforming males after controlling for variation of the other, are significant.

For all 15 samples, the multiple regression equation describing the plane of best fit for the three factors is

$$P_t = -.361 + .0443 \bar{X} - .187 \left(\frac{P_a}{1 - P_a} \right)$$

and the regression as a whole is significant ($R^2 = .402$, $F(12, 12) = 4.038$, $P = .05$). A much better fit can be obtained by limiting the analysis to the ten largest samples:

$$P_t = -1.319 + .0963 \bar{X} - .369 \left(\frac{P_a}{1 - P_a} \right)$$

($R^2 = .696$, $F(2, 7) = 8.020$, $P = .015$).

Partial correlation coefficients for the ten largest samples are

$$r_{y1.2} = .828 [t(7) = 3.90, P = .005]$$

$$r_{y2.1} = -.803 [t(7) = .356, P = .005]$$

where x_1 , x_2 , and y are $\bar{X}$, $P_a/(1 - P_a)$, and P_t , respectively. That is, about 70 percent of the variability in the proportion of transforming males is accounted for by variability in nonadult size and in the proportion of adults present. Each of these factors alone accounts for a significant portion of the variation not accounted for by the other.

These relationships explain some of the demographic characteristics of *Xiphophorus* populations. Figure 2 shows the size distribution of adults, transforming males, and juveniles for three different samples. In sample A, juveniles were highly inhibited because they were small and there were many adults present. In sample B, although the nonadults were small, few adults were present, so there was less inhibition. In sample C, many adults were present, but the nonadults were large and able to overcome the inhibition. Sample A contained few maturing males and B and C contained many. Furthermore, in consequence of the high proportion of adult males in samples A and C the sizes of juveniles and transforming males were significantly different [$t(41) = 2.87$, $P = .005$, and $t(22) = 4.95$, $P = .001$, respectively].

Of interest is a comparison of the two 1977 samples from Sarco pool 6. When visited on 25 November 1976, pool 6 was filled and few adult fish were seen. When visited on 20 March 1977, the pool had dried to the point that the upper and

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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References and Notes

1. H. M. Bruce [J. Anim. Sci. 25 (Suppl.), 83 (1966)] described a direct effect on fecundity. M. E. Brown [J. Exp. Biol. 21, 118 (1946)] saw an indirect effect.
2. L. Fishelson, *Nature (London)* 227, 90 (1970); D. R. Robertson, *Science* 177, 1007 (1972).
3. R. L. Borowsky, *Nature (London)* 245, 332 (1973).
4. ———, *Physiol. Zool.* 46, 22 (1973).
5. J. J. Sohn, *Science* 195, 199 (1977).
6. D. E. Rosen and R. M. Bailey, *Bull. Am. Mus. Nat. Hist.* 126, 1 (1963).
7. The localities, Encino and Sarco, are located near the town of Encino, Tamaulipas, Mexico. A locality map will be published (R. L. Borowsky, *Evolution*, in press).
8. Sizes reported are standard lengths. All males with fully differentiated gonopodia were classified as adults. The criterion for transforming males was at least 13 divisions in the third anal-fin ray. All immature males in a collection equal to or longer than the shortest transforming or adult male were classified as juveniles. The stages of development have been detailed (3).
9. B. H. Seghers, thesis, University of British Columbia (1973); J. A. Farr, *Evolution* 29, 151 (1975).
10. R. L. Borowsky, thesis, Yale University (1969).
11. F. E. McKay, *Ecology* 52, 778 (1971).
12. G. Gandolfi, *Boll. Zool.* 38, 35 (1971).
13. J. J. Sohn, *Copeia* 1977-11, 224 (1977).
14. I thank B. Borowsky and J. J. Sohn for criticism and suggestions. Supported in part by NSF grant BMS 75-13464. Permission to collect was granted by the Mexican government and is gratefully acknowledged.

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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 fa-

vored 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 spartea*, *Agropyron 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;