

COMPETITION AND GROWTH OF
BLUEGILLS, GREEN SUNFISH, AND
THEIR HYBRIDS AND THE POSSIBLE
ROLE OF AGGRESSIVE BEHAVIOR

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THESIS



This is to certify that the

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COMPETITION AND GROWTH OF
BLUEGILLS, GREEN SUNFISH, AND
THEIR HYBRIDS AND THE POSSIBLE
ROLE OF AGGRESSIVE BEHAVIOR
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A handwritten signature in dark ink, appearing to read "E. W. Rodger".

Major professor

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ABSTRACT

COMPETITION AND GROWTH OF BLUEGILLS, GREEN SUNFISH, AND THEIR HYBRIDS AND THE POSSIBLE ROLE OF AGGRESSIVE BEHAVIOR

By

John Andrew Janssen

A series of pond and laboratory aquarium experiments were conducted to determine the competitive relationships of bluegills, green sunfish, and their hybrids and the possible role of aggressive behavior. The aggressive behavior of monospecific and dispecific pairs of sunfish in aquaria was observed. In ponds, growth was used as a measure of relative competitive ability. Aggressive behavior in the experimental ponds was also observed.

Male hybrids of either reciprocal appear to grow at least as well as bluegills and green sunfish and probably better. For bluegill δ x green sunfish ϕ hybrids females grew less than males. No females were found among green sunfish δ x bluegill ϕ hybrids. Green sunfish males also grew faster than females but in bluegills the difference in growth by sex was slight or absent. Male hybrids were usually more variable in size than bluegills.

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In aquaria, hybrids were always dominant over bluegills. Green sunfish were more aggressive than green sunfish ♂ x bluegill ♀ hybrids but about equally aggressive as bluegill ♂ x green sunfish ♀ hybrids. In pairs of bluegills and green sunfish no aggression was observed for about a week, then green sunfish were dominant. No difference in aggressiveness of male and female bluegill ♂ x green sunfish ♀ hybrids was found.

Three types of agonistic behavior were observed in the experimental ponds. One, associated with reproductive activities, has been observed by others. An apparently interspecific hierarchical behavior, not immediately associated with feeding, was observed in spring. In summer fish were observed to defend feeding areas on the bottom.

Based on the results of this study, an hypothesis is developed on the role of aggression and defense of a food resource on the competitive relationships of sunfish.

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INTRODUCTION

Hybrid sunfish have generated much interest among people interested in fish and fisheries. Much of the first work on interspecific hybridization of freshwater fish was on sunfish hybrids (Hubbs, 1955). The early work of Hubbs and his co-workers stimulated the interest of fishery biologists because sunfish hybrids seemed to grow faster than the parent species and they were largely infertile and would not overpopulate lakes and ponds (Hubbs and Hubbs, 1931, 1933). In an effort to explain hybrid vigor on a molecular basis, Manwell et al (1963) studied the hemoglobin of sunfish hybrids. Those interested in phylogenetic relationships have used the viability of interspecific and intergeneric centrarchid hybrid zygotes at various stages of development to demonstrate phylogenetic affinities (Hester, 1970).

This paper is primarily concerned with the hybrids of the bluegill (Lepomis macrochirus Rafinesque) and the green sunfish (L. cyanellus Rafinesque). In this paper, when the name of a hybrid is given the male parent is listed first. A cross between a male bluegill and a female green sunfish is called a bluegill x green sunfish hybrid (hereafter BxG)

and the reciprocal hybrid is a green sunfish x bluegill hybrid (hereafter GxB). For natural populations of hybrids between bluegills and green sunfish in which the sex of the parents is not known the population is referred to as a wild bluegill x green sunfish population.

In my discourse I treat the hybrids as if they were species when discussing topics such as interspecific competition. While a sunfish hybrid is certainly not a reproducing species, it has some of the usual attributes of a species in that it is morphologically and functionally distinct from the parent species.

Hubbs and Hubbs' (1931, 1933) conclusion that hybrid sunfish grow faster than the parent species was based on work on wild populations of pumpkinseed (Lepomis gibbosus (Linnaeus)) x green sunfish, pumpkinseed x bluegill, and bluegill x green sunfish hybrids. Childers (1967) criticized this conclusion as follows: because of similar behavioral and morphological characters, intraspecific competition is usually more intense than interspecific competition. The hybrids were less numerous than the parent species in the ponds that Hubbs and Hubbs studied. Therefore the hybrids were subject to less intraspecific competition and increased growth would be expected. Childers and Bennett (1961) could demonstrate no difference in growth of either green sunfish x redear (L. microlophus (Gunther)) hybrids vs. the parent species or BxG hybrids vs. green sunfish when hybrids and the parent species were stocked

in equal numbers and at densities less than 1300 per hectare. Childers (1967) suggested that high density stocking of equal numbers of parent species and hybrids might be necessary to demonstrate a difference in growth.

Following Childers' suggestion, I studied the growth of BxG hybrids in comparison with bluegills at densities of about 7400 fish per hectare (Janssen, 1972). In that study male hybrids grew significantly faster than male and female bluegills but female hybrids grew significantly slower than bluegills. There was no difference in the growth rate of male and female bluegills. The difference in growth of male and female hybrids was curious. Lewis and Heidinger (1971) found that at densities of about 3700 fish per hectare GxB males grew faster than females when fed artificially. When stocked at about 1300 fish per hectare with no artificial feeding, they found no difference in growth of males and females. W. C. Latta (pers. comm.) found no difference in size between BxG males and females stocked at about 1300 fish per hectare in two Michigan lakes. It seemed that density was an important factor in the relative growth of male and female hybrids between bluegills and green sunfish.

Instances in which male sunfish grew faster than females in wild populations have been reported for green sunfish (Hubbs and Cooper, 1935) and for pumpkinseeds, bluegills, and their hybrids (Hubbs and Hubbs, 1933).

Various workers have reported a tendency for male sunfish to be more aggressive in aquarium situations. Allee

et al (1947) and Greenberg (1947) found that male green sunfish were usually dominant in aquarium hierarchies, but males were also usually larger to begin with. Pumpkinseed males were reported by Erickson (1967) to be usually dominant over females in aquaria. Allee et al (1947) and Greenberg (1947), working with green sunfish, and McPhee (1967), working with pumpkinseeds, found that dominant fish obtained more food and grew faster. Based on these aquarium studies and results from pond studies, I suggested that aggressive behavior may be responsible for the difference in growth of male and female BxG and GxB hybrids under crowded conditions and that aggressive behavior may also be important in interspecific sunfish relations (Janssen, 1972).

Most work on the role of intraspecific and interspecific aggressive behavior in fish population dynamics and growth has concerned salmonids. In salmonids both territorial and hierarchical behavior have been reported: in riffles feeding territories form and in pools hierarchies form (Chapman, 1966). Jenkins (1971) has shown aggressive activities to be important in determining the spatial distribution of trout in streams. Newman (1956) studied the role of interspecific aggression on the distribution of brook trout (Salvelinus fontinalis (Mitchell)) and rainbow trout (Salmo gairdneri Richardson). The interspecific behavior of Atlantic salmon (Salmo salar Linnaeus) and brown trout (Salmo trutta Linnaeus) was studied by Kalleberg (1958). Symons

(1968) reported that aggression and the strength of social hierarchy increased when Atlantic salmon were deprived of food.

Magnuson (1962) studied the relationship between distribution of food and amount of food on aggressive behavior and growth of the medaka (Oryzias latipes Temminck and Schlegel). Medaka were aggressive only when food was limited. When food was clumped the dominant medaka guarded the food, would eat the most food, and grow fastest. If food was dispersed so the dominant fish could not guard it, all fish would grow equally well. The ability to guard a food supply confers definite advantages to the territorial fish.

The nature of agonistic behavior in sunfish has been described in detail by Miller (1963). Certain agonistic behaviors are commonly observed in aquaria. The following list is adapted from my own observations and those of Greenberg (1947), Miller (1963), and Fabry (1972).

1. Lateral (Threat) Display.--One fish turns its side to another and extends its fins. The Lateral Display is usually given when the fish is threatened by another.

2. Frontal (Threat) Display.--The posture is similar to the Lateral Display except the threatening fish faces the other fish. The Frontal Display is often followed by nipping or chasing.

3. Tail Beating.--A pair of fish are parallel and one apparently slaps the other with its tail. Actual contact

is not made.

4. Drive.--One fish chases another in an aggressive manner. Driving may follow a Frontal Display and often bumping and nipping are involved.

5. Attitude of Inferiority.--A submissive fish folds its fins and leans to one side, usually toward the dominant fish. The Attitude of Inferiority is usually given when the fish is threatened.

Other behaviors can be observed and the above behaviors can be analyzed and dissected further. The list includes only the more obvious behaviors and is not intended to be complete.

Greenberg (1947) noted some relations between coloration and hierarchy position in laboratory populations of green sunfish and Fabry (1972) studied the relations intensively. A dominant green sunfish is typically light in color, has little or no barring, and has a white or red iris whereas a submissive fish is dark in color and has a black iris. Iris color is the best indicator of dominance.

In spite of the number of publications on aggressive behavior among sunfish in aquaria, only Fabry (1972) has observed aggressive behavior in the field other than that of the male when defending the nest. Fabry's observation concerned a lone territorial green sunfish in a small Michigan lake. This was the only incident of non-breeding aggression that she observed in three summers of watching green sunfish in the lake.

Typically she saw groups of green sunfish swim by the littoral zone, all in dominant coloration. One interesting aspect of her study was that, except during spawning season, she saw only male green sunfish in the littoral zone. The fish were large (150-180 mm) and males of this size can be recognized by their coloration.

It is likely that aggression among sunfish is more common in aquaria than in the wild because the fish are crowded and a submissive fish cannot escape. It seems unlikely that aggression occurs only in aquaria. That sunfish do have threatening and submissive displays suggests that they must have some function in natural populations. The function and nature of agonistic behavior in natural populations must be a subject of inquiry before much of the meaning of aquarium studies can be understood. It is also important for designing meaningful aquarium experiments.

Among fish, usually the first response of a population to competition is a decrease in individual growth rate (Weatherly, 1963). Sunfish hybrids are morphologically intermediate between the parent species (Hubbs and Hubbs, 1932). As the feeding niche is usually dependent in part on morphology and the feeding behavior is probably intermediate between the two parent species, a hybrid sunfish is likely to have a feeding niche intermediate between that of the parent species. A species that has a niche sandwiched between those of two competing species is at a competitive

disadvantage (MacArthur, 1972). A hybrid is at a further disadvantage because its genotype and phenotype are not the result of generations of natural selection as is the case for the parent species. One way that the hybrid can overcome its disadvantage is through aggressive behavior. It then seems that a sunfish hybrid would grow more slowly than the parent species unless it was more aggressive and could inhibit the feeding of the parent species.

In an effort to explore some of the competitive relations of sunfish hybrids and their parent species, I undertook a series of experiments with bluegills, green sunfish, and their hybrids (BxG and GxB). The experiments dealt with the growth of the sunfish in ponds in which various combinations of the hybrids and parent species were stocked and with the aggressive behavior of fish stocked in aquaria. Two types of experimental ponds were studied. In one type equal numbers of one hybrid reciprocal and one parent species were stocked so that hybrids in each pond were competing with only one parent species. In the other type of pond experiment equal numbers of a hybrid sunfish reciprocal and each parent species were stocked so that the hybrids were competing with both parent species. Experimental aquaria contained pairs of fish, one a hybrid and one of the parent species. As I was also interested in the aggressive relations between BxG males and females, pairs of BxG hybrids in aquaria were also studied.

Before describing the experiments in detail it is useful to briefly examine the genetics of sunfish hybridization. There are a total of 24 pairs of chromosomes in sunfish (Roberts, 1964). Not much is known about sex determination in sunfish as the autosomes and sex chromosomes are indistinguishable. However, Krumholz (1950) suggested that female sunfish are heterozygous for the sex chromosomes because when one sex of a hybrid is less common than the other that is usually the heterozygous sex. In hybrid sunfish the males outnumber the females (Hubbs and Hubbs, 1933; Childers, 1967). Assuming that female bluegill and green sunfish are heterozygous, the chromosomes of bluegills and green sunfish can be listed as:

	Sex Chromosomes		Autosomes
	male	female	
Bluegill	$X_b X_b$	$X_b Y_b$	BB
Green sunfish	$X_g X_g$	$X_g Y_g$	GG

A cross between a male bluegill and a female green sunfish and a cross between a female bluegill and male green sunfish yields:

	Sex Chromosomes		Autosomes
	male	female	
BxG	$X_b X_g$	$X_b Y_g$	BG
GxB	$X_b X_g$	$X_g Y_b$	BG

Note that the males of both reciprocal hybrids have the same autosomes and sex chromosomes and the female reciprocal hybrids differ by the sex chromosomes. Males of the reciprocal hybrids would be expected to be identical in morphology and behavior. Differences between female hybrid reciprocals would probably be due to the different sex chromosome complement. Of course, maternal effects could also influence the morphology and behavior of reciprocal hybrids. If females were homozygous for the sex chromosomes, then female hybrid reciprocals would have the same chromosome complement and males would differ by their sex chromosomes. More work on the nature of sunfish chromosomes will someday, hopefully, provide insights into the nature of sex determination in sunfish.

MATERIALS AND METHODS

The pond experiments and the preparation of most experimental fish were conducted at the Limnological Research facility at Michigan State University, East Lansing, Michigan. Aquarium experiments were conducted in a room in the Natural Resources Building at Michigan State University.

Preparation of Fish

Most experimental sunfish, both hybrids and the parent species, were prepared during June and July, 1972 by stripping eggs and milt from ripe adults collected in the East Lansing vicinity. A few BxG hybrids used in aquarium studies were obtained from the Wolf Lake Fish Hatchery, Mattawan, Michigan. The hatchery fish were the result of natural spawning.

The method of stripping eggs and milt generally followed the procedure outlined by Childers and Bennett (1961). Eggs were stripped into a glass petri dish partly filled with water. A few drops of milt, collected in an eyedropper, were mixed with the eggs. After about a minute the petri dish and eggs were transferred to a 40-liter aquarium and aerated constantly. The eggs were adhesive and



would stick to the bottom of the aquarium and petri dish. Dead eggs were removed via an eyedropper several times daily. After four to seven days the larvae became free swimming and were then transferred to outside ponds. Ponds were 7.3 m square with a gravel bottom and vertical concrete sides. Water depth was about 2 m. A total of six ponds was used, two for each hybrid reciprocal and one each for bluegills and green sunfish. In each pond, larvae were stocked at 100 to 200 fish at a time over a period of a few weeks until about 1000 larvae had been stocked. Most fish remained in the ponds until April, 1973, but about 100 bluegills, green sunfish, and each of the reciprocal hybrids were transferred to indoor storage tanks, about 700-liter capacity, in November, 1972 to be used in aquarium studies.

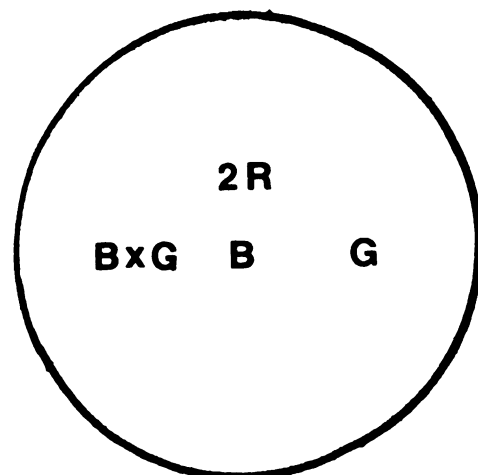
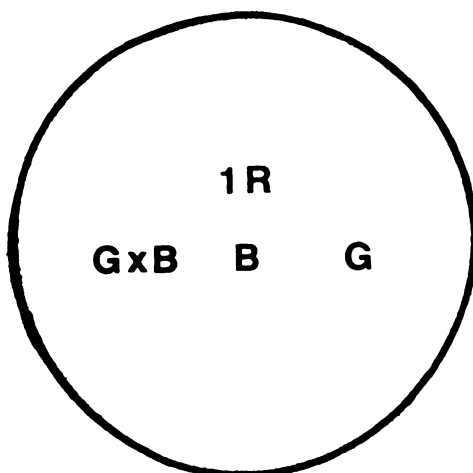
Although I made no attempt to monitor egg mortality, the viability of hybrid zygotes was considerably lower than that of the parent species zygotes. This differs from Childers' (1967) results in which he found little difference in BxG and GxB zygote viability as compared to zygotes of the parent species.

Pond Experiments

Two pond types were used for the pond experiments during 1973. Figure 1 is a diagrammatic representation of the experimental ponds. The eight square ponds (7.3 m square) had a gravel bottom, vertical walls, and were filled to a

Figure 1. Diagrammatic representation of the experimental ponds. Square ponds were 7.3 m square and stocked with 20 of each sunfish type shown for the pond. Round ponds were 13.5 m in diameter and stocked with 25 of each of the sunfish types shown for the pond. B = bluegill; G = green sunfish.

1 GxB B	2 GxB G	3 BxG G
4 GxB B	5 BxG G	6 BxG B
7 BxG B	8 GxB G	



depth of about 1.5 m. Some of the square ponds were used during 1972 to raise the sunfish to be used in these experiments. The two circular ponds were 13.5 m in diameter, had vertical walls and a soil bottom.

Figure 1 also shows the combinations of fish stocked in each experimental pond. Each of the square ponds was stocked with 20 of one of the hybrid reciprocals and 20 of one of the parent species. Each hybrid reciprocal appears with each parent species in two square ponds. Treatments were assigned randomly. Circular ponds were stocked with 25 bluegills, 25 green sunfish, and 25 of one hybrid reciprocal. Lengths and weights of the fish stocked, date stocked, and the date of termination are summarized in Table 1. For each pond I selected fish in a narrow range of total lengths (TL) in hopes of lessening the size variability at the end of the experiment. Fish not used in the pond experiments were transferred to the indoor tanks. These fish were then used in the aquarium experiments.

During 1973 measurements of alkalinity, hardness, pH, and dissolved oxygen were made at approximately two-week intervals. Water samples were collected in the afternoon and determinations made immediately. Additional dissolved oxygen measurements were frequently taken shortly after dawn. Temperatures were recorded on a maximum-minimum thermometer, usually daily. These measurements were taken mainly in the interest of pond maintenance. Previous experience indicated

Table 1. Type of fish, numbers of fish, mean and range of lengths and weights at time of stocking, and stocking and termination dates for the pond experiments. B=bluegill; G=green sunfish.

Pond		Number of fish	Length (mm)		Weight (g)		Term of experiment
			mean	range	mean	range	
1	GxB	20	50.0	(49-50)	1.84	(1.6-2.1)	May 3--
	B	20	50.1	(49-51)	1.54	(1.3-1.7)	Oct. 2
2	GxB	20	45.6	(44-47)	1.34	(1.2-1.7)	April 30--
	G	20	45.3	(44-47)	1.51	(1.3-1.8)	Sept. 27
3	BxG	20	38.0	(37-39)	0.67	(0.6-0.8)	May 7--
	G	20	38.0	(37-39)	0.82	(0.7-1.0)	Oct. 4
4	GxB	20	50.0	(49-51)	1.64	(1.4-1.9)	May 2--
	B	20	50.0	(49-51)	1.46	(1.3-1.6)	Oct. 1
5	BxG	20	42.0	(41-43)	1.04	(0.9-1.1)	May 1--
	G	20	42.1	(41-43)	1.17	(1.0-1.4)	Sept. 29
6	BxG	20	45.1	(44-46)	1.14	(1.1-1.5)	May 7--
	B	20	45.2	(44-46)	1.05	(0.9-1.2)	Oct. 5
7	BxG	20	48.2	(47-50)	1.63	(1.4-1.8)	April 27--
	B	20	48.1	(47-50)	1.33	(1.1-1.6)	Sept. 26
8	GxB	20	42.9	(41-44)	1.02	(0.9-1.3)	April 26--
	G	20	42.9	(41-44)	1.26	(1.1-1.5)	Sept. 25
1R	GxB	25	52.4	(50-54)	1.77	(1.5-2.0)	June 9--
	B	25	52.6	(51-55)	1.61	(1.4-1.9)	
	G	25	52.2	(50-54)	1.98	(1.7-2.4)	Sept. 16
2R	BxG	25	47.0	(45-50)	1.27	(1.1-1.5)	June 10--
	B	25	47.4	(46-50)	1.14	(1.0-1.4)	
	G	25	47.1	(45-48)	1.43	(1.1-1.7)	Sept. 18

that the ponds were subject to somewhat unusual physical and chemical conditions. The ponds are sheltered from wind agitation and are therefore not well mixed. Thermal stratification results, along with high levels of dissolved oxygen and high pH. During late summer oxygen levels can collapse if vegetation dies. In an effort to promote mixing in the square ponds, air was pumped into each via an Air-Aqua aeration system during the night and early morning. The round ponds were not aerated. The square ponds were also fertilized at a rate of about 25 lbs per hectare of a 20-10-5 mixture fertilizer. Pond 2R developed dense stands of Elodea and Potamogeton crispus which threatened to canopy the pond during July and August. I periodically removed sections of the macrophytes by hand. Water meal (Wolffia) was present in ponds 1, 3, 4, 5, and 6 and was periodically thinned manually.

Benthos and plankton samples were taken at two-week intervals. In the round ponds the benthos samples were taken with a 15 x 15-cm Ekman dredge. The Ekman dredge was an inadequate sampler for the gravel bottoms of the square ponds so a Ponar dredge (23 x 22-cm) was used. Samples were washed through a series of screens, the smallest with 12 meshes/cm, and the entire sample sorted by hand picking. Plankton samples were taken at night with a single vertical haul of a #25 Wisconsin "small net" and the contents filtered through a Nytex screen (20 meshes/cm). The Nytex screen retained

Ceriodaphnia sp. (Cladocera: Daphnidae), larger chydorids (Cladocera: Chydoridae), and larger zooplankters but passed small organisms such as rotifers, copepod nauplii and smaller copepodids. Samples were washed from the screen to a petri dish, killed, and counted through a binocular microscope. Samples of the fauna on pond walls were not taken. I examined the walls occasionally while snorkeling. The only organism I observed was Physa (Gastropoda: Physidae).

I conducted seining operations on the square ponds at the end of June and again at the beginning of August. The fish were measured (TL) and quickly returned to the pond. Seining was difficult due to heavy growths of macrophytes, but did yield some information on growth.

Termination of Pond Experiments

Pond experiments were terminated in mid-September for the round ponds and in late September to early October for the square ponds. The exact termination date for each pond is given in Table 1. Each pond was drained as much as possible and the stranded fish collected. Draining required about ten hours for the round ponds and about three hours for the square ponds. The green sunfish had reproduced in all ponds in which they were present. I attempted to collect all the green sunfish offspring in the square ponds but this proved impossible in the round ponds because of the muddy bottoms. I probably also lost a few experimental fish in the mud of the round ponds.

Experimental fish were anesthetized in MS-222 (Tricaine Methanesulfonate), weighed to the nearest 0.1 g, and measured to the nearest millimeter total length. A slip of paper with an identification number was inserted into the fishes mouth and the fish preserved in 10% formalin. The MS-222 solution was strong enough that fish did not regurgitate stomach contents when placed in formalin. Volumetric determinations of stomach contents were made and food organisms identified and enumerated. Young green sunfish were preserved in 10% formalin and those from each pond counted and weighed as a group at a later date. The stomach contents of a few young green sunfish from each pond were analyzed.

Behavior

Behavior was studied mainly in aquarium experiments although some observations were made in the experimental ponds. Pond observations were made when possible and I used polarized sunglasses, binoculars, and snorkeling equipment. The pond methods are more fully described in the results section.

Aquarium experiments were conducted in a series of twenty 20-liter aquaria. Each aquarium was constantly aerated and the bottom covered with gravel. A short section of plastic pipe was placed in each aquarium as a refuge. Between experiments aquaria were drained, rinsed with a light solution of HCl, and rinsed again with 90% Ethanol. A 15 hr light-9 hr

dark artificial photoperiod was maintained. Temperatures varied from 18-20 C. Aquarium experiments were conducted during 1973 and part of 1974.

For an experiment each aquarium was stocked with two sunfish. For experiments comparing aggressiveness in two "species", one of each species was stocked. The following pairs were compared: BxG-green sunfish; BxG-bluegill; green sunfish-bluegill; GxB-bluegill; GxB-green sunfish. Three experiments were conducted to compare the aggressiveness of male and female BxG hybrids. A pair of BxG hybrids was stocked in each aquarium. As I could not determine the sex until the fish were dissected, I depended on chance pairings of males and females for data points. Fish for two of these experiments were fish I produced during 1972; for the third experiment I used fish from the Wolf Lake Fish Hatchery. Fish used ranged from 35-55 mm at stocking except for those obtained from the Wolf Lake Fish Hatchery which were 27-30 mm. Pairs of fish were matched to the nearest millimeter total length and their weights recorded.

Each experiment lasted about five weeks except for the experiment using Wolf Lake Hatchery fish which lasted about 12 weeks. This time period was necessary to allow sufficient growth of fish so that sex could be determined, and sometimes for the two-level hierarchies to stabilize. Fish were fed a dry commercial fish food. For the first three experiments (BxG-green sunfish, BxG-bluegill, and

green sunfish-bluegill), I observed each aquarium five minutes daily. This long observation period proved unnecessary because the dominant fish was readily identified. The dominant fish (alpha) frequently chased the submissive fish (omega) and attacks by the omega were infrequent. Beginning with the fourth experiment (BxG-BxG) I observed each aquarium until the alpha fish was noted, generally every day. When aquaria contained pairs of hybrids I only noted if there was aggressive behavior. When one fish became larger I noted the relative size of the alpha.

At the conclusion of each experiment all fish were anesthetized in MS-222, weighed and measured (TL), and preserved in 10% formalin. In some cases the alpha killed the omega during the experiment and in other cases I sacrificed the alpha when it too severely inhibited the omega's growth. The fish were later dissected and the gonads examined microscopically to determine sex.

RESULTS

Pond Characteristics

Temperatures at the beginning of the square pond experiments (late April) were about 10 C. By early June temperatures rose to about 15 C. From mid-June to early September temperatures generally ranged from 20-23 C and were about 15 C by October. The daily temperatures usually fluctuated about 1 C but as much as 3 C, and there was often as much as a 4 C difference between surface and bottom temperatures.

Pond hardness and total alkalinity were initially about 250 ppm as CaCO_3 but from July to the end of the experiment averaged about 140 ppm. The pH was typically about 9.0-9.5 for square ponds and about 10.0-10.5 for the round ponds. Measured oxygen levels ranged from a low of about 5 ppm to a high of about 16 ppm in square ponds; in round ponds dissolved oxygen was usually near 20 ppm in the afternoon and still supersaturated at dawn.

All of the square ponds except numbers 7 and 8 sustained high densities of macrophytes. Elodea sp. and Potamogeton crispus were the dominant macrophytes and Myriophyllum spicatum was usually present. Pond 7 had only

sparse stands of macrophytes and the filamentous green alga, Cladophora, carpeted its bottom. Pond 8 supported only a few patches of Myriophyllum. The square ponds had periodic blooms of the phytoplankters Ceratium and Volvox. Pond 1R had a dense bloom of Ceratium until August when the water cleared and large stands of Elodea and P. crispus developed. Elodea and P. crispus dominated in pond 2R and, as mentioned above, areas of these macrophytes were removed periodically when they threatened to canopy the pond.

Large numbers of young-of-the-year green sunfish (about 10-50 mm TL) occurred in all green sunfish ponds except 1R. The young green sunfish were observed in these ponds by late June. Pond 1R had only a small population of young green sunfish and I did not detect them until I snorkeled in the pond in August. Bluegills and hybrids did not reproduce.

Pond Food Organisms

The dominant organisms in the benthos were midge larvae (Diptera: Chironomidae) and tubificid worms (Oligochaeta: Tubificidae). Hyalella azteca (Amphipoda: Talitridae) was numerous in ponds 1, 2, 3, 5, and 7. Other organisms usually found in benthos samples included naiads of Siphonurus (Ephemeroptera: Siphonuridae), Caenis (Ephemeroptera: Caenidae), and damselflies (Odonata: Coenagrionidae), larvae of Agraylea (Trichoptera: Hydroptilidae) and

biting midges (Diptera: Ceratopogonidae), and the snails Physa (Physidae) and Gyraulus (Planorbidae). All these organisms except tubificid worms and Caenis were found in fish stomachs.

Zooplankton during May in the square ponds consisted mainly of cyclopoid copepods and ostracods. In early June Daphnia pulex (Cladocera: Daphnidae) and Simocephalus sp. (Cladocera: Daphnidae) appeared in the zooplankton, but by mid-June Daphnia disappeared and Ceriodaphnia appeared. Simocephalus is largely a benthic animal and also attaches to plants and in my ponds often concentrated near walls. My sampling technique was probably inadequate for Simocephalus. In square ponds containing bluegills, Ceriodaphnia usually dominated the zooplankton for the remainder of the experiments. Pond 7 was unusual because it usually had large numbers of Diaphanosoma brachyurum (Cladocera: Sididae), Diaptomus pallidus (Copepoda: Diaptomidae), and sometimes Bosmina longirostris (Cladocera: Bosminidae). These zooplankters occurred in other square ponds, but rarely in large numbers. The square ponds stocked with green sunfish had high numbers of Ceriodaphnia until July when young green sunfish appeared and apparently decimated the Ceriodaphnia populations. Plankton hauls from bluegill ponds typically contained about 100-1000 Ceriodaphnia, but in green sunfish ponds the number of Ceriodaphnia seldom exceeded 20. The young green sunfish had no apparent effect on cyclopoid copepods or on benthic organisms.



Pond 1R had few zooplankters until August when the Ceratium bloom disappeared. Ceriodaphnia, Diaphanosoma, and Diaptomus then dominated the plankton. I observed dense clouds of Simocephalus near the bottom when snorkeling. Pond 2R contained large numbers of Daphnia and Ceriodaphnia in June. These disappeared in July when young green sunfish became numerous and mainly copepods and ostracods remained. Pond 1R was not subject to as intense planktivory by young green sunfish as pond 2R and so maintained higher numbers of Cladocera.

Stomach Analysis

Tables 2-5 summarize the results of stomach content analysis of experimental fish from square ponds. The tables include only the more important items. The results may not be indicative of feeding habits earlier in the experiments as the fish were killed at the end of the growing season.

The foods consumed by hybrids and the parent species is generally similar. However, bluegills consumed large numbers of Ceriodaphnia while only a few hybrids consumed any. Using the Chi-square test (Conover, 1971) to test the null hypothesis that the fraction of fish consuming a food item is the same for both species in a pond, other differences are scattered. As a large number of comparisons can be made, some "significant differences" may be due to chance. In pond 4 a greater fraction of hybrids consumed large (>10mm)

Table 2. Summary of food items found in stomachs of experimental fish in ponds 1 and 4 (bluegill (B) and BxG ponds). Sample=total number of a food item in two benthos or plankton samples; No.=number of fish containing an item; Median and Range in number refer to those fish that contained the item.

POND 1							
Food item	Sample	B (20 fish)			GxB (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	21	2	1.0	(1-1)	2	1.5	(1-2)
5-10 mm	8	0			3	3.0	(1-7)
< 5 mm	13	9	4.0	(1-64)	7	2.0	(1-7)
Zygoptera	37	9	3.0	(1-7)	9	3.0	(1-16)
<u>Agraylea</u>	0	5	1.0	(1-4)	5	4.0	(1-9)
<u>Hyalella</u>	474	18	8.5	(1-118)	19	7.0	(1-117)
<u>Simocephalus</u>	44	12	2.5	(1-19)	11	4.0	(1-43)
<u>Ceriodaphnia</u>	433	18	34.0	(2-402)	2	26.5	(3-50)

POND 4							
Food item	Sample	B (20 fish)			GxB (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	17	3	1.0	(1-3)	11	4.0	(1-33)
5-10 mm	34	6	1.5	(1-2)	7	2.0	(1-8)
< 5 mm	60	18	6.5	(1-85)	9	2.0	(1-4)
Zygoptera	0	4	1.0	(1-1)	1	1.0	(1)
<u>Agraylea</u>	0	3	1.0	(1-2)	6	1.5	(1-2)
<u>Siphonurus</u>	10	15	3.0	(1-6)	15	8.0	(2-64)
<u>Ceriodaphnia</u>	1634	20	417.5	(110-1000+)	7	3.0	(1-29)

Table 3. Summary of food items found in stomachs of experimental fish in ponds 6 and 7 (bluegill (B) and BxG ponds). Sample=total number of a food item in two benthos or plankton samples; No.=number of fish containing an item; Median and Range in number refer to those fish that contained the item.

POND 6							
Food item	Sample	B (20 fish)			BxG (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	195	0			0		
5-10 mm	228	0			0		
< 5 mm	195	14	34.0	(3-78)	16	7.0	(1-109)
Zygoptera	0	4	1.0	(1-1)	11	1.0	(1-6)
<u>Simocephalus</u>	110	13	10.0	(2-101)	17	15.0	(1-279)
<u>Ceriodaphnia</u>	554	14	77.0	(1-1000+)	0		
<u>Ostracoda</u>	66	1	1.0	(1)	8	2.5	(1-30)

POND 7							
Food item	Sample	B (19 fish)			BxG (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	31	0			0		
5-10 mm	4	5	1.0	(1-1)	1	1.0	(1)
< 5 mm	27	11	25.0	(3-101)	7	2.0	(1-8)
<u>Agraylea</u>	17	7	1.0	(1-3)	8	1.5	(1-13)
<u>Siphonurus</u>	8	5	2.0	(1-6)	10	2.0	(1-16)
<u>Hyaella</u>	736	15	5.0	(1-22)	15	4.0	(1-80)
<u>Physa</u>	1	5	1.0	(1-3)	4	5.0	(1-8)
<u>Gyraulus</u>	1	7	2.0	(1-2)	8	2.0	(1-3)
<u>Ceriodaphnia</u>	104	4	4.0	(1-67)	1	3.0	(3)

Table 4. Summary of food items found in stomachs of experimental fish in ponds 2 and 8 (green sunfish (G) and GxB ponds.). Sample=total number of a food item in two benthos or plankton samples; No.=number of fish containing an item; Median and Range in number refer to those fish that contained the item.

POND 2							
Food item	Sample	G (17 fish)			GxB (19 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	0	0			0		
5-10 mm	32	1	1.0	(1)	7	4.0	(1-6)
< 5 mm	13	0			13	4.0	(1-25)
<u>Agraylea</u>	0	2	1.0	(1-1)	7	1.0	(1-2)
<u>Hyaella</u>	38	4	2.5	(1-5)	6	3.0	(1-11)
<u>Physa</u>	28	5	1.0	(1-3)	11	3.0	(1-11)
Terrestrials	-	12	1.0	(1-3)	5	1.0	(1-1)

POND 8							
Food item	Sample	G (18 fish)			GxB (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	0	0			2	2.0	(1-3)
5-10 mm	0	0			3	2.0	(1-2)
< 5 mm	5	1	1.0	(1)	7	1.0	(1-4)
<u>Physa</u>	2	1	1.0	(1)	3	1.0	(1-3)
<u>Gyraulus</u>	2	2	3.0	(1-5)	5	2.0	(1-2)
<u>Simocephalus</u>	5	5	2.0	(1-4)	7	2.0	(1-7)
Cyclopoids	4	6	2.0	(1-8)	11	2.0	(1-12)

Table 5. Summary of food items found in stomachs of experimental fish in ponds 3 and 5 (green sunfish (G) and BxG ponds). Sample=total number of a food item in two benthos or plankton samples; No.=number of fish containing an item; Median and Range in number refer to those fish that contained the item.

POND 3							
Food item	Sample	G (16 fish)			BxG (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	18	3	1.0	(1-3)	3	4.0	(2-6)
5-10 mm	19	2	2.0	(1-3)	2	3.0	(1-5)
< 5 mm	94	3	2.0	(1-3)	7	7.0	(2-39)
<u>Zygoptera</u>	3	3	5.0	(1-8)	3	1.0	(1-1)
<u>Agraylea</u>	1	8	1.5	(1-3)	8	1.0	(1-20)
<u>Siphonurus</u>	0	3	3.0	(1-5)	4	1.5	(1-2)
<u>Hyaella</u>	36	5	10.0	(2-29)	10	3.0	(1-30)
<u>Physsa</u>	147	5	1.0	(1-3)	10	3.0	(1-11)

POND 5							
Food item	Sample	G (16 fish)			BxG (20 fish)		
		No.	Median	Range	No.	Median	Range
Chironomids							
>10 mm	9	0			0		
5-10 mm	103	2	5.0	(1-9)	6	1.0	(1-10)
< 5 mm	256	7	1.0	(1-13)	19	6.0	(1-34)
<u>Agraylea</u>	2	12	2.5	(1-19)	19	2.0	(1-23)
<u>Siphonurus</u>	3	1	1.0	(1)	8	1.5	(1-5)
<u>Hyaella</u>	49	1	1.0	(1)	8	1.5	(1-9)
<u>Physsa</u>	61	4	11.5	(2-20)	2	3.5	(3-4)
<u>Simocephalus</u>	0	6	2.5	(1-4)	13	3.0	(1-9)

midge larvae while a greater fraction of bluegills consumed small (<5 mm) midge larvae ($P < 0.02$ in both cases). A greater fraction of green sunfish than hybrids consumed terrestrial arthropods in pond 2 ($P < 0.05$) and a greater fraction of hybrids than green sunfish consumed midge larvae (all sizes) in ponds 2, 5, and 8 ($P < 0.01$). The most striking difference is in the use of Ceriodaphnia by bluegills and hybrids. In wild populations of bluegills, green sunfish, and their hybrids, Etnier (1971) found hybrids and green sunfish did not use Cladocera while bluegills used them extensively. Etnier found other differences in feeding habits, the main difference being that hybrids and green sunfish consumed larger food items than bluegills. One green sunfish in each of ponds 2, 3, 5, and 2R consumed a young green sunfish. Ostracods and copepods were found only in low numbers in fish stomachs and despite high numbers of Diaphanosoma in pond 7 (about 900 per vertical haul), only a few were found in stomachs.

I had hoped that the round ponds would yield good comparisons of the food habits of hybrids, bluegills, and green sunfish. In pond 1R, however, nearly all fish consumed mainly midge pupae and in pond 2R very few food items were found in stomachs, mainly midge larvae.

I examined the stomach contents of about 15 young green sunfish from each pond containing them. The items found were generally similar to those found in stomachs of

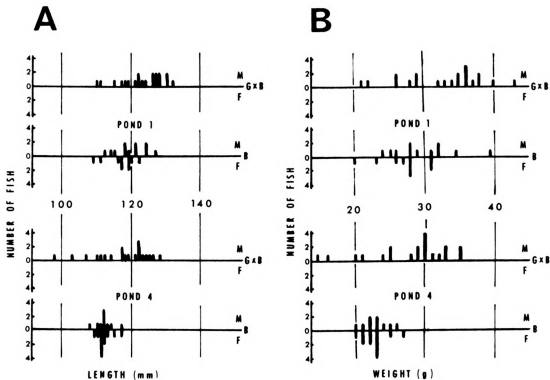
experimental fish and included Hyaletella, naiads of Siphonurus and damselflies, and midge larvae. Large numbers of smaller food organisms were also found including copepods, ostracods, and chydorids. There was, then, overlap in the food habits of the experimental fish and young green sunfish.

Growth of Fish in Ponds

The final lengths and weights of the fish in experimental ponds are shown in Figures 2-7. The figures are arranged in groups of three, A, B, and C: A is the final total lengths; B is the final weights; C is the mean lengths and weights and statistical summary. The Mann-Whitney test (Conover, 1971) was used to compare means. A level of 0.05 was considered statistically significant. A total of 61 two-way comparisons can be made and of these, $0.05 \times 61 =$ about 3 significant differences are expected from random chance.

When results from different ponds are compared, there are some consistencies and inconsistencies between ponds. The BxG males grew significantly larger than BxG females in all ponds except pond 7 which had only two females. The results from pond 7 are inconclusive because of the low number of female hybrids. No female GxB hybrids were found. Male green sunfish were significantly larger than female green sunfish in ponds 2 (length only), 3, 8, 1R, and 2R, but in pond 5 males and females were about the same size. In pond 1 and in pond 6 (length only) male bluegills were significantly larger than female bluegills. Based on these

Figures 2A-C. Results of growth of GxB hybrids and blue-gills (B) in ponds 1 and 4. 2A is the lengths; 2B is the weights (rounded to the nearest gram); 2C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences are not significant at the 0.05 level; underlining with a dashed line indicates that differences are not significant at the 0.01 level. M = male; F = female.



C

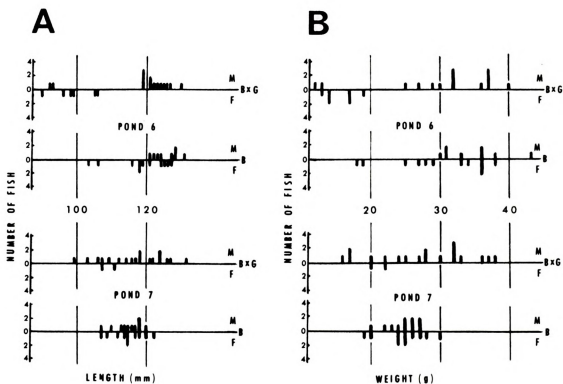
POND 1		
LENGTH (mm)		
GxBd (122.8)	Bd (119.4)	B* (116.7)
(20 fish)	(11 fish)	(9 fish)

WEIGHT (g)		
GxBd (32.6)	Bd (29.8)	B* (26.5)

POND 4		
LENGTH (mm)		
GxBd (116.9)	Bd (112.1)	B* (112.0)
(20 fish)	(9 fish)	(11 fish)

WEIGHT (g)		
GxBd (27.6)	Bd (23.0)	B* (22.7)

Figures 3A-C. Results of growth of BxG hybrids and blue-gills (B) in ponds 6 and 7. 3A is the lengths; 3B is the weights (rounded to the nearest gram); 3C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences are not significant at the 0.05 level; underlining with a dashed line indicates that differences are not significant at the 0.01 level. M = male; F = female.



C

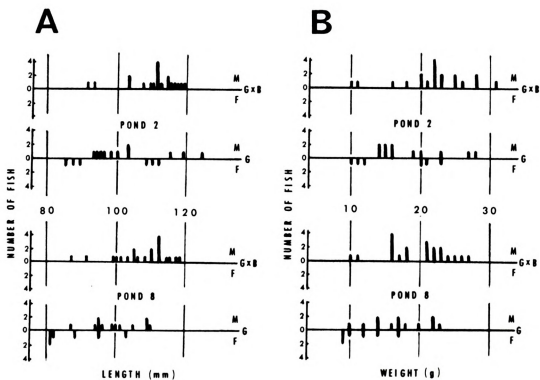
POND 6			
LENGTH (mm)			
Bd (125.4) (8 fish)	Bx0d (118.6) (14 fish)	BW (118.5) (11 fish)	Bx0W (98.8) (6 fish)

WEIGHT (g)			
Bd (34.8)	Bx0d (30.6)	BW (29.4)	Bx0W (15.8)

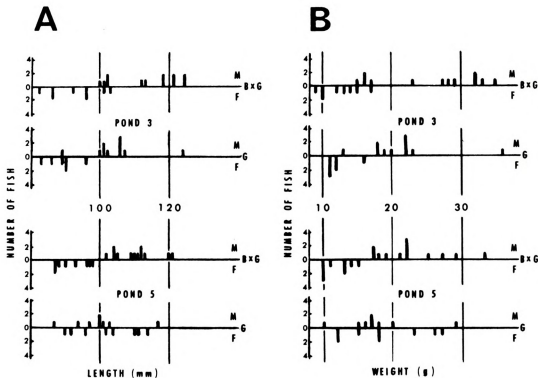
POND 7			
LENGTH (mm)			
Bx0d (116.4) (18 fish)	BW (114.9) (10 fish)	Bd (114.8) (10 fish)	Bx0W (109.0) (2 fish)

WEIGHT (g)			
Bx0d (27.6)	BW (24.7)	Bd (24.4)	Bx0W (20.0)

Figures 4A-C. Results of growth of GxB hybrids and green sunfish (G) in ponds 2 and 8. 4A is the lengths; 4B is the weights (rounded to the nearest gram); 4C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences are not significant at the 0.05 level; underlining with a dashed line indicates that differences are not significant at the 0.01 level. M = male; F = female.

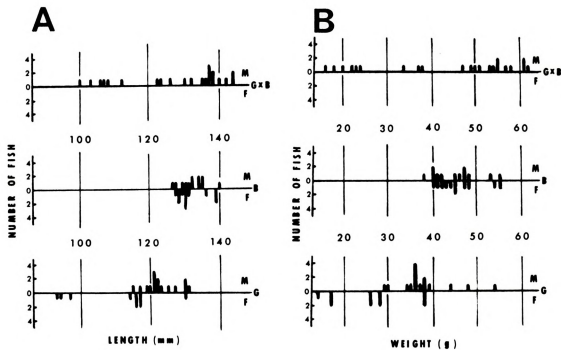


Figures 5A-C. Results of growth of BxG hybrids and blue-gills (B) in ponds 3 and 5. 5A is the lengths; 5B is the weights (rounded to the nearest gram); 5C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences are not significant at the 0.05 level; underlining with a dashed line indicates that differences are not significant at the 0.01 level. M = male; F = female.

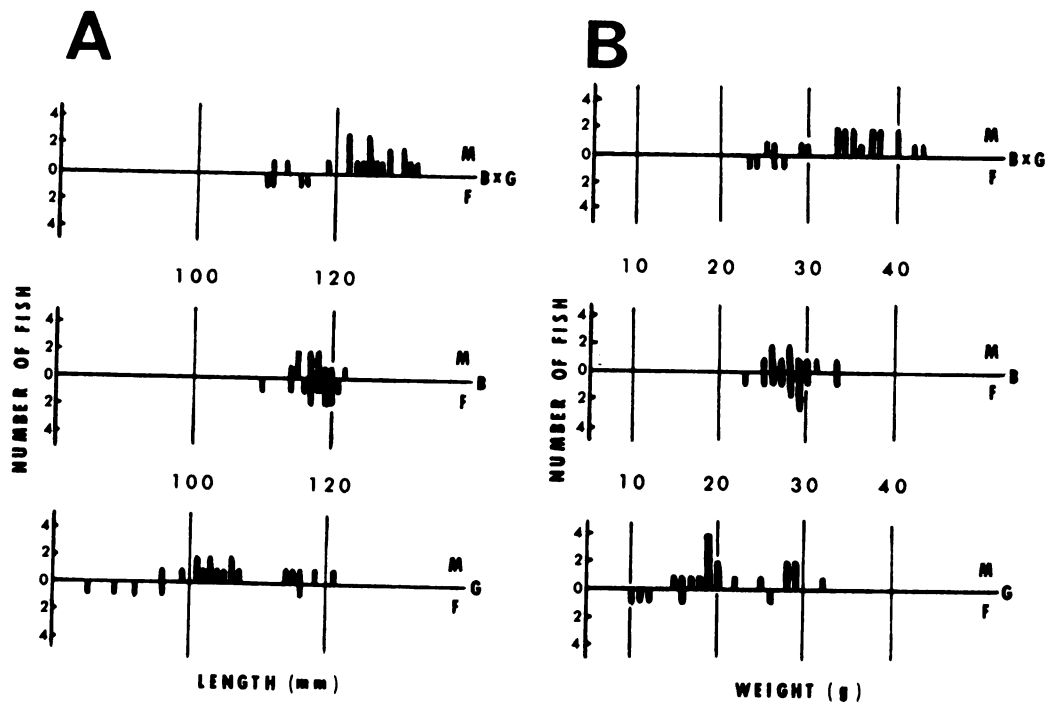
**C**

POND 3			
LENGTH (mm)			
BxGd (113.0) (12 fish)	Gd (104.2) (10 fish)	BxG# (92.8) (8 fish)	G# (89.0) (6 fish)
WEIGHT (g)			
BxGd (25.5)	Gd (21.4)	BxG# (12.4)	G# (12.1)
POND 5			
LENGTH (mm)			
BxGd (110.2) (12 fish)	G# (102.4) (8 fish)	Gd (99.9) (8 fish)	BxG# (92.0) (8 fish)
WEIGHT (g)			
BxGd (22.8)	G# (19.0)	Gd (17.9)	BxG# (12.0)

Figures 6A-C. Results of growth of GxB hybrids, blue-gills (B), and green sunfish (G) in pond 1R. 6A is the lengths; 6B is the weights (rounded to the nearest gram); 6C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences not significant at the 0.05 level; underlining with a dashed line indicates differences not significant at the 0.01 level. M = male; F = female.



Figures 7A-C. Results of growth of BxG hybrids, bluegills (B), and green sunfish (G) in pond 2R. 7A is the lengths; 7B is the weights (rounded off to the nearest gram); 7C is the statistical summary. Statistical analyses were made with the Mann-Whitney test. Underlining with a solid line indicates differences not significant at the 0.05 level; underlining with a dashed line indicates differences not significant at the 0.01 level. M = male; F = female.

**C**POND 2B

LENGTH (mm)

BxGd (19 fish) (124.4)	Bd (10 fish) (117.5)	Bf (11 fish) (117.4)	BxGf (4 fish) (113.0)	Od (17 fish) (106.9)	Of (5 fish) (95.6)
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WEIGHT (g)

BxGd (34.9)	Bd (28.2)	Bf (28.0)	BxGf (25.1)	Od (21.9)	Of (15.2)
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results it seems that in BxG hybrids and green sunfish, males grow faster than females. There is some evidence that male bluegills grow faster than female bluegills, but the difference seems slight.

Male hybrids were significantly larger than female green sunfish except for pond 5 and for pond 2 (weight only). Ponds 5 and 2R were the only ponds in which male hybrids (BxG) averaged significantly larger than male green sunfish. There is no clear pattern in the relative size of female BxG hybrids and male and female green sunfish. In both square ponds (3 and 5), but not on pond 2R, male green sunfish were significantly larger than female BxG hybrids. Female green sunfish were significantly larger than female BxG hybrids in pond 5. In the round ponds female green sunfish were always significantly smaller than any other group of fish and male green sunfish were always significantly smaller than bluegills.

The relationship between bluegills and male hybrids is obscure. Janssen (1972) reported that male BxG were significantly larger than bluegills of either sex. That study utilized the same ponds and fish densities as the present study. The present results do not indicate any large differences in growth of bluegills and male hybrids, but male hybrids are significantly larger than both male and female bluegills in ponds 4 and 2R and significantly larger than only female bluegills in ponds 1 and 6 (length only). The



male hybrid growth seems no less and probably greater than bluegill growth. In ponds 6 and 2R BxG females averaged significantly smaller than bluegills.

Seining operations conducted on the square ponds during late June indicate that both BxG and GxB hybrids averaged larger than bluegills in ponds 1, 4, and 6 ($P < 0.05$ using the Mann-Whitney test). Insufficient fish were seined from pond 7 for statistical analysis. Seining in August was not very successful. It seems, then, that hybrids grew faster than bluegills at the beginning of the experiments.

The bluegills in pond 2R may have been more affected by competition from young green sunfish than hybrids or green sunfish were. The stomach analysis on young green sunfish indicated a high utilization of zooplankters which was also an important food item for bluegills. Previously I noted that young green sunfish seemed to be responsible for the collapse of Ceriodaphnia populations in pond 2R.

One curious result from ponds containing bluegills was that in all ponds except numbers 1 and 6 the male hybrids were more variable in size than bluegills ($P < 0.01$ for weights in ponds 4, 7, 1R, and 2R using the Siegal-Tukey test (Conover, 1971)). The size of green sunfish seems also to be highly variable.

Male hybrids grew less in square ponds with green sunfish than in ponds with bluegills, apparently due to competition with green sunfish offspring. The total biomass



in green sunfish ponds is partitioned below:

Green sunfish ponds

	total biomass	biomass of experimental fish	no. of young green sunfish
2	1055 g	715 g	449
3	1052 g	691 g	769
5	1138 g	663 g	580
8	943 g	466 g	727

and the total biomass in bluegill ponds is:

Bluegill ponds

	total biomass
1	1217 g
4	1008 g
6	1125 g
7	1027 g

When the biomass of young-of-the-year green sunfish is included, the total biomass in green sunfish ponds is similar to that in bluegill ponds. Swingle and Smith (1942) found similar total biomass in ponds stocked with considerably different bluegill densities. Hall et al (1970) reported similar results for ponds containing adult bluegills and their offspring. The present results are consistent with Swingle and Smith's and Hall et al's but are obtained from mixed-species populations. They indicate that young green sunfish competed with experimental fish for food.

Behavior of Aquarium Fish

Table 6 summarizes results from the aquarium experiments. Results for each sex are given only for experiments with aquaria containing pairs of BxG hybrids. There were no

Table 6. Results of aquarium experiments comparing aggressiveness of pairs of fish types. Statistical tests were made using the binomial test (Conover, 1971) on the null hypothesis that each fish type in an experiment is equally aggressive.

Experiment 1-comparing BxG hybrids and green sunfish, 20 pairs.

Dominant BxG - 9

Dominant green sunfish - 11

Conclusion: BxG hybrids and green sunfish are equally aggressive.

Experiment 2-comparing BxG hybrids and bluegills, 20 pairs.

Dominant BxG - 20

Dominant bluegills - 0

Conclusion: BxG hybrids are more aggressive than bluegills ($P < 0.001$).

Experiment 3-comparing bluegills and green sunfish, 20 pairs.

Dominant bluegills - 5

Dominant green sunfish - 15

Conclusion: green sunfish are more aggressive than bluegills ($P < 0.05$).

Experiments 4 and 5-comparing male and female BxG hybrids, 12 pairs.

Dominant male BxG - 6

Dominant female BxG - 6

Conclusion: male and female BxG hybrids are equally aggressive.

Table 6. (cont'd)

Experiment 6-comparing GxB hybrids and bluegills, 20 pairs.

Dominant GxB - 20

Dominant bluegills - 0

Conclusion: GxB hybrids are more aggressive than bluegills
($P < 0.001$).

Experiment 7-comparing GxB hybrids and green sunfish, 20 pairs.

Dominant GxB - 2

Dominant green sunfish - 18

Conclusion: green sunfish are more aggressive than GxB
hybrids ($P < 0.001$).

apparent differences between males and females in other experiments. The table includes a statistical test on the hypothesis that both species in an experiment are equally aggressive (binomial test, Conover, 1971). Aggressive behavior was observed in most aquaria within a day for most experiments. The lone exception was the experiment using a bluegill and a green sunfish in each aquarium. Here it was from 5 to 22 days (median=8) before aggression was observed in an aquarium. Green sunfish and bluegills may not recognize each other as potential competitors or aggressors. Pairs of bluegills or green sunfish in aquaria are usually aggressive within a day (pers. obs.).

Alpha fish were nearly always larger than omega fish at the end of experiments. Exceptions occurred only in the bluegill-green sunfish experiment where in one aquarium a bluegill was dominant and smaller than the green sunfish and in another aquarium a green sunfish was dominant and smaller than the bluegill.

Some alpha fish killed omegas in nearly every experiment. Killing was most severe in hybrid-bluegill experiments; more than half of the bluegills were killed.

In order to obtain sufficient male and female pairs for experiments comparing male and female BxG aggressiveness I had to select small fish as the larger fish in my holding tanks were nearly all males. At the time of these experiments the fish had been indoors for over four months and had



grown. This presents a problem when interpreting results because if growth and aggressiveness are correlated, then fish of nearly equal size should be nearly equally aggressive regardless of sex. I chose fish of nearly equal size for these experiments. In October, 1973 I obtained some small (27-30 mm) BxG hybrids from the Wolf Lake Hatchery to test for differences in aggressiveness of males and females not exposed to holding tank conditions. In this experiment five males were dominant out of six male-female pairs. The results are not statistically significant ($P > 0.20$), but are suggestive.

Hybrids always dominated bluegills. This would lead one to expect that, if aggressiveness was the most important factor in competition, hybrids would always be larger than bluegills in the experimental ponds. Similarly, BxG hybrids and green sunfish should average about the same size and green sunfish should average larger than GxB hybrids. In the round ponds green sunfish should average larger than bluegills. My pond experiments largely conflict with these expectations. The problem of coordinating pond and aquarium experiments is considered further in the discussion.

Pond Observations

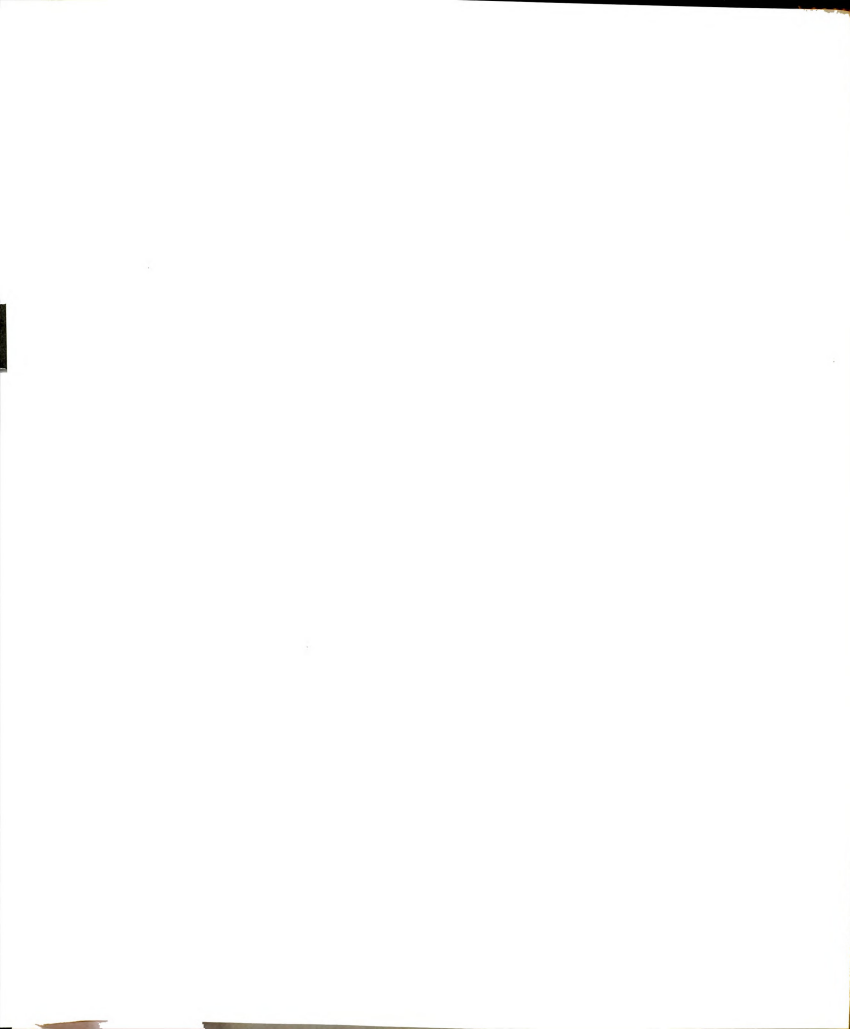
My observations on the experimental ponds are treated here in approximately chronological order. In some of the

square ponds during late May and through June, fish would aggregate near the surface on sunny days. Aggregations could be observed through a careful approach and observing through binoculars. I observed aggregations in all bluegill ponds except pond 7, but only in pond 3 of the green sunfish ponds. The aggregations nearly always contained over 20 fish and as many as 35 so both hybrids and the parent species were present. I observed all of the typical sunfish agonistic behaviors described in the introduction including Drives, Frontal Displays, Lateral Displays, Tail Beating, and Attitude of Inferiority. At one point a GxB hybrid and two bluegills separated from the main group and swam in my direction. The hybrid chased and nipped the bluegills and the trio dispersed. Apparently both hybrids and bluegills were involved in the agonistic behavior. Although fish would occasionally pick food from the surface, they were not feeding actively and the agonistic behaviors were apparently not food related. As sunfish spawn in nests on the bottom, the behavior was probably not related to reproductive activities. Nor did it seem to be territorial; fish often travelled nearly a meter to attack another fish, passing closer fish. The behavior suggests that the fish were forming a hierarchy.

The remaining observations were made in pond 7. They involve behaviors conducted near the bottom. Other ponds were either too weedy or turbid for observations. From late June to mid-July I observed spawning activity in

pond 7. I entered the pond with diving mask and snorkel many times to examine nests but never saw any eggs and offspring were never found. Up to seven nests could be found; both hybrid and bluegill males were guarding them. On July 23 I observed several fish guarding nests and one fish guarding a patch of exposed gravel that apparently was not a nest. This fish appeared to be feeding from the patch when it was not chasing others from the patch. I entered the water and was immediately surrounded by inquisitive fish. There were no eggs on any of the nests, nor on the gravel patch. I picked up some of the Cladophora which carpeted the bottom to examine it. Immediately about six fish began feeding near the exposed gravel, all large hybrids, and within a minute one hybrid chased the others from the patch and proceeded to defend the patch and feed. The Cladophora held large numbers of midge larvae, Hyalella, and Simocephalus. I repeated the experiment of removing a piece of Cladophora regularly until September. During July and early August the result was always the same: within a minute a large hybrid was defending the patch and feeding from it. Toward the end of August often several hybrids occupied a patch of exposed gravel and by September fish were only rarely interested in freshly exposed gravel even though numerous large food organisms were exposed. The fish seemed to be less aggressive toward summer's end.

I could observe feeding in pond 7 in the morning if

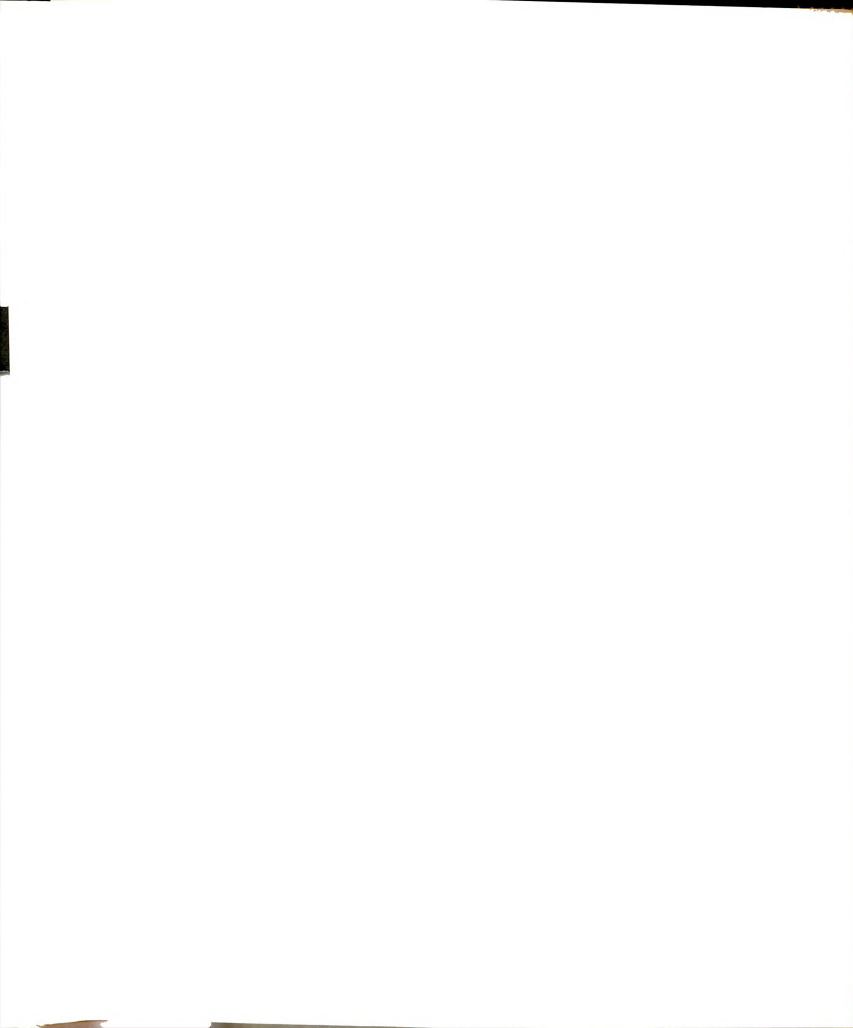


I approached carefully. There was always one group of fish feeding on zooplankton. Ceriodaphnia and Diaphanosoma were numerous at the time. Another group was feeding on the bottom and occasionally driving others from it. Both large and small fish were feeding on zooplankton. Large fish made about 30 feeding movements per minute, small fish made less than five feeding movements per minute. As the bluegills were more planktivorous than hybrids, I suspect that the larger fish feeding on zooplankton were bluegills and the smaller fish were hybrids. The large fish feeding from and defending the bottom were probably hybrids. I observed no aggression between plankton feeding fish.

In a non-experimental pond at the Limnological Research facility, containing numerous green sunfish (50-100 mm), I observed sunfish feeding on the bottom and chasing intruders away. The sunfish defended the area immediately around their feeding position and, upon leaving, another fish would begin feeding in the area. In a park pond in Oakland County, Michigan, bluegills are commonly fed by visitors. When people approach the pond, bluegills "jockey" for a good feeding position and threaten and chase each other. I suspect that this type of behavior occurred in Lewis and Heidinger's (1972) study where males outgrew females when crowded and fed artificially.

In summary, I observed three types of aggressive behavior in my experimental ponds. One, mainly during June,

among fish in aggregations near the surface; the second between males defending spawning nests; and the third among fish feeding from the bottom.



DISCUSSION

A conclusion that hybrids between bluegills and green sunfish grow faster than the parent species is not well supported by the present results. Results from some ponds indicate that male hybrids grew faster than the parent species but results from other ponds are inconclusive. The male hybrids seem to grow at least as well as the parent species. They are also more variable in size than bluegills and about as variable as green sunfish. Green sunfish seem to be competitively inferior when stocked with both bluegills and hybrids.

No female GxB hybrids were found in any of the experiments. For the BxG hybrids, 72% were male. This differs from results obtained by Childers (1967) in which males constituted 97% of the BxG hybrids and 68% of the GxB hybrids. Lewis and Heidinger (1971) had 71% males for GxB hybrids. Janssen (1972) found 72% males for BxG hybrids spawned naturally at the Wolf Lake Hatchery. Parents for Childer's hybrids were obtained from Illinois waters. There may be some geographic variability in the viability of female zygotes.

The fact that the percentage of females is different

for the reciprocal hybrids of bluegills and green sunfish perhaps supports Krumholz's (1950) suggestion that female sunfish are heterozygous for the sex chromosomes. If female sunfish are heterozygous, then reciprocal male hybrids have the same chromosome complement and females differ by their sex chromosomes. The difference in sex chromosome complement in females may explain differences in viability of reciprocal female hybrid zygotes.

The low numbers of female green sunfish in ponds 2R and 1R are unexplained, but possibly due to selection of certain sizes for stocking. Larger sizes of green sunfish were stocked in the round ponds than in the square ponds. It seems that male green sunfish were larger than female green sunfish even before the experiments began.

In green sunfish the males grew larger than females, as was found earlier for GxB hybrids (Lewis and Heidinger, 1971) and BxG hybrids (Janssen, 1972 and present study). Hubbs and Cooper (1935) reported that male green sunfish grew faster than females. In the fish family Cichlidae, males also grow faster than females (Fryer and Iles, 1972). The best studied genus is Tilapia. The mechanism of growth dimorphism seems to vary within the genus, however (Van Someren et al, 1960). In T. mossambica females grow as fast as males when raised in separate ponds and are thus unable to breed. But in T. nigra males grow faster than females even when males and females are raised in separate ponds.

The female green sunfish did spawn in my ponds and the loss of biomass to eggs may have contributed to their lowered growth. However, as noted previously, the female green sunfish seemed to average smaller even when stocked; i.e. before they spawned. For BxG hybrids this explanation is probably inoperative as females apparently did not spawn. It is possible that female hybrids did extrude some non-viable sex products.

My results from aquarium experiments do not support the conclusion that aggressive behavior is responsible for the difference in growth of male and female BxG hybrids. Nor do they seem to explain the results of interspecific competition from the pond experiments. Several aspects of my aquarium experiments can be criticized. Although I maintained fish to be used in the aquarium experiments in large tanks (700-liters) aggressive behavior was pronounced. Many sunfish were killed in aggressive encounters and so the remaining fish were the more aggressive ones. This, and the possible physiological and psychological effects of crowding may have had profound effects on the aquarium experiment results. Also, I purposely selected small fish and I may have selected for less aggressive fish. Results from aquarium experiments are always somewhat suspect because of the artificiality of the environment.

One purpose of the aquarium experiments was to determine the relative aggressiveness of male and female

BxG hybrids. It is possible that the aggressiveness of males depends on the presence of other males. Here it is useful to examine the work of Erickson (1967). Erickson did not report results from statistical tests, so I have conducted tests on his reported data where appropriate. Erickson worked with groups of four pumpkinseeds in aquaria. As with my fish, he could not discern males from females until the fish were sacrificed. Fish were ranked from most dominant to most submissive. Out of a total of 21 experimental aquaria, four contained three males and one female. In each of these the female was most submissive. The probability of this occurring, if males and females are equally aggressive, is $(\frac{1}{4})^4 = 1/256$. Eleven of the aquaria contained two males and two females. Of the 22 males, 16 occupied either the dominant or second most dominant position. If males and females are equally aggressive, the probability of this is $P < 0.05$ (binomial test of the hypothesis that males are as likely to occupy the two most submissive hierarchy positions as the two most dominant positions). In aquaria with three females and one male, a female is dominant in five of six aquaria. Erickson concluded that the effect of maleness in pumpkinseed hierarchies is more pronounced when other males are present. It is likely that the dominance of male BxG hybrids over females also requires the presence of other males.

An important aspect of the present study is that aggressive behavior other than that which occurs while guard-



ing nests does occur among sunfish in pond situations. This behavior seems to be of two types: one is associated with feeding from the bottom and is territorial in nature and one is apparently not associated with feeding and appears to be hierarchical. The effect that these behaviors have on intra-specific and interspecific competition is yet to be determined. I conclude this paper with an hypothesis.

For my hypothesis I require three assumptions:

1. Either aggression does not occur among sunfish feeding on zooplankton or the aggressive behavior of one fish feeding on zooplankton has little effect on the feeding and growth of others feeding on zooplankton;

2. Because benthic organisms such as midge larvae are larger than most zooplankters, sunfish will prefer to feed there and, within a species, those that do feed there will grow faster;

3. A fish feeding on benthos will defend a certain area around its present feeding position and the size of the area will depend on the size of the fish and the density of food.

Results from my observations of aggression in the experimental ponds support assumptions 1 and 3. Also personal observations of groups of five bluegills in 40-liter aquaria indicate that when fed midge larvae on the bottom, two or three fish will defend the bottom while searching for food. When fed Daphnia

all fish fed and no aggression during feeding was observed. The observation of Patriarche and Ball (1949) and Hall et al (1970) that bluegills begin looking for food on the bottom when about 40-50 mm total length supports assumption 2.

I begin with a hypothetical pond stocked only with small (ca 50 mm) bluegills. The fish are crowded enough that some portion of the population is restricted to feeding on zooplankton by more aggressive bluegills defending and feeding from areas of the bottom. Compared to the benthic feeding fish, the plankton feeders are restricted in their growth. As the benthos feeders grow their defended areas increase in size. More aggressive benthos feeders gradually displace less aggressive benthos feeders which now feed mainly on zooplankton and have restricted growth. Eventually some equilibrium is reached and the bluegill population has a wide size range.

If bluegills and some other sunfish species (species X) are stocked and species X is more aggressive than bluegills, the entire bluegill population is restricted to feeding on zooplankton. If aggression among bluegills feeding on zooplankton is non-existent or ineffective, the bluegills will all be of similar size. Species X will show considerable size variability because the more aggressive individuals are feeding on benthos and those less aggressive are feeding on zooplankton. If large and equal numbers of bluegills and species X are stocked, and bluegills are better planktivores

and species X is at least as efficient as bluegills at feeding on benthos, then the least aggressive members of species X will grow more slowly than bluegills and more aggressive members will grow faster than bluegills.

If true, this hypothesis would explain some of the phenomena from my experimental ponds. If species X is a BxG or GxB hybrid, hybrids should be more variable in size than the bluegills, as was found in most ponds. With hybrids, there is the interesting possibility that the hybrids may be less efficient at feeding on benthos than bluegills. In this case it is possible for the plankton feeding bluegills to grow faster than hybrids. Earl Werner (pers. comm.) has found that bluegills raised alone show more size variability than when raised with pumpkinseeds and green sunfish. Here the pumpkinseed is probably species X. Werner's observations indicate that pumpkinseeds feed on the bottom and he observed pumpkinseeds chasing bluegills from the bottom.

That female BxG hybrids may grow less than bluegills (Janssen, 1972 and pond 6 of the present study) need not conflict with the conclusion drawn from aquarium experiments that BxG hybrids are more aggressive than bluegills. If the male hybrids keep bluegills and female hybrids from feeding on the bottom, and the hybrids are less efficient planktivores than bluegills, then female hybrids should grow less than bluegills.

That male green sunfish may restrict females from

the littoral zone is indicated by the observations of Fabry (1972). Fabry observed the behavior of green sunfish in the littoral zone of a small Michigan lake for three summers. Fabry observed females in the littoral zone only during the breeding season.

Aggressive relationships of some salmonids are similar to those suggested here for sunfish. In the ayu (Plecoglossus altivelis Temminck and Schlegel) all fish are territorial when population densities are low and the fish grow well (Kawanabe, 1969). The ayu feeds on attached algae in streams and the individual benefits by defending its food source. At medium densities some fish are territorial and grow well, and the rest school and have poor growth. Newman (1956) found that both brook trout and rainbow trout preferred feeding positions near the bottom in an artificial stream. When both brook trout and rainbow trout were present the brook trout forced rainbow trout into feeding positions near the surface.

The hypothesis can be tested through direct observation of feeding and aggressive behavior of monospecific and multi-specific assemblages of sunfish. Laboratory experiments of intraspecific and interspecific sunfish competition should take account of feeding habits and feeding micro-habitats. That sunfish are aggressive in ponds as well as in the laboratory is now evident. The role of intraspecific and interspecific aggression in sunfish must be determined before much of sunfish population dynamics can be understood.

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