

TWO'S COMPANY, THREE'S A CROWD: DIFFERENCES IN DOMINANCE RELATIONSHIPS IN ISOLATED VERSUS SOCIALLY EMBEDDED PAIRS OF FISH

by

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Summary

We performed experiments with cichlid fish to test whether several basic aspects of dominance were the same in isolated pairs as in pairs within a social group of three or four. We found that the social context, whether a pair was isolated or within a group, strongly affected the basic properties of dominance relationships. In particular, the stability of relationships over time, the replication of relationships in successive meetings, and the extent of the loser effect were all significantly less in socially embedded pairs than in isolated pairs. We found no significant winner effect in either isolated or socially embedded pairs. These findings call into question many current approaches to dominance that do not consider social context as an important factor in dominance behavior. These findings also cast serious doubt on the validity of empirical and theoretical approaches based on dyadic interactions. Among these approaches are game theoretic models for the evolution of aggressive behavior, experimental designs evaluating how asymmetries in attributes influence the outcome of dominance

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contests, and mathematical models and computer simulations accounting for the common occurrence of linear hierarchies.

Introduction

Consider two pairs of animals about to form a dominance relationship: One pair forms its relationship by itself, out of the sight of other animals. The second pair develops its relationship in the presence of other animals, or establishes its relationship by itself and then is joined by several additional individuals. In the first case the pair is an isolated unit, not affected by others. In the second case, the pair is a 'socially embedded' unit, at least in principle no longer separate and independent but potentially dependent and influenced by others. Do these pairs establish their relationships in exactly the same manner? Or do the characteristics of their dominance relationships and the factors that affect them differ in some major ways?

Present research gives little clear guidance in answering these questions. Many current experimental and theoretical approaches simply do not consider the question of social context, and so, by default, seem to imply that it is not of consequence (by social context, we mean being in the presence of other animals). But other approaches assume that social context does matter — to a greater or lesser extent — in the formation of dominance relationships. Which assumption is correct? How important is social context to the creation and maintenance of dominance relationships? Does it really affect the qualities of dominance behavior within pairs?

Here we provide some experimental evidence to help answer these questions by comparing several basic aspects of dominance relationships in separate and socially embedded pairs of individuals using cichlid fish as model animals. More specifically, we investigate the stability of relationships over time, the replication of relationships in successive meetings, and the presence and strength of winner and loser effects in pairs by themselves *versus* pairs within 'crowds' of three and four animals.

Current approaches to dominance can be roughly divided into three classes depending upon their position concerning the importance of social context as a factor in the formation and maintenance of dominance relationships: those that do not consider social context at all, those that hold it of some moderate importance, and those that regard it of crucial importance. Many of the approaches at the core of our experimental and theoretical approaches to dominance simply do not consider the importance of

social context. Among these are most experimental studies investigating the effect of differences in intrinsic attributes, such as weight, on the outcome of dominance contests (*e.g.* Clutton-Brock *et al.*, 1984; Beacham, 1988; Drews, 1993; Holekamp & Smale, 1993; Sapolsky & Share, 1994) and game theoretic models for the evolution of tactics in aggressive encounters (*e.g.* Parker, 1974; Maynard Smith, 1982; Enquist & Lelmar, 1983; Riechart, 1998). In experiments examining the effects of differences in attributes, the typical design is to match pairs of animals differing by specified amounts in attribute measures, say, by 10 to 20% in weight. The experimenter then reports how these differences in attributes affect the outcome of dominance contests, *e.g.* the percentage of contests in which the heavier animals prevailed. Experiments of this sort have indicated that differences in a variety of attributes, such as weight, age, *etc.* have significant influences on the outcome of contests, especially if the differences are reasonably large. However, since these experiments are carried out in isolated pairs, we do not know whether or not the results would be either stronger or weaker for pairs with the same differences in attributes forming relationships in group settings.

Virtually all of the classical models attempting to account for the evolution of commonly seen behavioral tactics in aggressive encounters, such as hawk-dove, prober-retaliator, war of attrition, are two-individual game theoretic models (*e.g.* Parker, 1974; Maynard Smith, 1982; Enquist & Lelmar, 1983; Riechart, 1998, but see Broom & Cannings, 2002 and the literature reviewed there). By definition, these models only depict how separate pairs of individuals should interact with one another and not how their actions might be altered by the presence of others. These models have helped us to understand the adaptive advantage of many of the behavioral responses commonly observed in animal contests, but they do not consider in what ways it might be adaptive for animals to change their tactics when third parties are present at their dominance interactions. Oliveira *et al.* (1998) have called attention to this point indicating that dominance relationships often form within networks of animals rather than in isolated pairs.

Some experimental and theoretical approaches take an intermediate position on the importance of social context. They assume that what one animal experiences in interacting with a second animal can materially change how it interacts with a third animal: what happens in a first pair carries over to influence what happens in another pair. Third parties do not actually have to be present, but after one contest, the participants have to have access to

the third parties. Some of the chief representatives of this proposition are experimental studies of winner and loser effects and the mathematical models and computer simulations that use these effects in attempting to explain the common occurrence of linear hierarchy structures. In the winner effect, an animal winning one contest increases its probability of winning a second with another animal, and in a loser effect an animal losing an earlier contest has an increased probability of losing a subsequent one with a different animal. The way these experiments are usually done is to match an animal that has received either a winning or a loser experience in a contest with a single new opponent (after removing the individual that provided either the winning or losing experience). Researchers have found loser effects in a broad range of species; these effects usually last for a while, perhaps a day or longer; and sometimes even animals quite a bit smaller can dominate previous losers (Frey & Miller, 1972; Burk, 1979; Bakker & Sevenster, 1983; Francis, 1983, 1987; Beacham & Newman, 1987; Beacham, 1988; Bakker *et al.*, 1989; Drummond & Osorno, 1992; Zucker & Murray, 1996; Drummond & Canales, 1998; Hsu & Wolf, 1999). Researchers also report winner effects in a variety of species, but they do not find them as commonly as loser effects, and where they occur, winner effects are apt to be short-lived (Frey & Miller, 1972; Burk, 1979; Bakker & Sevenster, 1983; Bakker *et al.*, 1989; Chase *et al.*, 1994; Drummond & Canales, 1998; Hsu & Wolf, 1999). However, as in the case of experiments on the effect of differences in attributes, there are no reports in the literature investigating how the strength of winner and loser effects might change in a group context, that is, how the presence of one or more other animals might affect the relationship between a winner or a loser and a new animal.

Most of the current mathematical models and computer simulations attempting to account for the common occurrence of linear hierarchy structures do so by relying on winner and/or loser effects plus one or more other behavioral mechanisms (*e.g.* Hogeweg, 1989; Theraulaz *et al.*, 1995; Skvoretz *et al.*, 1996; Hemelrijk, 2000). In doing this, most of these models and simulations assume that winners are very likely to win again and losers to lose again. But since the models and simulations necessarily apply to animals forming relationships in group contexts, it is important to know whether winner and loser effects are present in social contexts and if they are, whether their levels of strength match those that the models and simulations require.

Other experimental and theoretical studies take a yet stronger position concerning the importance of social context and explicitly assume that it can have a direct influence on the formation of dominance hierarchies and relationships. Much of this work is fairly recent, but some dates back to the earlier years of research in dominance. Among the recent experimental studies are those investigating 'eavesdropping' and audience effects: how observation of a contest in a pair affects third parties or how being observed by third parties affects the participants in a pair contest (*e.g.* McGregor, 1993; Johnson & Akerman, 1998; Oliveira *et al.*, 1998; Herb *et al.*, 2003). This research indicates, for example, that observers in Siamese fighting fish behave differently towards animals that they have seen either win or lose a contest than they behave towards animals that have either won or lost but have not been observed to do so (Oliveira *et al.*, 1998). In particular, they are slower to approach and display to observed winners than to observed losers and equally quick to approach and display to unobserved winners and losers. Also in Siamese fighting fish individuals that observe contests experience hormonal changes in comparison to non-observers (Oliveira *et al.*, 2001), and male Siamese fighting fish that have lost contests 'prefer' females that have not observed them losing over those females that have observed them losing (Herb *et al.*, 2003).

Experimental work of another sort also indicates the importance of social context in ensuring the formation of linear hierarchy structures. In groups of cichlid fish that met only as pairs to form dominance relationships, out of the sight of the other members of their groups, only about 50% of the groups formed linear hierarchies (Chase *et al.*, 2002). In contrast, when all members of a group met in one tank at the same time, *i.e.* when members of groups formed their hierarchies in a social context, over 90% of the groups formed linear structures.

As far as we are aware, the jigsaw puzzle model is the only current theoretical approach examining empirical patterns of interaction within a social context during hierarchy formation (Chase, 1982, 1985) and maintenance. This model describes the possible sequences occurring in groups of three or more animals, either in terms of dominance relationship formation or in single attacks, and it points out that some sequences guarantee transitivity and thus promote linear hierarchies while others do not ensure transitivity and thus can lead to non-linear hierarchies. Researchers using this model have found that the sequences guaranteeing transitivity occur at high rates

in groups across a broad range of species including chickens, rhesus monkeys, Japanese macaques, cichlid fish, crayfish (Chase, 1982, 1985; Mendoza & Barchas, 1983; Barchas & Mendoza, 1984; Eaton, 1984; Nelissen, 1985; Goessmann *et al.*, 2000) and even some species of ants (Jürgen Heinze, pers. comm.).

Beyond the study of dominance hierarchies, there is a large and growing empirical and theoretical literature concerning how social context affects many aspects of behavior in animals. This literature includes, for example, theoretical 'selfish herd' models and empirical observation of behavior in groups responding to predators, theoretical and empirical investigation of information flow concerning food sources, and of course the extensive experimental and theoretical research on the coordination of effort in animals working together.

In the three experiments described below, we tested for any differences in the stability of dominance relationships, the replication of relationships in successive meetings, and the extent of winner and loser effects in isolated and socially embedded pairs of fish. In the experiment on the stability of relationships, we let two fish form stable relationships and then either remain by themselves or be joined by other fish. We wanted to know in a relationship once formed, whether or not a subordinate was more likely to contest the relationship and attack the dominant in either isolated pairs or pairs in a group setting. In the second experiment on replication of relationships, we let either separate pairs or groups of four fish form dominance relationships, separated them long enough to forget one another, and then brought the separate pairs or groups back together to form dominance relationships once again. Here we wanted to know if there was any differences in the tendency for the isolated pairs or the ones in groups to form the same relationships each time they met (having the same individuals dominant and subordinate each time they met). In the experiment on winner and loser effects, we let either a winner or a loser meet one new fish by itself, or we let a winner and loser together join a third or a third and a fourth fish. Here we wanted to compare how often winners won again or losers lost again when they either met just one additional fish or they met one additional fish along with yet other fish.

Experiment 1: Stability of dominance relationships in isolated pairs versus pairs within groups of three and four fish

Stability, in the sense of one animal in a pair consistently delivering all or most of the aggressive actions and the other all or most of the submissive actions over a period of time, is the defining characteristic of a dominance relationship. Without stability, we would not be able to even consider dominance relationships as a behavioral phenomenon. In this experiment we tested for any differences in the stability of dominance relationships in isolated versus socially embedded pairs. Our aim was to determine whether or not social context could influence this most basic property of dominance relationships in pairs. If, after a pair formed a dominance relationship, the initial subordinate was never observed to direct aggressive acts towards the initial dominant, we considered the relationship stable. If, on the other hand, the initial subordinate did act aggressively toward the initial dominant — by delivering one or more aggressive acts to it — we considered that the relationship was unstable.

Subjects

In this experiment we used female *Pseudotropheus tropheops*. This fish is native to Lake Malawi in east Africa and readily forms both dominance relationships and dominance hierarchies in the laboratory. We obtained the fish from a commercial breeder in Florida. Before experiments the fish were housed in 475 l stock tanks kept at 25.5°C; the light dark regimen was 13 : 11 with lights on at 0700 hours. Approximately 220 fish were used in total.

Procedure

We took fish from their stock tanks and placed them in separate chambers, approximately 19 liters in volume, for at least two weeks before a trial in order to remove any possible effects of relationships established in their stock tanks (Johnsson, 1997; Miklosi *et al.*, 1997). The chambers were made by dividing either 57-liter or 76-liter tanks with commercial aquarium partitions (Penn Plax). These partitions were opaque with very small holes allowing water pass from one chamber to another. Fish in adjacent chambers were not used in the same trial. Approximately two days before a trial, we weighed the fish and made up pairs, groups of three, or groups of four. The larger fish in a pair was no more than 5% heavier than the smaller, and in a group the largest was no more than 7% heavier than the smallest in a group.

After their two-week period of isolation we transferred the fish that would form either a pair or a group to a 76-liter observation tank that was separated into four compartments of equal size. We used two adjacent compartments in an observation tank for a pair experiment, three adjacent compartments for a group of three, and all four for a group of four fish. For all experiments we placed the fish in their compartments the afternoon before and returned 24 hours later to remove the partitions separating the fish and to begin observations.

In both pairs and groups of three and four fish, we considered one fish to be dominant to another when it delivered any combination of eight nips, chases, lunges (one fish rapidly moves at least one-half of its body length toward another fish and then returns to its original position with the other fish retreating from the area), or displaces (one fish approaches to within one body length of a second fish and the second immediately leaves the area) in a row to the other without any return of aggressive actions. We considered mouth fighting to be a mutually aggressive act and started counting aggressive acts by either fish from zero after an instance of this behavior (Barends & Barends-Van Roon, 1950). In pairs, after one fish achieved dominance over the other, we carefully monitored them for a period of 24 hours making observations of which fish was dominant at the four-hour and 24-hour points using a criterion of six consecutive aggressive acts. In the trials involving three and four fish we initially followed the same procedure as in the trials with pairs: we introduced a pair of fish and observed them until one of the pair became dominant by delivering eight consecutive acts to the other without return. However at this point, rather than letting the pair stay by themselves, we introduced a third fish or a third and a fourth fish to the original pair in order to form groups of either three or four fish in total, respectively. We again monitored the groups for 24 hours noting the dominance relationships among the group members at the four- and 24-hour points using the same six-act criterion as in the isolated pairs.

Results

When the pairs met in isolation, initial relationships were remarkably stable. In all 36 trials, the initial relationship persisted over the 24-hour period with no aggressive behavior directed by the initially subordinate fish against the dominant (Table 1). In groups of three and four, initial relationships in the socially embedded pairs were significantly less stable, with about 20% and 35% of the initially subordinate fish, respectively, showing aggressive behavior — and often outright reversal of initial relationships — against the initially dominant fish (Table 1). Stability was significantly less in both groups of three ($p < 0.01$, Fisher exact test, Table 1) and in groups of four *versus* isolated pairs ($p < 0.001$, Fisher exact test, Table 1). We also compared the rates of stability of pairs embedded in groups of three with those embedded in groups of four to see if there was a significantly stronger ‘crowd’ influence in the larger groups. There was not ($p = 0.26$, Fisher exact test, Table 1).

Discussion

The results indicate that initial dominance relationships were less stable for pairs within social contexts than for pairs in isolation. Once a relationship was formed, initial subordinates in isolated pairs never acted aggressively toward their dominants, while initial subordinates in socially embedded pairs

TABLE 1. *The stability of relationships in isolated and socially embedded pairs*

	Isolated pairs	Pairs in groups of three	Pairs in groups of four
Percent stable	100.0	78.9	65.2
Percent unstable	0.0	21.1	34.8
Number of pairs	36	19	23

often did so and occasionally even reversed their relationships to become dominant over the fish that had initially dominated them. The presence of other individuals — being in a social context — significantly affected a basic quality of dominance relationships in pairs of fish.

While our experiments do not show how these results come about, it seems reasonable to consider the variety of interactions and observations that can occur in a group context. That is, in social contexts individuals have the possibility of observing encounters between other individuals and altering their behavior in their own future encounters with the individuals observed or yet other individuals when the observer encounters them. One or both of the added fish can dominate the initial dominant in the pairs; the initial subordinates may observe these encounters and respond by attacking their initial dominants. Or, at other times, the initial dominants may prevail over one or both of the added fish, not giving the initial subordinates an ‘invitation’ to attempt to reverse their relationships with their initial dominants. There are also additional possibilities: the initial subordinate might dominate one of the added fish, and because of this experience, go on to attack its initial dominant in an ‘effort’ to reverse its initial relationship. Or, at other times, the initial dominant might also dominate one or both added fish, and as a result, also repeatedly attack its initial subordinate thereby ‘making sure’ that the initial relationship did not become unstable.

Although we controlled the influence of weight in these experiments, we did not control differences in any other attributes (*e.g.* hormone levels, degree of aggressiveness, genotype). Therefore, to the extent that differences in these uncontrolled attributes influenced the outcomes of the initial encounters in the pairs, the impact of these differences was significantly lessened in social contexts — even in spite of the fact that the initial dominants and initial subordinates had already set up stable relationships. Thus these results

suggest that the ability of asymmetries in attributes to predict the outcome of dominance encounters is much lower in social contexts than it is in isolated pairs.

We also considered an alternative design for the part of this experiment examining the stability of relationships for pairs within groups. Instead of letting a pair form a relationship and then adding a third or a third and a fourth fish, we thought about just assembling groups of either three or four fish simultaneously and following the stability of a randomly selected pair within the group. However, the problem with that design would have been that we would have had no control over how the pair selected, or any other pair for that matter, established its relationship. Consequently, it would have been very likely that the pairs within groups would not have formed their relationships in the same way that the isolated pairs would have. For example, a socially embedded pair might have had one or two interactions, separated from one another, had separate interactions with the third and fourth members of the group, and finally have come back together again to finish establishing their relationship. In short, since it was impossible to make sure, using this alternative design, that isolated and socially embedded pairs would meet the same criteria in forming their relationships, they could not have been fairly compared, and as a consequence, we rejected this design.

Experiment 2: Replication of relationships in isolated pairs *versus* pairs within groups of four fish

In this experiment we tested the degree to which isolated *versus* socially embedded pairs formed the same relationship when they met on two separate occasions. If the same individual dominated both times a pair met, the pair replicated their relationship, but if not, the pair did not replicate their relationship. Our purpose was to determine whether or not social context could influence this basic property of dominance relationships in pairs: which individual was dominant and which subordinate.

Subjects

We used female *Metriaclima zebra* (formerly *Pseudotropheus zebra*), OB morph, also native to Lake Malawi and from the same commercial breeder as the fish in Experiment 1. This species also readily forms dominance relationships and hierarchies in the laboratory. They were kept in stock tanks of the same size and under the same light dark regimen as the *P. tropheops* used in Experiment 1.

Procedure

We isolated the fish before trials and formed pairs and groups of four fish using the same techniques and apparatus as in Experiment 1. After their two-week period of individual isolation we transferred fish to the same kind of 76-liter observation tank used in the previous experiment. In trials with pairs, only two adjacent compartments were used and in groups of four all the compartments were used. In the case of pairs we returned 24 hours later, removed the partitions, and observed the fish at the one-hour and two-hour points after the removal of the partitions. With groups of four we removed the partitions and returned 24 hours later to observe the relationships among the fish. We observed both pairs and groups of four from behind one-way mirrors and recorded all instances of nips, chases, and mouth fighting. We considered that two fish had a stable dominance relationship if one of the fish (the dominant) delivered six aggressive acts, in any combination of nips and chases, to the other without retaliation. We again considered mouth fighting as a mutually aggressive act and began recounting consecutive aggressive acts by either fish after an instance of this behavior. In the pairs we used the six-act criterion to determine which fish, if either, was dominant over the other at the one- and two-hour points of observation. In the groups of four we began observing at the 24-hour mark after the removal of the partitions since it usually takes larger groups considerably longer for all relationships to become stable than just an isolated pair of fish. If after approximately 30 minutes of observation all the pairs in a group of four had stable dominance relationships, we terminated observations. If all the relationships were not stable, we observed the group for two or three more sessions that day, and if all the relationships were not in place we returned the next day to continue our observations. After the two-hour point of observation was completed in a pair or when all the relationships in a group of four were in place, we returned the fish to their isolation chambers for two weeks so that they would forget one another (Johnsson, 1997; Miklosi *et al.*, 1997). Finally, we reassembled the earlier pairs and groups of four to let the fish form dominance relationships once again using the same procedures as in their first meetings. The fish within a pair or group received identical rations over the course of a trial (approximately 1.5% of body weight).

Results

As shown in Table 2, separate pairs almost always replicated their relationships, reversing in only 7% of the trials, while pairs in groups of four had a considerably lower rate of replication with reversals occurring in nearly one-quarter (24%) of the trials. Using all the pairs in the groups of four, the rate of replication would be significantly lower in the socially embedded than isolated pairs ($p < 0.02$, Fisher exact test). However, it could be argued that including all the pairs in the groups of four is not a proper way to perform a statistical test of these results. This is because the pairs within the groups of four are not independent in the sense that each fish in a group is a member of three different pairs and what happens to a fish in one pair might influence what happens to it in another pair. For example, in a group with members A, B, C, and D, fish A is a member of pairs AB, AC, and AD, and perhaps if

TABLE 2. *The replication of relationships in isolated and socially embedded pairs*

	Isolated pairs	All pairs in groups of four	Randomly sampled pairs in groups of four
Percent replication	93.5	75.8	68.2
Percent non-replication	6.6	24.2	31.8
Number of pairs	31	132	22

A repeats its relationship with B, it is more likely to repeat it with C and D. To get around this potential dependency problem and to perform a very conservative statistical test, we randomly selected one pair of fish from each of the 22 groups and compared the rate of replication in these pairs with that in the isolated pairs. Table 2 shows the results of this, and once again the rates of replicability in the isolated and socially embedded pairs are significantly different ($p = 0.02$, Fisher exact test).

Discussion

These results clearly show that having other fish present significantly lowers the probability that two fish will have the same relationships they did in a first meeting when they come together for a second time. As in the previous experiment, this experiment does not show how the inconsistency in the relationships of socially embedded pairs comes about, but again it seems reasonable to think about them arising from the complexities of interaction among pairs in groups of four forming their relationships. Besides the possibilities arising from observation, what happens to an individual in one encounter may influence what it does in successive encounters: winner and loser effects could be relevant examples. Since the order of encounters is not under experimental control when groups of four meet, an individual A may have an early encounter when a group is assembled for the first time, lose this encounter, and go on to do badly with other individuals because of this early loss. However, the next time the group meets, A may not be involved in the early encounters, but may dominate one or more of those that lose some of the early encounters in this meeting, and thereby reverse some of the relationships it had during the first meeting of the group.

Also as in the previous experiment, although we controlled for weight differences, we did not control for differences in any other attributes. Therefore, to the extent that differences in attributes influenced the outcomes of

contests in the isolated pairs, the ability of differences in attributes in socially embedded pairs to control the direction of contest outcomes appears to have been moderated by the presence of other animals — perhaps through observation as we mentioned for Experiment 1 or the loser effect as we have just indicated (but see the results of Experiment 3).

There is, however, another factor that could have been at play. As the references we have cited above indicate, most studies of how long fish remember one another put the time at considerably less than the two-week period of separation that we used (Johnsson, 1997; Miklosi *et al.*, 1997). But what if our fish could remember each other and their previous relationships longer than two weeks? If that were the case in our species, then in addition to differences in intrinsic attributes, the high rate of replication in isolated pairs could also have been due to fish remembering their previous relationships with one another. To the extent that memory did play a role in reproducing the relationships formed at first meetings in isolated pairs, the results here would suggest that the forces at play in social contexts can undermine the effects of memory so as to change relationships when socially embedded pairs meet again.

Experiment 3: Winner and loser effects in isolated pairs *versus* pairs within groups of three and four fish

In this experiment we compared the presence and magnitude of winner and loser effects in isolated *versus* socially embedded pairs. That is, we examined the magnitude of winner and loser effects using the standard experimental model — when the winner or loser met a single, new opponent — *versus* the magnitude of these effects when the winner or loser met one or more new opponents in a group context. As discussed in the Introduction, the presence of winner and loser effects indicates at least a minimal effect of social context: what happens in one pair influences what happens in another (when a participant in one pair, the winner or loser, meets another animal). But what we wanted to test here was whether or not the embedding of the target pair itself — the winner or loser and a new individual — in a social context would influence the presence and magnitude of winner and loser effects.

In designing this experiment, we had the choice of using either randomly selected or ‘self-selected’ winners and losers (Chase *et al.*, 1994). To get

a randomly-selected winner or loser, an experimenter randomly selects an animal and places it in a situation in which it will either win or lose an initial dominance encounter, say, by matching it either with a considerably smaller or considerably larger individual, respectively. After its win or loss, the experimenter matches the animal with a new individual to determine the effect of the earlier winning or losing experience. To get a self-selected winner or loser, an experimenter simply brings two animals together for a dominance contest; the one winning is the self-selected winner and the one losing is the self-selected loser. We chose to use self-selected winners and losers to be more in keeping with what might happen when a dominance encounter occurred within an already assembled group in which, of course, encounters always produce self-selected winners and losers.

Subjects

We used female *P. tropheops* from the same subject pool as described for Experiment 1 and housed under the same conditions.

Procedure

In testing winner and loser effects in isolated pairs, we placed a group of four fish in the four separate compartments of a 76-liter observation tank and left them there overnight. The fish were randomly assigned to their compartments. Twenty-four hours later we returned, removed the partitions between the fish in the two middle compartments and observed which of the two became dominant using an eight-act criterion. After this we separated the two fish, moving each back to her original compartment, and then we removed the partition between the winner and the fish in the compartment nearest her and between the losing fish and the fish nearest her. This allowed the winning fish and the losing fish to each separately meet a new fish in order to determine the effect of winning or losing a prior contest, respectively.

The trials in which we tested for how the presence of other fish might influence winner and loser effects were the same as those used in Experiment 1 to determine the stability of dominance relationships in socially embedded pairs; however here we collected data on the interactions between initial winners or initial losers and either an added third fish or added third and fourth fish. In these trials we put either three or four fish in a 76-liter observation tank the afternoon before and returned 24 hours later to remove the partitions between two of the fish and to determine which was the winner and which the loser using the same eight-act criterion as above. When this relationship had been settled we removed the partition between the initial pair and the third fish in the trials using groups of three fish or between the initial pair and the third and fourth fish in the trials using groups of four fish. We determined the dominance relationships among the fish at the four-hour and 24-hour points using the same procedure as in the isolated pairs.

TABLE 3. *The winner effect in isolated and socially embedded pairs*

	Isolated pairs	Pairs in groups of three	Pairs in groups of four
Percent winning	62.5	61.1	64.7
Percent not winning	37.5	38.9	35.3
Number of pairs	24	18	17

Results

In groups of four, we faced the same kind of problem of potential statistical dependence that we had in Experiment 2. There were two opponents for both the initial winner and the initial loser and what a winner or loser did with one opponent might not have been independent of its outcome with the other opponent. We again decided to perform a very conservative statistical test by using a technique similar to that used in Experiment 2: randomly choosing only one contest for each winner and one for each loser in a group (using separately generated random numbers for the winners and the losers).

The percents of trials in which winners won again in isolated and in socially embedded pairs in groups of both three and four fish were all virtually identical, falling in the range from 61% to 65% (Table 3). These proportions are not significantly more than random, assuming that by chance individuals should win half of their contests ($p = 0.15$, $p = 0.24$, $p = 0.17$, isolated pairs, pairs in groups of three, pairs in groups of four, respectively, one-sided binomial tests). In the case of self-selected winners an argument can be made that in order to be significantly different from chance, the winners must win more than two-thirds of their trials rather than simply one-half of them. That argument is as follows. Assume that, *a priori*, the dominance relationships among A, B, and C are equally likely to follow each of the six possible linear orderings: ABC, ACB, BAC, BCA, CAB, and CBA. Each of these orders has probability 1/6. After we observe A dominating B, the orderings BAC, BCA, and CBA are ruled out. The remaining three orderings are consistent with A dominating B. Thus the conditional probability distribution (given that A has dominated B) is ABC (1/3), ACB (1/3), and CAB (1/3). Under this conditional probability distribution the probability is two-thirds that A dominates C (ABC, ACB) and one-third that C dominates A (CAB). Using this higher standard, these data are of course not different from chance levels ($p = 0.75$, $p = 0.78$, $p = 0.68$, isolated pairs, pairs in groups of three,

TABLE 4. *The loser effect in isolated and socially embedded pairs*

	Isolated pairs	Pairs in groups of three	Pairs in groups of four
Percent losing	86.7	61.1	58.8
Percent not losing	13.3	38.9	41.2
Number of pairs	30	18	17

pairs in groups of four, respectively, one-sided binomial tests). As expected from the nearly identical fractions of winners winning in all three situations, and the absence of any significant winner effect, no significant decrease of the winner effect in crowds is found ($p = 0.59$, $p = 0.68$, isolated pairs *versus* pairs in groups of three, isolated pairs *versus* pairs in groups of four, respectively, Fisher exact tests, Table 3).

Table 4 shows our results comparing the loser effect in isolated and socially embedded pairs. The extent of the loser effect, 87%, was significantly more than chance in the isolated pairs, setting chance at both one-half and two-thirds ($p < 0.001$ for chance = 0.5, $p = 0.012$, for chance = 0.67, one-sided binomial tests). But the loser effect was not different from chance in either groups of three or four fish ($p = 0.24$, pairs in groups of three; $p = 0.31$, pairs in groups of four; both for chance = 0.5; $p = 0.78$, pairs in groups of three; $p = 0.83$, pairs in groups of four; both for chance = 0.67; one-sided binomial tests). Given these findings, not surprisingly, the magnitude of the loser effect was significantly higher in the isolated pairs than it was in pairs in groups both of three fish ($p = 0.047$, Fisher exact test) and four fish ($p = 0.037$, Fisher exact test).

Discussion

Our results indicate a lack of winner effects in both isolated and socially embedded pairs. Given that this effect was not present in isolated pairs, it was not too surprising that it also did not occur in group situations. As noted above, some studies do find winner effects in separate pairs, and it would be interesting to investigate how social contexts might alter the extent of the winner effect in those species and experimental conditions in which it does occur.

However, our results with the loser effect were more surprising: we did find loser effects in isolated pairs but not in socially embedded ones. While

losers lost nearly all of their second contests (87%) in isolated pairs, they lost only a little over half of them (61% and 59%, respectively) in groups of three and four. These findings are in sharp contrast to the large number of studies finding significant loser effects in isolated pairs across many species (Frey & Miller, 1972; Burk, 1979; Bakker & Sevenster, 1983; Francis, 1983, 1987; Beacham & Newman, 1987; Beacham, 1988; Bakker *et al.*, 1989; Drummond & Osorno, 1992; Zucker & Murray, 1996; Drummond & Canales, 1998; Hsu & Wolf, 1999). Many of the mathematical models and computer simulations attempting to explain the mechanisms behind linear hierarchies assume that either winner or loser effects or both are present and of high magnitude in group contexts (*e.g.* Hogeweg, 1989; Theraulaz *et al.*, 1995; Skvoretz *et al.*, 1996; Hemelrijk, 2000). As far as we are aware, our research here is the first to investigate the presence and extent of these effects in social contexts, and our experiments do not support the assumptions of most of this work. It is of course possible that winner or loser effects or both do occur in social contexts in other species, and more experimental work is needed to investigate this possibility.

Could it be possible that a loser effect is still at work in groups but masked by our results? For example, what if C, the third fish in a group of three, were to first meet A, the winner in the initial pair, lose this fight, and then meet B, the initial loser? In this case, B would not be at a disadvantage when meeting C. If this happened in many groups, even though B fish were initial losers, many of them would win over C fish, and we would not see a loser effect (from the point of view of B). However, we would see a loser effect from the point of view of C! If this were to happen, we could still argue that there was a strong loser effect in groups, but just not one involving the initial losers — the ones we examined in our data analysis.

In order to consider this possibility in a more rigorous and general way, we examine it using a simple mathematical model. This model is as follows: Assume that when C joins A and B after their contest, that it is equally likely to first meet either A or B to have an encounter (probability of 0.5 for either meeting). Assuming prior attributes differences, A would win with probability $2/3$ and C with probability $1/3$ (see the explanation earlier about the $2/3$ probability assumption and given, as in our experiments, no winner effect). If A dominates C, C and B are both losers, and each has a 0.5 probability of dominating the other. On the other hand, if C beats A when

they meet, then assuming a loser effect (as postulated by this explanation), C dominates B with very high probability.

So assuming the first meeting in the group context is between A and C, the (unconditional) probabilities of the ordering among the fish are ACB (1/6), ABC (1/6), and CAB (1/6).

If, however, the first meeting is between B and C, C is very likely to beat B (since B is a loser and we are assuming that the loser effect is operating in groups). But C still has only a 1/3 probability of beating A since there is no evidence of a winner effect in these fish, and we are assuming a random difference in attributes (again see the explanation above concerning the 2/3 probability assumption and remember that we have the information that A has previously dominated B). So assuming that the first meeting is between C and B gives the following probabilities for the final ordering of the fish: ACB (1/3), CAB (1/6).

The total probabilities for the various orders, given both possibilities for which fish C meets first are: ACB (1/2), CAB (1/3), and ABC (1/6).

Therefore, making the argument that the loser effect still operates in groups gives the prediction that indeed there should be a strong loser effect when viewed from the perspective of C: specifically, that C should beat B in 5/6 (83%) of the groups. However, the actual data do not show such an outcome as predicted by this argument, but instead show that C wins over B in only 61% of the groups.

Let us summarize this mathematical argument. In some of the possible sequences of interaction, a loser effect involving C could operate to moderate the loser effect that we observe for B. Therefore, at first glance, it seems very reasonable to suggest that, overall, a loser effect could still be operating in the groups. However, our mathematical analysis shows that when all the possible sequences of interaction are considered, one should see strong evidence of the loser effect in the group experiments, but our data did not show this.

General discussion

Taken together, the results of our experiments demonstrate that several core aspects of dominance relationships are different in pairs of animals by themselves than in pairs of animals within larger groups. In three out of the four aspects of dominance relationships that were investigated, we found significant differences between the dominance behavior of isolated *versus* socially

embedded pairs of fish. In socially embedded pairs the fish had less stability in their relationships, replicated their relationships at lower rates, and showed an absence of loser effects as compared to isolated pairs. In the fourth aspect of relationships that was investigated, we found that the strength of the winner effect was low and not significantly different from chance in both contexts (but see Chase *et al.*, 1994 for cases in which isolated pairs of animal in several species do show winner effects).

The findings reported here strongly suggest that dominance relationships in separate pairs are not the proper unit of analysis for understanding dominance behavior in groups. In every case in which we found a property of dominance relationships operating in isolated pairs, that property was significantly reduced or vanished altogether when we looked at pairs in social contexts. Our findings corroborate those in a variety of species also showing that relationships in dyads can be fundamentally altered by the presence of other individuals (*e.g.* see the reviews by Holekamp & Smale, 1991; Chapais, 1995 and the literature cited below in the discussions of experimental studies of transitive inference and of application of the jigsaw puzzle approach). Taken together, this research, including such diverse species as fish, primates, birds, and hyenas, has fundamental implications for how we must study dominance behavior, including the design of experiments, the formulation of evolutionary models, and the explanation of dominance hierarchy formation and maintenance.

In the case of experimental design, these combined findings raise the issues of control *versus* applicability. On one hand, doing experiments in separate pairs, as for example, using the standard design in winner and loser experiments, gives the experimenter greater control of the animals and of the variables that might affect experimental outcomes. But when experiments are carried out in social contexts, the experimenter usually must relinquish some of this control. An example in point would be our experiments on winner and loser effects in social contexts where we could not control how third and fourth fish added to a group might interact with each other before they had a contest with either the winner or loser. Of course, intermediate designs are also possible in which the experimenter exerts considerable control over animals in pairs, but in which social context can also be manipulated. Some of the experiments on observation and eavesdropping are particularly good examples of this kind of design.

Overall, the relevance of these findings for experimental design is that they suggest that the results of experiments on isolated pairs, no matter how well executed, may often have limited, or sometimes even no relevance, to understanding dominance in groups of animals. The significance of experiments in isolated pairs cannot simply be assumed, but it must be itself an object of investigation in further experiments in socially embedded pairs or in whole groups.

In the case of evolutionary models, our results support the conclusions of Oliveira *et al.* (1998) that the evolution of various aspects of dominance behavior must be seen as contextual to networks of individuals rather than to independent dyads. The great body of evolutionary theory using two-animal games has been very helpful as a first approximation to understanding many of the common tactics used in aggressive and territorial encounters, but the results of research on observational and eavesdropping effects, as well as the results here, increasingly demonstrate that animals gain information from the interactions of other animals, and at least in part because of that information, act differently in groups than they do in separate pairs. While multi-individual game theoretic and other models for the evolution of dominance behavior may present considerable mathematical challenges over those for just two individuals, experimental results now indicate the need for this new class of evolutionary models.

In the case of explanations of hierarchy formation, the results here, plus those of observation, eavesdropping, and recent studies of the cognition of relationships, all indicate that this phenomenon is a much richer and more complex one than it is now usually considered to be in animal behavior. These results suggest that it is simply no longer tenable to consider hierarchy formation as a simple agglomeration of behaviors occurring in separate pairs of individuals. If this conjecture is correct, one result will be that our theoretical approaches to the common occurrence of linear hierarchies must be revamped. Nearly all of these theoretical approaches, as indicated in the Introduction, use some combination of winner and loser effects, plus usually some additional behavioral mechanisms, in order to account for linear hierarchies. Some of this work assumes only the most minimal role for social context: other animals have to be present in order for a winner or loser effect to occur but they do not consider, for example, that social context could change the nature or even the very occurrence of these effects. Given our results, the dependence of these models on winner and loser effects may be a

limitation in their explanations for the development of linear hierarchy structures that cannot be supported by empirical observations.

How can the importance of social context be reflected in new and more adequate explanations of hierarchy formation? Several lines of investigation seem promising here. A first line of research would be studies of observation and eavesdropping. As reviewed in the Introduction, research in these areas is indicating that animals observe the interactions of other animals and that they alter their subsequent behavior, depending upon what they have observed, when they interact with those they have observed, or even when they later interact with animals they have not observed. Social contexts naturally provide rich environments for observations of encounters and reactions to what has been observed. We speculated that some of our experimental results showing differences between behavior in isolated and socially embedded pairs might have resulted from such possibilities.

A second line of research is the study of the cognition of relationships. Some of the recent work in this area has been influenced by the 'social hypothesis' and is of particular note. This hypothesis holds that animals that live in groups with complex and varied relationships among members have been selected to develop a variety of cognitive abilities that allow them to work well in their groups: recognition of their own relationships and those between other individuals, memory of many different relationships, capacity to make inferences concerning relationships, *etc.* (Cheney & Seyfarth, 1990; Kummer *et al.*, 1997). The capacity to make what are known as transitive inferences is of particular pertinence in linear hierarchy formation. In linear hierarchies, by definition, all dominance relationships are transitive: for any sub-group of animals, A, B, C, within a larger group, A will dominate B, B will dominate C, and A will also dominate C. If a hierarchy is not linear, it contains at least one sub-group with an intransitive dominance relationship: A dominates B, B dominates C, but C dominates A. Experiments have indicated that several species, including monkeys, pigeons, rats, and corvids, can make transitive inferences (Fersen *et al.*, 1991; Roberts & Phelps, 1994; Terrance & McGonible, 1994; Steirn *et al.*, 1995; Treichler & van Tilburg, 1996; Wynne, 1997; Bond *et al.*, 2003). That is, after they have been trained to make a series of rewarded pair comparisons of the sort $A > B$, $B > C$, $C > D$, $D > E$; they can make choices that will be rewarding even in pairs on

which they have never been tested, *e.g.* between B and D. It seems possible that this cognitive ability to make such inferences may be one of the mechanisms that operate in group contexts to help produce linear hierarchies.

A third line may be the formulation of theoretical models that attempt to explain or describe linear hierarchy formation at the level of typical patterns of behavior in groups rather than at the level of typical behaviors that individuals use, as most current models attempt to do. That is, instead of relying upon an individual-based explanation — how individuals should act in various circumstances, for example, after winning or losing — a more successful approach might come with explanations based upon kinds of behavioral sequences or patterns occurring during hierarchy formation — without trying to predict which individuals will execute the sequences or patterns (*e.g.* see Chapais, 1995 for some patterns concerning interactions among three or more individuals in primates). An example of a sequence- or pattern-based approach is the jigsaw puzzle model, reviewed in the Introduction (Chase, 1982, 1985; Mendoza & Barchas, 1983; Barchas & Mendoza, 1984; Eaton, 1984; Nelissen, 1985; Goessmann *et al.*, 2000). Researchers using this approach have shown that a diverse range of species use the same sequential patterns for forming dominance relationships or for sequences of attacks when they establish or maintain their hierarchies. It seems likely that this kind of approach could be developed further. If that is the case, it will require the collection of detailed records of dominance interactions among groups during hierarchy formation and maintenance and the methodological tools that are needed to analyze these interactions. Researchers rarely collect data of this type at the present time and these tools have yet to be developed.

The experiments reported here also point up a general problem in the study of systems, whether social, biological, mechanical, or physical. To analyze a system we typically break it into its component parts. This in fact is the definition of 'analyze'. We tend to think of the components comprising a system as existing independently of the system itself, and we study the properties of the components and the relationships between them, separate from the entire system. But what if the properties of the elements and their relationships are affected by their participation in the system? How can we analyze a system if its components have different properties *in situ* than in isolation? This general problem arises in many guises in many disciplines. The findings that we report here compel us to face this challenge in the study of dominance hierarchies.

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