

# Merging social hierarchies: Effects on dominance rank in male green swordtail fish (*Xiphophorus helleri*)

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## Abstract

When the same set of individuals are placed in different social contexts, some groups members often experience a change in dominance status. We examined the context-dependence of social status using a group fusion protocol in male green swordtail fish (*Xiphophorus helleri*). Six individuals were matched for size and separated into two groups of three fish. Each triad established a stable hierarchy after which time the two subgroups were merged into one larger assemblage. The maintenance of within- and between-group rank relationships was examined. Relative rank was preserved within each subgroup across social contexts but we found no evidence that familiarity with dominant animals assists individuals of one subgroup in achieving higher rank (coat-tail effects). Dominant individuals from the pre-fusion groups were significantly likely to obtain high status in the merged group and vice versa for subordinate pre-fusion animals. These results demonstrate that social rank in swordtails is relatively impervious to changes in social context, but we address some deviations from this trend. Small differences in standard length were a significant predictor of the most dominant rank in the post-fusion hierarchy, with the largest animals tending to occupy the alpha position. We discuss our results in terms of the potential factors involved in within- and between-group rank maintenance, including individual recognition, winner and loser effects, or asymmetries in dominance-related characteristics.

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## 1. Introduction

The initial stages of hierarchy formation are marked by social instability but, at least in small groups, linear dominance orders often emerge and ranks are maintained for relatively long periods of time when individuals are kept under static conditions. If the hierarchy is disturbed or the individuals are placed in a different context, however, there is a non-negligible probability that some individuals will experience a change in status. For instance, Dugatkin et al. (1994) demonstrated that groups of cockroaches (*Nauphoeta cinerea*) establish different hierarchies if placed together at different times with intervening periods of isolation. This phenomenon of context-dependent dominance appears to be widespread across taxonomic categories. From invertebrates to primates, there is evidence that the status an ani-

mal acquires, even relative to individuals that it had dominated or was dominated by in the past, depends in part on the context in which it is obtained (e.g., presence of familiar/unfamiliar animals, place of residence; Bernstein and Gordon, 1980; Nelissen, 1985; Cristol et al., 1990; Wiley, 1990; Verbeek et al., 1999; Chase et al., 2002).

Group fusion, a method that entails merging two small groups of equal size into one larger assemblage, has been utilized to detect the effects of prior residence or familiarity on status acquisition in avian species (*Junco hyemalis*; Balph, 1979; Yasukawa and Bick, 1983; Cristol et al., 1990; Wiley, 1990; Cristol, 1995a). Before the groups are merged, individuals within each subgroup establish a stable dominance hierarchy. The context in which the animals re-form (with familiar opponents) or establish (with unfamiliar opponents) dominance relationships following the merger is inherently different from that which they experienced prior to fusion. The purpose of this study was to examine the effects of group fusion, a change of social context, on within- and between-subgroup rank relationships in male green swordtail fish (*Xiphophorus helleri*). Will individuals retain rank relationships with ani-

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imals of their original subgroup in the larger assemblage, as is often the case in avian group fusion studies (e.g. Wiley, 1990)? Is familiarity with the incumbent dominant member of the larger group an asset in terms of status acquisition (e.g., coat-tail effects; Cristol, 1995a)? Is dominance rank in the small group transferable to a large group context (e.g., initially dominant/subordinate animals retain high/low ranks)? Swordtails were chosen as a model species for this investigation because individuals exhibit stereotypical agonistic behavior (Franck and Ribowski, 1989) and because their behavior in social groups under laboratory conditions (Beaugrand et al., 1984) reflects field observations (Franck and Ribowski, 1993; Franck et al., 1998).

## 2. Materials and methods

### 2.1. Test subjects

Heterosexual groups of *X. helleri* were obtained from Sunshine Aquatic Farms (Tampa, FL) and were transferred to laboratory aquariums ranging in size from 189 to 429 l. Each holding tank was equipped with chemical and biological filtration, substantial aeration, gravel substrate at a depth of 6 cm, and plants and clay pots as refuge. The temperature was maintained between 25 and 27 °C and the pH at 7.6 with a photoperiod of 12 h light:12 h dark. Aquarium salt and Stress Coat™ were added as needed to reduce osmotic stress, condition the water, and replenish the natural slime coat of the fish (e.g. following a water change). The fish were fed TetraMin™ flake food daily with occasional supplements of brine shrimp (*Artemia*) nauplii. One day prior to experimentation male *X. helleri* were removed from the holding tanks for measurement. Six males were matched for total length (standard length + sword length, cm), and body and sword characteristics were noted for identification purposes. The fish used in this study exhibited substantial variation in macromelanophore body patterns (Franck et al., 2001) and sword characteristics (e.g., upper/lower black stripe presence, width, and continuity; color variation from orange/yellow to green; see also Basolo and Trainor (2002)), which, together with differences in sword length (see below), allowed for accurate discrimination among the six grouped animals. Subjects had a mean ( $\pm$ S.E., cm) total length of  $6.98 \pm 0.08$ , standard length of  $4.44 \pm 0.05$ , and sword length of  $2.54 \pm 0.04$ . Total length was measured from the tip of the snout to the posterior tip of the sword; standard length was measured from the tip of the snout to the caudal peduncle; sword length was measured from sword origin to its posterior tip. The mean difference ( $\pm$ S.E., cm) between the six matched individuals was  $0.309 \pm 0.024$  (4.4%) for total length,  $0.117 \pm 0.015$  (2.6%) for standard length, and  $0.295 \pm 0.021$  (11.6%) for sword length. These six males were arbitrarily separated into two groups of three fish; each individual was assigned a letter (e.g. Group #1 consisted of individuals A–C and Group #2 of individuals D–F) for purposes of data recording. Hereafter, these three-member groups will be referred to as pre-fusion hierarchies or groups. 40 pre-fusion groups were established and utilized in the analyses.

### 2.2. Experimental apparatus and observational methods

Each pre-fusion group was placed into a 38 l experimental aquarium with similar conditions to the holding tanks. A heater and aeration stone were separated from the experimental arena by a porous partition to prevent the fish from seeking refuge behind the devices during aggressive interactions. In doing so, the animals were prevented from removing themselves from the interaction space, which would interfere with assessment of rank relationships over time (see below). The lack of refuge did not result in injuries or death due to aggressive interactions during the trial period. A 60 W bulb positioned 10 cm above the center of the aquarium provided illumination. The tanks were covered on three sides with white paper in order to prevent visual contact between fish in adjacent aquariums. The fish were allowed 16 h to acclimate to the experimental tanks. All observations were conducted between 08:00 and 18:00 h.

Behavior was viewed from behind a mesh screen to minimize distraction of the fish by the observer. Each of the three fish in both Groups #1 and #2 were observed, in random order, for a period of 15 min each day for a maximum of 7 days. During the 15 min observation period, all aggressive and submissive behavior was noted, including the aggressor and recipient of the act as well as the behavior type (Altmann, 1974). Observing the fish in random order minimized the possibility of overlooking rank reversals that could have occurred on a given day. Five types of aggressive behavior (approach, attack, bite, chase, and threat display) and two types of submissive behavior (avoid, retreat) were recorded; see Franck and Ribowski (1989) for behavioral descriptions.

Each group was observed until a stable, linear hierarchy arose, which we defined as a hierarchy in which no intransitive relationships existed and where each individual occupied the same rank for at least 3 days. If a group did not establish a stable linear hierarchy after 7 days, the group and its pre-fusion counterpart were discarded ( $N=3$  group pairs). The number of days required to reach the stability criteria varied between 4 and 7 days depending on the groups. High-, intermediate-, and low-ranking fish were designated the  $\alpha$  (alpha),  $\beta$  (beta), and  $\gamma$  (gamma) members of the pre-fusion hierarchy, respectively.

When the hierarchies in both groups stabilized, the six fish were removed from the initial experimental aquariums and were immediately (and simultaneously) transferred to a neutral tank with the same conditions and design as described above. This was termed the ‘fusion event’ and the resultant six-member group will be referred to as the post-fusion hierarchy or group. The substrate was changed to small, multi-colored gravel at a depth of 5 cm in order to eliminate familiarity with aquarium characteristics. The fish were given 16 h to acclimate to novel tank during which time no behavioral data were collected.

Each fish in the post-fusion hierarchy was observed, in random order, for 15 min each day for a maximum of 7 days. During each 15 min observation period, aggressive and submissive behavior was tallied as in the pre-fusion groups (see above for behavior recorded). The six individuals were allowed to interact until a stable linear hierarchy formed; all hierarchies met the stability criteria (see above description) within 7 days. The

top-ranking individual was assigned a rank of 1 and the lowest-ranking fish was assigned a rank of 6. Twenty post-fusion groups derived from the initial 40 pre-fusion groups were established and utilized in the analysis.

### 2.3. Statistical analyses

There was a significant negative correlation between the aggressive and submissive behavior exhibited by individuals both before and after fusion (pre-fusion:  $r_{119} = -0.43$ ,  $p = 0.0001$ ; post-fusion:  $r_{119} = -0.53$ ,  $p = 0.0001$ ). In keeping with the majority of studies on hierarchy formation in animals (e.g. Moore et al., 1988; Oliveira and Almada, 1996), we chose to use aggressive behavior in the statistical analyses.

In both the pre- and post-fusion hierarchies, the average proportion of total group aggression directed by one individual toward another across the days required for stability was calculated to control for differences in the absolute number of interactions among groups. A one-factor analysis of variance determined whether  $\alpha$ ,  $\beta$  and  $\gamma$  of the pre-fusion groups exhibited different patterns of aggression during hierarchy formation. Given the large number of interaction pairs in the post-fusion groups (36) relative to the pre-fusion groups (6) we utilized the  $\tau_{KR}$  statistic, which evaluates the number of aggressive acts an individual directs toward versus receives from each other group member, to examine trends in directionality of aggression (Goessmann et al., 2000). A  $p$ -value corresponding to the  $\tau_{KR}$  was obtained for each group each day and these  $p$ -value were summed across groups to determine the overall daily trends for directionality using a technique for combining probabilities ( $-2\sum \ln P$ ; Sokal and Rohlf, 1995). Of main interest were the  $p$ -value corresponding to the left tail of the distribution ( $-\tau_{KR}$ ) because these indicate the degree of unidirectionality of aggression in the hierarchy. Unidirectionality refers to a situation where  $\alpha$  directs aggression toward each of the remaining group members without reciprocation,  $\beta$  directs aggression toward all others except  $\alpha$  without reciprocation, and so on.

Coat-tail effects were assessed using interdependence and difference-in-rank scores (see Wiley (1990), Cristol (1995a) for details). The interdependence score assesses the likelihood that subgroup members occupy adjacent ranks; this score ranges from 0 to 4 for six-member hierarchies with a score of 4 indicating that all members of one subgroup rank above all members of the other subgroup. High difference-in-rank scores (range:  $-2$  to  $3$ ) indicate that members of the subgroup containing the highest-ranking fish in the combined group achieved higher status than members of the other subgroup (Cristol, 1995a). Average interdependence and difference-in-rank scores for the 20 post-fusion hierarchies were compared against the scores of the 20 possible hierarchies for groups of 6 individuals under the constraint that relative pre-fusion ranks are maintained after fusion (see Section 3; Wiley, 1990) using a Mann–Whitney  $U$ -test with  $n_1 = 20$  and  $n_2 = 20$ . Logistic analysis assessed relationships between pre- and post-fusion ranks both within and between subgroups. We tested the influence of size on rank using the standard normal approximation for the Page statistic (Page, 1963; Hollander and

Wolfe, 1999). The  $\alpha$ -level of significance was set at 0.05 for all statistical analyses.

## 3. Results

In total, we conducted 403.5 h of observation of the sword-tail groups. For the three-member groups, average observation time was 5.14 h per group (1.71 h per individual per group) and for the six-member groups, average observation time was 9.9 h per group (1.65 h per individual per group) over the 4–7 days interaction periods.

### 3.1. Pre-fusion hierarchies

Across all three-member groups, the minimum number of unidirectional aggressive interactions between any two individuals, in which aggression by one animal resulted in submissive behavior by its opponent, was 16. The mean for minimum unidirectional aggressive interactions among three-member groups was calculated by averaging across groups the number of unidirectional aggressive encounters that occurred between the dyad of each group that interacted least frequently. The mean for minimum unidirectional aggressive interactions for all pairwise encounters in the three-member groups was  $165.83 \pm 17.5$  S.E. (range 16–578) and the median was 148 (inter-quartile range: 113.5). The  $\alpha$ ,  $\beta$ , and  $\gamma$  individuals exhibited significantly different patterns of aggressive behavior ( $F_{5,234} = 32.7$ ,  $p < 0.0001$ ; Fig. 1). On average,  $\alpha$  individuals accounted for the majority (73%) of total group aggression; the proportion of aggression directed by  $\alpha$  toward both  $\beta$  and  $\gamma$  was significantly higher

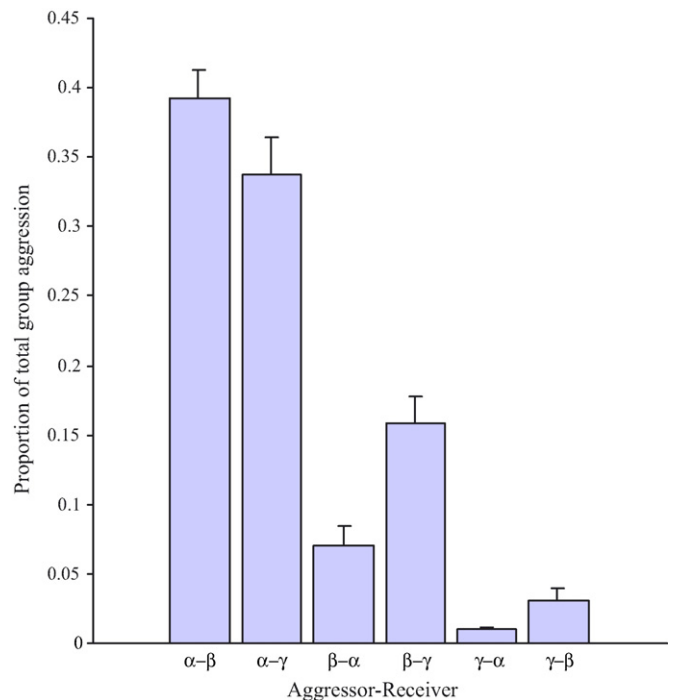


Fig. 1. Directionality of aggressive interactions in the pre-fusion groups. Notation on the x-axis follows the form 'aggressor-receiver' with ranks  $\alpha$ ,  $\beta$ , and  $\gamma$ . Error bars represent the mean proportion of total group aggression  $\pm$  S.E.

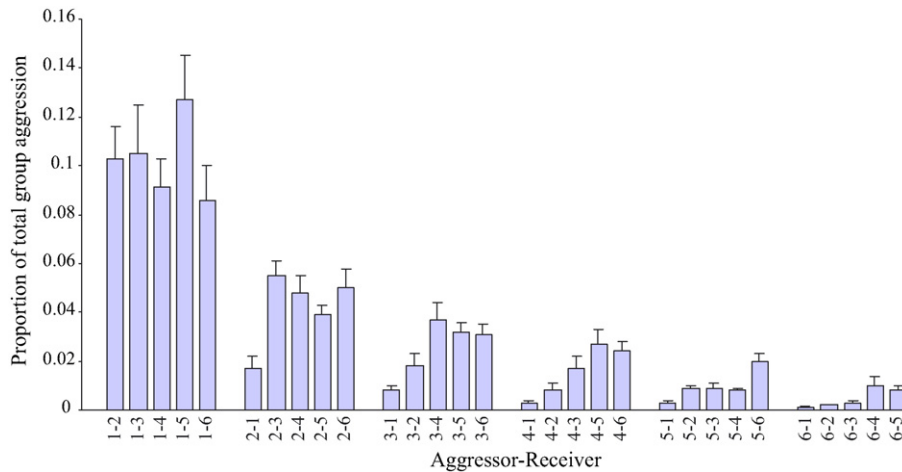


Fig. 2. Directionality of aggression in the post-fusion groups. Notation on the x-axis follows the form ‘aggressor-receiver’ with ranks 1–6. Error bars represent the mean proportion of total group aggression ± S.E.

than by  $\beta$  or  $\gamma$  toward any group member (Tukey’s post hoc;  $p < 0.05$ ). Dominant individuals distributed aggressive behavior equally among  $\beta$  and  $\gamma$  animals. Beta individuals accounted for approximately 23% of the total group aggression and directed aggression significantly more toward  $\gamma$  than toward  $\alpha$  (Tukey’s;  $p < 0.05$ ). Gamma individuals accounted for only 4% of the total group aggression and directed aggression toward  $\alpha$  and  $\beta$  at equally low frequencies (Fig. 1).

3.2. Post-fusion hierarchies

3.2.1. Directionality of aggression and hierarchy linearity

Across all six-member groups the minimum number of unidirectional aggressive interactions between any two individuals, in which aggression by one animal resulted in submissive behavior by its opponent, was 8. The mean for minimum unidirectional aggressive interactions among six-member groups was calculated by averaging across groups the number of unidirectional aggressive encounters that occurred between the dyad of each group that interacted least frequently. The mean for minimum

unidirectional dyadic interactions for all pairwise encounters in the six-member groups was  $47.9 \pm 7.6$  S.E. (range 8–132) and the median was 45.5 (inter-quartile range: 52.5). The degree of unidirectionality in the post-fusion groups was highly significant on days 1–4 (all days:  $\chi^2_{40} > 77.6, p < 0.001$ ), significant on days 5 ( $\chi^2_{36} = 51.9, p < 0.05$ ) and 7 ( $\chi^2_{32} = 46.2, p < 0.005$ ), and marginally significant for day 6 ( $\chi^2_{36} = 48.6, p < 0.1$ ). Dominant members of the post-fusion groups accounted for a substantial majority of the total group aggression (51%) followed sequentially by the second (20%), third (13%), fourth (8%), fifth (5%), and sixth (3%) ranking individuals (Fig. 2).

3.2.2. Within-subgroup rank maintenance

Logistic analyses examined whether the ranks obtained in the pre-fusion hierarchies were maintained within each subgroup in the larger assemblage. There was a highly significant relationship between pre- and post-fusion ranks within subgroups (Wald  $\chi^2_1 = 22.6, p < 0.0001$ ; Table 1; Fig. 3), indicating that original pre-fusion ranks are maintained when the individuals interact in the context of a larger group.

Table 1

Raw data for the relationship between pre-fusion rank and final within-subgroup post-fusion rank, expressed as the: (1) number of times an animal with a given pre-fusion rank ( $\alpha, \beta, \gamma$ ) obtained each within-subgroup post-fusion rank ( $\alpha, \beta, \gamma$ ), (2) observed probability of each event, and (3) predicted probability derived from logistic analysis (see Section 3 and Fig. 3)

Pre-fusion rank	Post-fusion rank (within subgroup)	Number	Observed probability	Logistic probability
$\alpha$	$\alpha$	25	0.625	0.608
	$\beta$	9	0.225	0.281
	$\gamma$	6	0.150	0.111
	Total: 40			
$\beta$	$\alpha$	8	0.200	0.250
	$\beta$	19	0.475	0.382
	$\gamma$	13	0.325	0.367
	Total: 40			
$\gamma$	$\alpha$	7	0.175	0.155
	$\beta$	12	0.300	0.331
	$\gamma$	21	0.525	0.514
	Total: 40			

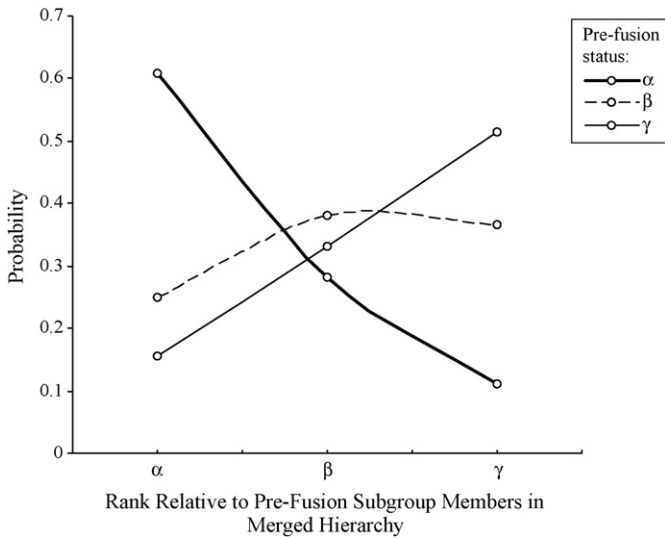


Fig. 3. Probability that  $\alpha$ ,  $\beta$ , and  $\gamma$  from the pre-fusion hierarchies would obtain any of the ranks  $\alpha$ ,  $\beta$ , or  $\gamma$  relative to their original subgroup members in the post-fusion hierarchy; all probabilities are derived from logistic analysis on the original data (see Table 1). Smoothed lines are drawn for convention only, not to indicate that rank is a continuous variable.

3.2.3. Effects of familiarity: coat-tail effects

Neither the interdependence (Mann–Whitney  $U = 194$ ,  $U' = 206$ ,  $z = -0.162$ ,  $p = 0.87$ ) nor the difference-in-rank (Mann–Whitney  $U = 189$ ,  $U' = 211$ ,  $z = -0.298$ ,  $p = 0.77$ ) scores deviated from the null expectation given relative rank maintenance, indicating a lack of coat-tail effects in merged hierarchies.

3.2.4. Between-subgroup dynamics

Logistic analyses examined whether final post-fusion status could be predicted by final rank in the pre-fusion hierarchies (*finalpre*; ranks  $\alpha$ ,  $\beta$ , and  $\gamma$ ), and rank on the first day of the post-fusion hierarchy (*initialpost*; ranks 1–6). The overall logistic model was highly significant (Wald  $\chi^2_3 = 43.1$ ,  $p < 0.0001$ ); both *finalpre* (Wald  $\chi^2_1 = 5.82$ ,  $p = 0.016$ ) and *initialpost* (Wald  $\chi^2_1 = 8.80$ ,  $p = 0.003$ ) had a substantial influence on final rank in the post-fusion hierarchy. However, the *finalpre*  $\times$  *initialpost* interaction was not significant (Wald  $\chi^2_1 = 0.91$ ,  $p = 0.34$ ) indicating that previously high-ranking animals (i.e., final pre-fusion or initial post-fusion status) were likely to obtain more dominant positions in the final post-fusion hierarchy (Tables 2 and 3; Figs. 4 and 5).

3.3. Effects of size on rank

Although the fish in both the pre-fusion and post-fusion groups were matched closely for total length, small variation in size could potentially influence rank acquisition. None of the measures of size (total length, standard length, sword length) predicted rank in the pre-fusion groups ( $L^* < 1.06$ ,  $p > 0.14$ ,  $k = 3$ ,  $n = 40$ ). Neither sword length nor total length predicted rank in the post-fusion groups ( $L^* < 0.56$ ,  $p > 0.29$ ,  $k = 6$ ,  $n = 20$ ). Despite standard length being less variable than the other size measures, it was a significant predictor of post-fusion status ( $L^* = 2.5$ ,  $p = 0.007$ ,  $k = 3$ ,  $n = 20$ ). Significance was due primarily to the highest-ranking individual of the post-fusion hierarchy being among the largest of the group; ranks 2–6 had similar size distributions.

Table 2  
Raw data for the relationship between pre-fusion rank and final between-subgroup post-fusion rank, expressed as the: (1) number of times an animal with a given pre-fusion rank ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) obtained each between-subgroup post-fusion rank (1–6), (2) observed probability of each event, and (3) predicted probability derived from logistic analysis (see Section 3 and Fig. 4)

Pre-fusion rank	Post-fusion rank (between subgroups)	Number	Observed probability	Logistic probability
$\alpha$	1	15	0.375	0.329
	2	9	0.225	0.259
	3	5	0.125	0.174
	4	2	0.050	0.111
	5	6	0.15	0.075
	6	3	0.075	0.052
	Total: 40			
$\beta$	1	4	0.100	0.124
	2	6	0.150	0.168
	3	9	0.225	0.189
	4	9	0.225	0.184
	5	7	0.175	0.175
	6	5	0.125	0.160
	Total: 40			
$\gamma$	1	1	0.025	0.063
	2	5	0.125	0.100
	3	6	0.150	0.141
	4	9	0.225	0.179
	5	7	0.175	0.229
	6	12	0.300	0.288
	Total: 40			

Table 3

Raw data for the relationship between post-fusion rank on day 1 and final post-fusion rank, expressed as the: (1) number of times an animal with a given initial post-fusion rank (1–6) obtained each final post-fusion rank (1–6), (2) observed probability of each event, and (3) predicted probability derived from logistic analysis (see Section 3 and Fig. 5)

Post-fusion rank day 1	Post-fusion rank final	Number	Observed probability	Logistic probability
1	1	16	0.800	0.759
	2	0	0.000	0.185
	3	1	0.050	0.034
	4	2	0.100	0.013
	5	0	0.000	0.006
	6	1	0.050	0.003
	Total: 20			
2	1	2	0.100	0.197
	2	12	0.600	0.367
	3	0	0.000	0.207
	4	3	0.150	0.113
	5	3	0.150	0.071
	6	0	0.000	0.045
	Total: 20			
3	1	0	0.000	0.037
	2	3	0.150	0.132
	3	5	0.250	0.178
	4	3	0.150	0.200
	5	4	0.200	0.223
	6	5	0.250	0.230
	Total: 20			
4	1	0	0.000	0.032
	2	1	0.050	0.117
	3	7	0.350	0.165
	4	1	0.050	0.195
	5	7	0.350	0.233
	6	4	0.200	0.257
	Total: 20			
5	1	2	0.100	0.049
	2	3	0.150	0.167
	3	3	0.150	0.202
	4	4	0.200	0.202
	5	4	0.200	0.199
	6	4	0.200	0.181
	Total: 20			
6	1	0	0.000	0.029
	2	1	0.050	0.107
	3	4	0.200	0.155
	4	7	0.350	0.191
	5	2	0.100	0.239
	6	6	0.300	0.280
	Total: 20			

#### 4. Discussion

The aims of this correlational study were to characterize the dynamics of hierarchy formation in male green swordtails and to determine whether relative ranks within subgroups and rank trends (e.g., dominant/subordinate) between subgroups were maintained from pre- to post-fusion social contexts. Both the pre- and post-fusion hierarchies exhibited significant unidirectionality of aggression, providing quantitative support for the existence of asymmetrical rank relationships among group members. Individuals rarely challenged rank-order superiors but directed aggression with approximately equal frequency toward all individuals of lower rank, a result consistent with [Beaugrand](#)

[et al. \(1984\)](#) investigation of heterosexual swordtail hierarchies in captivity.

Rank maintenance, both within and between subgroups, was remarkably robust in the post-fusion hierarchies indicating little variation in status with social context. Familiarity with dominant animals did not assist low-ranking animals of one subgroup in achieving higher status (coat-tail effects), which contrasts aviary studies on birds ([Wiley, 1990](#); [Cristol, 1995a](#); but see [Wiley et al. \(1999\)](#)), though little is known about the importance of coat-tail effects in wild bird populations. The ability to identify familiar opponents via individual recognition, however, might explain rank stasis within subgroups. Several species of swordtails (*X. helleri*, *X. multilineatus*, and *X. nigrensis*) are capable of individ-

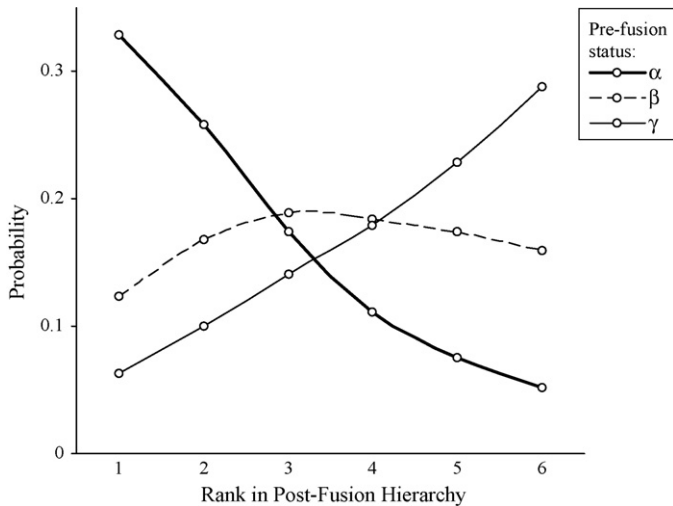


Fig. 4. Probability that  $\alpha$ ,  $\beta$ , and  $\gamma$  from the pre-fusion hierarchy would obtain any of the ranks 1–6 in the final post-fusion hierarchy; all probabilities are derived from logistic analysis on the original data (see Table 2). Smoothed lines are drawn for convention only, not to indicate that rank is a continuous variable.

ual recognition and familiarity with past opponents influences dyadic contest dynamics in these species; subordinate animals submit quickly when encountering previous dominants a second time (Zayan, 1974; Morris et al., 1995a). Thus, it is reasonable to suppose that individual recognition could preserve rank relationships within existing subgroup hierarchies, particularly in small groups (e.g., Barnard and Burk, 1979). Concordance between pre- and post-fusion status might also reflect uneven distribution of unmeasured dominance-related asymmetries among subgroup members (e.g., intrinsic aggression levels).

Significant overall correspondence between pre- and post-fusion ranks (e.g., high-ranking animals generally retain dominant positions) is a bit more perplexing due to the number of possible explanations for the trend. Individual recognition *per se* cannot explain between-subgroup rank maintenance but status or class recognition (Appleby, 1993) might provide a mechanism by which individuals gauge relative rank. Postural changes or alterations in skin pigmentation patterns (e.g., Morris et al., 1995b; O'Connor et al., 1999; Hoglund et al., 2000), which occur in *Xiphophorus* in response to changes in social status, could serve as cues for such recognition mechanisms. If status parallels the distribution of some unmeasured trait that affects dominance across subgroups, asymmetries in this attribute might also be responsible for between-group patterns of rank acquisition. Small differences in body size in swordtail males, as measured in this study, do not appear to be important at least insofar as explaining the eventual status of each member of the larger assemblage.

Previous dominant or subordinate experiences affect success in dyadic contests between male swordtails, with prior winners having a significant advantage in contests against previous losers (e.g., Thines and Heuts, 1968; Franck and Ribowski, 1987, 1989; Beaugrand et al., 1991; Beaugrand, 1997a; Beaugrand and Goulet, 2000; see Hsu et al. (2006) for a review). Simulation models implicate these so-called winner and/or loser effects in the process of linear hierarchy formation, and demonstrate that

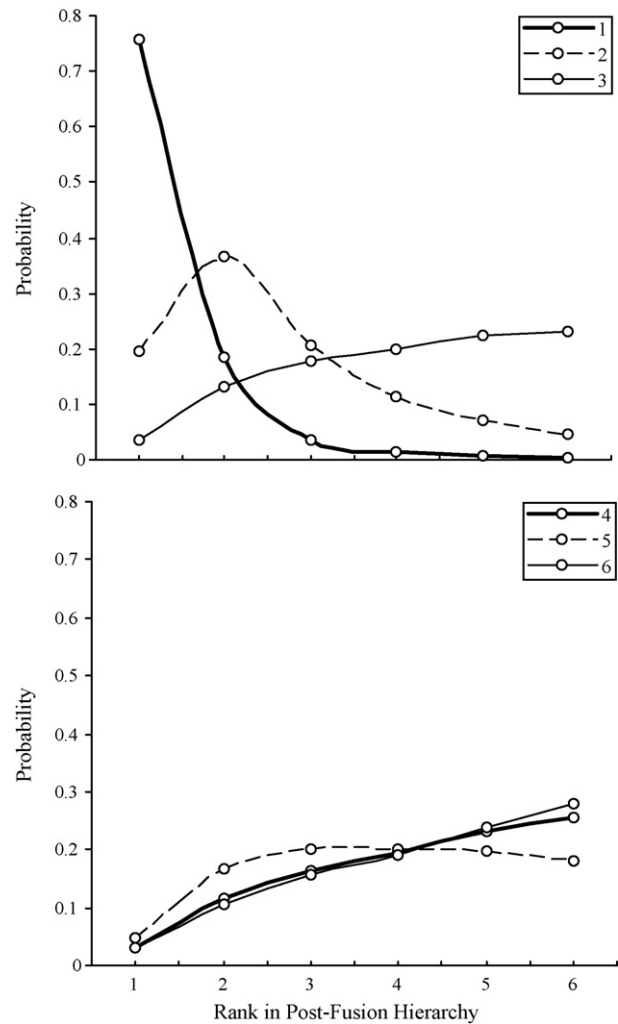


Fig. 5. Probability that individuals ranking 1–3 (upper panel) or 4–6 (lower panel) on the first day post-fusion would obtain any of the ranks 1–6 in the final post-fusion hierarchy; all probabilities are derived from logistic analysis on the original data (see Table 3). Smoothed lines are drawn for convention only, not to indicate that rank is a continuous variable.

dominance experience exerts an influence on hierarchy structure even when measurable asymmetries in fighting ability exist between group members (e.g. Bonabeau et al., 1996; Beaugrand, 1997b; Dugatkin, 1997). In an empirical test of these models, Dugatkin and Druen (2004) employed a random selection procedure (see Chase et al., 1994) in which size-matched green swordtail males were given winning, losing, or no experience and then placed together to form a dominance hierarchy. Hierarchies in which previous winners achieved the dominant rank, naïve animals the middle rank, and prior losers the subordinate rank were significantly overrepresented, providing compelling evidence that winner and loser effects can affect the ordering of individuals in a social hierarchy. Thus, it is possible in our study that status in the post-fusion group reflects prior dominant or subordinate experiences in the pre-fusion hierarchy.

Despite the highly significant correspondence of individual status between the two social contexts, there was some variation in how well pre-fusion rank forecasted final post-fusion status (Fig. 4). Several interesting patterns of rank shifting were evi-

dent in the post-fusion hierarchies. For instance, at least one pre-fusion  $\alpha$  occupied a dominant post-fusion rank (1 or 2) in 95% of the observed hierarchies but,  $\alpha$ 's that failed to secure a dominant position in the post-fusion group on day 1 were more likely to drop to the subordinate positions (5 or 6; 45% of observed hierarchies) than to adjacent intermediate positions (3 or 4; 35% of observed hierarchies). This suggests that maintaining pre-fusion dominance status might be costly enough to precipitate significant loss of rank should a previous  $\alpha$  lose early on. Cristol (1995b) revealed a similar trend for dark-eyed juncos where previous dominants experienced substantial loss of status and elevated metabolic rates when introduced into the home aviary of another flock (e.g. Cristol et al., 1990; Wiley, 1990). One such cost for dominant swordtails could come in the form of chronically elevated corticosteroid levels, which can prohibit energy regulation and homeostasis (Goymann and Wingfield, 2004). Hannes et al. (1984) demonstrated in *X. helleri* that both dominant and subordinate members of a pair experience elevated corticosteroid levels after 72 h, and up to 14 days, of cohabitation relative to control animals that had not engaged in an agonistic encounter. Furthermore, Netherton (2005) revealed in *X. helleri* that losers of aggressive interactions show a more pronounced increase in corticosteroids immediately after a contest relative to winners and isolated controls. Together, these data suggest that maintenance of dominance in the pre-fusion groups could have been stressful, and that pre-fusion dominants that became subordinate in post-fusion groups could have experienced even greater hyperactivity of the neuroendocrine stress axis. Although we did not examine corticosteroid levels in this study, it is possible that losing an initial encounter in the post-fusion groups exacerbates the already vulnerable homeostatic state of previously dominant animals and thus precipitated, or at least contributed to a dramatic loss in status.

Our empirical results for pre-fusion  $\alpha$  individuals are consistent with a recent model developed by Dugatkin and Earley (2003), which demonstrated that under certain social circumstances, one pre-fusion  $\alpha$  would drop to a subordinate rank following group fusion. This model, however, did not reveal increases in rank for pre-fusion  $\gamma$  animals under any condition while this study showed that at least one of the previous  $\gamma$ 's often achieves intermediate (3 or 4) status in the post-fusion group (70% of observed hierarchies), but occupies a dominant position considerably less often (30% of observed hierarchies). Our study does not permit us to tease apart the mechanisms responsible for rank shifts. These trends could be a manifestation of differences among individuals in characteristics associated with dominance or they could indicate that 'social factors' such as winner/loser effects or eavesdropping are operating during post-fusion hierarchy establishment (Dugatkin, 1997, 2001).

Given existing evidence that winner/loser effects and eavesdropping affect contest dynamics at both the dyadic and group levels in swordtails (e.g., Beaugrand et al., 1991, 1996; Beaugrand and Cotnoir, 1996; Earley and Dugatkin, 2002; Dugatkin and Druen, 2004), it is possible that 'social factors' have a substantial impact on post-fusion hierarchy formation in this species. Future experiments could address the relative contribution of previous fighting experience, eavesdropping, and

dominance-related characters to hierarchy formation by systematically manipulating these variables and examining the emergent rank-order. The dearth of empirical field research on *X. helleri* social behavior, particularly social organization, points to a greater need for rigorous testing of these laboratory findings in a natural setting (see Franck et al., 1998), as has been done for other swordtail species (e.g., Morris et al., 1992). The relationship between field and laboratory research on *X. helleri* is of particular concern because animals purchased from the breeder could be hybridized (e.g., with *X. maculatus* or *X. variatus*; see Kazianis and Walter (2002)), inbred, or artificially selected for traits that might alter contest competence (e.g., body size, coloration patterns, aggressiveness; see Doyle and Talbot (1986)). We attempted to eliminate the use of hybrid animals, which have distinct phenotypes (Kazianis and Walter, 2002), but an investigation of additional aquarium breeding pressures might be spearheaded first by using wild-caught animals to examine hierarchy formation in the laboratory and subsequently validating these findings in the field.

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### References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–265.
- Appleby, M.C., 1993. How animals perceive a hierarchy: reactions to Freeman et al. *Anim. Behav.* 46, 1232–1233.
- Balph, M.H., 1979. Flock stability in relation to social dominance and agonistic behavior in wintering dark-eyed juncos. *Auk* 96, 714–722.
- Barnard, C.J., Burk, T., 1979. Dominance hierarchies and the evolution of "individual recognition". *J. Theor. Biol.* 81, 65–73.
- Basolo, A.L., Trainor, B.C., 2002. The conformation of a female preference for a composite male trait in green swordtails. *Anim. Behav.* 63, 469–474.
- 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.
- Beaugrand, J.P., 1997a. Erratum to "Resolution of agonistic conflicts in dyads of acquainted green swordtails (*Xiphophorus helleri*): a game with perfect information". *Behav. Process.* 41, 293–310.
- Beaugrand, J.P., 1997b. Relative importance of initial individual differences, agonistic experience, and assessment accuracy during hierarchy formation: a simulation study. *Behav. Process.* 41, 177–192.
- Beaugrand, J., Goulet, P.C., 2000. Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophorus helleri*). *Behav. Process.* 50, 131–142.
- Beaugrand, J.P., Caron, J., Comeau, L., 1984. Social organization of small heterosexual groups of green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity. *Behaviour* 91, 24–60.
- Beaugrand, J.P., Cotnoir, P.-A., 1996. The role of individual differences in the formation of triadic dominance orders of male green swordtail fish (*Xiphophorus helleri*). *Behav. Process.* 38, 287–296.

- Beaugrand, J.P., Payette, D., Goulet, C., 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience and prior residency. *Behaviour* 133, 303–319.
- Bernstein, I.S., Gordon, T.P., 1980. The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). *Anim. Behav.* 28, 1033–1039.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1996. Mathematical model of self-organizing hierarchies in animal societies. *Bull. Math. Biol.* 58, 661–717.
- Chase, I., Tovey, C., Spangler-Martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc. Natl. Acad. Sci. U.S.A.* 99, 5744–5749.
- Chase, I.D., Bartolomeo, C., Dugatkin, L.A., 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning? *Anim. Behav.* 48, 393–400.
- Cristol, D.A., 1995a. The coat-tail effect in merged flocks of dark-eyed juncos: social status depends on familiarity. *Anim. Behav.* 50, 151–159.
- Cristol, D.A., 1995b. Costs of switching social groups for dominant and subordinate dark-eyed juncos (*Junco hyemalis*). *Behav. Ecol. Sociobiol.* 37, 93–101.
- Cristol, D.A., Nolan, V., Ketterson, E.D., 1990. Effect of prior residence on dominance status of dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.* 40, 580–586.
- Doyle, R.W., Talbot, A.J., 1986. Artificial selection on growth and correlated selection on competitive behaviour in fish. *Can. J. Fish. Aquat. Sci.* 43, 1059–1064.
- Dugatkin, L.A., 1997. Winner and loser effects and the structure of dominance hierarchies. *Behav. Ecol.* 8, 583–587.
- Dugatkin, L.A., 2001. Bystander effects and the structure of dominance hierarchies. *Behav. Ecol.* 12, 348–352.
- Dugatkin, L.A., Druen, M., 2004. The social implications of winner and loser effects. *Proc. R. Soc. Lond. (Suppl.)* 271, S488–S489.
- Dugatkin, L.A., Earley, R.L., 2003. Group fusion: the impact of winner, loser and bystander effects on hierarchy formation in large groups. *Behav. Ecol.* 14, 367–373.
- Dugatkin, L.A., Alfieri, M.S., Moore, A.J., 1994. Can dominance hierarchies be replicated? Form–re-form experiments using the cockroach (*Nauphoeta cinerea*). *Ethology* 97, 94–102.
- Earley, R.L., Dugatkin, L.A., 2002. Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proc. R. Soc. Lond. B* 269, 943–952.
- Franck, D., Ribowski, A., 1987. Influences of prior agonistic experiences 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.
- Franck, D., Ribowski, A., 1993. Dominance hierarchies of male green swordtails (*Xiphophorus helleri*) in nature. *J. Fish Biol.* 43, 497–499.
- Franck, D., Klamroth, B., Taebel-Hellwig, A., Schartl, M., 1998. Home ranges and satellite tactics of male green swordtails (*Xiphophorus helleri*) in nature. *Behav. Process.* 43, 115–123.
- Franck, D., Dikomey, M., Schartl, M., 2001. Selection and the maintenance of a colour pattern polymorphism in the green swordtail (*Xiphophorus helleri*). *Behaviour* 138, 467–486.
- Goessmann, C., Hemelrijk, C.K., Huber, R., 2000. The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behav. Ecol. Sociobiol.* 48, 418–428.
- Goymann, W., Wingfield, J.C., 2004. Allostatic load, social status and stress hormones: the costs of social status matter. *Anim. Behav.* 67, 591–602.
- Hannes, R.-P., Franck, D., Liemann, F., 1984. Effects of rank-order fights on whole-body and blood concentrations of androgens and corticosteroids in the male swordtail (*Xiphophorus helleri*). *Z. Tierpsychol.* 65, 53–65.
- Hoglund, E., Balm, P.H.M., Winberg, S., 2000. Skin darkening, a potential social signal in subordinate Arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *J. Exp. Biol.* 203, 1711–1721.
- Hollander, M., Wolfe, D.A., 1999. *Nonparametric Statistical Methods*, 2nd ed. John Wiley and Sons Inc., New York, pp. 284–287.
- Hsu, Y., Earley, R.L., Wolf, L.L., 2006. Modulation of aggressive behavior by fighting experience: mechanisms and contest outcomes. *Biol. Rev.* 81, 33–74.
- Kazianis, S., Walter, R.B., 2002. Use of platyfishes and swordtails in biological research. *Lab Anim.* 31, 46–52.
- Moore, A.J., Ciccone, W.J., Breed, M.D., 1988. The influence of social experience on the behavior of male cockroaches, *Nauphoeta cinerea*. *J. Insect Behav.* 1, 157–168.
- Morris, M.R., Batra, P., Ryan, M.J., 1992. Male–male competition and access to females in the swordtail *Xiphophorus nigrensis*. *Copeia* 1992, 980–986.
- Morris, M.R., Gass, L., Ryan, M.J., 1995a. Assessment and individual recognition of opponents in *Xiphophorus nigrensis* and *Xiphophorus multilineatus*. *Behav. Ecol. Sociobiol.* 37, 303–310.
- Morris, M.R., Mussel, M., Ryan, M.J., 1995b. Vertical bars on male *Xiphophorus multilineatus*: a signal that deters males and attracts females. *Behav. Ecol.* 6, 274–279.
- Nelissen, M.H.J., 1985. Structure of the dominance hierarchy and dominance determining “group factors” in *Melanochromis auratus*. *Behaviour* 94, 85–107.
- Netherton, J.D., 2005. Temporal Decay of Cortisol in Green Swordtail Fish (*Xiphophorus helleri*) Following an Aggressive Encounter: Differences Between Winners and Losers? MS Thesis, Georgia State University, Atlanta, USA.
- O’Connor, K.I., Metcalfe, N.B., Taylor, A.C., 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Anim. Behav.* 58, 1269–1276.
- Oliveira, R.F., Almada, V.C., 1996. Dominance hierarchies and social structure in captive groups of the Mozambique tilapia *Oreochromis mossambicus* (Teleostei Cichlidae). *Ethol. Ecol. Evol.* 8, 39–55.
- Page, E.B., 1963. Ordered hypotheses for multiple treatments: a significance test for linear ranks. *J. Am. Stat. Assoc.* 58, 216–230.
- Sokal, R., Rohlf, F., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. WH Freeman and Co., San Francisco.
- Thines, G., Heuts, B., 1968. The effect of submissive experiences on dominance and aggressive behaviour of *Xiphophorus* (Pisces, Poeciliidae). *Z. F. Tierpsychol.* 25, 139–154.
- Verbeek, M.E.M., DeGoede, P., Drent, P.J., Wiepkema, P.R., 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour* 136, 23–48.
- Wiley, R.H., 1990. Prior-residence and coat-tail effects in dominance relationships of male dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.* 40, 587–596.
- Wiley, R.H., Steadman, L., Chadwick, L., Wollerman, L., 1999. Social inertia in white-throated sparrows results from recognition of opponents. *Anim. Behav.* 57, 453–463.
- Yasukawa, K., Bick, E.I., 1983. Dominance hierarchies in dark-eyed juncos (*Junco hyemalis*): a test of a game–theory model. *Anim. Behav.* 31, 439–448.
- Zayan, R.C., 1974. Le rôle de la reconnaissance individuelle dans la stabilité des relations hiérarchiques chez *Xiphophorus* (Pisces. Poeciliidae). *Behaviour* 49, 268–312.