

COMBAT AND COMMUNICATION IN THE EVERGLADES PYGMY SUNFISH

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Abstract. Changes in population density and resource patterning affect the aggressive behaviour of pygmy sunfish (*Elassoma evergladei*) in many ways. Increases in density significantly reduce the proportion of fights directly over clumped prey, the likelihood of initiators winning contests or acquiring clumped prey, and the length of contests. Increases in prey dispersion also reduce the proportion of resource fights in low- and high-density populations, the greater tendency for subordinates to initiate fights directly over resources, the likelihood of initiators acquiring a contested prey item in low-density populations, and the length of contests. Such increases, however, increase the likelihood of initiators winning contests at moderate competitive levels, and increase the effectiveness of rapid sequential communication in populations that abandon territoriality. In addition, some of these findings, such as the inverse relationship between contest length and both prey dispersion and rank differential, are consistent with predictions of cost-benefit models of fighting behaviour, namely, that escalated contests become more likely as asymmetries in fighting ability decrease and asymmetries in resource valuation simultaneously increase.

Animals competing for resources often engage in aggressive contests ranging from peaceful bouts of display to violent tournaments of strength. Recent theoretical advances (Maynard Smith & Parker 1976; Hammerstein 1981; Parker & Rubenstein 1981) have suggested that three factors: the value of the resource, the disparity in fighting ability between opponents, and the energetic and damage costs associated with alternative tactics, interact to determine the amount of physical aggression that will produce the selectively most advantageous fighting strategy. The purpose of this paper is to show how changes in predator density and patterns of prey dispersion, by altering the net value of the resource and the distribution of fighting abilities in pygmy sunfish (*Elassoma evergladei*) populations, affect their fighting behaviour and in particular, those aspects associated with communication.

Most animal contests involve some form of communication. When communication is visual it can be simple, involving approaches which show opponents each other's size, or it can be complex, involving elaborate movements of body and extremities. But no matter how simple or complex, communication occurs because animals attempt to acquire information about each other's fighting ability or valuation of the resource before deciding whether to fight for a

resource or retreat. By doing so they assess and influence their probability of success. Thus it is not surprising that contests are often sequences of actions and reactions and that such sequences change as the contest progresses.

Because of the sequential nature of most contests, 'communication' is often defined operationally as 'the process by which behaviour of one individual influences the probability of behavioural acts in other individuals' (Wilson 1975). The advantage of this operational definition is that it allows sequences of behaviour between organisms to be analysed quantitatively using information theory to determine the extent and effectiveness of an animal's communication system under different environmental and social conditions.

Materials and Methods

Pygmy sunfish were collected from the Green Swamp, North Carolina, and divided at random into two replicate populations of 4, 8, or 16 fish. The populations were kept in a 38-litre aquarium containing a sandy substrate, four small clay flower pots and four plants. The photoperiod was 13.5 h light, the water temperature was 25 ± 2 C, and the water was continuously filtered.

Each aquarium, regardless of density, was provided with 20 *Tubifex* worms daily. Because fish at higher densities were competing more vigorously for food, the value of the resource varied with density. The intensity of competition

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was also altered by changing the prey dispersion. During the first experiment the prey appeared predictably in a centrally located clump, but during the second experiment the prey were randomly distributed. Growth measurements clearly showed that competition was more intense when prey were presented in a clump (Rubenstein, in press).

During the last eight days of each 20-day experiment, 10 min of activity immediately following feeding were recorded on video tape. From these recordings, aggressive actions and reactions of fish individually identifiable by spot patterns (see Rubenstein 1981) were coded for the analyses. Comparisons involving proportions or probabilities are presented in the Tables as overall results, but testing the significance of these relationships involved subdividing the data into daily intervals.

After extensive preliminary observations, aggressive actions involving stereotyped fin and body movements were classified according to three components: (1) the extent, direction, and type of movement; (2) the position of the body relative to that of the opponent; and (3) the positions and movements of various fins. The displays are listed in the Appendix. Although these displays were stereotyped, there was variability among situations and among animals in the details of execution.

Information theory (Shannon & Weaver 1949) in the form of character analysis (Estabrook 1967) was applied to the collection of all aggressive interactions involving two contestants. From the video tapes, each aggressive interaction was analysed and coded as a sequence of behavioural acts. Given that each act in the sequence was treated as a character having 20 possible character states, one for each posture listed in the Appendix, it was possible to use character analysis to ask the following question: how much dependence exists between acts in a sequence? In other words, do the postures used by animals in act 1 affect the distribution of postures used by responding animals in act 2? Do the postures used by the respondents in turn affect the distribution of postures used by the initiators in act 3? And so on.

The mathematical treatment of the data begins with estimation of the information content, in bits, of any two adjacent acts (X and Y) in the sequence as

$$H(X) = - \sum_i p(i) \log_2 p(i)$$

$$H(Y) = - \sum_j p(j) \log_2 p(j)$$

where $p(i)$ and $p(j)$ are the probabilities of occurrence of each posture in X and Y respectively. On a Venn diagram of information space the space enclosed by a circle represents the information content associated with the act. The magnitude of $H(X)$ and $H(Y)$ reflect the difficulty of predicting a priori which posture an animal will adopt. Thus $H(X)$ and $H(Y)$ take on large values if the repertoire is large or each posture occurs at about the same frequency.

After computing $p(i, j)$, the joint probability of posture i in act X being followed by posture j in act Y , and $p(j|i)$, the conditional probability of posture j occurring in act Y given that posture i occurred in act X , it is possible to measure how much information remains in act Y given that all the uncertainty about act X has been removed. The conditional information content of act Y is measured as

$$H(Y/X) = - \sum_{i,j} p(i, j) \log_2 p(j|i)$$

Similarly the conditional information content in act X can be computed as

$$H(X/Y) = - \sum_{i,j} p(i, j) \log_2 p(i|j)$$

On the Venn diagram of information space, these conditional entropies are represented by the crescents of the respective acts. The amount of information transmitted, in bits/display, is the intersection of the two characters and can be measured as

$$\begin{aligned} T(X, Y) &= H(X) - H(X/Y) \\ &= H(Y) - H(Y/X) \end{aligned}$$

Estabrook (1967) has computed a measure of independence

$$I(X, Y) = \frac{H(Y/X) + H(X/Y)}{H(Y/X) + T(X, Y) + H(X/Y)}$$

which has the value of 1 when the information contained in the acts are completely different and the value of 0 when they are completely the same. In terms of communication, when $I(X, Y) = 1$, there is no information common to acts X and Y , indicating that the behaviour of an animal in act X has no influence on the behaviour of the other animal in act Y . Conversely, when $I(X, Y) = 0$, the acts share all their information, indicating that the behaviour of an animal in act X precisely determines the behaviour of the other animal in act Y .

Results

General Aspects of Fighting

Contests among pygmy sunfish do not occur only over food. In fact, as Table I shows, the proportion of the total number of fights directly over food is never very high (less than 40%), and decreases as population density increases or as prey dispersion is changed from clumped to random. When the prey appear in a clump the density reductions are significant (Clumped: $F_{2,15} = 3.98$, $P < 0.05$; Random: $F_{2,15} = 3.06$, $P < 0.10$), as are the dispersion reductions in both low- and high-density populations (low: $t_{10} = 2.57$, $P < 0.05$; intermediate: $t_{10} = 0.43$, NS; high: $t_{10} = 2.31$, $P < 0.05$).

The frequency at which individuals initiate contests directly over food is affected by dominance rank. Table II shows the correlation bet-

ween rank (highest rank = 1) and the ratio of the number of contests initiated for food to the number of contests initiated not for food. When prey are clumped there are significant inverse relationships between dominance and the ratios for all densities. This suggests that subordinates initiate contests directly over food whereas dominants initiate contests to achieve dominance, with presumably future resource control as well.

Changes in density and prey dispersion also affect the likelihood of initiators winning contests and acquiring contested prey items. Initiators always have better than a 50% chance of winning, and this advantage is significantly greater when fights are not directly over food (Table III) (low: $t_{10} = 2.60$, $P < 0.05$; intermediate: $t_{10} = 2.71$, $P < 0.05$; high: $t_{10} = 2.33$, $P < 0.05$). But only when contests are for food is an initiator's probability of winning affected by prey dispersion (Table III). Increased dispersion generally increases an initiator's probability of winning, but only significantly so in low- and intermediate-density populations (low: $t_{10} = 3.11$, $P < 0.02$; intermediate: $t_{10} = 2.84$, $P < 0.02$; high: $t_{10} = 0.35$, NS). Although there is some indication that initiators are more likely to win contests in small populations (Table III), the density differences are not significant.

When it comes to acquiring prey during resource fights, initiators are somewhat less successful than they are at winning contests. An initiator's probability of obtaining a contested prey item is increased by decreasing the dispersion of the prey, although only significantly so in low density populations (Table IV) (low: $t_{10} = 2.37$, $P < 0.05$; intermediate: $t_{10} = 1.41$, $P < 0.2$; high: $t_{10} = 1.87$, $P < 0.10$), and by decreasing the number of its competitors (Clumped: $F_{2,15} = 3.73$, $P < 0.05$; Random: $F_{2,15} = 0.96$, NS). The effects of density, however, only are significant when prey are clumped.

Table I. Effects of Fish Density and Prey Presentation on the Proportion of Fights over Food

Density	Prey	
	Clumped	Dispersed
4	0.39 (156)	0.27 (92)
8	0.27 (190)	0.22 (156)
16	0.25 (404)	0.15 (266)

Sample sizes in brackets.

Table II. Effects of Fish Density and Prey Presentation on Correlations of Rank and Ratio of Initiations With and Without Food

Density	Prey	
	Clumped	Dispersed
4	0.90* (4)	0.86 (4)
8	0.77** (8)	0.31 (8)
16	0.83*** (16)	0.23 (15)

Significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$. Sample sizes in brackets.

Table III. Effects of Fish Density and Prey Presentation on the Probability of Initiator Winning Resource and Dominance Fights

Density	Resource fights		Dominance fights	
	Clumped prey	Dispersed prey	Clumped prey	Dispersed prey
4	0.67 (61)	0.83 (25)	0.90 (95)	0.86 (67)
8	0.53 (51)	0.81 (34)	0.72 (139)	0.73 (122)
16	0.65 (101)	0.67 (40)	0.77 (303)	0.76 (226)

Sample sizes in brackets.

Determinants of Fight Length

Both density and dispersion significantly influence the length of contests, but not independently (Table V). Under conditions of clumped prey, increases in density reduce the number of acts in a fight sequences (Fig. 1). Furthermore, for low- and intermediate-density populations, increasing prey dispersion also reduces contest length. In high-density populations, however, fight length is not significantly affected by patterns of prey dispersion ($F_{1,665} = 0.43$, NS).

Despite the significant effects of density and resource patterning on fight length, most of the variance (92%) remains to be explained by other factors. First, the length of a contest depends on whether the contest is directly for resources. Resources fights are always shorter than dominance fights and significantly so for low- and high-density populations receiving a clump of prey (Table VI). Second, the length of resource fights depends on prey dispersion. For all densities, resource fights are longer when prey are clumped (Table VI). These differences are not significant, but it should be noted that increased activity in the vicinity of a clump causes interruptions that will tend to shorten average fight length. Third, contest length depends on whether the eventual winner is the initiator or defender (Table VII). In low-density populations, contests are slightly but not significantly longer when the initiator wins, but in intermediate- and high-

density populations resource fights on average are often significantly longer when the defender wins. Elsewhere I have shown that males in all densities defend feeding territories when prey are clumped and that males in intermediate densities continue to do so even after prey dispersion becomes random (Rubenstein 1980). It is interesting to note that defender-won contests are significantly longer when competition is moderately severe and males defend territories. Lastly, contest length depends on the rank differential of the opponents. As shown in Table VIII, there are inverse correlations between rank differential and fight length for all populations. These are significant in high-density populations where competitive intensity is greatest. Thus the more equally two opponents are matched, the longer the contest is likely to be.

Communication Effectiveness

Population density and patterning of the resource do not significantly affect the size of the repertoire or the frequency with which particular displays are used. They do influence, however, both the amount and effectiveness of information transfer in the pygmy sunfish.

Under all experimental conditions, the amount of information transferred between adjacent acts in a sequence increases as a fight progresses. An example of this increase appears in Fig. 2 as a decreasing independence value. An analysis of covariance was used to determine whether there were significant differences among densities and between different patterns of prey dispersions in the slopes of these lines and therefore the effectiveness of information transfer throughout an interaction. The regression of the independence value and act number are significant for all densities and feeding treatments. Within a feeding treatment, however, the slopes of the regressions for the various densities differ significantly (Clumped: $F_{2,32} = 3.73$, $P < 0.005$; Random: $F_{2,32} = 3.96$, $P < 0.05$). Under both

Table IV. Effects of Fish Density and Prey Presentation on the Probability of Initiator Acquiring Contested Prey

Density	Prey	
	Clumped	Dispersed
4	0.58 (61)	0.33 (25)
8	0.45 (51)	0.41 (34)
16	0.39 (101)	0.33 (40)

Sample sizes in brackets.

Table V. Significance of Factors Affecting Fight Length

Source	df	Sum of squares	Mean square	F	P	Coeff. of variation
Density	2	1353.2	676.6	31.3	0.001	4.6
Dispersion	1	282.2	282.2	13.0	0.001	1.0
Density × dispersion	2	601.9	301.0	13.9	0.001	2.1
Residual	1258	27 224.0	21.7			
Total	1263	29 461.2	23.3			

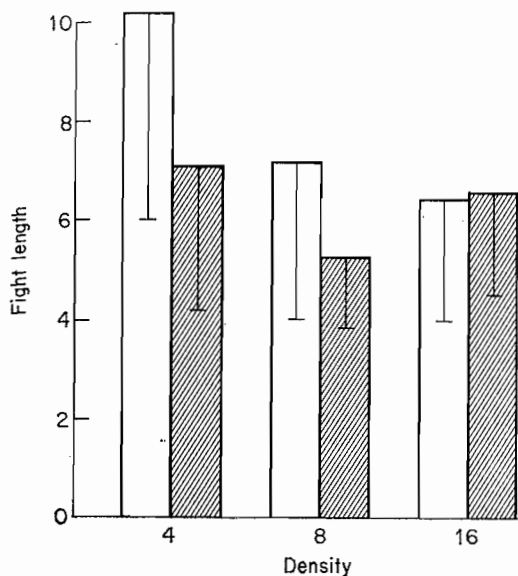


Fig. 1. Means and standard deviations of fight lengths in different-density populations. Open bars represent clumped-prey presentations and hatched bars dispersed-prey presentations.

feeding regimes, the slope becomes steeper as population density decreases, indicating that as a fight progresses the increase in the amount of information per act is greater at lower population densities. Inspection of the lines in Fig. 2 suggests that the average amount of information transferred per act is a non-linear function of density. More information appears to be transferred in low-density populations than in high-density populations, but both amounts are higher than the amount transferred in intermediate-density populations. The fact that the regressions have significantly different slopes precluded analysing the statistical significance of differences in the adjusted means.

The pattern of prey dispersion has a strong effect on the amount of information transferred during aggressive encounters, but this effect differs with respect to the density of the population. For each density, the slope of the regression of the independence value on act number does not differ significantly between feeding treatments of clumped or randomly-dispersed prey (Table IX). It was thus possible to compare the adjusted independence values between feeding treatments. In both the high- and low-density

Table VI. Effects of Fish Density, Prey Presentation and Fight Context on Fight Length

Density	Clumped prey		Dispersed prey	
	Resource fight ‡	Dominance fight	Resource fight	Dominance fight
4	7.6*	11.5	6.0	7.1
8	6.4	7.6	5.5	5.6
16	4.8**	6.7	4.1†	5.7

Pairs differ significantly at * $P < 0.05$; ** $P < 0.01$.

†The difference between resource fights when prey are clumped and dispersed is almost significant: $t_{10} = 2.01$, $P < 0.10$.

‡The effects of density on resource fight length when prey are clumped are significant ($F_{2,15} = 4.16$, $P < 0.05$).

Table VII. Effects of Fish Density, Prey Presentation and Type of Winner on Fight Length

Density	Clumped prey				Dispersed prey			
	Resource fight		Dominance fight		Resource fight		Dominance fight	
	Initiator	Defender	Initiator	Defender	Initiator	Defender	Initiator	Defender
4	7.8	6.9	11.7	10.0	6.3	4.0	7.1	8.2
8	4.2**	8.9	6.5	6.7	5.3*	8.0	5.1	6.1
16	4.4**	6.5	6.6	7.4	5.9	6.5	6.6	6.9

Pairs differ significantly at * $P < 0.05$; ** $P < 0.01$.

Sample sizes can be computed from Table III.

populations, information transfer increases significantly as the pattern of prey dispersion is shifted from clumped to random. The increase in the amount of information transfer occurring in the intermediate-density populations is not significant (Table IX). In general, increases in prey dispersion increase the importance of sequential signal communication in high- and low-density populations, but not in the intermediate-density populations. It is in the high- and low-density populations that presentation of dispersed prey leads to the abandonment of male territoriality (Rubenstein 1980).

Discussion

The results clearly show that changes in both the physical and social environment influence many aspects of fighting behaviour. Increases in population density significantly reduce: (a) the proportion of fights directly over clumped resources; (b) the likelihood of initiators winning non-resource contests; (c) the likelihood of the

initiator acquiring a disputed clumped prey item; and (d) the length of contests. Increases in prey dispersion also significantly reduce: (a) the proportion of fights directly over resources in low- and high-density populations — those in which territoriality was abandoned (Rubenstein 1980); (b) the distinction between dominants and subordinates in the types of contests they initiate in moderately competitive situations; (c) the likelihood of initiators acquiring contested prey items; and (d) the length of contests. Increases in prey dispersion, however, significantly increase: (e) the probability of initiators winning resource contests in low- and intermediate-density populations; and (f) the effectiveness of rapid sequential communication in low- and high-density populations.

It is difficult to compare these findings with those of other studies of agonistic behaviour because many suffer from the absence of contested resources or the lack of social and physical environmental manipulations. Despite these differences, some parallels can be made. For example, in pygmy sunfish there is a significant inverse relationship between contest length and rank differential in high-intensity situations. In the blue gourami (*Trichogaster trichopterus*) Frey & Miller (1972) found a similar inverse relationship between fight length and size differential; and in the bluegill sunfish (*Lepomis macrochirus*) Henderson & Chiszar (1977) found that contests between a large intruder and a large resident are significantly longer than those involving a large intruder and a small resident.

Table VIII. Effects of Fish Density and Prey Presentation on Correlation between Fight Length and Rank Differential

Density	Prey	
	Clumped	Dispersed
4	-0.28 (6)	-0.31 (6)
8	-0.16 (22)	-0.25 (24)
16	-0.43* (24)	-0.40* (20)

* $P < 0.05$. Sample sizes in brackets.

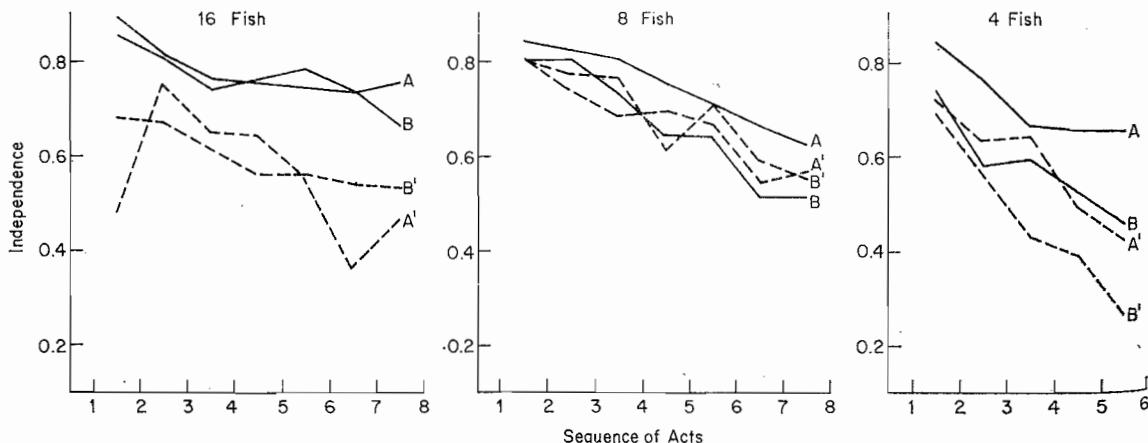


Fig. 2. Relationship of the independence measure, $I(X, Y)$, and act number. Solid lines denote clumped-prey presentations whereas dashed lines denote dispersed-prey presentations. A and A' represent one population while B and B' represent the replicate population.

Table IX. Analysis of Covariance of the Measure of Independence on Act Number between Clumped and Random Pattern of *Tubifex* Dispersion

Equality of slopes						
Density	Source	df	Sum of squares	Mean square	F	P
4	Among	1	0.0141	0.0141	2.0	0.17
	Within	16	0.1123	0.0070		
8	Among	1	0.0008	0.0008	0.3	0.56
	Within	24	0.0557	0.0023		
16	Among	1	0.0012	0.0012	0.2	0.70
	Within	24	0.1893	0.0079		

Equality of adjusted means						
Density	Source	df	Sum of squares	Mean square	F	P
4	Among	1	0.0605	0.0605	8.1	0.01
	Within	17	0.1264	0.0074		
8	Among	1	0.0082	0.0082	3.6	0.07
	Within	25	0.0560	0.0023		
16	Among	1	0.1344	0.1344	17.7	0.0003
	Within	25	0.1905	0.0076		

Thus for all three species, fight length increases as differences in a measure of fighting ability decrease; and if escalation is measured by changes in intensity as well as changes in duration, further evidence exists supporting this relationship. Sinclair (1977) showed that stone crabs (*Menippe mercenaria*) very similar in size were significantly more likely to be involved in fights, as opposed to bouts of display, than those more different in size. Similarly, Clutton-Brock & Albon (1979) have demonstrated in red deer (*Cervus elaphus*) contests that the most intense forms of advertisement — parallel walks and roaring — rarely occur when there are visible discrepancies between opponents.

Another parallel concerns the relationship between fight length and type of winner. In pygmy sunfish, resource contests won by defenders are longer than those won by initiators, but the reverse occurs in fiddler crabs (Hyatt & Salmon 1978) and spiders (Reichert 1978). One possible reason for this discrepancy lies in the nature of the asymmetry between opponents. In fiddler crabs and spiders, residents defending a burrow or web site have a fighting advantage and usually win contests; but when initiators do win they are invariably larger. This suggests that when two asymmetries are contradictory (*sensu* Parker and Rubenstein 1981), escalation which

leads to longer contests is a likely result. In the pygmy sunfish the situation is reversed as the advantage belongs to the initiator (see Tables III and IV). But the same rule appears to apply, because when the advantage is negated and the defender wins, contests are longer. This suggests that in fights over resources, defending pygmy sunfish also escalate when a contradiction in asymmetries arises. What generates this contradiction is discussed below.

Although the purpose of this study was to find out whether or not these changes were in accordance with the predictions of cost-benefit models of contest behaviour, there are a number of difficulties. One is that the models are based on assumptions about decision rules and the accrual of costs and benefits that are simple and somewhat unrealistic. Thus caution is necessary when applying data to evaluating models. Unfortunately, this will exclude from evaluation many aspects of fighting behaviour that are environmentally influenced. For example, changes in resource value and the distribution of fighting ability might be responsible for the reductions in resource fighting that occur with increases in density or prey dispersion, but such relationships are not easily extracted from the models. It may turn out that the reductions are not due to these factors at all, but result from diminished for-

aging time at high densities, or reduced interference under conditions of dispersed prey. However, it is not possible to distinguish between these possibilities, using current models.

Another problem with comparing predictions of models with data is that of expressing the many types of changes that can result from general environmental alterations in the specific terms of the models. Determining whether the effect is on resource valuation, distributions of fighting ability, or both and in what proportion, is extremely difficult. For example, under conditions of clumped resources, fight length increases. Since resource value is inversely related to the ease with which an alternative resource can be acquired (Parker 1974), resources predictably appearing in a centrally-located clump should be of high value. Simple Hawk-Dove models (Maynard Smith & Parker 1976) predict that escalation should be favoured as the value of the resource increases. Thus under clumped prey conditions, one might expect pygmy sunfish to invest more in fighting than under dispersed prey conditions. That fight length is longer under clumped rather than dispersed conditions, despite the increased interference resulting from congregations around a clump, is consistent with the predictions of the model.

If this were the sole explanation for long contests, why does contest length decrease as density increases? Surely resource value should be high in high-density populations, because foraging time constraints decrease the likelihood of finding another acquirable resource. This divergence from the prediction of the model probably arises because altering density also alters parameters other than resource value, some of which are not explicitly included in the model. It is possible that despite high resource value, the shortness of the foraging period in conjunction with large variances in competitive ability (Rubenstein 1981, in press) and high levels of confusion, favour early assessment of relative ability and, from the perspective of the less able contestant, rapid withdrawal. Withdrawing early should increase an individual's chances of acquiring at least one rapidly-disappearing prey. So despite high resource valuation, fights might be short, contrary to the predictions of the model.

Despite these difficulties, there are two situations in which the fighting data and measurements of fight 'context' are in a form appropriate for evaluating some of the fighting models. In both cases, the experimental results are con-

sistent with the predictions of the models. First, the simple Hawk-Dove model, incorporating asymmetries (Maynard Smith & Parker 1976), predicts that for any given value of the resource and damage cost, the likelihood of both opponents escalating should increase as asymmetry in fighting ability between opponents decreases, especially the more the value of the resource exceeds the costs of damage. In all populations of pygmy sunfish, contest length increases as the rank differential between opponents decreases (rank is correlated with size; Rubenstein 1981). This inverse relationship is most significant in high-density populations where competitive intensity and resource value are highest.

Second, the 'war of attrition' model (Maynard Smith & Parker 1976) predicts that in contests in which the contestants are of equal fighting ability and possess perfect assessment capabilities, if they value the resource differently, the contestant with the most to gain should escalate while the other should withdraw. Complications arise when assessment is imperfect and fighting abilities differ, but in general a contestant should escalate when it has more to gain. Two results support this prediction. First, subordinates tend to initiate more contests when resources are involved than when they are not (see Table II). This suggests that only when there is something to be gained directly do subordinates engage in and escalate contests. Second, though defenders rarely win contests, when they do so these contests are significantly longer than when they are defeated (see Table VII). It is interesting to note that when prey are clumped, a victory increases enormously their prospect of acquiring the resource (compare conditional probabilities of prey acquisition given a victory (low: $P = 0.92$; medium: $P = 0.86$; high: $P = 0.74$) with the unconditional acquisition probabilities in Table IV). This suggests that defenders escalate those contests in which they can derive a feeding advantage. Supporting evidence for this hypothesis comes from fights in which defenders lose. In these contests initiators attack the defender and grab the prey almost simultaneously. Usually the defender counter-attacks, but if the worm is not regurgitated, the defender retreats. As a result, fights are shorter than when the prospects of obtaining a prey are higher.

Apart from these comparisons with models, the results show a striking correlation between how animals use space and the effectiveness of their communication. Under conditions that in-

duce individuals to abandon territorial behaviour, there is a significant increase in the amount of information transmitted by sequential displays among aggressively interacting individuals. When changes in prey dispersion do not result in a change in the pattern of spatial dispersion of the fish, there is no significant change in the levels of communication by means of postural movements. That such a correlation exists suggests that territorial behaviour and rapid sequential signalling, although both means of communication, have different functions. In situations where space is not defended, animals are interacting with a greater variety of opponents but each infrequently. In order to avoid costly contests, there will probably be a premium on probing for information about an opponent's ability (Parker & Rubenstein 1981) and in return conveying information, either incidentally or deliberately, about its own. The use of stereotyped signals, which effectively force controlled responses from an opponent, would serve this function. Conversely, in territorial situations, consistency in the position of individuals will probably be sufficient to indicate ownership. Furthermore, the importance of stereotyped signalling will be reduced, because economic considerations, generated by the experimental territorial situations, reduce the importance of probing for or the broadcasting of information about an opponent's or one's own ability. This adjustment occurs because one consequence of long-term control of a limited food resource by some individuals in a population is that the condition of the others will deteriorate, while at the same time their need for the resource will increase. As a result, territorial intrusions will occur in which subordinate attackers value the resource so highly that they pursue prey despite stereotyped signals of the owner and regardless of the physical consequences that such 'inappropriate' responses inevitably entail. The effectiveness of communication will necessarily be reduced. Thus, because the need for 'probing' for recent information about the resident's present ability will be superseded by the absolute need for the resource, and the control of the initiator's behaviour, via display by owners, will be limited, the importance of stereotyped signalling in such combat situations will be diminished. That situations can be created which dramatically change the patterns of information transfer, underscores the importance of examining the ecology of animal communication.

Appendix: Displays of Interacting Pygmy Sunfish which were Used as States in Character Analysis of Signal Communication

- A: rapid approach.
- B: lunge and nip.
- C: sidle approach; flank to flank; caudal fin motionless.
- D: sidle approach; head to flank; caudal fin motionless.
- E: sidle approach; flank to flank; slow caudal fin wave.
- F: sidle approach; flank to flank; rapid caudal fin wave.
- G: sidle approach; flank to flank; dorsal and pelvic fin movements.
- H: sidle approach; flank to flank; tail droop.
- I: sidle approach; flank to head; caudal fin motionless.
- J: sidle approach; flank to head; caudal fin wave.
- K: circling sidle 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: sidle withdrawal; flank to flank; caudal fin motionless.
- Q: sidle withdrawal; head to flank; caudal fin motionless.
- R: circling sidle withdrawal.
- S: rapid retreat.
- T: sidle withdrawal; flank to flank; tail droop.

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