

POPULATION DENSITY, RESOURCE PATTERNING, AND TERRITORIALITY IN THE EVERGLADES PYGMY SUNFISH

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Abstract. The means by which pygmy sunfish compete for food are influenced by the density of the population and the dispersion of the prey as well as by the sex and dominance status of the individual. At all densities when the prey were predictably located in a central clump, males established territories. When prey were dispersed randomly in both the high and low density population, males abandoned territorial behaviour and, like females, swam freely about the aquaria. Only in the intermediate density populations did the males maintain territories and continue to defend resources. Development of a simple cost-benefit model shows that male territorial behaviour is governed to a large extent by economic considerations. Despite these overall patterns, differences in competitive strategies were observed within populations. Dominant individuals tended to possess territories nearest the central patch of prey, and use the most intense and physiologically exhausting displays. Only under the most stressful conditions did they acquire significantly more food than subordinates, and even then these benefits were not translated into increased growth, largely because dominant fish engaged in disproportionately more energy-consuming contests.

One of the most striking features about competition is its diversity of form. Although all animals, when faced with a scarcity of resources, compete by diverting resources from others to themselves for their own reproductive advantage, they often do so by a variety of means. These can range from exploiting common and equally accessible resources, to interfering with each other's access to resources (Miller 1964). Interference can be effected by defending areas and gaining exclusive and prolonged access to resources, by dominating others and gaining priority of access to resources regardless of location, or by contesting resources individually as they are located. Furthermore, aggressive contests can range from peaceful assessments to physical tournaments. It is not therefore surprising that an animal's competitive arsenal is potentially large. With this diversity arises the intriguing problem as to how animals 'choose' particular competitive tactics for particular situations.

Ultimately, animals should choose tactics that maximize their fitness. Usually these will be ones which enable them to acquire the most resources with a minimum of effort or risk. It follows then that characteristics of the resource and of the contestants, by determining the costs and benefits associated with particular behavioural alternatives, should play a major role in influencing the mechanisms of competition.

Some evidence suggests that environmental and social factors do affect the means by which animals compete. For example, Brown's (1964) principle that territoriality should only occur when the energetic costs of defence are exceeded by the energetic benefits associated with the exclusive use of the area, has been corroborated by a variety of field studies on sunbirds (Gill & Wolf 1975), hummingbirds (Feinsinger 1976) and honeycreepers (Carpenter & MacMillen 1976). At least for the sunbirds, flower nectar levels determine the economic feasibility of territoriality. At normal nectar levels the birds defend territories; the savings in energy from reductions in foraging time more than offset the energetic costs of defence. But at higher nectar levels they abandon them when the costs of repelling the increased number of intruders exceed the energetic gains derived from exclusive use of the flowers.

The purpose of this report is (1) to provide further support for the idea of economically motivated territoriality by demonstrating how environmental and social factors, such as prey dispersion and population density, interact to adjust the costs and benefits of alternative competitive tactics, (2) to show how individuals vary markedly in their response — in terms of fighting ability, fighting frequency, and displaying tactics — to changing economic considerations, and (3) to show, by measuring growth, how these different responses can have profound effects on an

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individual's future competitive ability and reproductive potential.

The Fish

The pygmy sunfish, *Elassoma evergladei*, is a small benthic centrarchid about 3 cm long that lives in sluggish waters amongst the submerged vegetation. Adults feed upon small annelids, chironomid larvae, daphnia, copepods, and ostracods (Barney & Anson 1920; Rubenstein, unpublished data). They mature at about one year and rarely live more than three years (Barney & Anson 1920). They do not shoal, and occasionally they establish territories.

The pygmy sunfish was chosen for this study for the following reasons. (1) It is carnivorous and eats only living prey; therefore its diet could be accurately controlled and manipulated. (2) It is small and could be kept in 38-litre aquaria without markedly distorting its behaviour (but see Martin 1975). (3) It is hardy and showed no apparent ill effects associated with transport or experimental handling. (4) It is primarily a benthic fish. The fact that it naturally confines its activity to two dimensions facilitated the manipulation of prey dispersion and the analysis of various aspects of its social behaviour. (5) It normally lives in small ponds that undergo radical seasonal changes in volume, and therefore under natural conditions the pygmy sunfish experiences wide fluctuations in population density.

General Methods

The experiments consisted of raising individually identifiable adult pygmy sunfish at different densities under semi-natural conditions. The fish were collected at the end of July 1976 from the Green Swamp in Brunswick County, North Carolina, and placed in separate containers for two weeks. This period of isolation served to minimize differences in past experience and to allow identification of fish damaged by handling. Then each fish was weighed and sexed. At this time of year males can be distinguished from females because they are darker and have blackish fins. The unique spot pattern of each individual was recorded on fish silhouettes to avoid the need to artificially mark individuals. During the five months of the experiment, no major changes in the spot patterns of any of the fish were observed.

A total of 12 experimental populations were established: two populations of 16 fish, two of eight fish, two of four fish, and six of only a

single fish which served as competition-free controls. Both males and females were divided into two weight classes. From each weight class, equal numbers of males and females were randomly assigned to one replicate of each competitive density. Three males and three females chosen at random were used as controls. Populations were randomly assigned to aquaria. Fish dying during the first half of the experiment were replaced using fish of similar weights taken from holding tanks.

The experimental systems used in this study were similar to those used in previous experiments on pygmy sunfish growth (Rubenstein, in press). Therefore only a brief description will be presented here. Twelve 38-litre aquaria were equipped with under-gravel filters and filled with sterilized stream sand to a depth of 3 cm. Four small clay flower pots and four plastic plants were placed in each aquarium. Each tank was covered with a translucent lid and illuminated by a 15-W cool white fluorescent bulb. All aquaria were maintained on a fixed photoperiod with 13.5 h of light and water temperature was maintained at 25 ± 2 C, simulating the conditions of early summer in the swamps of eastern North Carolina.

The experiments were designed so that the fish at the higher densities would compete more vigorously for food. Therefore each aquarium, regardless of fish density, was supplied with an identical amount of food. The types, abundances, and dispersion patterns of the prey were manipulated. The experimental design was modelled after a $4 \times 3 \times 2$ factorial analysis of variance in which the main effects were population density (16, 8, 4, and 1 fish per tank), relative abundance of two naturally eaten species of prey (20 chironomid larvae (*Chironomus* sp.), 20 Tubifex worms (*Tubifex* sp.), and 10 chironomid larvae plus 10 *Tubifex* worms) and food dispersion (predictably clumped or randomly dispersed).

Placing benthic prey on the bottom of the aquaria both quickly and precisely required a special feeding device. It consisted of 60 quarter-inch (0.63-cm) glass tubes glued into holes in a piece of Plexiglass. The tubes were arranged in six rows of ten columns. The apparatus was loaded by placing it into a 38-litre aquarium filled with water to the same level as the experimental tanks. If the food was to be presented in a randomly dispersed fashion, twenty tubes were selected at random by rolling a die to determine the row and selecting a number from a table of random numbers to determine the column. If the

food was to be presented in a clump, the two most central tubes were selected. The chosen tubes were then corked, and the feeding apparatus was removed from the tank and suspended from ring clamps. Water remained only in the tubes containing corks. Prey were inserted with forceps into the bottom of the tubes containing water. The device was then lowered into an experimental aquarium. The corks were dislodged in two or three seconds, after which the apparatus was removed from the tank. Thus in a total of 5 s, specific food items could be placed precisely in predetermined locations on the sandy substrate. Fish were fed every day, and each feeding arrangement was presented to a population for 20 days. The order of feeding treatments was randomized, and the sequence was: 20 *Tubifex*, clumped; 20 *Tubifex*, random; 20 chironomid larvae, random; 10 *Tubifex* + 10 chironomid larvae, random; 10 *Tubifex* + 10 chironomid larvae, clumped; and 20 chironomid larvae, clumped.

After the last feeding of any experimental treatment the fish were given one day to empty their digestive tract before being removed, identified, and weighed. They were returned to their aquaria within 1–2 h, depending on the size of the population, and were permitted to re-acclimatize to the experimental units for another day before the initiation of the next feeding treatment.

Only during the last eight feeding days were feeding and social behaviour recorded. The first twelve feeding days allowed the fish to adapt to the new feeding regime. All feeding and social behaviour that occurred during a 10-min interval beginning with the removal of the feeding apparatus was recorded on video tape. My verbal accounts of the activities were also recorded. Two 10-min control periods were recorded at non-feeding times for each treatment. The level of activity during these periods was generally lower, but the patterns of social behaviour did not differ from those occurring immediately after feeding. In the discussions that follow, the data from the first two feeding treatments, 20 *Tubifex* in a clump and 20 *Tubifex* dispersed randomly, will be presented in detail. The results from the other feeding treatments, in which the relative abundance of the prey species was changed, will be mentioned either to emphasize similarities or to stress differences.

Description of Behaviour

The pygmy sunfish performs most feeding, locomotory, and social activities within 5 cm of the

bottom of the aquarium. When feeding, a fish approaches prey slowly and obliquely from the side. As it approaches the prey item, it tilts its head downward, focusing on the prey with only one eye. After a brief period of time, while only a few centimetres from the prey, the fish will lunge, grasp the item in its mouth and swim away. Pygmy sunfish appear to respond to prey items from as far as 10 cm away. While approaching particular prey items, fish often will pass by other prey items even if they are of similar size and of the same species.

When pygmy sunfish move about, they dart forward in short, rapid bursts. During forward swimming, body undulations propel the fish, while dorsal, anal, pectoral and pelvic fins are held against the body. These fins are spread to stop. In aggressive situations this pattern of forward motion is sometimes modified slightly; these modifications will be discussed below.

Elassoma are not highly social fish and do not aggregate or form schools. Instead, each individual moves about independently of others in the aquarium. Aggressive interactions occur often, especially over contested food items. Such interactions are not limited to males: fights involving females or members of both sexes are not uncommon.

The form of aggressive contests is highly variable. An interaction usually begins with one or both opponents swimming rapidly forward. The initial approach is usually directed toward the flank or head of the opponent. At other times, one or both fish may sidle (Miller 1963) towards the opponent's flank. During this approach, the caudal fins are maximally spread, the dorsal fin is held erect, and the pelvic fins are spread and extended perpendicular to the ventral surface. Meanwhile, the pectoral fins are vigorously vibrated and serve to move and orient the fish. In very intense situations, a fish may slightly alter the form of the sidle approach by allowing its tail to droop or it may slowly ruffle or rapidly vibrate the caudal fin.

Many responses may follow these approaches. The opponent may flee, it may turn and sidle towards the attacking fish, or it may remain motionless in place. If the interaction continues, the contestants, usually within 2 cm of each other, exchange displays in sequence. One animal may sidle forwards while the other sidles backwards. Alternatively, one animal may lunge and nip the other, inducing either a retreat or a lunge and nip by the opponent. During some interactions, one or both fish will remain motionless

for long periods; then one fish will raise and lower the dorsal fin while moving the pelvic fins alternately up and down in a scissor-like motion. The responses of opponents to this semaphore movement are highly variable and include retreats, lunges, sidle withdrawals, sidle approaches, with and without caudal fin vibrations, as well as continued motionlessness. Colour changes, to shades ranging from light tan to dark blue-black may accompany any of these displays, especially the sidle approach. If one contestant withdraws, either by sidling away or by rapidly retreating, the interaction is terminated, although it is not uncommon for the withdrawing fish to be pursued and involved in another aggressive interaction.

Reproductive behaviour is similar to aggressive behaviour but involves characteristic bobbing behaviour that is only directed by males to females. In male-female aggressive interactions, males sidle up to a female and move their fins in semaphore patterns, but if they want to court the female and have her follow, males bob rapidly up and down. Bobbing is characterized by repeatedly raising the head and lowering the tail, then lowering the head and raising the tail. When males swim away from the female in a bobbing display with the female following, males undulate in the vertical plane.

Spatial Dispersion and Resource Defence

Under certain conditions, many mammals (Smith 1968; Koford 1957; Neville 1968), birds (Hailman 1960; Yeaton & Cody 1974; Stiles & Wolf 1970; Gill & Wolf 1975; Wiley 1973), reptiles (Rand 1967), and fish (Magnuson 1962; Jenkins 1969; Keenleyside 1972; Symons 1974) restrict their aggressive activities to particular areas in order to control resources. In this section, I investigated the conditions affecting the pygmy sunfish's use of space by examining: (1) whether patterns of spatial dispersion are affected by population density and resource dispersion, (2) whether these patterns are similar for males and females, and (3) whether these patterns remain constant or change depending on whether an animal is feeding, fighting, winning, or just moving about.

Methods

Video-taping all of the feeding and social behaviour of the fish in a population provided an accurate record of where each fish travelled, fought, won contests, and captured prey. Maps of the aquaria were drawn and divided into

thirty quadrats, each 40 cm². By treating the edges of the aquarium bottom as an abscissa divided into 10 equal compartments, and as an ordinate divided into three equal compartments it was possible to give each quadrat an X-Y score. Then, by stopping the videotapes every 30 s, it was possible to sample and spatially score all aspects of a fish's behaviour. At the end of each 10-min period, a fish would have twenty X-Y scores. From the 120 measurements obtained for a feeding treatment, inferences could be drawn regarding a fish's overall pattern of space utilization. In a similar fashion, the location of every aggressive interaction, victory, and captured prey item was given the X-Y scores of the quadrat in which the activity took place.

Using these data, it was possible to determine objectively, using a multivariate analysis of variance, whether individual fish formed territories or used space in some other way. Just as an analysis of variance tests whether the means of two univariate samples are significantly different, a multivariate analysis of variance determines whether the centroids of a multivariate distribution (bivariate in this case) are significantly different. To show that fish in a population have established territories entails rejecting the null hypothesis that there are no significant differences among their bivariate spatial distributions. This technique was applied to spatial distributions associated with general, aggressive, and foraging activities of fish in the different populations.

Results

The multivariate analyses of variance revealed that a variety of factors influenced the ways in which pygmy sunfish use space. Table I shows that sex is the most important factor determining whether a fish will establish a territory. Regardless of the experimental conditions, females never established areas of preferred use. Within a population, females showed no significant differences with respect to where they swam or rested, behaved aggressively, defeated conspecifics and, in all but one case, captured prey.

The pattern of spatial dispersion for males of a population was more complex and was affected by the spatial dispersion of the prey as well as by the density of the population. Table I shows that regardless of the population density and the relative abundance of the two prey species, when the prey repeatedly appeared in a centrally-located clump, males partitioned space, restricting their movements to separate areas of the

aquaria. Figures 1-3 show the overall patterns of male dispersion for each density when *Tubifex* worms were presented in a centrally-located clump. Although adjacent males often overlapped in their use of space, especially at the higher densities, males tended to limit their general activity to areas smaller than the total substrate. In high and intermediate density populations, male aggressive activity also was confined to particular areas (Table I). As these areas are virtually identical, males apparently successfully defend their preferred areas of activity. Only during feeding, when the males were drawn to the clumped prey, were there no significant differences in their patterns of space utilization. Since there are only two males in the low density populations, it is not surprising that their aggressive areas overlap (Table I).

It is interesting to note a relationship between an animal's aggressive ability and the quality of the territory it holds. In all the feeding treatments involving clumped prey, the four highest-ranking males in the high density population, those hav-

ing dominated the greatest number of conspecifics or those having won the greatest proportions of their encounters, acquired the territories closest to the area where the clumped prey was predictably located (Fig. 1B). The other males had peripheral territories, some of which did not even intersect the feeding area (Fig. 1A). The central territories were considered of higher quality than the peripheral ones, not only because of their proximity to the food but also because, as a group, the four males occupying the central territories (in each replicate) acquired more food when *Tubifex* was presented in a clump than did the males with the peripheral territories (see correlation in Table VIII).

At some densities, the pattern of male spatial dispersion changed when the prey were dispersed randomly. Males in both the lowest and highest density populations no longer remained spatially segregated; they showed no significant departure from random dispersion with respect to their general, aggressive, and foraging activity (Table I). Only in the intermediate density popu-

Table I. Analysis of Spatial Dispersion of Various Activities under Different Feeding Regimes. Null Hypothesis Was that Fish Did Not Concentrate their Activity to Particular Areas of the Aquaria

Density	Replicate	Sex	Situation	<i>Tubifex</i> clumped	<i>Tubifex</i> random	<i>Chironomus</i> random	<i>Chir./Tub.</i> random	<i>Chir./Tub.</i> clumped	<i>Chironomus</i> clumped
16	B	M	All	62.8***	1.1	1.2	0.8	43.6***	58.2***
			Fights	9.6***	0.7	1.6	1.0	19.3***	10.2***
			Wins	8.7***	0.8	0.6	0.9	11.2***	6.5***
			Food	NV	1.8	0.3	0.7	NV	0.3
	B	F	All	0.7	0.4	0.6	0.4	1.4	0.9
			Fights	1.2	1.3	0.8	1.6	1.8	0.7
			Wins	1.3	1.8	1.1	1.4	0.9	1.7
			Food	NV	0.7	0.7	0.9	1.1	NV
8	B	M	All	50.5***	108.2***	92.1***	68.9***	60.1***	42.6***
			Fights	3.1**	14.6***	11.7***	12.6***	5.5***	4.2***
			Wins	4.3***	11.8***	15.9***	10.8***	7.2***	5.9***
			Food	0.9	15.1***	12.3***	12.0***	0.7	1.1
	B	F	All	0.9	2.1	1.7	2.0	1.1	0.8
			Fights	0.7	1.4	1.1	0.9	0.5	1.2
			Wins	0.8	0.6	0.9	0.6	0.7	1.0
			Food	0.5	0.9	1.0	0.5	0.7	0.9
4	A	M	All	57.0***	0.1	0.5	1.1	46.2***	37.6***
			Fights	2.7	0.1	0.3	0.5	1.3	2.1
			Wins	1.7	1.8	2.0	1.6	2.1	1.4
			Food	2.5	0.2	0.7	1.3	1.6	1.9
	A	F	All	2.6	0.5	0.6	1.1	1.9	2.2
			Fights	0.9	0.2	0.9	0.4	0.8	1.1
			Wins	1.7	1.3	1.7	0.9	1.5	0.8
			Food	3.9*	3.1	2.0	1.7	2.0	1.2

Numbers in feeding treatment columns are *F* values based on the Hotelling Trace. Significance: **P* < 0.05, ***P* < 0.01, ****P* < 0.001. NV means that there was no variation among individuals in the population.

lations did males continue to limit their activities to particular areas even after the pattern of prey dispersion was switched from clumped to random. Moreover, these males established 'feeding' territories (Table I).

Although the general nature of territoriality in the intermediate density populations was not altered by changes in the patterning of the resource, several aspects of the territories themselves were changed (Table II). There were significant shifts among males with respect to the spatial components of general and foraging activity, but not with respect to those of aggressive activity. Most of these changes involved territorial separations resulting from the abandonment of a central focus of activity. A major change occurred when two males exchanged territories (Fig. 2). But even with these rearrangements, the locations of the four territories changed little after the pattern of prey dispersion was altered.

Changes also occurred in the details of territoriality in the high density populations at the end of the experiments, when the prey were again presented in a predictable centrally-located clump. Of the four central positions found to be occupied in each replicate, at the end of the experiment a total of three (38%) were held by

previously subordinate males (e.g. male 41, see Table VII). As before these central males, as a group, were the most successful in aggressive encounters and in acquiring food. Apparently, individual competitive abilities changed during the intervening feeding conditions.

Discussion

The pattern of prey dispersion exerted a strong influence on the pattern of male spatial dispersion, but the nature of this influence differed among densities. At low and high densities, males maintained territories when the food was clustered in one location but ranged freely when prey were randomly distributed about the substrate. At the intermediate density, males maintained territories regardless of the dispersion pattern of the prey. The generality of these patterns is supported by the finding that even after 63 days of prey appearing randomly distributed, the territorial behaviour of the males reappeared in the high and low density populations when prey again predictably appeared in one centrally-located patch. Individual locations changed, but these changes can be accounted for by changes in

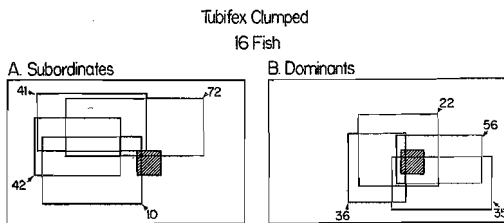


Fig. 1. Maps of male territories in population 16B. The rectangles represent ± 1 standard deviation, in both the X and Y direction, about a fish's centre of activity (centroid). The rectangle corresponds to the area where a fish spent 67% of its time. Each territory is labelled with the identification number of the fish holding it. The hatched area represents the predictable location of the clumped *Tubifex*.

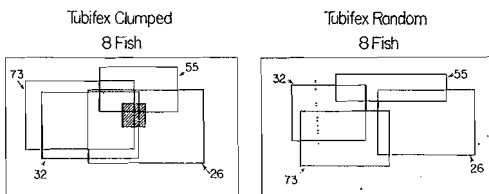


Fig. 2. Maps of male territories in population 8B.

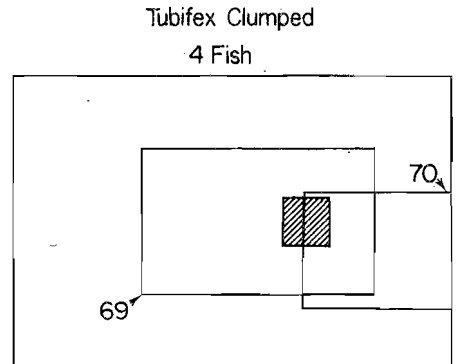


Fig. 3. Maps of male territories in population 4A.

Table II. Comparison of the Spatial Pattern of the Males of Population 8B under Clumped and Random Presentations of *Tubifex*. Null Hypothesis was that a Male Did Not Change its Area of Activity

Fish no.	All	Fights	Wins	Food
73	20.7***	1.3	4.6*	1.8
32	12.7***	3.0	2.9	7.4*
26	7.0**	0.7	1.2	10.9***
55	0.7	2.2	0.4	20.8***

Numbers in activity columns are *F* values based on the Hotelling Trace.

Significance: **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

competitive ability that arose under the different feeding regimes (see below).

Are these changes in spatial dispersion consistent with an economic interpretation of territoriality? In order to answer this question a simple model was constructed to predict minimum utilization rates for economical territorial defence and against which to compare actual utilization rates.

The pygmy sunfish in these studies only exhibited two types of foraging behaviour: territorial defence of the resource or continuous searching for the resource. For territorial defence to be economically feasible

$$B_T \cdot R_T > B_S \cdot R_S \quad (1)$$

where B_T and B_S are the gross benefits of territorial and searching foraging behaviour respectively, and R_T and R_S are the respective cost reduction factors associated with each foraging technique. A cost reduction factor of the form $1 - (C/[C + M])$, where C represents energetic expenditures on competitive activities associated with resource acquisition, and M expenditures on all other activities such as maintenance, growth and reproduction, would be suitable because it takes a value of 1 (no reduction) when there are no costs associated with resource acquisition and a value of 0 (total reduction) when 100% of the energy budget is devoted to such activities. Furthermore, given that the gross benefits to an individual can be expressed as some proportion of the total food available to the population (F), the net gain inequality can be rewritten as

$$\alpha F \left(1 - \left[\frac{S}{S + M} \right] \right) < \beta F \left(1 - \left[\frac{T}{T + M} \right] \right) \quad (2)$$

where α and β represent the proportion of the food acquired by a searching and a territorial fish respectively, and S and T are the respective costs of competing for food by searching or by establishing and maintaining a territory. Since the costs of territorial aggression can be expressed as a function of the costs of non-territorial aggression ($T = \gamma \cdot S$ where γ represents the conversion factor) the inequality simplifies to

$$\frac{M}{S} < \frac{\beta - \alpha\gamma}{\alpha - \beta} \quad (3)$$

From my detailed time budgets and measurements on the cost of activity in small fish (ranging from 1.5 to 4 times resting levels (Prosser 1973))

it appears that 30–40% of the energy budget of a non-territorial pygmy sunfish is devoted to searching and contesting food items. Although this is likely to be an overestimate (Li & Brocksen (1977) found that the expenditure by juvenile salmon was 20–30% of the energy budget), it provides a conservative M/S ratio of 1.5. After substituting and rearranging, the net benefit inequality simplifies to

$$\beta > \frac{\alpha(1.5 + \gamma)}{2.5} \quad (4)$$

In other words, territoriality will only be feasible if the proportion of the resource a territorial individual can acquire is greater than $(1.5 + \gamma)/2.5$ times what it could have obtained by not being territorial. And as γ , a measure of the relative magnitude of the costs of territorial aggression to non-territorial aggression increases, the resource gains necessary to make territoriality economically viable increase.

From the data it is possible to estimate γ and α and hence predict what β is necessary for territoriality to be economically viable. As a first approximation we will assume that the cost of aggression is proportional to the number of fights an animal is involved in. From Table III it appears that 10% fewer fights occurred when fish maintained territories when prey were randomly dispersed than when prey were presented in a clump; thus $T_R = 0.9T_C$. Similarly, 30% fewer fights occurred when animals abandoned the territorial defence of a clumped resource and searched for dispersed prey; thus $S_R = 0.7T_C$. Combining these relationships produces $T_R = 1.3S_R$: hence $\gamma = 1.3$ for situations of random prey dispersions. If we assume that when searching for randomly distributed prey fish will have an expectation of deriving an equal and average share of the total food available, then $\alpha = 1/n$. Only at the intermediate density did the males maintain territories when prey were randomly

Table III. Means and Standard Errors of the Number of Fights per Treatment for Three Clumped and Three Random Feeding Treatments

Density	Clumped		Random	
	Mean no. fights	SE	Mean no. fights	SE
4	154.7	17.4	83.3	7.5
8	166.0	12.5	144.7	12.4
16	386.3	7.5	257.3	11.0

distributed. By substituting $\gamma = 1.3$ and $\alpha = 1/8$ into equation (4), $\beta \geq 0.14$ for territoriality to be economically feasible. That the territorial males in the intermediate population acquired 0.18, 0.16, 0.18, and 0.09 of the randomly distributed resource demonstrates that three males defending territories derived net energetic benefits by doing so; the fourth male may have been 'defending' his territory only because his movements were being curtailed by the activities of the other territorial males.

It is more difficult to ascertain whether the male territorial defence of clumped prey is consistent with an economic interpretation. All males defended territories under these conditions so there are no data on the level of non-territorial aggression. However, if conservatively we assume that the level of non-territorial aggression when the prey are distributed at random would have been only 10% lower than the level of non-territorial aggression when prey were clumped, then γ for the clumped situation is again 1.3. Table IV shows the threshold values of β and the actual proportions of food acquired by males of each density.

As in the case of randomly dispersed prey, three of the males at the intermediate density established economically viable territories. Similarly, four of the males in the high density population maintained economically viable territories. But in the lowest density population, males were defending territories despite the fact that they appeared to be an economic liability — from an energetic perspective. Thus it appears that when food was scarce at least 50% of the males in each population established territories in accordance with economic considerations. Nevertheless, the intriguing problem remains as to why some males appeared to behave in an 'irrational' way when establishing territories. At least for populations experiencing some competitive stress (intermediate and high densities), it appears that the economically viable actions of some members, those

defending the central areas, constrain the actions of other members. Since the way in which these constraints arise is related to individual variation in competitive ability it will be discussed below.

The results clearly show that population density and resource patterning interact to influence the costs and benefits of alternative competitive tactics. Determining exactly how this interaction actually influences the economic feasibility of behaviour is difficult. In the intermediate density population changes in the distribution of food from clumped to random increased the benefits of territoriality slightly and also reduced the costs of territorial defence. Thus it is not surprising that territorial behaviour, once established when the prey are clumped, is maintained when the prey are distributed at random. In the high density populations, however, had the males maintained their territories established during the clumped prey dispersion, they would have on average received 2.0 prey items/day, which would have been more than the theoretically required ration of 1.5 prey items/day (0.075×20 items) for territoriality to be economical. Furthermore, if the costs of territorial aggression would have decreased slightly, as they did in the intermediate density population, then the high density males should also have maintained their territories. That they did not suggests that under the changed conditions the costs did not decrease, and/or the expectation of receiving the minimum number of worms was not fulfilled. By imagining that each male initially maintained his same territory during the initial presentation of randomly dispersed prey, it is clear that there were large daily differences in the rate of prey appearance among territories; some territories received no prey for four consecutive days. Given such variances it might be that low marginal success rates in relation to the higher marginal success rates derived from the previous prey dispersion or from sampling outside the territory, induced males to abandon territorial behaviour. Furthermore, in the territories receiving higher than average prey, attentive free-swimming females and 'sampling' males might also have locally depleted the resource before the resident obtained its critical ration, or have made the defence of the ration extremely expensive. Both these factors could have induced the males to abandon their territories. Although observations during the acclimatization period (first 12 days) after the prey dispersion change support these hypotheses, manipulations are needed before they can be evaluated.

Table IV. Comparisons of Predicted Threshold Values of Economical Territoriality and Actual Proportions of Food Acquired by Males for Each Density

Density	Predicted values	Actual values
16	$\beta > 0.075$	0.12, 0.12, 0.09, 0.08 0.05, 0.05, 0.02, 0.02
8	$\beta > 0.14$	0.17, 0.16, 0.15, 0.09
4	$\beta > 0.29$	0.25, 0.22

Despite the fact that a majority of males in populations experiencing moderate levels of competition appeared to use economic considerations in deciding their competitive behaviour, it would be wrong to state unequivocally that territoriality in the pygmy sunfish is influenced by the economics of energy acquisition. If food resources were the only factor influencing the decision to be territorial, then why were females never territorial? Certainly individuals of both sexes will be selected to maximize their reproductive success, but in doing so their energy needs and strategies of acquiring this energy may be different. In effect males are most probably attempting to maximize the number of matings they can achieve. Thus acquiring more food, growing quickly to a large body size, establishing dominance, and attracting large numbers of females all become inter-related and almost certainly will be facilitated by the male defending a food resource that he and all the females require. If the defence of the food can be accomplished economically, the male will not only derive a disproportionate immediate energetic benefit but a reproductive one as well. If the defence of the food resource can only be accomplished at a net gain which is less than a non-territorial strategy, it may still pay, in an evolutionary sense, for him to defend the territory as long as the reproductive gains of doing so exceed those of the more energetically economical strategy. Of course as the net gains become much less than the alternative strategy, or even negative, the long-term costs in terms of diminished future reproductive success would select against the establishment of energetically uneconomical territoriality.

Females, on the other hand, are most probably trying to invest as much of their resources in offspring as possible. Thus they will attempt to maximize food intake but by minimizing expenditures on swimming and fighting, and by reducing chances of risk. As a result it is not surprising that females, by being involved in only approximately 10% of the fights, and acquiring almost as much food as the males (approximately 90%), grow as quickly as the best males. Thus because of sexual differences in the allocation of resources to mating and parental activities, defence of a food resource is always important to males as energy maximizers, but rarely so for females as cost minimizers. Whether or not males exhibit territorial behaviour, however, appears to depend on the relative costs and benefits associated with exclusive control, which in this

system at least are affected by population density and resource patterning.

It should be noted, however, that although male territories may not be strictly related to food, they are probably not strictly related to mating either. If they were only for mating they should have persisted at all densities as the prey dispersion changed from clumped to random.

Individuals, Dominance, and Competitive Success

The effects of resource patterning and population density on the typical mechanisms of competition exhibited by the 'average' individual in a population has been shown to be quite striking. But individuals are different and vary in their ability to acquire resources (Table IV), in their use of space, and in their growth (see Rubenstein, *in press*). The purpose of this section is to show why these differences arise and what consequences they have on individual life histories, by examining dominance relationships among individuals.

In populations where animals are able to recognize each other as individuals or are able to associate competitive ability with specific physical or behavioural attributes, the intensity of aggressive interactions is often reduced as patterns of social dominance are established. These patterns arise because animals that are consistently defeated either avoid interacting altogether or, when involved in interactions, quickly submit or withdraw. As a result, few overt aggressive interactions occur, and those that do differ markedly in intensity and in form from those occurring before dominance relationships were established.

Clearly dominant individuals benefit by this arrangement. By dominating others, they gain priority of access to resources (Murton *et al.* 1966; Jenkins 1969). In addition, they often derive considerable reproductive advantages (De Fries & McClearn 1970; De Vore 1971; Le Boeuf 1974). But what do subordinates derive from this arrangement? In the short run, definitely much less than the dominants. Given their phenotype, subordinates are minimizing their losses: in short, making the best of a bad job (*sensu* Maynard Smith 1979). But even though their fitness is low relative to that of the dominant individuals, it could be even lower if less peaceful conditions prevailed. Peaceful interactions reduce the likelihood of incurring physical damage and of wasting time and energy, and by remaining undamaged a subordinate has a

chance of eventually acquiring higher status and thus increased fitness.

The purpose of this section is to examine what sorts of dominance relationships exist in these 'closed' experimental populations of pygmy sunfish and to determine by what mechanisms dominance is achieved. In particular, I examined (1) how density and resource patterning affected dominance relationships, (2) whether dominant individuals achieved success by using particular behaviour patterns, and (3) whether dominant individuals also showed increased competitive success in the short term as measured by prey consumption and in the long term as measured by growth.

Methods

Aggressive sequences were analysed to determine winners and losers. Distinctions between various types of retreats provided the criteria for determining the winner and loser of an interaction. In 97% of the interactions, the loser was the animal first to retreat in either a rapid swimming or sidle away posture. In 3% of the cases, the animal leaving first was not designated the loser. These departures differed markedly from the retreats of the losers. When a winner departed, it did so gradually, by first moving a few centimetres and then performing dorsal and pectoral fin movements. If the other fish remained absolutely motionless, the withdrawing animal turned and swam away and was designated the winner. If the other fish moved or attempted to withdraw, it was often reapproached and the interaction continued.

Once a winner and a loser were determined for each encounter, it was possible to devise two indices of dominance. One index was determined by dividing the total number of fights won by the total number of fights engaged in. The other measure is more complex and was determined by counting the number of fish against which an individual won more fights than it lost. For every fish against which the number of victories exceeded the number of defeats, a score of 1 was recorded; for every fish against which the number of losses exceeded the number of victories, a score of -1 was recorded. A zero was recorded if the number of wins equalled the number of losses or if no interactions occurred with a particular fish. The dominance score was the sum of these values. The higher the score, the higher a fish's rank. This procedure had the advantage of linearizing the dominance scores of potentially non-linear dominance systems, yet it

retained some information on the magnitude of the inequality of competitive abilities that exist among individuals in a population. Although these indices were highly correlated, both were used to investigate the first two propositions outlined above. References to rank indicate that dominance scores were used in the analysis.

A complex procedure was used to determine whether dominant individuals used particular behaviour patterns to achieve competitive success. Multiple regression analysis could not be used directly to examine the relationship between rank and the proportional occurrence in the repertoire of the 20 visual signals, because the number of variables always exceeded the number of fish to be compared. Instead, principal components analysis was used to create a reduced set of uncorrelated signal variables that accounted for most of the original total variance. For each fish these new uncorrelated variables were computed using the following equation

$$Z_{ik} = \sum_{j=1}^{20} a_{jk} x_{ij} \quad (5)$$

where Z_{ik} represents the k th new variable score for the i th fish, a_{jk} represents the j th eigenvector score associated with the k th principal component, and x_{ij} represents the i th fish's value for the j th standardized original variable. Some of these new variables, those derived from components cumulatively accounting for a minimum of 70% of the total variance, were regressed against rank, using the following equation

$$y_i = \sum_{k=1}^m \beta_k Z_{ik} + \beta_0 + e_i \quad (6)$$

where y_i is the rank of the i th fish, β_k is the regression coefficient of the k th new variable, β_0 is the intercept and e_i is the error term. By substituting the first equation into the second the model becomes

$$y_i = \sum_{k=1}^m \sum_{j=1}^{20} \beta_k a_{jk} x_{ij} + \beta_0 + e_i \quad (7)$$

in which $\beta_k a_{jk}$ is a coefficient reflecting the relationship among the original variables and the importance of each in accounting for variance in the dependent variable rank.

Dominance Relationships

Density and the pattern of prey dispersion had significant effects on pygmy sunfish dominance relationships, as illustrated in Fig. 4. A completely flat distribution of ranks would have in-

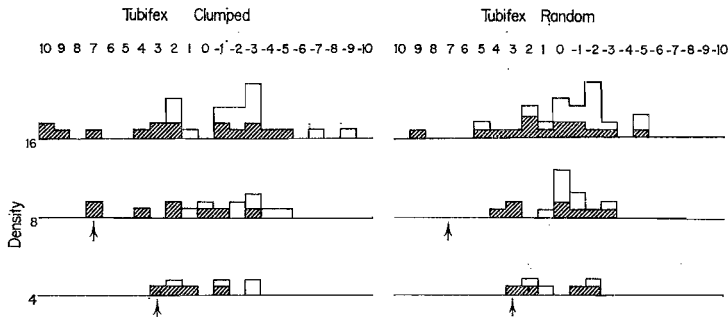


Fig. 4. Frequency histograms of dominance scores (rank) at various population densities and under different patterns of *Tubifex* dispersion. The hatched area represents males and the clear area represents females. Arrows indicate maximum dominance score of linear hierarchies.

indicated a linear dominance hierarchy. Only the low and intermediate density populations exhibited indications of linear hierarchy, and then only under conditions of clumped prey. In the high density population, there was much variation in rank, but no individual dominated all the others as was the case at more moderate densities.

The location of prey also affected dominance relations. In both the high and intermediate density populations, the variance in rank was significantly higher when the prey were clumped than when the prey were dispersed randomly ($F(31,31) = 2.28, P < 0.05$ (high density); $F(15, 15) = 3.33, P < 0.025$ (intermediate density)). Increased prey dispersion increased the competitive equality among members of these populations. In the low density populations, the patterning of the resource had no significant effect on variance in rank. Similar changes in rank occurred during feeding treatments involving other prey species.

Sex had an effect on rank. Although the distributions of male and female ranks overlapped, males generally had higher ranks than females (Fig. 4). The amount of overlap between these distributions increased as the dispersion of the prey increased. Under all conditions the range of male ranks was larger than that of females.

There were significant correlations among dominance rankings of adjacent feeding treatments (Table V). An individual was more likely to maintain its rank when population density was low and when prey were dispersed randomly about the aquarium: that is, when the intensity of competition was low. Despite this constancy, large changes in rank occurred. For example, the dominant male (74) in population 16A had a

dominance score of 9 and won 74% of its encounters when *Tubifex* worms were located in a central patch. But when the *Tubifex* were randomly distributed, it was only able to win 60% of its fights and dropped to third, with a dominance score of 2. A female (14) that ranked eighth in population 16B, won only 40% of her fights and had a dominance score of -2, rose in rank to a tie for second when the pattern of prey dispersion was changed from clumped to random. Her ability to win encounters rose to 65% and her dominance score increased to 2. Similar changes occurred, but with decreasing frequency, throughout the experiment.

Determinants of Dominance

In pygmy sunfish, dominant individuals tend to be larger than subordinates and tend to use different behaviour patterns during contests (displays). Table VI shows that at all densities and under both prey dispersions, rank is positively correlated with body size as measured at the end of the experimental period: thus, the heavier fish tend to rank higher. This relation-

Table V. Correlation Coefficient of Rank Constancy across Adjacent Feeding Groups. 1-2 Clumped *Tubifex* to Random *Tubifex*; 2-3 Random *Tubifex* to Random Chironomid Larvae; 3-4 Random Chironomid Larvae to Random Mixture of Prey; 4-5 Random Mixture of Prey to Clumped Mixture of Prey; 5-6 Clumped Mixture of Prey to Clumped Chironomid Larvae

Density	1-2	2-3	3-4	4-5	5-6
16	0.55	0.75	0.81	0.76	0.70
8	0.57	0.84	0.85	0.83	0.74
4	0.85	0.92	0.92	0.90	0.89

All correlation coefficients significant at the 0.95 level or greater.

ship, however, is only significant for low and high density populations under conditions of randomly dispersed prey, and therefore suggests that body size, although a contributing factor, is not always a major determinant of an animal's rank. It is interesting to note that body size takes

Table VI. Correlations of Weight and Rank

Density	Clumped prey	Random prey
16B	0.35	0.56**
8B	0.44	0.54
4A	0.59	0.93*

* $P < 0.05$; ** $P < 0.025$.

on a significantly more prominent role when males abandon territorial defence of the resource.

Figure 5 shows that a fish's ability to dominate others is correlated with the use of particular displays, and that changes in resource patterning affect the make-up of the repertoire more than do changes in density.

Under conditions involving clumped *Tubifex*, there was a positive correlation between an animal's ability to win aggressive encounters and its use of approaches, and a negative correlation between winning and retreating, especially rapid retreats (S) and side withdraws (P). These victorious individuals did not use all approaches

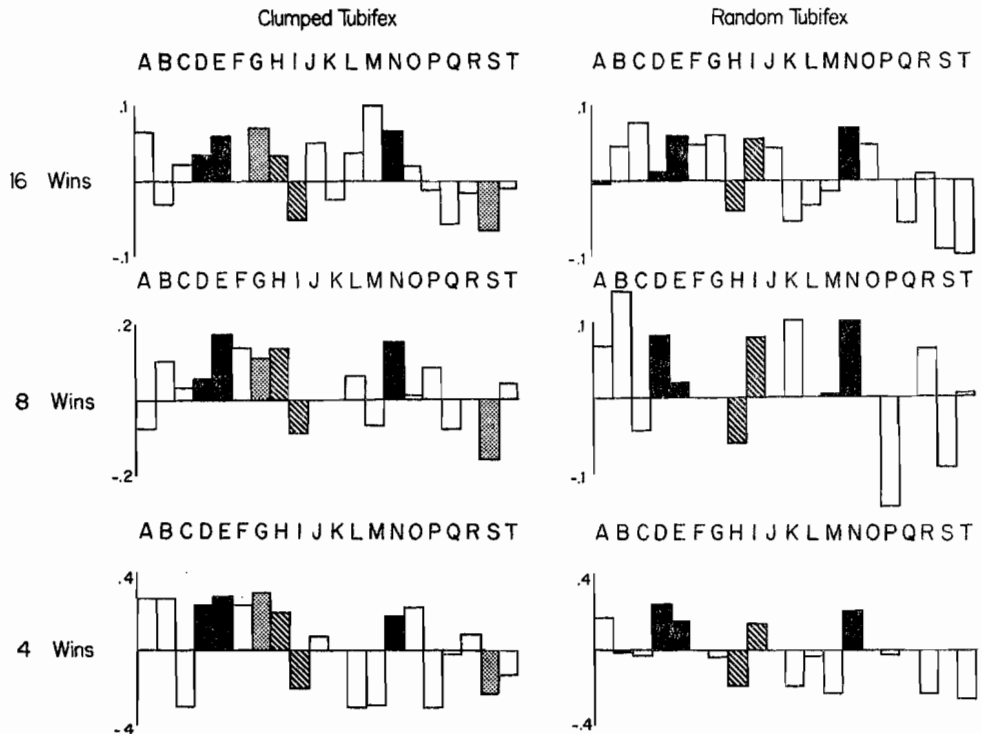


Fig. 5. Correlations among the 20 visual displays and the proportions of fights won by individuals in populations 16B, 8B, and 4A. The height of the bars reflects the magnitude of the correlation. Dark bars depict displays used by dominants at all densities and all dispersions. Stippled bars depict displays consistently used by dominants at all densities but only when prey were clumped. Hatched bars depict displays used by dominants under one dispersion and subordinates under the other. A = rapid approach; B = lunge and nip; C = side approach, flank to flank, caudal fin motionless; D = side approach, head to flank, caudal fin motionless; E = side approach, flank to flank, slow caudal fin wave; F = side approach, flank to flank, rapid caudal fin wave; G = side approach, flank to flank, dorsal and pelvic fin movements; H = side approach, flank to flank, tail droop; I = side approach, flank to flank, caudal fin motionless; J = side approach, flank to head, caudal fin wave; K = circling side approach; L = stationary, head to flank, caudal fin motionless; M = stationary, flank to flank, caudal fin motionless; N = stationary, dorsal and pelvic fin movements; O = stationary, caudal fin wave; P = side withdrawal, flank to flank, caudal fin motionless; Q = side withdrawal, head to flank, caudal fin motionless; R = circling side withdrawal; S = rapid retreat; and T = side withdrawal, flank to flank, tail droop.

indiscriminately. Their repertoire was composed primarily of rapid approaches (A), sidle approaches especially to the flank of the opponent with the tail dipped or waving (D and E), or sidle approaches involving raising and lowering dorsal and pelvic fins (G). Rarely did dominants sidle to an opponent's flank with no fins moving (C), nor did they often approach from the flank to an opponent's head (I). During the stationary phase of the contest, dominants rarely pointed their head at an opponent's flank and kept their fins motionless (L). Instead, especially in high and intermediate density populations, they showed a propensity to orient parallel or anti-parallel to their opponent and raise and lower their dorsal and pelvic fins (N). These displays comprised the typical dominant individual's repertoire under all combinations of prey, as long as it appeared in a centrally located clump.

Under conditions involving randomly distributed prey, the general aspects of the repertoire remained the same, but many of the details were different. In high density populations, dominants continued to use sidle approaches with fin movements frequently, but added sidle approaches without fin movements (C) to their repertoire. The stationary phase of contests remained basically the same and mostly involved displays emphasizing movements of the dorsal and pectoral fins (N). Although there were a number of minor differences among repertoires of dominants within densities resulting from changing prey dispersion patterns, there was one consistent difference across densities. Whereas dominants sidled to their opponent flank to flank with the caudal fin dropped (H) when the prey were clumped, they sidled to their opponent flank to head with the caudal fin motionless but erect (I) when the prey were randomly distributed.

The ways in which density and prey dispersion interacted to influence the repertoire of dominants is shown most clearly by the shaded areas in Fig. 5. Some displays, such as sidle approaches with the tail moving or dipped, and stationary postures involving dorsal and pelvic fin movements, were always used by dominants at all densities and both prey dispersions (dark bars). Other displays, such as sidle approaches with dorsal and pelvic fin movements, were used by dominants at all densities, but only when the prey were clumped (stippled bars). Still others, such as sidles with the caudal fin dropped or erect, were used consistently by dominants under one prey dispersion but by subordinates under the other (hatched bars).

Consequences of Dominance

Although some fish are dominant over others and use particular displays when contesting resources, these individuals do not necessarily achieve greater competitive success. The success of each fish, as measured by the percentage of the total food ration it acquired and by its growth rate for each feeding treatment, is shown in Table VII. The extent to which dominant individuals were able to acquire more resources and grow more rapidly is shown by the correlation of rank (dominance scores) on these two variables (Table VIII). Only in the high density populations did the amount of food an individual ate correlate significantly with its rank. This occurred irrespective of the pattern of prey dispersion. But even then there was no correlation between rank and growth rate.

It appears that only when competition is extremely severe do dominant individuals succeed in acquiring a significant and disproportionate share of the food resource. High ranking individuals, however, do not appear to translate these feeding benefits into increased growth. The reason for this appears to be related to the fact that there is a significant correlation between rank and the proportion of the total fights which an animal was engaged in (Table VIII). Thus increased aggression offsets the immediate growth benefits associated with high rank. This can be seen clearly by comparing the ratios of the proportion of food eaten to proportion of fights engaged in for dominant and subordinate males in the high density population. The mean benefit/effort ratios for dominants was 0.46 whereas it was 0.41 for the subordinates. Thus the subordinates, by adopting peripheral territories, avoided the clumps of prey and certainly acquired significantly less food than the dominants, but by reducing their costs they minimized their losses to such an extent that neither their B/E ratios nor growth rate differed significantly from those of the more central territorial dominants. From these results it appears that maintaining dominance is extremely costly in terms of time and energy. Even if dominant individuals succeeded in getting a significantly greater percentage of the food, they metabolized it before it could be used to significantly increase their growth rate above that of the subordinates.

Discussion

Populations of pygmy sunfish exhibit patterns of social dominance that are affected by the density of the population and by the dispersion of

the food resource. Reducing the density of the population and increasing the dispersion of the prey ameliorated the effects of competition (see growth rate variation, Table VII) and, in different ways, altered the patterns of social dominance. Whereas density reductions increased differences in dominance, changes in prey dispersion from clumped to random decreased differ-

ences in dominance. This is interesting because ordinarily increases in density should accentuate differences. Such differences did not appear in this study because the subordinates altered the rules of the game. They withdrew from competing for food almost completely and by doing so avoided most contests. As a result the inherent differences in dominance were never expressed.

Table VII. Individual Differences in Success and Aggressiveness

Density	Fish	Sex	Clumped prey				Random prey			
			Rank	% Food eaten	Growth rate (mg/day)	% Fights engaged	Rank	% Food eaten	Growth rate (mg/day)	% Fights engaged
16B	36*	M	1.5	8	0.2	28	1	11	1.2	37
	56*	M	1.5	12	0.4	25	2.5	9	0.8	20
	22*	M	3	12	0.8	23	4.5	8	1.4	19
	35*	M	4	9	0.0	12	9	8	1.4	19
	3	F	5	7	0.0	13	7	6	1.7	12
	42†	M	6	5	0.2	14	14	7	1.3	22
	14	F	8	10	1.4	13	2.5	8	1.6	12
	40	F	8	1	-0.1	2	died			
	59	F	8	4	0.1	6	4.5	4	0.0	8
	72†	M	12	2	-0.2	6	12	4	0.3	6
	66	F	12	7	-0.1	12	7	6	0.2	6
	49	F	12	4	-0.1	18	10.5	4	1.1	5
	51	F	12	6	0.7	4	14	5	-0.5	6
	41†	M	12	5	1.0	10	7	10	1.7	12
	10†	M	15	5	0.5	14	10.5	6	1.2	11
6	F	16	4	0.1	11	14	5	0.5	6	
8B	73	M	1	16	0.7	56	1	18	1.3	57
	26	M	2	9	1.0	40	4.5	18	2.2	21
	68	F	3	8	0.5	17	3	9	1.1	11
	32	M	4	17	1.4	36	2	16	1.2	33
	30	F	5.5	10	0.2	17	8	9	1.1	17
	63	F	5.5	11	0.4	19	7	11	2.1	28
	55	M	7.5	15	0.9	13	4.5	9	1.3	17
	45	F	7.5	13	0.4	21	6	11	1.0	17
4A	69	M	1	26	1.6	70	1	22	2.7	69
	70	M	2	20	1.2	41	3	18	1.1	60
	57	F	3	30	1.6	46	2	35	2.4	33
	62	F	4	25	0.4	43	4	26	1.7	38

* = dominant males centrally located.

† = subordinate males peripherally located.

Table VIII. Correlations of a Fish's Dominance Scores (Rank) with the Proportion of Prey it Captured, its Growth Rate (mg biomass/day) and the Proportion of the Total Fights it was Involved in

Density	Clumped <i>Tubifex</i>			Random <i>Tubifex</i>		
	Food	Growth	Fights	Food	Growth	Fights
16	0.41*	0.16	0.54**	0.60***	0.33	0.59***
8	0.20	0.36	0.68**	0.07	-0.23	0.55*
4	0.44	0.69	0.78*	0.50	0.55	0.51

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Based on data from both replicates.

In general, dominant individuals were not significantly more successful than subordinates in acquiring resources. Only at the highest density where competition was most intense did dominants eat significantly more food than the subordinates, but this gain was not translated into accelerated growth. If the energetic costs of maintaining dominance seemingly outweigh the energetic gains associated with it, why should fish persist in dominating others? Acquiring food and growing fast are only partial measures of success. Ultimately these energetic gains should be converted into increased reproductive success. But to increase its chances of successfully reproducing, a male may have to divert a significant portion of its energy from growth and invest it in the maintenance of dominance. Dominant males repeatedly drive opponents away. Thus when females are ready to lay eggs, dominant males, because of their aggressive ability, have the greatest chances of successfully mating with the females. If the breeding system involves female choice, dominants are most likely to be selected by females, either because they are the most visible of all the males (they often are darker and hold central territories near the food) or because repeated demonstrations of their competitive prowess makes them more attractive to the females. In either case, if the dominants breed successfully, the energetic costs in terms of reduced growth would be offset by gains in fitness. In long-lived iteroparous species these gains would have to be very large in order to offset the long-term costs associated with present reductions in growth.

It is ironic, however, that subordinates, by removing themselves from the intense competition, probably attenuate the costs associated with the dominants' increased reproductive success. Such subordinates nevertheless are most probably doing the best they can given the existing asymmetries in size and ability. Although they may only have a small chance of acquiring a few matings as sneaky raiders (they are producing sperm (Rubenstein, in press)), they are at least growing as well as the dominants, and if the growing season is long there is a chance of rising in rank and taking over the prime territories after the dominants have exhausted their energy reserves.

Recent studies on fish provide some support for this hypothesis. Sohn (1977) has demonstrated that once a male platyfish establishes dominance, it is assured of mating first because the maturation of the other male is delayed.

Once it begins to breed, however, the subordinate surpasses it in size. During favourable periods when breeding seasons are long, these males might achieve significant reproduction. Furthermore, growth studies on gobies and rainbow trout have also demonstrated that dominance has its costs. Yamagishi and his co-workers (1974) have shown that the dominant goby was not the largest fish in the population and that it did not exhibit the highest growth or feeding rates. Li & Brocksen (1977) showed that as a group, dominant individuals grew significantly faster than subdominants, and that there were no significant differences among the groups with respect to levels of routine metabolism. Nevertheless, there was much variation among individuals, and in a number of cases subdominants grew faster than the dominants. Although more studies are needed in which both energetic and reproductive benefits and costs are measured, these findings suggest that there are situations in which dominant individuals incur energetic costs for immediate reproductive gains and that subordinates minimize energetic costs in order to increase the likelihood of acquiring future gains.

Conclusions

These experiments have shown that the mechanisms of competition in the pygmy sunfish change as the environment changes, and that to a large extent the change is governed by the economic viability of defending a renewable food resource. When the prey are economically defendable males establish territories, dominance differences are magnified and, as I have shown elsewhere (Rubenstein 1981), the use of sequential displaying to transfer information during prolonged aggressive encounters is low. Doubtless predictability associated with continual defence of a particular area facilitated the process of social conditioning (McDonald et al. 1968) necessary to establish these long-term associations, and under such conditions the accuracy of early assessments was high enough to reduce the need for many long signalling contests. When resources were not economically defendable, however, territoriality was abandoned, dominance differences were reduced, and the amount of information transferred by means of visual displays during aggressive encounters increased markedly (Rubenstein 1981). Obviously, competition for non-defendable resources relied less on memory and more on assessment of the particular situation.

It should be emphasized, however, that defendability of a resource did not require that the resource be clumped. Even when prey were randomly dispersed, males in the intermediate density populations continued to defend areas in which the renewable food would appear. That they continued to do so regardless of the pattern of prey dispersion underscores the fact that the costs and benefits of alternative behaviour patterns may be affected by complex interactions among a variety of environmental factors.

It is also important to note that even when territories were defended they did not necessarily conform to Brown's (1964) principle of economic defendability. One possible reason for this discrepancy is that territories may serve a variety of functions, one of which may be to acquire energy, but another of which might be to keep competitors away from potential mates. Thus although a territory may in fact yield too few energetic gains to make it energetically profitable, the combined gains, in terms of energy as well as offspring, may make a territory highly profitable when compared to any other overall reproductive strategy. Such an expanded concept of gains almost certainly accounts for the fact that males in the low density populations where competition for food was negligible defended 'uneconomic' territories. Nevertheless, it is likely that animals might establish uneconomic territories even when the overall combined gains are still insufficient to make such defence profitable. This may arise when defence of an area is actually a form of confinement: either dominants are constraining a subordinate to such an extent that it takes up refuge in a protected area, or subordinates attempt to cut their losses by withdrawing and reducing the extent of their activity. In the latter case, returning to a focal and well-known area may be more energetically efficient than stopping and resting at random locations, where frequent disturbances might result in unnecessary expenditures of energy.

In this study dominance was measured by an animal's ability to win fights, and correlated with dominance was the use of particular displays. If displays serve to inform others of one's fighting ability it is not surprising that dominant animals exhibited particular displays more frequently than subordinate animals. In general, displays by a dominant pygmy sunfish involved its sidling with its flank oriented towards an opponent's flank, or remaining stationary close to the opponent and moving the dorsal and pectoral fins up and down rapidly. Both these dis-

plays are energetically expensive and place the animals at risk, but most importantly they are good indicators of a dominant's fighting ability. Whereas the semaphore movements of the fins dramatize an animal's overall size and could give a clue as to its fighting ability (the extent of fin damage is inversely related to fighting ability), the vibratory thrusts of the sidle approach, especially from a flank to flank orientation, provide a good measure of an animal's strength, endurance, and agility. Not only is the vibratory activity of the sidle approach energetically costly, it exposes the animal's flank to damaging nips. The dorsal and pectoral fin waves may also be energetically expensive. Fish performing these semaphores often do so at the rate of two per second for many seconds. Furthermore, they may perform 10-20 such bouts at various stages during a contest. Thus it is likely that both these displays push fish close to their physiological limit during contests. If so, they are not easily increased by cheating and serve as reliable indicators of a fish's fighting ability. Therefore, one might expect that they would appear more often in the repertoire of dominant fish, either as signals of their ability or as probes to determine an opponent's ability (Parker & Rubenstein 1981). It is also possible that the semaphore movements serve another, less immediate, function as well. Because semaphore movements are so visible, they could also serve to draw the attention of females in the vicinity to the fight and to the dominant's ability.

One of the most interesting findings of the study was that dominance was not highly correlated with success in acquiring food unless competition was very intense. It was then surprising to find that this increased feeding success was not apparently translated into increased growth. Clearly the role of subordinates must not be ignored when evaluating the functional significance of social organization. It appears that subordinates, rather than continuing to contest vigorously for resources when their chances of acquiring them were virtually zero, adopted an alternative strategy that minimized their losses. In fact, since the dominants continued to fight among themselves, the outcome of the subordinate's strategy was not all that bad. They grew almost as well as the dominants, and if the environment were to change or the dominants were to exhaust their reserves, the subordinates would have been in the best possible condition to abandon the peripheral territories and engage in the costly struggles for the central territories

and a disproportionate share of the food and females. In fact, subordinate male 41 (population 16B), holding a peripheral territory under the initial clumped presentation of prey, later outcompeted some of the centrally territorial dominant males during the 63-day period of randomly dispersed prey. That he became a dominant centrally-territorial male at the end of the experiment when prey again appeared in a clump, underscores the significance of adopting the most economical behaviour possible even if in the short run the reproductive benefits may be far less than those of another type of behaviour.

The fact that some equally successful alternative feeding strategies may produce totally different reproductive gains points to an important problem: easily obtainable operational measures of success that logically should be good estimates of ultimate reproductive success may not always be so. Such differences underscore the danger of assuming, as often is the case with optimal foraging models, that strategies achieving the highest net energy intake will necessarily be those favoured by natural selection because they will automatically produce the highest reproductive success as well.

From these studies it is apparent that the mechanisms of competition are varied and that an individual's competitive tactics will be affected by the nature of the resource and the attributes and behaviour of other individuals in the population. How these factors interact to determine the costs and benefits associated with particular behavioural alternatives is often complex and thus difficult to discern; but if a comprehensive understanding of the mechanisms of competition is to emerge and be incorporated into ecological theory these relationships must be deciphered.

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