Molly R. Morris · Leila Gass · Michael J. Ryan

Assessment and individual recognition of opponents in the pygmy swordtails *Xiphophorus nigrensis* and *X. multilineatus*

Received: 27 June 1994/Accepted after revision: 2 June 1995

Abstract We examined factors that determine the outcome of agonistic encounters between male pygmy swordtail fish. Xiphophorus nigrensis and X. multilineatus males formed dominance relationships based on body size in staged laboratory encounters. There was a significant negative correlation between size asymmetry and fight intensity, suggesting that males assessed size in the encounters. However, a significant proportion of the variation in fight intensity in contests that escalated to bites could not be explained by size asymmetry. Aggressive motivation may also influence the outcome of contests and could be assessed in agonistic encounters. Theory suggests that signals of aggressive intention will be evolutionarily stable if individuals can recognize opponents and encounter one another repeatedly. In addition, individual recognition is one way that dominance hierarchies can be maintained. Here we demonstrate that males from both species can recognize individuals. In addition, at least some X. nigrensis males were site-faithful in the field, suggesting males encounter the same opponents repeatedly.

Key words Aggression · Communication · Individual recognition · Resource holding potential · Swordtails

Introduction

A productive area for examining the function and evolution of intraspecific communication is agonistic encounters between conspecifics. Contests over resources often consist of ritualized displays rather than

M.R. Morris (⊠)¹ · L. Gass · M.J. Ryan Department of Zoology, University of Texas, Austin, TX 78712,

Present address:

¹Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, MD 21853, USA

physical combat. It has been argued that displays in agonistic confrontations communicate information about either resource-holding potential (RHP, Parker 1974) or aggressive motivation (Morris 1957; Cullen 1966; Smith 1977). The function of display communication would be to settle disputes based on who is more likely to win an escalated contest without the high costs of physical combat (Hammerstein and Riechert 1988).

Asymmetry in body size is used to determine the outcome of agonistic encounters or dominance in many animal species (for review, see Archer 1988), including fish in the genus Xiphophorus (Collins et al. 1967; Beaugrand and Zayan 1985; Beaugrand et al. 1991; Ribowski and Franck 1993) and therefore body size is often a good indicator of RHP. RHP can be assessed in contests through signals correlated with RHP. It is possible to determine if contestants are assessing RHP by comparing the intensity of a fight to the degree of asymmetry in RHP. Because assessment should be easier when the relative difference is great, contests between individuals with a large relative difference in RHP should be settled at a lower cost than contests in which the relative difference is small (Parker and Rubenstein 1981; Enquist and Leimar 1983).

Intrinsic RHP does not always explain why some individuals win contests (Parker 1974). Several other factors have been implicated in determining the outcome of contests, including asymmetries in resource ownership (e.g., Braddock 1949; Hyatt and Salmon 1978), payoff asymmetries (Parker and Rubenstein 1981; Maynard Smith 1982), and prior fighting experience. The contribution of prior experience to the outcome of fights has been examined in *Xiphophorus helleri* (Beaugrand and Zayan 1985; Franck and Ribowski 1987, 1989; Beaugrand et al. 1991). Beaugrand and Zayan (1985) demonstrated that prior dominance experience could reverse the effects of a small asymmetry in RHP. If a factor like prior fighting experience can influence the outcome of a fight, a signal might evolve

that conveys information about motivation due to this factor.

There is little dispute that signals containing information about RHP can be evolutionarily stable (Parker 1974). Signals conveying information about more transitory factors like motivation, however, could be more easily exaggerated or concealed. This would make it easier for these signals to be invaded by cheaters, which would render them unreliable over time (Maynard Smith and Parker 1976; Dawkins and Krebs 1978; Caryl 1979; Maynard Smith 1982). Axelrod and Hamilton (1981) demonstrated that apparent altruistic behavior (reciprocal altruism, Trivers 1971) could be evolutionarily stable against cheaters if the same individuals interact repeatedly. The conditions under which signals that convey information about intention might be evolutionarily stable against cheaters are similar (van Rhijn and Vodegel 1980; Turner and Huntingford 1986; Hauser and Nelson 1991). Recognizing previous opponents makes it possible for individuals that cheat to be distinguished from reliable individuals (van Rhijn and Vodegel 1980).

We were interested in examining communication between males during agonistic encounters in Xiphophorus nigrensis and X. multilineatus. First, we examined the role that size plays in determining the outcome of fights and the possibility that males assess size in aggressive encounters. We then investigated behavior patterns that may indicate aggressive motivation to determine their influence on the outcome of contests. Since encountering and recognizing a previous opponent can prevent the invasion of cheaters and maintain a signal of motivation (van Rhijn and Vodegel 1980), and individual recognition appears to play a role in dominance hierarchies (e.g., Barnard and Burk 1979), we also examined the ability of males to identify individuals and the probability of encountering the same opponent repeatedly in the field.

Methods

Study organisms

X. nigrensis is found in the Río Choy and X. multilineatus in the Río Coy, both of the Pánuco River drainage in San Luis Potosí, Mexico (Rauchenberger et al. 1990). X. nigrensis males vary in size from 18 to 42 mm standard length (SL) and X. multilineatus from 18 to 44 mm SL. Much of the variation in size is due to a genetic polymorphism at the pituitary (P) Y-linked locus (Kallman 1984, 1989). X. nigrensis has three P alleles, producing three size classes of males (large, intermediate and small), X. multilineatus has four P alleles, producing four size classes (large, intermediate I, intermediate II, small). Field studies have shown that large males of X. nigrensis have greater reproductive success than small males (Ryan et al. 1990), and that this advantage is due at least in part to male-male competition for access to females (Morris et al. 1992). Larger males chased smaller males away from females in the field and were better at blocking access to females in the laboratory. Therefore, the dominance a male gains through aggressive interactions should increase his fitness.

Males used in this study were either collected as adults in the field or were raised to sexual maturity in large breeding tanks at the Brakenridge Field Station at the University of Texas. All males were kept in communal tanks in the laboratory for no longer than three weeks prior to testing, and were returned to the outdoor breeding tanks after testing. Water temperature was kept at approximately 24° C and light on a 12-h cycle.

Assessment

We determined if males were assessing body size during aggressive encounters by analyzing contests staged between pairs of males in which we varied the degree of asymmetry in size. Combinations of males from all size classes were used (Table 1). Tests were conducted in a $45 \times 90 \times 41$ cm tank, with gravel on the bottom, and black plastic covering the ends and back side. Two males were taken from community tanks, measured for standard length (mm), and placed on either side of the experimental tank that was divided into two equal compartments by an opaque partition. After 24 h, the partition was removed and the behavior of both fish was recorded on video.

The behavior and patterns of agonistic interactions used by *X. nigrensis* and *X. multilineatus* are similar to those described by Franck (1964) for *X. helleri*. Contests can be divided into three phases. In the first phase, males *approach*, raise their dorsal fins, *circle* and then use a series of *S-threats* (for descriptions of behavior, see Franck 1964). The second phase begins when one male *bites*. These first two phases are the same as the "threat period" (period I) of Franck and Ribowski (1987). In the third phase, bites are returned by both males (period II, Franck and Ribowski 1987).

We recorded 13 encounters between *X. nigrensis* males, and 14 between *X. multilineatus* males. The average size asymmetries in the contests were similar for the two species (Table 1). From the video tapes of each contest we noted which male approached first, which male delivered the first bite, number of displays (S-threats), number of bites, length of contest, and which male became dominant (or won the contest). Contest length was measured as the length of time from when the first male approached to the time when one male became dominant. A male was judged dominant if the other male put down his dorsal fin and swam away when approached.

We used bites/minute as a measure of the intensity of a fight, and thereby the cost of the contest. Enquist and Leimar (1983) predicted that fights between more evenly matched opponents will last longer if assessment is taking place. Parker and Rubenstein (1981) made the more general prediction that cost will be greater in such contests. Fights in *X. nigrensis* and *X. multilineatus* often contained periods when males did not bite but rested or circled. Therefore, bites/minute is probably a better indicator of fight intensity (or cost) than contest duration.

We also compared the number of S-threats, number of bites, first male to approach, and first male to bite between winners and losers with a Wilcoxcon signed-rank test to determine if these behavior patterns were predictive of the outcome of the contest. Differences between the behavior of losers and winners can be expected in contests where differences in RHP are assessable (Archer 1988). However, when RHP is not easily assessed and the contests are symmetrical, winners and losers should not differ in predictable ways (Maynard Smith 1982).

Individual recognition

Individual recognition experiments were conducted for 17 male pairs of *X. nigrensis* and 11 of *X. multilineatus*. Two larger males, matched for size within 0.2 mm, were designated as the "dominant" males in each test. Another pair of males, 0.5–2 mm smaller than the test males and also matched for size were designated as the "subordinate" males. All males used were over 30 mm in size. Each

subordinate male was put with one dominant male in a tank with an opaque divider and left to acclimate for 24 h. The next day, the divider was removed and the number of bites and displays was recorded for each individual for 30 min. We also recorded time until one male gave up, and which male won or became dominant. Most fights were over before 30 min, however, the dominant male continued to occasionally chase, bite and display to the subordinate. Males were left together for 3 days, and the number of bites and displays for each male recorded for 30 min at the same time on each day for 17 of the 28 pairs (10 X. nigrensis, and 7 X. multilineatus). On the 3rd day, the divider was replaced and the subordinate males were either switched between the two tanks (treatment = strange), or simply removed and then replaced in the same tank (treatment = familiar). Males were then left to acclimate for 24 h. On the 4th day, the divider was removed and the number of bites and displays recorded again for each pair of males (n = 28) for 30 min. Total number of bites by both males over the 30-min observation period was used as a measure of fight intensity.

We matched the size of pairs of subordinate males (switched between tanks in the strange treatment) and pairs of dominant males to control for the effect of size difference on fight intensity. Both familiar and strange subordinate males were placed on the same side of the tank to control for recognition based on location alone ("dear enemy effect", Ydenberg et al. 1988). Comparisons were made within treatments between the 1st and 4th day to control for differences in aggressiveness between males. If males can recognize individuals, we predicted that for each pair, fight intensity would be less on the 4th day than on to the 1st day in the familiar treatment, but not in the strange treatment.

Beaugrand et al. (1991) have shown for *X. helleri* that previous fight experience influences fight intensity (i.e., males who were subordinate in previous encounters were less aggressive in future encounters, although see Franck and Ribowski 1989). We controlled for prior fight experiences by comparing fight intensity between the familiar and the strange treatment on the 4th day. If males are recognizing individuals, and not simply altering their fighting behavior due to previous experiences, we would predict that fight intensity would be less in the "familiar" treatment than in the strange treatment on the 4th day.

A variable that we did not control for, and which may have influenced fight intensity, was familiarity of environment. Subordinate males in the strange treatment were not only placed with a new opponent, but into a new environment, while subordinate males in the familiar treatment were removed and then replaced into the same tank. From our experience, however, the effect of a strange environment on male aggressive behavior is to reduce male aggression. When two males were placed in a divided tank and allowed to acclimate for a much shorter time than in the experiments presented here, interactions between the males once the divider was removed were much reduced. The influence of this variable would have been to bias the results in the opposite direction to our results, or to decrease the aggressive behavior in the fights in the strange treatment. We suggest, therefore, that controlling for this variable would not have changed our conclusions.

Site fidelity in the field

We collected by seining 38 adult males of X. nigrensis (23 large, 11 intermediate, and four small) on 9 March 1991, from a site just below the headwaters of the Río Choy. Two areas were seined, one approximately 3 m \times 9 m, one 3 m \times 12 m, and both surrounding large rocks that protruded from the water. Each male was anesthetized with tricaine methanesulfonate (MS-222), measured (standard length, mm), and then marked with a unique combination of tail clips and freeze burns (Raleigh et al. 1973; Hert 1986) for individual identification. We have used freeze-branding in the laboratory for other experiments and have had no increase in mortality due to this technique. All males were then released within 20 m of where they had been captured. The next day (10 March) using

SCUBA, we observed all males in the two areas where we had previously seined, to determine if they were marked. We recorded the identity of marked males and where they were observed. Each location was marked with a numbered bobber tied to a rock. Observations were made from 1200 to 1600 hours. On the morning of 11 March, we made observations with SCUBA in the same areas from 1030 to 1145 hours, checking each male again to see if he was marked, and checking the locations of the bobbers to determine which males were found there.

Results

Assessment

Of the 27 contests, 18 escalated to period II, while 7 contests were resolved without bites. In one case in each species, the contest ended after the second phase, with only one of the two males escalating to bites. Even though males made contact while biting, they showed no signs of injury even after the most intense fights. Franck and Ribowski (1986) also stressed that escalated fights were not dangerous in the sense of injury for *X. helleri*. Because losers were aggressive right up to the point at which they terminated a contest, losers are evidently not forced into submission by the physical strength of the dominant male. Therefore, even contests that escalated to bites had a ritualized component.

We examined the effects of asymmetry in size on the outcome and intensity of contests to determine if males were assessing size in agonistic encounters. Of the 25 contests in which males differed in standard length, the larger males won significantly more often in both X. nigrensis and in X. multilineatus (Table 1). Of the 27 encounters 20 escalated to physical contact, with either both males biting (mean size difference = 2.2 mm, SD = 2.55, n = 18) or one male biting (mean size difference = 2.6 mm, SD = 2.26, n = 2). Contests with no bites had an average size difference of 11.36 mm (SD = 6.07, n = 7), which was greater than the size difference for fights that escalated to both males biting (Mann-Whitney U, Z = 3.2, P = 0.001). In all seven of the contests that did not escalate to bites, the larger male was dominant (Table 1). These data suggest that body size is a good indicator of RHP, and that males are assessing size in these contests.

We also examined the relationships between various measures of the cost of an encounter and relative asymmetry in size (Table 2). Bites/min was the only measure of fight intensity that was significantly correlated with difference in size for *X. multilineatus*, while all measurements except length of contest correlated with size difference in *X. nigrensis* (Table 2, Fig. 1). The difference between the number of significant relationships in the two species may suggest that in *X. nigrensis* difference in size accounts for more of the variation in fighting behavior than in *X. multilineatus*.

Fight intensity was highly variable when the asymmetry between males was small (Fig. 1). Considering

Table 1 Size difference, fight outcome, and fight intensity of staged laboratory encounters in two species of *Xiphophorus*

	Difference in size (mm)	First bite	Winner	Bite/min	Bite/total acts
X. multilineati	us				
	0.0	loser	-	8.59	0.45
	0.3	winner	smaller	0.34	0.21
	0.5	loser	smaller	0.27	0.29
	0.8	loser	larger	0.5	0.41
	0.9	loser	larger	2.68	0.74
	1.4	loser	larger	11.39	0.44
	3.1	loser	larger	6.07	0.68
	4.0	winner	smaller	5.06	0.62
	4.2	loser	larger	4.18	0.85
	4.2	*winner	larger	0.39	0.42
	6.3	loser	larger	0.2	0.10
	9.8	loser	larger	1.03	0.62
	11.1	0	larger	0	0
	16.9	0	larger	0	0
Avg	4.54		3/13	2.90	0.42
SD	4.97		P = 0.03	3.66	0.27
X. nigrensis					
0	0.0	winner	_	4.7	0.33
	0.4	loser	larger	7.78	0.38
	0.5	loser	smaller	12.86	0.36
	1.0	*winner	smaller	0.23	0.39
	1.0	loser	larger	10.67	0.25
	1.9	loser	larger	0.41	0.33
	2.2	winner	larger	6.72	0.25
	2.4	0	larger	0	0
	2.7	loser	larger	2.11	0.71
	6.0	0	larger	0	0
	8.7	0	larger	0	0
	15.5	0	larger	0	0
	18.9	0	larger	0	0
Avg	4.70		2/12	3.50	0.23
SD	6.08		P = 0.01	4.59	0.22

Relative size of winners and losers compared with binomial statistic

Table 2 Relationships between measures of fight intensity and asymmetry of male size. Acts include bites, S-threats, and chases

		tilineatus	for relations X . nigrensis $(n = 13)$	
Measures of intensity	Z	P	Z	P
Contest length (min)	0.98	0.33	0.73	0.47
Total number of acts	1.68	0.09	2.56	0.01
Total number of bites	1.49	0.14	2.55	0.01
Bites/total acts	1.04	0.30	2.05	0.04
Contest intensity (bites/min)	1.91	0.05	2.56	0.01

only those contests that escalated to period II (both males bite), we found that the correlation between fight intensity and size difference was not significant (Spearmann rank correlation, Z = 1.49, P = 0.13, n = 20). The large degree of variability in fight intensity that cannot be explained by size asymmetry suggests that a factor in addition to size asymmetry influences fight intensity when size asymmetries are small.

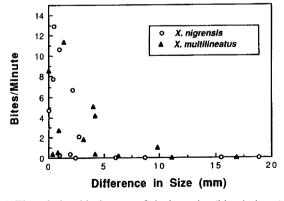


Fig. 1 The relationship between fight intensity (bites/minute) and size asymmetry

We examined the relationship between the different behavior patterns and the outcome of contests to determine if behavior could be used to predict outcome. Combining data from both species and including all contests, first approach did not predict fight outcome (Table 3). In those contests that escalated to bites, the number of bites given by winners as compared to losers

^{*} only one male escalated to bites

Table 3 Relationships between behaviors, and fight outcome and relative size

	Individual performing behavior					
	Winner	Loser	Binomial	Larger	Smaller	Binomial
First approach	11	15	NS	10	14	NS
First bite	6	14	P = 0.05	4	15	P = 0.007
Winner		-		20	5	P = 0.001
2 (All 1874) - 1	W > L	L > W	Binomial	Lg > Sm	Sm > Lg	Binomial
No. bites	9	10	NS	11	8	NS
No. S-threats	16	7	P = 0.05	12	11	NS

Table 4 Average number of bites for pair of males (and SDs) in male-male recognition contests. In first encounters (day 1), all males were strangers. On day 4 some males were given "familiar" males, and some males were given "strange" males

X. multilineatus	Treatment Familiar	n	Strange	n	Mann-Whitney U-test
Day 1	48.6 (84.0)	5	62.8 (133.7)	6	Z = 0.09 P = 0.93
Day 4	2 (3.9)	5	38.7 (59.3)	6	Z = 2.23 $P = 0.03$
Wilcoxon signed-rank	Z = 2.03; P = 0.05		Z = 0.63; P = 0.86		
	Treatment				
X. nigrensis	Familiar	n	Strange	n	Mann-Whitney U-test
Day I	31.6 (25.3)	7	58.7 (72.1)	10	Z = 0.07 P = 0.94
Day 4	7.4 (7.0)	7	31.1 (31.5)	10	Z = 2.6 $P = 0.008$
Wilcoxon signed-rank $Z = 2.03$; $P = 0.05$		Z = 0.64; P = 0.87			

did not differ significantly. However, the winners used more S-threats than the losers (Table 3). In addition, losers were more likely to bite first than winners, and small males were more likely to bite first than large males (Table 3).

Individual recognition

The number of bites and displays decreased after males had been together for 24 h in both species. The average number of bites during the 30-min observation period on the first day for X. nigrensis was 27.2 (n = 10, SD = 14.83) and 40.5 (n = 7, SD = 68.69) for X. multilineatus. On the 2nd day, the number of bites observed in a 30-min period had dropped to 0.3 (n = 10, SD = 0.48) for X. nigrensis, and to 2 (n = 7, SD = 1.85) for X. multilineatus, which was a significant decline (Wilcoxon signed-rank test, Z = -2.81, n = 10, P = 0.005; Z = -1.86, n = 7, P = 0.06).

We tested for individual recognition while controlling for differences in the aggressive levels of males and the relative size asymmetries by comparing differences in number of bites between day 1 and day 4 across treatments. The difference in the number of bites for a pair of males between day 1 and day 4 in the strange treatment for either species was not significant (Table 4). However, the number of bites decreased significantly in both species when males were presented with a familiar male on day four (Table 4).

We controlled for the effects of prior fight experience by comparing the number of bites on the fourth day between treatments. The smaller male in both treat-

ments had been subordinate and the larger male dominant for 3 days. In both species, there were more bites in the strange treatment than the "familiar" treatment on the last day (Table 4). Differences in the intensity of fights between familiar and strange males was therefore not due to prior experience.

Site fidelity in the field

Of the 38 marked males, 17 were observed again after being released (52% of the males in the large size class, 27% of the intermediate size class, and 60% of the small size class). Ten males were observed only once, four on the 1st day of observations and six on the 2nd day of observations. Of the males seen on both days (four large, one intermediate, and two small), all were found within 1 m of the same location on both days. One male (large) was observed twice on the 2nd day, and was not at the same site for one of the two observations. We suggest that at least some males are site-specific, remaining at or returning to the same site in subsequent days.

Discussion

Assessment

We demonstrate that body size is a good indicator of RHP in *Xiphophorus nigrensis* and *X. multilineatus*, and that males are apparently gaining information about

relative size during aggressive encounters. Because small males were more likely to bite first, males probably had significant information about size asymmetry by the time a contest escalated to the first bite. However, if fight outcome is determined on size asymmetry alone, then once information is complete, theory predicts that the contest would be settled at that point based on the asymmetry (Maynard Smith 1982).

There are at least two possible explanations why contests might escalate even though information about the asymmetry in size had already been conveyed. First, information about size may still not be complete. Males could be gaining more precise information about the asymmetry in size by escalating. If so, we would expect to find a significant negative relationship between asymmetry in size and fight intensity in fights that escalated. We did not. While the reduced asymmetry in size in contests that escalated would make it more difficult to detect a relationship between size difference and fight intensity, another possible explanation is that fight outcome was not determined by size alone. Although larger males won significantly more contests, they did not win all of the staged encounters. Beaugrand et al. (1991) examined the relative contribution of prior experience and asymmetries in size to the outcome of contests in Xiphophorus helleri. They found that prior dominance experiences could reverse the effects of small asymmetries in size (but see Franck and Ribowski 1986). Although we isolated fish for at least 24 h before each test in this study, we only controlled for a male's prior fighting experience in the individual recognition experiments. Variability in fighting intensity, as well as wins by smaller males in the other staged encounters, could be due to differences in aggressive motivation based on variability in prior fighting experience.

The behavior of biting first in a contest has been viewed as an indicator of aggressive motivation in several fish studies (Barlow 1986; and see articles cited in Figler and Einhorn 1983). In this study, losers were more likely to bite first than winners, even when fights continued well after the first bite. In addition, winners used more S-threats than losers. The detailed study by Simpson (1968) of the behavior of Siamese fighting fish was one of the first studies to ask if winners of fights can be predicted by certain behavior patterns. The "war of attrition" model predicts that the behavior of an individual in a contest should not carry information about long-term intentions, or in particular, about who will be the ultimate winner (Maynard Smith 1982). Predictions from this model, however, only apply to situations in which there are no asymmetries influencing fight outcome (Archer 1988). Because asymmetry in size decided the outcome of most of the contests in this study, the differences in the behaviors used by the winners and losers may simply reflect that differences in behaviors used by males based on knowledge of their relative size.

Further tests on the role of aggressive motivation in male-male interactions in these fish are needed and should consider contests in which the size asymmetry is held constant. Barlow et al. (1986) demonstrated that persistent differences in aggressive behavior effected the outcome of contests in the midas cichlid. They suggest that an individual's inherent aggressiveness in this case would be a component of its RHP. Differences in aggressive motivation could represent an asymmetry correlated with RHP. It may be impossible to assess motivation and RHP independently (Richner 1993), especially if motivation varies as a function of RHP (Archer 1988).

Why, however, would a smaller male escalate first? It seems counter-intuitive to suggest that individuals who know their relative RHP is less than that of their opponents are initiating aggressive encounters. However, as size did not determine the outcome of all contests, smaller males have some probability of winning an escalated contest, which could counter the costs of fighting. In addition, if information about RHP or other factors was not complete, the benefit of escalating for the male with a perceived lower RHP could be to gain more information about asymmetry in these other components. Small males might escalate in either of these cases if the costs of fights were fairly low in comparison to the benefits of being a dominant male. These conditions may be met for these fish. The fight intensity we observed in the staged laboratory contests was much greater than what we observed in the field, and even then we saw no evidence of injury from these fights. In addition, it has been demonstrated that males do gain access to females in the field through malemale competition (Morris et al. 1992).

Franck and Ribowski (1989) have found results similar to ours for *X. helleri*. In contests where the size asymmetry was held to a minimum, males with a prior subordinate experience had a significantly higher tendency to escalate. They suggested that it should pay subordinates to be more aggressive if there is an asymmetry in payoffs between subordinate and dominant males. This argument could hold for small males biting first as well as for subordinate males biting first. For example, if the only chance a small male had of winning was by being more aggressive or motivated, then differences in payoffs could lead small males to risk more (Parker and Rubenstein 1981).

Individual recognition and site fidelity

We demonstrated that males can identify individuals in *X. nigrensis* and *X. multilineatus*, and that they have the opportunity to encounter the same opponent repeatedly in *X. nigrensis*. Many animals that maintain either territories or dominance hierarchies are able to recognize familiar individuals (for review see van Rhijn and Vodegel 1980; also Halpin 1980; Godard 1991;

Caldwell 1992), and individual recognition has been suggested for at least one other poeciliid (*Xiphophorus helleri*, Zayan 1975; Beaugrand and Zayan 1985). We have shown that the degree of escalation observed in contests may depend on the familiarity of the contestants with each other. This observation has important consequences for studies of aggressive interactions in these fish. First, individual recognition could be used to maintain dominance hierarchies (Barnard and Burk 1979). Second, because van Rhijn and Vodegel (1980) demonstrated that revealing information about long-term intentions can be evolutionarily stable if individuals are able to recognize one another and encounter the same opponent repeatedly, we suggest that a signal of aggressive motivation could be stable in these fish.

Acknowledgements Thanks are due to Michelle Mussel, Christy Foran, and Ken Casey for assisting in collecting the data. We thank George Barlow for constructive comments on the manuscript. We also thank the Mexican Government for the collecting permits (permit numbers 15088113031726 and 40070201838) and Sr. Gaston Santos for permission to work on his property. This study was supported by a grant from the National Science Foundation (BSR 8800231) to M.R.M., a Reeder Fellowship and a National Science Foundation grant (IBN 92217033) to M.J.R.

References

- Archer J (1988) The behavioral biology of aggression. Cambridge University Press, Cambridge
- Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211:1390–1396
- Barlow GW, Roger W, Fraley N (1986) Do midas cichlids win through prowess or daring? It depends. Behav Ecol Sociobiol 19:1-8
- Barnard CJ, Burk T (1979) Dominance hierarchies and the evolution of 'individual recognition'. J theor Biol 81:65-73
- Beaugrand J, Zayan R (1985) An experimental model of aggressive dominance in *Xiphophorus helleri* (Pices, Poeciliidae). Behav Proc 10:1–52
- Beaugrand J, Goulet C, Payette D (1991) Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. Anim Behav 41:417–424
- Braddock JC (1949) The effect of prior residence upon dominance in the fish *Platypoecilus maculatus*. Physiol Zool 22:161–169
- Caldwell RL (1992) Recognition, signalling and reduced aggression between former mates in a stomatopod. Anim Behav 44:11–19
- Caryl PG (1979) Communication by agonistic displays: what can game theory contribute to ethology? Behaviour 68:136–169
- Collins JM, Cramer J, Wechkin S (1967) Nip frequency and dominance in male swordtails and platies. Am Zool 7:806
- Cullen JM (1966) Reduction in ambiguity through ritualization. Phil Trans R Soc Lond B 251:363–374
- Dawkins R, Krebs JR (1978) Animal signals: information or manipulation. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 282–309
- Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. J Theor Biol 102:387-410
- Figler MH, Einhorn DM (1983) The territorial prior residence effect in convict cichlids (*Cichlasoma nigrofasciatum* Gunther). Temporal aspects of establishment and retention, and proximate mechanisms. Behaviour 85:157–181

- Franck D (1964) Vergleichende Verhaltensstudien an lebendgebarenden Zahnkarpfen der Gattung Xiphophorus. Zool Jb Physiol 71:117–170
- Franck D, Ribowski A (1987) Influence of prior agonistic experience on aggression measures in the male swordtail (*Xiphophorus helleri*). Behaviour 103:217–240
- Franck D, Ribowski A (1989) Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): effects of prior rank-order experience and information transfer. Behav Ecol Sociobiol 24:133–143
- Godard R (1991) Long-term memory of individual neighbors in a migratory songbird. Nature 350:228–229
- Halpin ZT (1980) Individual odors and individual recognition; review and commentary. Biol Behav 5: 233–248
- Hammerstein P, Riechert SE (1988) Payoffs and strategies in territorial contest: ESS analysis of two ecotypes of the spider *Agelenopsis aptera*. Evol Ecol 2:115–138
- Hauser MD, Nelson DA (1991) "Intentional" signalling in animal communication. Trends Ecol Evol 6:186–189
- Hert E (1986) Freeze branding in fish, a method for eliminating color patterns at the skin surface. Ethology 72: 165–162
- Hyatt GW, Salmon M (1978) Combat in the fiddler crabs *Uca pugilator* and *Uca pugnax*: a quantitative analysis. Behaviour 65: 182–221
- Kallman KD (1984) A new look at sex determination in poeciliid fishes. In: Turner BJ (ed) Evolutionary genetics of fishes. Plenum, New York, pp 95-171
- Kallman KD (1989) Genetic control of size at maturity in *Xiphophorus*. In: Meffe GK, Snelson FF (eds) Ecology and evolution of livebearing fishes (Poeciliidae). Prentice-Hall, Englewood Cliffs, pp 163–184
- Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge
- Maynard smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:154–157
- Morris D (1957) 'Typical intensity' and its relationship to the problem of ritualization. Behaviour 11:1-12
- Morris MR, Batra P, Ryan MJ (1992) Male-male competition and access to females in the swordtail *Xiphophorus nigrensis*. *Copeia* 1992:980–986
- Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223-243
- Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Anim Behav 29:212-240
- Raleigh RF, McLearen JB, Groff DG (1973) Effects of topical location, branding techniques, and changes in hue on recognition of cold brands in Centraarchid and Salmonid fish. Trans Am Fish Soc 102:637–641
- Rauchenberger M, Kallman KD, Morizot DC (1990) Monophyly and geography of the Rio Panuco Basin swordtails (Xiphophorus) with descriptions of four new species. Am Mus Novit 2975
- Rhijn JG van, Vodegel R (1980) Being honest about one's intentions: an evolutionarily stable strategy for animal conflicts. J Theor Biol 85:623-641
- Ribowski A, Franck D (1993) Demonstration of strength and concealment of weakness in escalating fights of male swordtails (Xiphophorus helleri). Ethology 93: 265-271
- Richner H (1993) Assessment of expected performance and Zahavi's notion of signal. Anim Behav 45:399-401
- Ryan MJ, Hews DK, Wagner WE Jr (1990) Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. Behav Ecol Sociobiol 26:231–237
- Simpson MJA (1968) The displays of the Siamese fighting fish *Betta splendens*. Anim Behav Monogr 1:1–73
- Smith WJ (1977) The behaviour of communicating. Harvard University Press, Cambridge

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Turner GF, Huntingford FA (1986) A problem for game theory analysis: assessment and intention in male mouthbrooder contests. Anim Behav 34:961–970

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbours,

strangers, and the asymmetric war of attrition. Anim Behav 36:343-347

Zayan RC (1975) Defense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poeciliidae). Behaviour 52: 266–312

Communicated by G.M. Klump