Socially Induced Inhibition of Genetically Determined Maturation in the Platyfish, *Xiphophorus maculatus*

Abstract. *Maturation in* Xiphophorus maculatus *(Pisces; Poeciliidae) is under control of the sex-linked* P *gene. However, when two individuals are reared together the socially dominant individual delays the maturation of the subordinate. Nevertheless, it is not a requirement that a fish be socially dominant to become mature. The data suggest that inhibition of maturity takes place when an individual is not dominant at a time near the genetically determined age of maturation. Two hypotheses are offered to explain these results.*

Small changes in the age of maturity of individuals may produce large changes in the rate at which a population grows (*1*). Although the causes of variability in the age at which individuals reach maturity in natural and exploited populations have been discussed (*2*), few investigators have examined the interactions of genetic and social factors that determine the age or size at maturity in vertebrates. I have studied these factors in the platyfish, *Xiphophorus maculatus* (Pisces; Poeciliidae), and report here that although the age or size of individuals at maturity is genetically determined, when two fish are reared together in an aquarium the socially dominant fish will cause changes in the age and size at which the other fish attains maturity.

Kallman and Schreibman (*3*) discovered that in *X. maculatus* a single sex-linked locus controls the approximate age when maturity is attained. The presence of different alleles at this *P* gene causes males (and females) to mature at different ages and sizes. These workers suggested that the *P* gene controls the age at which the gonadotropic zone of the adenohypophysis differentiates. This differentiation is correlated with testicular development and with the transformation of the anal fin into a gonopodium (*4*). Androgen from the developing testes causes a decrease in the growth rate, so that at maturity males have reached their final size (*3*). In males it is possible to record, by external examination of the anal fin, the date that maturity is attained (*3*, *5*).

In *X. variatus* and *Gambusia manni*, the size and time of maturity is under social control (*5*, *6*). In both of these poeciliids, the presence of a large adult or juvenile fish in an aquarium usually inhibits the maturation of the smaller males until they exceed the size of the larger fish. In both these species, as well as in other poeciliids, size appears to be important in determining position within a dominance hierarchy. In *G. manni*, the phenomenon provides an explanation for the shift in the size at maturity of individuals in populations without predators (*6*). The genetic basis of maturation has not been investigated for these two species.

If, in *X. maculatus*, inhibition of maturity occurs in the presence of another individual, and if such inhibition is related to a social factor, the first fish to reach maturity should consistently be either dominant or subordinate and a change in the dominance position might be expected during the time of maturation of the first and second fish. Furthermore, the first fish to mature should do so at a significantly earlier age and smaller size, and not earlier than fish reared alone (*7*).

In *X. maculatus*, YY males of the Belize stock homozygous for early maturity, P^eP^e, attain maturity between 10 and 16 weeks of age, while YY males heterozygous for maturity, P^eP^l, reach maturity between 14 and 25 weeks (*3*). Because *X. maculatus* is naturally polymorphic for sex chromosomes (*8*), it is possible to obtain all-male broods. I mated YY males heterozygous for maturity to XX females homozygous for early maturity and produced only XY males that mature either early, P^eP^e, or late, P^eP^l (*9*).

At 2 to 4 weeks of age, fish of the same brood were placed either individually or in pairs irrespective of size into 20.8-liter glass aquariums (*10*). Fish were fed twice daily with an excess of frozen brine shrimp. Fluorescent room lighting, turned on at 0900 hours and off at 2300 hours, supplemented the natural photoperiod throughout the experiments (*11*). The laboratory temperature was maintained at 22° ± 2°C. Fish anesthetized with Finquel (Ayrest) were examined once every 2 weeks during early growth and once every 3 or 4 days after the onset of maturation. At these times, fish were measured for standard length, and the stage of anal fin metamorphosis was recorded (*12*). Observations of behavior were made at least once a week beginning in the third week of life (*13*). An individual was termed dominant if, during an encounter it nipped the other individual and was not nipped in turn. If the nipped

Table 1. Effect of social dominance on age and maturity in *X. maculatus*. The age at which each fish in a pair matures is given by T_1 and T_2; S_1 and S_2 are the respective sizes of the fish at maturity. The difference in the relative growth rates during early growth (growth rate of the smaller fish minus growth rate of larger fish) is given by ΔRG. The average percentage difference in standard length between the larger and smaller fish during early growth is given in the column for size difference. The last column presents the changes in dominance position of the first fish to mature with respect to gonopodium development: D, dominant; S, subordinate; and CD, codominant. Subscripts refer to the stage of gonopodium development (*12*).

Replicate	T_1 (days)	S_1 (mm)	T_2 (days)	S_2 (mm)	ΔRG	Size difference (%)	Dominance position
				P^eP^e *fish*			
E6	86	23.0	101	27.0	+.002	.106	$D_3 \rightarrow S$
E8	86	23.4	111	27.6	−.001	.009	$D_4 \rightarrow S$
E11	86	26.2	101	28.9	+.003	.243	$D_4 \rightarrow S$
E21	93	25.4	107	28.0	+.003	.098	$D_3 \rightarrow S$
E25	88	25.2	112	28.9	+.004	.113	$D_6 \rightarrow S$
E28	85	24.5	101	29.5	−.006	.059	$D_6 \rightarrow S$
F5	93	23.9	106	25.3	−.004	.081	$D_3 \rightarrow S$
F2	90	22.5	116	25.0	+.003	.035	$D_3 \rightarrow S$
X3	90	19.9	101	23.7	−.003	.078	$D_3 \rightarrow S$
X4	90	19.7	104	24.3	−.002	.063	$D_3 \rightarrow S$
D1	101	24.5	101	24.3	.000	.006	CD
X2	101	23.0	101	23.0	.000	.024	CD
				P^eP^l *fish*			
L1	121	32.0	134	32.5	+.001	.101	$D_3 \rightarrow CD$
L2	129	34.5	129	34.1	+.001	.057	CD
L4	121	32.4	145	34.6	−.002	.051	$D_3 \rightarrow S$
L5	118	33.5	142	34.0	−.001	.279	$D_6 \rightarrow D$
L6	134	32.8	142	34.7	.000	.018	$D_3 \rightarrow S$
L13	129	33.7	129	33.5	−.001	.042	CD
L22	120	31.4	135	33.1	−.008	.044	$D_4 \rightarrow S$
L24	120	31.9	135	33.1	−.002	.014	$D_3 \rightarrow S$
LL2	123	29.9	136	31.6	.000	.044	$D_3 \rightarrow S$
L8	122	29.5	142	34.5	.000	.062	$D_3 \rightarrow S$
LL5	114	27.5	137	32.5	+.002	.045	$D_3 \rightarrow S$
L33	131	29.5	131	29.5	+.003	.049	CD

Table 2. The effects of pairing early- and late-maturing fish. T_1 and S_1 are the age and size at maturity for P^eP^e fish; T_2 and D_2 are the age and size at maturity of P^eP^l fish. ΔRG is the difference in the relative growth rates during early growth (growth rate of the smaller fish minus growth rate of the larger fish). Size difference refers to the average percentage difference in standard length between the larger and smaller fish during early growth. The last column presents the changes in the dominance position of the P^eP^e fish with respect to gonopodium development; D, dominant; S, subordinate; and CD, codominant. Subscripts refer to the stage of gonopodium development. (In replicates B7 and B26, P^eP^l fish were larger during early growth; in all other replicates, they were smaller. Replicates B10 and B9 had to be abandoned because fish jumped from one tank to another).

Replicate	T_1 (days)	S_1 (mm)	T_2 (days)	S_2 (mm)	ΔRG	Size difference (%)	Dominance position
B7	101	24.8	121	30.5	−.002	.159L	S
B3	86	25.6	129	33.5	+.001	.150	$D_3 \rightarrow S$
B15	86	25.5	121	31.6	+.001	.000	$D_6 \rightarrow S$
B14	118	29.4	126	33.4	+.002	.08	$D_2 \rightarrow CD \rightarrow S$
B12	118	29.5	129	32.5	.000	.000	S
B10	86	26.6			.000	.014	$D_3 \rightarrow ?$
B9	92	24.5			.000	.061	$D_3 \rightarrow S$
B23	88	25.4	119	30.4	+.001	.053	$D_3 \rightarrow S$
B26	88	24.5	119	33.0	−.002	.029L	$D_3 \rightarrow S$
B27	101	30.0	119	34.5	+.001	.065	$D_2 \rightarrow S$
B29	88	24.4	123	33.0	+.007	.098	$D_3 \rightarrow S$
B30	81	22.4	112	30.4	+.010	.153	$D_3 \rightarrow S$
B31	89	22.5	115	30.0	+.003	.123	$D_3 \rightarrow S$

fish reciprocated, the fish were scored as codominants (*14*).

In experiment 1 P^eP^e fish were paired; in experiment 2 P^eP^l fish were paired; and in experiment 3 P^eP^e fish were paired with P^eP^l fish (see Tables 1 and 2). Fish were also raised in isolation (*15*). When P^eP^e fish were paired, the dominant fish matured at a younger age and smaller size than the subordinate fish in ten out of ten replicates. The median latency for the subordinate fish was 15 days (the minimum delay was 11 days), and the median increment in standard length was 3.7 mm (the minimum increment was 1.4 mm). The dominant fish matured at ages not significantly different from the ages at which P^eP^e fish reared in isolation matured (the median age for fish reared alone was 86.5 days, and the median age of maturity for dominant individuals was 88 days; Mann-Whitney test, $t = 15.5$, $P > .05$). Similarly, when P^eP^l fish were paired, the dominant fish matured at an earlier age and smaller size in nine out of nine trials. The median latency for the subordinate was 15 (the minimal delay was 8 days), and the median increment in size was 1.9 mm (the minimal increment in standard length was 0.5 mm). The dominant fish attained maturity at ages not significantly different from fish reared alone (the median age of maturity for dominant fish in the paired experiment and for unpaired fish was 121 days). In experiments 1 and 2, fish that matured first were dominant through at least the third stage of gonopodium development. In cases of ties (D1, X2, L2, L13, L33) fish were codominant. Fish of replicates D1 and X2 matured as late as subordinate fish in experiment 1, and fish of replicates L2, L13, and L33 matured as late as subordinate fish in experiment 2. These differences in the time to and size at maturity do not reflect differing growth rates (*16*).

In experiment 3 (Table 2), the median age at maturity of P^eP^l fish that were subordinate to P^eP^e fish until the maturity of the latter, but which were dominant thereafter, was 121 days. This median age is identical to that of dominant males of experiment 2 (who were dominant through at least the third stage of gonopodium development). This suggests that an individual can be subordinate during its early development and that there is no inhibition of maturation provided that a dominant position is achieved before the genetically determined age of maturation.

The median age of maturity of dominant P^eP^e fish of experiment 3 was 88 days, which is identical to the median age of maturity for dominant fish of experiment 1. However, P^eP^e fish of experiment 3 that either were codominant with P^eP^l fish or lost their dominant position before attaining the third stage of gonopodium development were delayed (B14, B12, B27, B7).

Table 3. Difference in standard length of the larger fish compared with the smaller fish and the frequency with which the larger fish is socially dominant.

Difference in standard length (%)	Frequency of dominance	No. of pairs
0.0 to 2.5	0.50	6
2.6 to 5.0	0.56	7
5.1 to 7.5	0.80	10
7.6 >	1.0	14

The results indicate that there is a time (or size) beyond which a fish cannot delay maturity. Although P^eP^e males did not become dominant in replicates B14, B12, B27, and B7, they matured within the range of P^eP^e fish in experiment 1 that were delayed, but became dominant. This observation is true of replicate L5 of experiment 2, where the subordinate fish did not become dominant but matured. Likewise in the case of codominance, fish did not delay maturity indefinitely but matured at ages similar to inhibited fish which did become dominant.

Borowsky (*5*) found that in *X. variatus*, if one fish of a pair was larger than the other by 5 percent (standard length), it matured at an earlier age and smaller size than the other fish. If the pair were separated in length by less than 5 percent (standard length), the fish with the faster growth rate matured first. These results may be adequately explained by a dominance theory of inhibition. Size is an important determinant of position in a dominance hierarchy in fishes (*17*); and in *X. maculatus*, if the difference in standard length is greater than 7.5 percent, the larger fish will always be dominant (Table 3). To explain the correlation found by Borowsky (*5*), I suggest that a fish that is 5 percent larger will be dominant even with a slower growth rate and will remain dominant throughout the maturation process. On the other hand, if the difference is less than 5 percent and the larger fish has a slower growth rate, it is possible that it will lose its dominance position before the maturation process is completed.

Borowsky presumed that social inhibition of maturation was related to sexual selection (*5*). He considered that the phenomenon allowed males to mature at any size that optimized fitness. In the poeciliids, adult males compete intensely for females and size appears to be directly correlated to reproductive success (*5*, *18*). It is possible to consider that the relationship between position in a dominance hierarchy and inhibition might provide a mechanism by which a male determines the probability of reproductive success and responds to that determination. Thus, if a male is dominant, the probability of reproductive success is high and maturity is initiated as soon as possible. If, however, the male is subordinate or codominant, the probability of reproductive success is lower, maturity is delayed, and growth continues.

There is another interpretation of this phenomenon which is not directly related to sexual selection. In a population that is declining, natural selection may favor individuals that delay maturity; in a growing population, it may favor immediate maturity (*19*). Growing populations are characterized by a high ratio of juveniles to adults while declining populations contain many adults and few juveniles (*1*). Presumably, a juvenile determines the growth rate of the population by its social interactions with adults and juveniles. If most interactions are with smaller, therefore younger, juveniles, this indicates that the population is growing and maturation is initiated as soon as possible. If, however, most interactions are with adults or larger, therefore older, juveniles, this indicates that the population is declining and maturity is delayed.

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References and Notes

1. L. Cole, *Q. Rev. Biol.* **29**, 103 (1954); R. C. Lewontin, in *The Genetics of Colonizing Species*, H. G. Baker and G. L. Stebbins, Eds. (Academic Press, New York, 1959), pp. 77–94.
2. G. Alm, *Inst. Freshwater Res. Drottingholm* **40**, 5 (1959); M. Gadgil and W. H. Bossert, *Am. Nat.* **104**, 1 (1970); R. Green and P. R. Painter, *ibid.* **109**, 1 (1975).
3. K. D. Kallman and M. P. Schreibman, *Gen. Comp. Endocrinol.* **21**, 287 (1973).
4. D. Grobstein, *Univ. Calif. Publ. Zool.* **47**, 1 (1940).
5. R. L. Borowsky, *Nature (London)* **245**, 332 (1973).
6. J. Sohn, *Copeia*, in press.
7. If dominant fish matured earlier than fish reared in isolation, there would be acceleration of maturity.
8. There are three types of females (WY, WX, and XX) and two types of males (XY and YY). XY males mated with WX females produce a 1:3 sex ratio, while XX females mated with YY males produce only males [K. D. Kallman, *Zoologica* **50**, 151 (1965)].
9. The YY males were Belize stock (3492) and the XX females were Rio Jamapa stock ($163B^{47}$) obtained through the courtesy of K. D. Kallman, Osborn Laboratories of Marine Sciences, New York Aquarium.
10. Newly born fish were fed on a diet of nauplii, mosquito larvae, and frozen brine shrimp in excess.
11. The experimental period lasted from 13 November 1975 to 1 June 1976.
12. The stages of anal fin metamorphosis are as described by Kallman and Schreibman (*3*) and Grobstein (*4*).
13. The arrangements of tanks in the laboratory permitted direct observations from a distance of about 1 m. Observations were made before and after feeding. Each individual could be identified by its markings resulting from the phenotypic expression of the *Sp* (spotted side) pigment gene.
14. R. Baeninger, *Psychonom. Sci. Sect. Anim. Physiol. Psychol.* **10**, 185 (1968); J. C. Braddock, *Physiol. Zool.* **18**, 176 (1945).
15. The ages at maturity of four P^eP^e fish raised in isolation were 73, 86, 86, and 85 days. The ages at maturity of five P^eP^l fish raised in isolation were 116, 125, 124, 118, and 125 days.
16. The medians of the relative growth rates for the first and second fish to mature in experiments 1 and 2 were 0.018 and 0.019, respectively. They are not significantly different (Wilcoxon sign rank test, $t = 86; N = 19$).
17. D. F. Frey and R. J. Miller, *Behaviour* **42**, 8 (1972).
18. F. E. McKay, *Ecology* **52**, 778 (1971); J. Sohn, in preparation.
19. L. Demetrius, *Math. Biosci.* **4**, 129 (1969); D. B. Mertz, *Am. Nat.* **105**, 437 (1971).
20. I thank R. C. Lewontin and E. O. Wilson for helpful discussions.

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Natural Selection for Juvenile Lizards Mimicking Noxious Beetles

Abstract. *Adult* Eremias lugubris *in southern Africa are concealingly colored and move with a typical lizard gait, but the jet-black and white juveniles are conspicuous and forage actively with arched backs. In color, gait, and size, juveniles mimic "oogpister" beetles (Carabidae:* Anthia*) that spray an acidic, pungent fluid when molested. This unique mimicry, which is believed to be the first reported case of a terrestrial vertebrate mimicking an invertebrate, seems to reduce predation on juvenile lizards.*

Batesian mimicry, the important evolutionary phenomenon (*1, 2*) in which selection by predators favors individuals of a palatable or unprotected species (mimic) that deceptively resemble those of an unpalatable or protected species (model), is traditionally established by satisfying several correlative criteria (*3*) or by manipulative experiments in the field or laboratory (*4*). Despite widespread interest in the phenomenon, however, natural field evidence of the selective advantage of Batesian mimicry is scant (*5*). Here we present correlative evidence for a bizarre and apparently unique case of mimetic resemblance, that of a palatable juvenile lizard mimicking a noxious beetle (*6, 7*), as well as indirect field evidence that this mimicry reduces predation rates.

Adult *Eremias lugubris* in the Kalahari semidesert of southern Africa are pale red-tan, a color that blends with the Kalahari sand (Fig. 1C). In contrast, juvenile *E. lugubris*, jet-black above and below with broken whitish lateral and dorsal stripes (tails black basiventrally, thereafter buff to red-yellow), are quite conspicuous (Fig. 1A). Metamorphosis into the adult coloration begins at snout-to-vent lengths (SVL's) of about 40 mm and is generally complete at SVL's of 45 to 50 mm. Ontogenetic color shifts are common in *Eremias*, but one of this magnitude is unparalleled (*8*).

Adults and juveniles also differ in foraging gait. Adults forage actively (*9*) with lateral undulations typical of lacertid lizards. Juveniles also forage actively, but walk stiffly and jerkily with strongly arched backs and tails pressed to the substrate. (Bilateral contraction of muscles in the ventral midline apparently produces the arch.) Pronounced bending curves in the body and tail, associated with lateral undulations in the adults (and most lizards), are not apparent in juveniles. The largest juvenile observed walking this way was 49 mm SVL, near the upper size of color metamorphosis. The juvenile gait, which persists in captivity, seems to be unique among lizards.

The evolutionary significance of the conspicuous coloration and arch-walking gait of these juvenile lizards needs evaluation. Metamorphoses in coloration and gait are unrelated to reproductive maturity, as lizards mature several months later. Black coloration can confer thermoregulatory advantages to insects with insulated elytra (*10*) but is more likely to be a thermoregulatory disadvantage to a small lizard active only during hot summer and autumn months. Furthermore, because juveniles arch-walk at both high and low body temperatures (*11*), arch-walking cannot be a heat avoidance posture.

We propose that these juvenile lizards are in fact behaviorally and morphologically mimicking abundant, sympatric, noxious "oogpister" (*12*) beetles [Carabidae: *Anthia* spp. (*13*)], which squirt an acidic pungent fluid [5*N* formic acid plus isovaleraldehyde, acetic acid, tiglic acid, and so forth (*14*)]. Juveniles resemble oogpisters in aposematic (*15*) coloration [beetles (Fig. 1B) are black with lateral white stripes on the elytral borders, sometimes also on the thorax and head] (*16*), in size (beetles range from about 30 to 52 mm in length) (*17*), and in gait (oogpisters are active foragers) (*18*). Juvenile lizards metamorphose into the adult coloration and gait at sizes corresponding roughly to the maximum sizes of beetles.

Beetles are generally considerably more abundant than juvenile lizards, are active over broader time periods daily and perhaps seasonally (*19*), and may have a broader geographic range. These noxious beetles are thus ideal models (*3*); juvenile lizards have apparently converged on them both in behavior and morphology. Indeed, on occasion we have initially mistaken juvenile lizards for oogpisters!

The arch-walk may have evolved from an arched-back, facing-off posture sometimes used by adult *E. lugubris* in aggressive encounters. Many African *Eremias* juveniles are darker than adults (*8*), and the black coloration of *E. lugubris* juveniles probably evolved as an exaggeration of this trend. Numerous lizard predators could be selective agents, including birds (several shrikes, secretary birds), mammals (bat-eared foxes, jackals, suricates), and snakes (horned adders, sand snakes).

If juvenile lizards mimic oogpisters,