

Desiccation, flooding, and the behavior of *Poecilia gillii* (Pisces: Poeciliidae)

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In tropical fresh waters, seasonal patterns of water level variation can result in strong cycles of population density, physico-chemical parameters, and the availability of food and refuge. This paper examines the behavioral correlates of desiccation and flooding in a small fish, *Poecilia gillii*, inhabiting an intermittent stream in northwestern Costa Rica. Focal observations were used to compare the behavior of fish from two isolated pools in the late dry season to one permanent pool and two newly flooded areas during the early wet season. Reduced feeding activity in the dry season pools relative to the wet season sites, loss of fish condition in the late dry season, and a negative relationship between feeding activity and fish density, suggest that food was scarcer in the late dry season when pool densities were very high. The incidence of aggression was lowest in the newly flooded habitat in the wet season. Over the five sites examined, the incidence of aggression was positively correlated with fish density and negatively correlated with feeding bout length. The major response to pool hypoxia was increased use of aquatic surface respiration which accounted for up to 16 % of fish activity in one pool. Variation in feeding activity and densities between sites in the wet season suggest that fish leaving dry season refuges may benefit from lower densities and higher feeding potential.

Introduction

The degree to which animals can select alternative habitats through movement influences the degree to which they can avoid or must tolerate environmental stresses, such as high density or low food availability. Dispersal has been recognized as one means of avoiding high densities and/or other unfavorable conditions (Krebs & Myers, 1974; Waser, 1985). However, when movement is restricted, animals must tolerate

existing densities and conditions. In some natural systems, changes in the physical environment have a strong effect on the ability of organisms to disperse and effectively enclose populations on a seasonal basis. This is particularly true of many seasonally flooding fresh waters where seasonal patterns of water level variation can be reflected in large scale changes in the availability of aquatic habitat and pathways for movement.

Flooding is particularly prevalent in the trop-

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ics where rainfall is often the most seasonally variable climatic factor. In the larger floodplain rivers, forests and savannas become flooded over enormous areas during the wet season, while in the dry season, waters may be confined to the main river channel or to residual pools on the floodplain (Lowe-McConnell, 1964, 1967, 1975; Welcomme, 1979; Goulding, 1980). Similarly, in smaller intermittent rivers and streams, fast flowing waters in the wet season may be reduced to isolated stagnant pools in the dry season. During low water periods, aquatic animals may be trapped for several months in isolated residual pools. In such pools, fish densities can become high as the dry season progresses, due to pool contraction, population growth in some species, and lack of dispersal opportunities (Lowe-McConnell, 1964, 1975; Welcomme, 1979). In addition, many isolated pools experience harsh physical or chemical conditions including hypoxia, high temperatures, and habitat desiccation (Lowe-McConnell, 1975; Welcomme, 1979; Kramer et al., 1978; Chapman & Kramer 1991a). In contrast, during wet periods, water bodies are connected, providing access to a number of habitats, and many fishes disperse (Lowe-McConnell, 1964, 1975; Goulding, 1980; Welcomme, 1979). Motivation for the invasion of flooded habitat includes factors such as the location of spawning and foraging areas, avoidance of predation, or the avoidance of high density areas (Lowe-McConnell, 1964, 1975; Welcomme, 1979; Chapman & Kramer, 1991b).

Since fishes may be trapped in dry season pools for several months, high densities and harsh physical conditions may lead to competition for diminishing resources as the dry season progresses, and behavioral patterns which reflect negative density feedback. In this study we report observations on the behavior of a small fish, *Poecilia gillii*, from an intermittent dry forest stream in Costa Rica. Focal animal observation was used to compare the behavior of fish in two isolated pools in the late dry season, when dispersal was restricted, to their behavior in one permanent pool and two areas of newly flooded habitat during the wet season, when fish were free to disperse into the newly available areas. We also considered spatial and temporal variation in population density, population structure, and the physical characteristics of the sites. Comparisons between sites and seasons are used to detect density effects.

Methods

Study site and species. The ecology and behavior of *P. gillii* were studied for 20 months over a 3-year period in Santa Rosa National Park, Costa Rica (10°50'N 85°38'W). Here, we report observations made primarily between March and June 1985 in a small intermittent stream, Quebrada (Q.) Costa Rica. The climate is highly seasonal. During the dry season (December to late May) all of the water courses within Santa Rosa are dry, with the exception of a few springs and permanent waterholes. During the rainy season, the streams and rivers flow in association with major rain events. For a description of the climate and habitat of the area see (Chapman & Kramer, 1991a-b).

Q. Costa Rica is an intermittent stream surrounded by low canopy forest and grassland. The upper section is on a relatively low gradient, and is separated by a 25-meter waterfall from its downstream sector which feeds directly into the Rio Poza Salada (Fig. 1). In the late dry season of 1985, the upper section of the stream contained five waterholes (Pools 2, 3, 4, 5, and 6; Fig. 1; Table 1). All were small (maximum depth 1 m, 2-7 m in diameter), with relatively high densities of *P. gillii* (Table 1). Pool 1 dried up completely in the early dry season killing all resident fish.

Poecilia gillii is a small livebearing fish (maximum size: 110 mm total length; maximum recorded length in Q. Costa Rica: 75 mm), that is often found in seasonally intermittent streams. It feeds primarily on detritus and algae, and can breed throughout the year when conditions are favorable (Bussing, 1987). In Santa Rosa, these fish remain in small isolated pools for up to 90 % of the year. During the rainy season when the stream flows, there is the opportunity for dispersal and the mixing of pool populations (Chapman & Kramer, 1991b).

In 1985, the first substantial rain (23.8 mm) occurred on May 9; there had been very little rain since early November of 1984. This rain increased the depth and surface area of the pools, but was not sufficient to induce stream flow. Similar small rain events occurred on a few other occasions in that month, but it was not until June 2, when 105 mm of rain fell over a 2-day period, that Q. Costa Rica was transformed into a running stream. The flood was mild, but the stream continued to flow through the com-

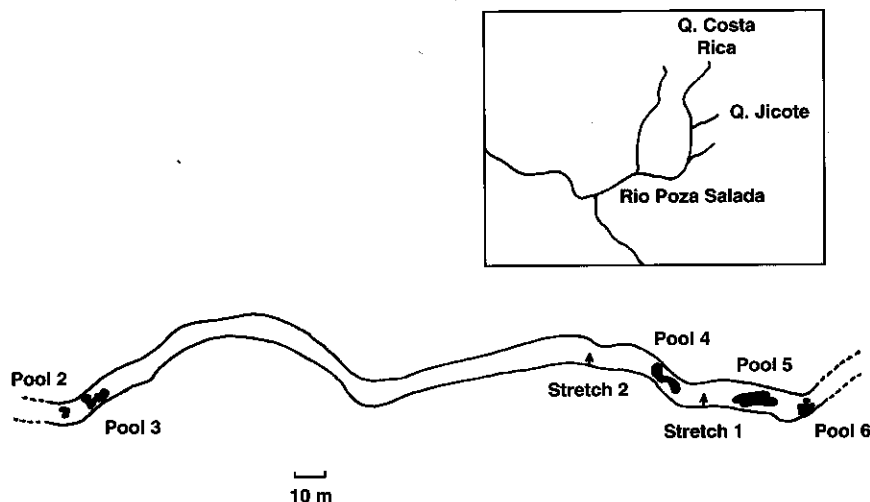


Fig. 1. Map of the location of the dry season pools and wet season sites examined in the study of *Poecilia gillii* in Quebrada Costa Rica.

pletion of our study on June 24. Many fish dispersed from the remaining dry season pools into the newly available areas. Regular surveys of the streambed indicated that some fish had travelled over 100 m upstream within a few days. The low gradient of Q. Costa Rica, upstream of Pool 5, and the quiet nature of the flood observed in 1985 may have facilitated upstream movement. Downstream movement was also detected and may represent voluntary departure from pools or flushing of individuals

by the force of the floodwaters.

Observations on the behavior of fish during the late dry season were recorded in two pools (Pools 2 and 5) that had good visibility. Pool 2 was a small pool (3.8 m²) with a mean depth of 29 cm in March (Table 1). The pool was at the base of a 2-m cavern in the streambed which limited direct sunlight. The surface area of Pool 2 decreased to 1 m² by April 25, and many fish died. A small amount of rain on April 26 increased the volume of the pool. However, only

Table 1. Characteristics of isolated dry season pools and wet season sampling sites in Quebrada Costa Rica. Sites used in the behavioral sampling program are indicated with an asterisk. The stream location indicates the distance upstream from Pool 6. Pool 1 dried up completely by February 12, and was not measured. Pool 3 was completely dry by May 2.

Site	Date	Maximum depth (cm)	Mean depth (cm) (±SD)	Pool area (m ²)	Stream location (m upstream of Pool 6)
Dry season pools					
Pool 2 *	March 11	50	28.8±14.6 (n=16)	3.8	270
Pool 3	March 11	140	79.9±21.0 (n=67)	91.4	260
Pool 4	March 11	50	19.3±14.7 (n=64)	16.2	55
Pool 5 *	March 11	100	37.1±25.7 (n=83)	87.3	15
Pool 6	March 8	100	43.9±32.9 (n=39)	7.0	0
Wet season sites					
Pool 4 *	June 10	50	20.6±10.4 (n=92)	61.2	55
Str. 1 *	June 12	50	9.4± 9.4 (n=79)	90.1	35
Str. 2 *	June 16	60	8.3± 8.6 (n=70)	54.0	70

a few fish remained, and behavioral observations in this pool were not continued after this date. In March, Pool 5 was one of the largest permanent pools in Q. Costa Rica (87 m²) with a mean depth of 37 cm and a maximum depth of 100 cm (Table 1). The area of this pool decreased to 14 m² before the first substantial rain on May 9. Behavioral observations were carried out on the fish in Pools 2 and 5 in the late dry season, beginning mid-March and continuing until April 24 in Pool 2 and continuing until May 9 in Pool 5 when the first substantial rain increased its water level by 20 cm and the surface area by a factor of 3.6.

During stream flow, three areas of the stream near Pool 5 were selected for wet season behavioral observations (June 3-24). Two areas (Stretch 1 and Stretch 2; Table 1; Fig. 1) had not contained standing water during the dry season. Both were shallow stretches of small pools connected by trickling water. Stretch 1 averaged 9 cm in depth with an area of 90 m². Stretch 2 averaged 8 cm in depth with an area of 54 m². Wet season observations were also carried out on Pool 4. This pool had increased substantially from 16 m² in March to 61 m² by June 10, and floodwaters had flushed out the heavy cover of duckweed which had minimized visibility in the dry season. Some fish had dispersed from Pool 4; however, densities here were still high relative to the stretches of new habitat. *Poecilia gillii* remaining in the deeper waters of Pools 2 and 5 could not be observed during the wet season due to high turbidity.

Behavioral sampling and estimates of population density and structure. A focal animal sampling regime (Altmann, 1974) was used to quantify the behavioral responses of the fish to changing environmental conditions. Fish were observed from the shoreline and were visually categorized into three approximate size classes: very small fish (<1.5 cm), small fish (>1.5 cm and less than <2.5 cm), and large fish (>2.5 cm). The two smaller size classes are combined as 'small' fish for analyses except where indicated. In addition, fish were captured using metal minnow traps, and large fish were marked as male or female by injecting acrylic paint subdermally with a fine gauge hypodermic needle (Riley, 1966; Thresher & Gronell, 1978).

Pools and stretches were divided into 1-m² grids by suspending ropes marked off at 1-m

intervals perpendicularly above the water. Grids for focal observations were selected randomly from the quadrat system. For each focal fish, a continuous record was made of the following: feeding, courting, aggression, swimming, aquatic surface respiration (ASR), and resting. Focal sessions were five minutes in duration, however it was sometimes difficult to follow one individual for the entire session. Thus, any session over 1 minute was considered in the analyses. For each randomly selected grid cell, focal animal selection was rotated once between size and sex categories so as to include one large male, one large female, one small fish, one very small fish, and one smaller member of the large size class. Observations were made from 0730 h to 1630 h, with an attempt to sample equally each of three periods (0730-1030; 1030-1330; and 1330-1630). For Pool 2, a grid system was not employed since the pool was only 3.8 m².

A total of 380 fish were observed in the late dry season with a mean focal duration of 4.1 minutes producing 1,942 behavioral bouts. In the wet season a total of 364 fish were observed with a mean focal duration of 4.5 minutes producing 1,444 behavioral bouts. Feeding activity in the smaller fish (<2.5 cm) was often difficult to differentiate from swimming activity that was close to the substrate. We therefore report overall activity budgets only for fish greater than 2.5 cm.

Population density and structure were assessed using visual counts of fish in different size classes in the 1 m² quadrats. One x or y coordinate was selected randomly, and all grid cells along that axis were censused for the number of large, small, and very small fish; and the percentage of the grid cell that was out of the water was estimated. Again, an attempt was made to give equal sampling effort to the three time periods. A total of 176 grid cells were sampled during the late dry season (Pool 5) and 352 cells in the wet season (114 in Pool 4, 125 in Stretch 1, and 113 in Stretch 2). In Pool 2, an attempt was made to count all fish in the pool, both through visual estimation and by capturing a large proportion of the fish.

Environmental measurements. During the dry season, the streambed was marked off into 10-meter segments, and all pools were mapped using the 1 m² grid system. Dry and wet season depth measurements were taken at 0.5-m intervals throughout the pools, and 1-m intervals in

the stretches of flowing water. Changes in area and depth were assessed by measuring changes in water level and periodically remapping the pool area and morphometry.

Water temperature and dissolved oxygen concentration (measured with an oxygen meter in the top 20 cm of water) were recorded at an average of 8 systematically selected sites in Pool 5, Pool 4, Stretch 1 and Stretch 2, and two sites in Pool 2. Data were recorded 3-4 times between 0700 hours and 1700 hours twice for Pools 2 and 5 in the dry season and once for Stretch 1, Stretch 2, and Pool 4 in the wet season. Additional early morning and midday observations were recorded in Pools 2 and 5.

Results

Fish density and proportion of young. The average density of fish (all size classes combined) was higher in the dry season pools (Pool 2: 72.3 fish·m⁻²; Pool 5: 30.7 fish·m⁻²) than the wet season sites (Pool 4: 8.6 fish·m⁻²; Stretch 1: 4.5 fish·m⁻²; Stretch 2: 4.0 fish·m⁻²; Fig. 2). These estimates are conservative, since smaller fish may have been missed. In addition, they represent average values over the sampling period during which time pool area declines. However, they do demonstrate the relative differences in densities among sites. When estimates are limited to large fish, again average densities in the two dry season pools were much higher (Pool 2: 34.9 fish·m⁻²; Pool 5: 18.0 fish·m⁻²) than the areas examined during the stream flow (Pool 4: 3.6 fish·m⁻²; Stretch 1: 3.3 fish·m⁻²; Stretch 2: 2.7 fish·m⁻²).

For Pool 5, there was a significant decline in the proportion of very small fish (<1.5 cm) from an average of 18.8 % of the population in the first 2 weeks of the sampling period to an average of 1.4 % in the last two weeks ($X^2=411.5$, $P<0.001$). During stream flow, new born fish were once again observed in all areas, particularly in Pool 4, where the proportion of very small fish was the highest of the three areas at 16.3 % ($X^2=31.4$, $P<0.001$). Very small fish represented 6.7 % of the population in Stretch 1 and 10.0 % of the population in Stretch 2. Grid counts were supported by the collection of 141 large female *P. gillii* (mean total length = 4.6 cm, range = 3.5-7.5 cm), collected from Pools 2-6 in the late dry season. The females were dissected,

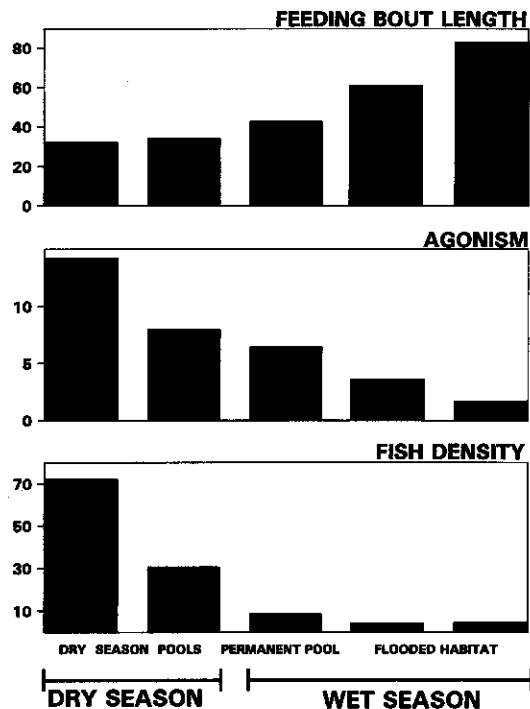


Fig. 2. The mean feeding bout length (seconds), incidence of aggression (expressed as a percentage of all behavioral bouts), and estimated total density (fish·m⁻²) of *Poecilia gillii* for two dry season pools, and three wet season sites in Q. Costa Rica. Order of sampling sites in the figure: Pool 2, Pool 5, Pool 4, Stretch 2, Stretch 1.

and the number of developing eggs and embryos were counted. Only 3 % of these large females had developing eggs or embryos, suggesting very little production of young in the late dry season.

Spatial and temporal variation in behavior. The percentage of time spent feeding by large fish increased from an average of 53.0 % prior to the flood, to an average of 73.9 % during stream flow (Table 2). The percentage of time spent feeding in the newly available habitats (Stretches 1 and 2) was higher than in the permanent Pool 4. Over the five sites considered, there was a negative correlation between the percentage of time spent feeding by large fish and both the density of large fish (Spearman rank correlation, $r_s=-0.90$, $P=0.037$, $n=5$) and total density ($r_s=-0.90$, $P=0.037$, $n=5$). The higher proportion of feeding associated with stream flow represented primarily an increase in the length

of feeding bouts which were highest in the newly flooded habitats, averaging 82 seconds per bout in Stretch 1 and 60 seconds per bout in Stretch 2 ($F=37.09$, $P<0.001$, $n=1228$). Feeding bout length averaged 32 seconds per bout in Pool 2, 34 seconds per bout in Pool 5, and 43 seconds per bout in Pool 4. Feeding bout length was negatively correlated with both the density of large fish ($r_s=-0.90$, $P=0.037$, $n=5$ sites) and total density ($r_s=-0.90$, $P=0.037$, $n=5$ sites; Fig. 2).

Longer feeding bouts and a greater percentage of feeding activity in the wet season may reflect greater food availability, either due to decreased densities, or more food, or a combination of the two factors. In contrast, it is possible that fish may require longer feeding bouts to collect food in short supply. To consider if food was limiting in the late dry season, we looked at the condition of the fish at this time to determine if shorter feeding bouts and a lower percentage of feeding time corresponded with weight loss. Fish collected from Pool 5 showed a significant loss of condition between March 15 (condition factor calculated as somatic weight(g)/length(cm)³ = 0.97) and late April (condition factor = 0.92, Mann-Whitney test, $z=-1.99$, $P=0.046$, $n=53$).

High densities of fish in pools might be expected to increase levels of stress. The frequency of aggression, expressed as a proportion of all

behavioral bouts, did not differ significantly between large and smaller fish (small and very small fish combined, G-tests, $P>0.05$). Thus, small and large fish were combined to examine differences among sites. Incidence of aggression was highest in the dry season but differed between Pools 2 and 5 (Pool 2: 14.2%; Pool 5: 8.0%, G-test, $P<0.05$, $df=1$). In the wet season, incidence of aggression was significantly lower in the newly flooded habitats than in the permanent Pool 4 (Pool 4: 6.5%; Stretch 1: 1.7%; Stretch 2: 3.6%, G-test, $P<0.05$, $df=1$). Over all sites, the incidence of aggression was positively correlated with the density of large fish ($r_s=0.90$, $P=0.037$, $n=5$ sites), and with total population density ($r_s=0.90$, $P=0.037$, $n=5$ sites; Fig. 2).

If aggression was related to competition for food resources, one would expect aggressive events to interrupt feeding activity. We examined this by comparing the percentage of aggressive events for large fish that were preceded by feeding activity, to the percentage expected if aggression was distributed at random. For Pools 5, 2, and 4, aggression was more likely to be preceded by feeding activity than expected by chance (Pool 2: $X^2=10.2$, $df=1$, $P<0.005$; Pool 5: $X^2=78.1$, $df=1$, $P<0.005$; Pool 4: $X^2=13.6$, $df=1$, $P<0.005$). In the newly available habitat, where rates of aggression were very low, aggression was not more likely to interrupt feeding activity

Table 2. Habitat characteristics, dissolved oxygen concentration and water temperature of dry season pools and wet season sites in Quebrada Costa Rica and the activity budget of large *Poecilia gillii*. Early morning (EM: 0700 - 0830 h) and midday (MD: 1000 - 1400 h) values are presented for dissolved oxygen and water temperature. Each behavior in the activity budget is expressed as a percentage of the total budget. Aquatic surface respiration is abbreviated as ASR.

	Pool 2	Pool 5	Pool 4	Stretch 1	Stretch 2
Habitat	dry season pool	dry season pool	wet season permanent pool	wet season flooded habitat	wet season flooded habitat
Oxygen (mg·l ⁻¹)					
EM	1.9	4.0	2.3	2.6	5.4
MD	3.6	7.8	4.2	5.1	7.2
Temperature (°C)					
EM	24.5	25.3	26.0	25.5	26.0
MD	32.1	33.1	27.2	29.5	30.1
Activity Budget					
Feed	57.9	48.3	65.1	77.7	78.5
Rest	12.8	14.0	9.4	0.5	1.2
Swim	10.8	30.2	16.8	19.0	19.4
ASR	16.3	4.6	4.8	2.3	0.1
Other	2.3	2.8	3.9	0.4	0.9

than other activities (Stretches 1 and 2 combined: $\chi^2=3.0$, $df=1$, $P>0.05$). Over the five sites examined, feeding bout length was negatively correlated with the incidence of aggression ($r_s=-1.0$, $P=0.00$, $n=5$ sites; Fig. 2).

Dissolved oxygen (DO) varied among dry season pools and wet season sampling sites. Early morning values (0630-0830 h) were generally low, but varied from an average of $1.9 \text{ mg}\cdot\text{l}^{-1}$ in Pool 2 to $5.4 \text{ mg}\cdot\text{l}^{-1}$ in Pool 5. In both dry season pools and wet season sites DO increased during the day producing midday (1000-1400) averages which ranged from $3.6 \text{ mg}\cdot\text{l}^{-1}$ in Pool 2 to $7.8 \text{ mg}\cdot\text{l}^{-1}$ in Pool 5 (Table 2). When oxygen depletion occurs, many fishes, including *P. gillii*, use aquatic respiration at the air-water interface to meet their oxygen demands (Aquatic Surface Respiration, ASR; Kramer & Mehegan, 1981; Kramer, 1983). When using ASR, *P. gillii* generally swam slowly along the surface with the mouth just below the air-water interface, producing a dimple in the water surface with each ventilation. Dissolved oxygen concentration was lowest in Pool 2 averaging only $2.3 \text{ mg}\cdot\text{l}^{-1}$ over the day. Correspondingly, the percent time engaged in ASR was highest in Pool 2 comprising 16 % of the activity budget. In the other sites, oxygen levels were higher and percent time engaged in ASR was lower ranging from 0.1 % in Stretch 2 to 4.8 % in Pool 4. Bout length for ASR averaged 20 s for large fish. Fish were often observed to engage in ASR as a group rather than as solitary individuals. In addition, there was a tendency for ASR behavior to be associated with more central deeper areas of water. Smaller fish (small fish and very small fish combined) spent less time using ASR than larger fish (Wilcoxon matched-pairs test, $z=-2.02$, $P=0.043$). Again, the highest proportion of ASR activity was observed in Pool 2 where small fish spent 4.5 % of their time at the surface.

Courtship was observed in large *P. gillii* throughout the observation period at all sites, even during the late dry season when very few females were producing young. The frequency of occurrence of courtship (expressed as a proportion of all behavioral bouts) averaged 4.1 % in the dry season and 6.1 % in the wet season. Courtship was not observed in smaller fish (<2.5 cm) in the dry season, but was observed on several occasions in the wet season (frequency of occurrence = 4.3 %) producing an overall increase in reproductive activity in the wet season.

Discussion

Correlates of pool isolation. In Q. Costa Rica, the comparative study of two dry season pools and three wet season sites provided several lines of evidence consistent with the idea that high population densities can affect behavioral and energetic patterns. Reduced feeding activity in the dry season pools relative to the wet season sites, loss of fish condition in the late dry season, and the negative relationship between feeding bout length and fish density, suggest that food was scarcer in the late dry season when pool densities were very high. In addition, there was evidence to suggest that high densities and lower food availability induced a higher incidence of aggression. Over the five sites examined, feeding bout length was negatively correlated with the incidence of aggression.

Observations in tropical floodplain pools suggest similar patterns in which large numbers of fish, crowded together in small pools at the end of the dry season, are inevitably forced to share the food resources. In these systems, such conditions are often reflected in the slowing or cessation of feeding, growth, and fat storage (Johnels, 1954; Lowe-McConnell, 1964, 1975; Welcomme, 1979; Junk, 1985). Similar resource depletion has been observed in some temperate intermittent streams (John, 1964; Larimore et al., 1959).

Poecilia gillii can breed throughout the year if conditions are favorable. However, in Q. Costa Rica, both behavioral observations and the dissection of females indicated very little production of young in the late dry season. Production of young in the late dry season may have been inhibited by high densities, low food availability, and the potential for higher rates of cannibalism which has been related to high densities of young or adults in other poeciliids (Rose, 1958; Thibault, 1974). We conducted our study of Q. Costa Rica in the late dry season when conditions were most severe. The large numbers of very small fish observed in the early part of the study in the pools suggest that fish were producing young well into the dry season. Production of young may cease only in the very late dry season when conditions become particularly extreme.

Hypoxia is widespread among shallow and stagnant fresh waters of tropical regions (Carter & Beadle, 1930; Carter, 1955; Kramer et al.,

1978), and has produced varied responses by fishes including change in activity, increased use of air breathing, increased use of ASR, and habitat shifts (Kramer, 1983, 1987). The major response that we observed in *P. gillii* was increased use of ASR, which accounted for up to 16 % of the activity of large fish in Pool 2. In Pool 5, ASR accounted for 4.6 % of the activity budget of large fish despite the fact that oxygen concentration was much higher than in Pool 2, Pool 4, or Stretch 1. Higher temperatures can increase metabolic demand for oxygen in fishes over certain temperature ranges (Davis, 1975; Cech et al., 1990). Further, it has been demonstrated that the percent time in ASR by *Poecilia reticulata* under laboratory conditions increases with temperature when the partial pressure of oxygen is held constant (Kramer & Mehegan, 1981). Thus, the daily temperature fluctuations averaging 8° and midday temperatures averaging 33 °C in Pool 5 may have increased oxygen demand. ASR was observed less frequently in small *P. gillii*, which may relate to microhabitat differences between small and large fish. Small fish often occupied very shallow peripheral areas in only a few centimeters of water.

Wet season behavior and the benefit of departure. Dry season desiccation of pools effectively isolates subpopulations confined to water on a seasonal basis, and these organisms must tolerate whatever conditions develop in dry season pools. Dispersal cannot regulate densities in such isolated pools, while habitat contraction can increase densities independent of population change. In such systems, motivation to move may increase in the late dry season as conditions deteriorate.

Chapman & Kramer (1991b) found that involuntary flushing during flooding and voluntary departure apparently interacted to produce the observed patterns of dispersal in *P. gillii* in Q. Jicote (a high-gradient, heavily forested tributary of the R. Poza Salada). In Q. Costa Rica the mild flood that we observed and the low gradient of the stream may have minimized the effect of floodwater force on fish dispersal. Downstream movement was detected in Q. Costa Rica and may represent involuntary movement; however, the upstream movement of fish clearly indicated signs of intentional movement. One potential advantage of seasonal exploitation of flooded areas by *P. gillii* is decreased

density in the newly flooded areas. Lower densities may reduce competition for food resources and lower the incidence of aggression. Chapman et al. (1991) found that population size and density of *P. gillii* increased during the dry season in pools of Q. Jicote; however, the average rate of population increase was low immediately after the floods. It was suggested that the availability of detritus and algae was potentially lower after flooding when the streambed has been scoured, light levels were reduced by seasonal leaf flush, and temporarily flooded areas become inaccessible. In Q. Costa Rica, the percentage of time spent feeding and feeding bout length were higher in the temporarily flooded sites than in the two dry season pools. Although temporarily flooded habitats may be scoured by flood waters, it is likely that the much lower densities in these areas reduce both competition for food and aggression. In addition, the low gradient of the upper section of Q. Costa Rica and the mild floodwaters of 1985 may have minimized the scouring effects of the floodwaters, while the high levels of incident light in Q. Costa Rica may produce higher levels of periphyton production than in heavily forested streams like Q. Jicote.

It is interesting that there were marked differences between the permanent Pool 4 in the wet season, which had been inhabited by *P. gillii* throughout the dry season, and the two newly available areas (Stretches 1 and 2). In Pool 4, density was higher, the frequency of aggressive encounters was higher, and feeding activity was lower than in Stretches 1 and 2. Since Pool 4 was occupied all dry season, food availability may have been very low at the onset of flooding. Lower densities in the newly available areas may reflect the costs of leaving a permanent refuge to exploit new habitat. The obvious disadvantage of movement away from a permanent refuge is the possibility of being trapped in a temporary pool when waters fall. The detailed study of dispersal in *P. gillii* in Q. Jicote documented the death of hundreds of fish trapped in desiccating pools (Chapman & Kramer, 1991b). These fish had dispersed from permanent refuge pools during seasonal flooding, but were unable to return when waters fell. In Q. Costa Rica, the lower densities of fish in the newly flooded stretches relative to Pool 4 may reflect the tradeoff between the costs of movement (travel, risk of entrapment) and the advantages

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Wet season behavior and the benefit of departure. Dry season desiccation of pools effectively isolates subpopulations confined to water on a seasonal basis, and these organisms must tolerate whatever conditions develop in dry season pools. Dispersal cannot regulate densities in such isolated pools, while habitat contraction can increase densities independent of population change. In such systems, motivation to move may increase in the late dry season as conditions deteriorate.

Chapman & Kramer (1991b) found that involuntary flushing during flooding and voluntary departure apparently interacted to produce the observed patterns of dispersal in *P. gillii* in Q. Jicote (a high-gradient, heavily forested tributary of the R. Poza Salada). In Q. Costa Rica the mild flood that we observed and the low gradient of the stream may have minimized the effect of floodwater force on fish dispersal. Downstream movement was detected in Q. Costa Rica and may represent involuntary movement; however, the upstream movement of fish clearly indicated signs of intentional movement. One potential advantage of seasonal exploitation of flooded areas by *P. gillii* is decreased

density in the newly flooded areas. Lower densities may reduce competition for food resources and lower the incidence of aggression. Chapman et al. (1991) found that population size and density of *P. gillii* increased during the dry season in pools of Q. Jicote; however, the average rate of population increase was low immediately after the floods. It was suggested that the availability of detritus and algae was potentially lower after flooding when the streambed has been scoured, light levels were reduced by seasonal leaf flush, and temporarily flooded areas become inaccessible. In Q. Costa Rica, the percentage of time spent feeding and feeding bout length were higher in the temporarily flooded sites than in the two dry season pools. Although temporarily flooded habitats may be scoured by flood waters, it is likely that the much lower densities in these areas reduce both competition for food and aggression. In addition, the low gradient of the upper section of Q. Costa Rica and the mild floodwaters of 1985 may have minimized the scouring effects of the floodwaters, while the high levels of incident light in Q. Costa Rica may produce higher levels of periphyton production than in heavily forested streams like Q. Jicote.

It is interesting that there were marked differences between the permanent Pool 4 in the wet season, which had been inhabited by *P. gillii* throughout the dry season, and the two newly available areas (Stretches 1 and 2). In Pool 4, density was higher, the frequency of aggressive encounters was higher, and feeding activity was lower than in Stretches 1 and 2. Since Pool 4 was occupied all dry season, food availability may have been very low at the onset of flooding. Lower densities in the newly available areas may reflect the costs of leaving a permanent refuge to exploit new habitat. The obvious disadvantage of movement away from a permanent refuge is the possibility of being trapped in a temporary pool when waters fall. The detailed study of dispersal in *P. gillii* in Q. Jicote documented the death of hundreds of fish trapped in desiccating pools (Chapman & Kramer, 1991b). These fish had dispersed from permanent refuge pools during seasonal flooding, but were unable to return when waters fell. In Q. Costa Rica, the lower densities of fish in the newly flooded stretches relative to Pool 4 may reflect the tradeoff between the costs of movement (travel, risk of entrapment) and the advantages

of dispersal into lower density areas. Fish leaving dry season refuges may benefit from lower densities and higher feeding potential but run the risk of unsuccessful return to a refuge when floodwaters recede.

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