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VARIATION IN THE STRUCTURE OF *POECILIA GILLII* POPULATIONS.—Fishes of the family Poeciliidae are one of the dominant groups in Central America and the West Indies and inhabit a wide range of habitats from large lowland rivers to fast flowing forest streams to small, isolated, stagnant pools (Rosen and Bailey, 1963; Bussing, 1987). Flexibility in diet (Dussault and Kramer, 1981), life-history strategies (Borowsky, 1987; Snelson, 1989; Trexler, 1989), and their ability to survive and reproduce under hypoxic conditions (Chapman, 1990; Kramer and Mehegan, 1981) may have facilitated exploitation of diverse habitats. There has been an increasing appreciation for the degree of variation that can be observed among poeciliid populations and the role of plasticity in their evolution (Stearns, 1983; Reznick and Miles, 1989; Trexler, 1989).

Here we compare the structure of *Poecilia gillii* populations (Kner and Steindachner, 1863) living in isolated residual pools of three inter-

mittent streams, to populations from two everflowing rivers in northwest Costa Rica. The intermittent streams we examined are highly seasonal and experience extreme physical conditions; some pool populations can be periodically decimated by severe floods or dry season desiccation (Chapman et al., 1991; Chapman and Kramer, 1991). The residual pools can remain isolated for up to 90% of the year, although during flooding there is the potential for movement and the mixing of pool populations (Chapman, 1990). In the everflowing rivers we examined, environmental conditions are less dynamic than in nearby intermittent streams, and *P. gillii* can potentially move throughout large stretches of the rivers providing the opportunity for sampling and selection of alternative habitats. We proposed that the fundamental differences between these habitats would be reflected in variation in the structure of *P. gillii* populations.

The ecology and behavior of *P. gillii* has been studied for 20 months over three years in Santa Rosa National Park, Costa Rica, and in nearby lowland areas (Chapman, 1990). Here we report data collected between Dec. 1987 and Feb. 1988. Sampling was initiated approximately 3.5 months after the major flood period of the 1987 rainy season. The climate of the region is characterized by two distinct seasons: the dry season, from mid-Dec. to late May in which virtually no rain falls, and the wet season which encompasses the remainder of the year. During the dry season, all of the water courses within Santa Rosa National Park are dry, with the exception of a few springs and permanent waterholes. In contrast, during the rainy season, the streams and rivers flow in association with major rain events. Lowland areas near the park have similar rainfall regimes, but there are both everflowing and intermittent rivers and streams. The everflowing rivers originate on the forested sides of volcanos and move down into the lowlands.

Residual pools from three intermittent streams within Santa Rosa National Park (Quebrada Jicote, Quebrada Costa Rica, and the upper section of Rio Calera) and sites within two everflowing rivers in nearby areas (Rio Tempisquito and Rio Centeno) were selected for study. The three intermittent watercourses lead into the large intermittent river, Rio Poza Salada. Sampling sites within the streams were upstream areas of the river system, and represented the more extreme areas of Santa Rosa

watercourses with respect to physical and chemical conditions of the pools. A series of two to four adjacent pools was selected from sectors of each of the intermittent streams. A midstream and downstream sector were selected from Q. Jicote. *P. gillii* was the only fish species in the pools examined (except the occasional goby in one pool of Q. Jicote). To document the structure of pool populations, fish were captured using baited minnow traps covered with 1 mm mesh netting. The size distribution of all fish was recorded in 0.5 cm size categories (total length, TL). In the everflowing rivers there were at least six fish species, and *P. gillii* were collected from a series of sites approximately 50 m apart, using 5 mm mesh seines. Results were limited to fish ≥ 2.5 cm in total length. For fish of this size, repeat sampling of an area of Q. Jicote during stream flow and a large isolated pool produced similar results for trapping and seining. Differences in the proportion of males and the proportion of large fish (≥ 4.0 cm) averaged 4.3% and 5.7%, respectively, between trap and seine samples, whereas the maximum size varied by less than 1 cm. Repeat sampling of the same areas on a different occasion using only traps resulted in similar differences in the proportion of males and the proportion of large fish between consecutive trap samples (4.3% and 3.5%, respectively). Generally, all fish were returned to the site of capture. Collections were minimal due to the small size of the *P. gillii* populations in the intermittent streams.

Maturity of males was judged on the basis of field examination of anal-fin morphology (Turner, 1941). Microscopic examination of the anal fin was not possible due to the nondestructive nature of the study. Fish were classified as males if the contour of the gonopodium was clearly foreshadowed or maturation had proceeded beyond this stage (see Chapman et al., 1991). Only a very small proportion of males with developed gonopodia were observed at less than 2.5 cm ($< 1\%$, TL).

Overall, the size frequency distributions of *P. gillii* from the permanent rivers differed from those from the isolated pools of the intermittent streams. Pool populations from the intermittent streams were characterized by a truncated size distribution with the maximum size seldom exceeding 5.5 cm (TL) (Table 1). This was significantly smaller than the maximum size of fish in the everflowing sites (> 9.5 cm, TL, Mann-Whitney test, $n = 20$, $P = 0.0002$). Similarly,

the mean size of mollies (≥ 2.5 cm, TL) was significantly smaller in the residual pools than in the everflowing river sites (Mann-Whitney test, $n = 20$, $P = 0.0070$).

The size range and distribution of males differed between the everflowing river sites and the residual pools. In the everflowing rivers, few recognizable males were < 3.5 cm (TL). The majority of the males were between 3.5 and 6.0 cm TL, and this was consistent among sites. The mean and maximum sizes of males in the everflowing sites were greater than in the residual pools where the majority of males were < 4.0 cm TL (mean size: Mann-Whitney test, $n = 20$, $P = 0.0003$; maximum size: $n = 20$, $P = 0.0002$). Among the residual pools examined, the maximum size of females was significantly greater than the maximum size of males (paired t-test, $t = 7.48$, $n = 13$, $P < 0.001$). However, in the everflowing river sites, there was no difference in the maximum size of males and females (paired t-test, $t = 1.90$, $n = 7$, $P = 0.106$).

Although data are not available for the size at maturity for females, as a conservative estimate of sex ratio, we considered the number of males expressed as a proportion of all other fish (females and immature males). In the everflowing rivers, this averaged 10% but ranged from 5% in Rio Centeno (Site 2) to 15% in Rio Tempisquito (Sites 1 and 3). In the residual pools, the proportion of males was significantly higher than the everflowing sites (Mann-Whitney test, $n = 20$, $P = 0.0003$), averaging 37% and ranging from 25% in Q. Jicote (midstream sector, Pool 4) to 58% in Q. Jicote (midstream sector, Pool 3).

In the everflowing rivers, the range between adjacent sites in the proportion of males was generally low (7% in Rio Tempisquito and 3% in Rio Centeno) compared to that observed among adjacent isolated pools in the intermittent streams (7% in Q. Costa Rica; 34% in Q. Jicote, midstream sector; 30% in Q. Jicote, downstream sector; and 17% in Rio Calera). Differences in the proportion of males were significant among pools in Q. Jicote (midstream sector: $\chi^2 = 21.52$, $P < 0.0001$; downstream sector: $\chi^2 = 14.09$, $P = 0.0009$) but not for Rio Calera ($\chi^2 = 4.72$, $P = 0.19$) or Q. Costa Rica ($\chi^2 = 1.55$, $P = 0.21$). There was no significant difference in the proportion of males between sites in the everflowing rivers (Rio Tempisquito: $\chi^2 = 4.89$, $P = 0.18$; Rio Centeno: $\chi^2 = 0.85$, $P = 0.65$).

TABLE 1. SIZE DISTRIBUTION OF *Poecilia gillii* FROM RESIDUAL POOLS IN THREE INTERMITTENT STREAMS (Q. JICOTE, Q. COSTA RICA, RIO CALERA) AND SITES IN TWO EVERFLOWING RIVERS (RIO CENTENO, RIO TEM-PISQUITO). Size classes are designated by their lower limit (e.g., 2.5 = 2.5–3.0 cm).

Size class		Q. Jicote midstream				Q. Jicote downstream		
		Pool 1	Pool 2	Pool 3	Pool 4	Pool 1	Pool 2	Pool 3
2.5	Male	12.3	15.5	30.0	7.7	9.1	26.2	20.2
	Female and imm.	20.6	27.8	17.9	18.5	8.3	23.5	16.0
3.0	Male	28.2	8.3	25.4	7.7	33.3	10.9	11.2
	Female and imm.	21.9	17.5	13.4	24.6	6.1	10.2	25.5
3.5	Male	1.4	3.1	—	7.7	7.6	4.1	1.1
	Female and imm.	5.5	8.3	9.0	10.8	15.2	10.5	11.7
4.0	Male	—	—	—	1.5	2.3	1.4	—
	Female and imm.	2.7	13.4	—	9.2	2.3	5.1	7.5
4.5	Male	1.4	1.0	3.0	—	2.3	—	1.1
	Female and imm.	4.1	4.1	—	6.2	7.6	4.4	3.7
5.0	Male	—	—	—	—	—	—	—
	Female and imm.	2.7	1.0	1.5	6.2	3.8	2.0	2.1
5.5	Male	—	—	—	—	—	0.7	—
	Female and imm.	—	—	—	—	0.8	—	—
6.0	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	1.1	0.1	—
6.5	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
7.0	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
7.5	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
8.0	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
8.5	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
9.0	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
9.5+	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—	—
Sample size		73	97	67	65	132	294	188

The variation in the size of males between everflowing rivers and intermittent streams may be explained either by differences between the systems in size at maturity or by seasonal termination of recruitment of young males into the mature fraction of the everflowing populations. Eleven months of continuous study of the population structure in the pools in Q. Jicote, a highly seasonal site, revealed continuous recruitment of males (Chapman et al., 1991). In addition, large numbers of small fish were captured at all intermittent and everflowing sites, suggesting that there was recruitment of young fish at the time of sampling. Thus, we believe

that the variation we observed in the size of males between the intermittent streams and everflowing rivers was not due to seasonal recruitment of juveniles into the populations.

Variation in the size and/or age at maturity has been documented for a number of poeciliid fishes (Borowsky, 1978, 1987; Farr, 1980). Delayed maturation of small males has been attributed to factors such as male-male behavioral interactions, or to stressful conditions such as a limited food supply (Borowsky, 1978, 1987; Snelson, 1989). In Q. Jicote, seasonal trends in the size distribution of males reported by Chapman et al. (1991) suggested that in *P. gillii* the

TABLE 1. CONTINUED.

Size class	Rio Calera				Q. Costa Rica		
	Pool 1	Pool 2	Pool 3	Pool 4	Pool 1	Pool 2	
2.5	Male	9.4	2.1	—	—	18.7	17.7
	Female and imm.	8.3	5.3	1.4	2.0	14.0	37.9
3.0	Male	14.4	15.8	13.0	14.3	8.0	9.7
	Female and imm.	22.7	24.2	13.0	4.1	22.0	17.7
3.5	Male	5.5	5.3	10.1	22.4	8.0	1.6
	Female and imm.	26.5	34.7	33.3	10.2	14.7	7.3
4.0	Male	2.2	3.2	4.3	2.0	2.7	—
	Female and imm.	5.0	7.4	17.4	30.6	4.7	1.6
4.5	Male	1.1	—	—	4.1	—	1.6
	Female and imm.	2.8	2.1	7.2	8.2	2.7	0.8
5.0	Male	—	—	—	—	0.7	0.8
	Female and imm.	1.1	—	—	2.0	1.3	1.6
5.5	Male	—	—	—	—	0.7	—
	Female and imm.	1.1	—	—	—	1.3	1.6
6.0	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	0.7	—
6.5	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
7.0	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
7.5	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
8.0	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
8.5	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
9.0	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
9.5+	Male	—	—	—	—	—	—
	Female and imm.	—	—	—	—	—	—
Sample size	181	95	69	49	150	124	

size at maturity was flexible, expressed on the population level as seasonal variation in the proportion of males in the smaller size classes. In Q. Jicote, the social environment was altered subsequent to a catastrophic population loss during seasonal flooding and the proportionately higher loss of large males from populations. These events were followed by a seasonal input of small males (Chapman et al., 1991). The question remains as to whether a similar argument can be invoked to explain the differences observed between the everflowing sites and the residual pools. Here we report data collected subsequent to flooding when the sea-

sonal recruitment of large numbers of small males into intermittent pool populations was reflected in small male size and a high proportion of males. It is reasonable to assume that such strong seasonal trends may not occur in everflowing rivers due to the less seasonal hydrological regime and perhaps as a result of no catastrophic loss of fish during flooding. Thus, the differential size at maturity in males between the everflowing rivers and residual pools that we examined may partially reflect the season at which the samples were taken. If comparisons had been made in the late dry season, the size distribution of males in the intermittent

TABLE 1. CONTINUED.

Size class		Rio Centeno			Rio Tempisque			
		Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 4
2.5	Male	—	—	—	—	0.5	—	—
	Female and imm.	33.3	42.4	36.0	18.8	49.3	29.4	20.9
3.0	Male	—	0.8	0.8	—	—	0.6	0.9
	Female and imm.	21.3	40.0	22.4	22.5	19.2	16.6	22.6
3.5	Male	—	1.6	—	—	1.9	0.6	0.9
	Female and imm.	8.3	4.0	8.8	1.3	7.4	11.0	14.8
4.0	Male	0.9	1.6	—	1.3	1.5	3.7	2.6
	Female and imm.	4.6	2.4	4.0	2.5	4.4	6.1	8.7
4.5	Male	2.8	0.8	1.6	1.3	2.0	3.1	1.7
	Female and imm.	6.5	0.8	1.6	1.3	1.0	1.2	6.1
5.0	Male	2.8	—	1.6	1.3	0.5	3.1	2.6
	Female and imm.	6.5	0.8	0.8	2.5	3.4	1.2	7.0
5.5	Male	—	—	0.8	7.5	1.0	2.5	0.9
	Female and imm.	3.7	0.8	0.8	—	2.0	1.2	1.7
6.0	Male	—	—	0.8	1.3	—	0.6	0.9
	Female and imm.	4.6	—	—	2.5	1.5	0.6	0.9
6.5	Male	—	—	—	—	—	0.6	—
	Female and imm.	—	—	0.8	3.8	0.5	2.5	2.6
7.0	Male	—	—	—	—	—	0.6	—
	Female and imm.	0.9	—	—	5.0	1.5	3.1	0.9
7.5	Male	0.9	—	0.8	—	0.5	—	—
	Female and imm.	0.9	—	—	10.0	1.5	4.3	—
8.0	Male	—	—	—	—	0.5	—	0.9
	Female and imm.	—	—	2.4	3.8	—	2.5	—
8.5	Male	—	—	0.8	1.3	—	—	0.9
	Female and imm.	1.9	0.8	—	3.8	—	1.2	—
9.0	Male	—	—	—	—	—	—	—
	Female and imm.	—	—	4.8	5.0	—	1.2	—
9.5+	Male	—	—	—	1.3	—	—	—
	Female and imm.	—	3.2	10.4	2.5	—	2.5	1.7
Sample size		108	125	125	80	203	163	115

stream sites would have been skewed toward larger males. However, in *Q. Jicote* even at the end of the dry season, when males in the 2.5–3.0 cm (TL) size range were rare, the modal size class for males was generally only slightly larger (3.0–3.5 cm, TL); and most males were <4.0 cm (TL). In the everflowing river sites, most males were >4.0 cm (TL), so differential seasonal trends in maturation do not offer a complete explanation.

It is conceivable that the difference in the size of males between the habitats examined may be attributed to differences in the availability of resources, growth rates, and/or the probability

of survival. The overall smaller size of males that we observed in the intermittent stream sites may be a response to a lower probability of survival; it may be of benefit to mature at small size if the probability of surviving to a large size is low. Alternatively, food availability may be higher in everflowing rivers, which are not subjected to the periodic desiccation. This may allow males to grow larger and reach a more competitive size before maturing.

In the residual pools of *Q. Jicote*, *Q. Costa Rica*, and *R. Calera*, the proportion of males averaged 41%, whereas it averaged only 10% in the everflowing systems. These observed dif-

ferences may reflect a more highly skewed sex ratio in the everflowing rivers or a much higher proportion of immature males. It is possible that the much larger size of males in the everflowing rivers and the higher proportion of large males may inhibit the maturation of males at a smaller size. To become competitive, males may have to achieve much larger sizes prior to maturing, thus producing a large component of immature males in the populations.

There were significant differences in the proportion of males between adjacent pools in Q. Jicote. Chapman (1990) documented divergence in a series of environmental parameters (dissolved oxygen concentration, periphyton productivity) in Q. Jicote over a five-month postflood period. *P. gillii* populations in these isolated pools are not free to sample alternative pools during the period of isolation but must respond to local conditions which diverge as the dry season progresses. Thus, the variability in the proportion of males that was observed in the residual pools may reflect a response to local conditions. In the everflowing rivers, stream flow minimizes divergence of water quality between stream areas and facilitates sampling of alternative habitats, equalizing opportunities in space.

The truncated size distribution typical of the intermittent stream pools may reflect a low probability of survival associated with catastrophic flooding and pool desiccation. In addition, lower growth rates may occur in stagnant pools due to pool desiccation, a decrease in water quality, and an increase in pool densities as the dry season progresses. Future studies which include comparisons of growth rates between sites may be useful in explaining variation in population size structure.

The residual pool populations that were examined in this study were from the upstream areas of watercourses which experienced extreme conditions and catastrophic population loss in some pools associated with seasonal flooding and dry season desiccation. This represents an extremely severe habitat for *P. gillii* populations. Downstream of the pools sampled in this study, where the streams feed into the large intermittent river, large *P. gillii* (>9.5 cm) have been observed in some residual pools. This may reflect less extreme conditions in downstream pools or more stability between years in the persistence of pool populations.

When compared to two nearby everflowing rivers, *P. gillii* populations in small, isolated pools

of three intermittent streams exhibited a higher proportion of males, smaller males, more variability among adjacent pools in the proportion of males, and a truncated size distribution. We believe this variation in population structure between the two habitats reflects differences in the seasonal regimes, in particular the more extreme conditions in the residual pools which can induce periodic catastrophic mortality of pool populations. Future studies which examine differential growth versus differential survival between these habitats and the extent to which the observed variation represents genotypic differences versus phenotypic plasticity will be useful in examining the life-history significance of these trends.

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INTERSPECIFIC FEEDING ASSOCIATIONS BETWEEN THE GOATFISH *MULLOIDES MARTINICUS* (MULLIDAE) AND A POSSIBLE AGGRESSIVE MIMIC, THE SNAPPER *OCYURUS CHRYSURUS* (LUTJANIDAE).—Interspecific feeding associations have been reported for a wide variety of vertebrates (e.g., Cody, 1971; Morse, 1977; Strand, 1988). Such associations typically involve a “nuclear” species that is the core or focus of the hetero-

specific group and one or more “attendant” species (Strand, 1988 and references therein).

Intraspecific feeding associations have been reported most often for tropical reef species, where attendant species are typically carnivores. Ormond (1980) described four interspecific feeding relationships among reef fishes involving carnivorous attendants. Different species of predators may hunt cooperatively when seeking the same prey (Hiatt and Strasburg, 1960; Fricke, 1972; Ormond, 1980), with little or no distinction between nuclear and attendant species. An attendant species may follow the nuclear species and feed on the organisms exposed by the latter's activity (Ormond, 1980; Dubin, 1982; Diamant and Shpigel, 1985). Attendant species may hide behind nonpredatory species, or species that feed on different prey, to facilitate access to visually wary prey (Hobson, 1968; Ormond, 1980; Aronson, 1983). Finally, the most specialized relationship is aggressive mimicry (Wickler, 1965), in which attendant species behaviorally or morphologically mimic the nuclear species (Russell et al., 1976; Thresher, 1978; Ormond, 1980).

The primary benefit of associating with and or resembling a nuclear species is likely increased foraging success of attendants (e.g., Montgomery, 1975; Diamant and Shpigel, 1985). Interspecific feeding associations have been reported for a wide variety of fishes, but few data assess enhancement of the foraging success of attendants. Here we describe feeding associations between a tropical western Atlantic goatfish, *Mulloidides martinicus*, and a species of snapper, *Ocyurus chrysurus*, which closely resembles the goatfish, in which the goatfish enhances the ability of the snapper to exploit benthic and demersal prey.

The yellow goatfish, *M. martinicus*, is a ubiquitous inhabitant of tropical and subtropical western Atlantic reefs (Randall, 1983) that attains 32 cm standard length (SL). Its coloration is pale olive dorsally, over white or pale silver on the sides, with a conspicuous yellow stripe running laterally and joining the yellow, forked caudal fin. It feeds by swimming near the bottom and probing with its chin barbels in the sand or rubble for infauna and other small invertebrates (Randall, 1983).

The yellowtail snapper, *Ocyurus chrysurus*, is also common on western Atlantic reefs at lengths up to 70 cm SL. It is pale blue or silver in background coloration and is the only fish sympatric with *M. martinicus* with a bright yellow lateral