Title
The making of winners (and losers): how early dominance interactions determine adult social structure in a clonal fish

Journal
Proceedings of the Royal Society B, 283(1830)

ISSN
0962-8452

Authors
Laskowski, Kate L
Wolf, Max
Bierbach, David

Publication Date
2016-05-11

DOI
10.1098/rspb.2016.0183

Peer reviewed

The making of winners (and losers): how early dominance interactions determine adult social structure in a clonal fish

Running head: Winners and losers in clonal fish

Kate L. Laskowski[1†], Max Wolf[1], David Bierbach[1]

[1] Leibniz Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, 12587 Berlin, Germany

[†] corresponding author: kate.laskowski@gmail.com

Word count: 5,313

ABSTRACT

Across a wide range of animal taxa, winners of previous fights are more likely to keep winning future contests, just as losers are more likely to keep losing. At present, such winner and loser effects are considered to be fairly transient. However, repeated experiences with winning and/or losing might increase the persistence of these effects generating long-lasting consequences for social structure. To test this, we exposed genetically identical individuals of a clonal fish, the Amazon molly (*Poecilia formosa*), to repeated winning and/or losing dominance interactions during the first two months of their life. We subsequently investigated whether these experiences affected the fish's ability to achieve dominance in a hierarchy five months later after sexual maturity, a major life-history transition. Individuals that had only winning interactions early in life consistently ranked at the top of the hierarchy. Interestingly, individuals with only losing experience tended to achieve the middle dominance rank, whereas individuals with both winning and losing experiences generally ended up at the bottom of the hierarchy. In addition to demonstrating that early social interactions can have dramatic and long-lasting consequences for adult social behaviour and social structure, our work also shows that higher cumulative winning experience early in life can counter-intuitively give rise to lower social rank later in life.

Keywords: aggression, dominant, subordinate, dominance hierarchy, development, winner effect

INTRODUCTION

In many animal species, dominance hierarchies are a key factor regulating individual access to resources and thus fitness. Several factors contribute to an individual's ability to achieve a higher dominance rank within a hierarchy, including intrinsic factors such as body size or age [1, 2]. One particularly important extrinsic factor is an individual's previous experience with fighting [reviewed in 3] where winners of previous contests tend to have an increased chance of winning future encounters just as losers are more likely to keep losing [3, 4]. While winner and loser effects are well documented across taxa, they are considered to be fairly transient, generally dissipating after a few hours to a few days [e.g. 5, 6], though one study demonstrated that effects persisted for up to one month in adult animals [7]. However, up to now, most research has investigated the impact of just one contest on later aggression [reviewed in 3, e.g. 8, 9], with just a few studies investigating the impact of two or three previous contests [7, 10, 11]. In sharp contrast, in many social species, individuals are continuously interacting with each other, especially during early life. This means most animals are likely to experience a larger number of contests over a longer period. At present, it is thus unclear whether these multiple and repeated contest experiences have long-lasting effects on social structure.

To address this question, we tested whether and how repeated dominance interactions early in life impact adult hierarchy formation. Early life experiences are known to interact with genetic background [e.g. 12], and both intrinsic and external factors can influence hierarchy formation [13]. We therefore used gynogenetic clonal Amazon mollies (*Poecilia formosa*). This parthenogenic Poeciliid species provides a unique opportunity to generate genetically identical ‘replicate individuals’ controlling for any intrinsic genetic differences and allowing us to pinpoint the effects of early social experience on later adult behaviour. These mollies are found in large shoals in the wild [14] and are known to exhibit considerable female-female aggression making repeated dominance interactions likely in this species [15]. Our experimental design manipulated an individual’s success at early dominance interactions by placing it in either a (i) winning, (ii) losing or an (iii) alternating winning and losing role for the first two months of life (prior to sexual maturity). We then examined hierarchy formation twenty weeks later in triads (after sexual maturity). If cumulative previous winning experience determines later success at achieving dominance, then we predicted that individuals that had repeatedly (and only) won as juveniles would rank highest in the hierarchy, followed by individuals that experienced half as many wins (and losses), and individuals that had repeatedly (and only) lost would rank lowest in the hierarchy.

METHODS

Animal care and maintenance

Stock populations of *P. formosa* (Amazon molly, obtained from Manfred Schartl, (University of Würzburg) are maintained in large (100 l) stock aquariums. The all-female Amazon molly originates from a single natural hybridization event between the sailfin molly *Poecilia latipinna* and the Atlantic molly *Poecilia mexicana* [16]. It reproduces gynogenetically and females require sperm from one of the parental species to stimulate egg production [17]. Therefore, several (2-4) males of *P. mexicana* were kept with each stock population aquarium. Stock populations experience ambient light conditions similar to the local light cycle (~14:10 L:D). Fish were fed ab libitum three times daily on standard flake fish food. We performed weekly water changes to replace ~10% of the total water volume of each tank. To generate the experimental individuals, we isolated gravid females from a single isogenic line (strain 269/223) in separate 35 l tanks containing a gravel bottom and plastic plant. This strain has been bred in captivity since 2002 and intermittent genetic samplings confirm that all individuals are clones (M. Schartl, personal communication). We checked females daily for evidence of offspring and removed the female immediately after giving birth. Offspring remained in these tanks for two weeks after birth, as newly born offspring were too fragile to be handled (netted). After two weeks, offspring were randomly assigned to one of our three early social experience treatments (see more details below; figure 1). We used a split-brood design to control for any potential maternal effects such that individuals from a single brood were placed into two different early social experience treatments. Additionally, we only used broods of similar size (10-15 offspring) to reduce the potential for differences in maternal provisioning. Finally, we note that all mothers were from a single isogenic line; therefore all experimental animals in all three treatments were genetically identical to each other. In total, six different mothers contributed to the experimental individuals.

Early social experience treatments: generating winning & losing experiences in dyads

Figure 1 provides a summary of our experimental design. Newly born offspring were assigned to one of three early social experience treatments approximately two weeks after birth: Winning, Losing or Variable treatment. Every week, for eight weeks, two individuals from different treatments were paired together to experience a dominance interaction. After one week in this pair, each individual was then paired with a new partner (see below for details). This new pairing each week continued for a total of 8 weeks.

Dominance in *P. formosa* (as in many other species) is tightly linked to body size with larger individuals generally achieving dominance (see works on *P. mexicana* [18]). This fact was used to generate individuals with three different types of social experiences (i.e. for each individual and each pair, we tightly controlled whether it was paired with a larger or a smaller individual). Specifically, individuals in the winning treatment were paired with other experimental individuals in such a way that they were always larger than their partner; individuals in the losing treatment were paired such that they were always smaller than their partner; and individuals in the variable treatment were paired with a larger individual one week and then with a smaller individual the next week and so on, for the duration of the treatment. So for example, winning individuals would be paired with smaller losing individuals, or smaller variable individuals; losing individuals would be paired with larger winning or larger variable individuals; and variable individuals would be paired with larger winning (or variable) individuals one week, and then smaller losing (or variable) individuals the next week. Thus at the end of the early social experience treatment period (8 weeks, figure 1) all individuals had experienced eight dominance interactions. We chose 8 total pairings to ensure that all individuals, but especially the variable individuals, had sufficient and repeated experiences in both the larger and smaller roles.

All individuals entered their treatments at the same chronological age (12-21 days) and assignment of experimental individuals to the treatments was staggered over the course of two weeks to allow for proper size differences among individuals in the larger or smaller role. Individuals from all three treatments were paired with each other in a semi-random round robin design constrained by the need to maintain a body size difference of at least 20% between partners (to ensure that the larger of the two partners achieved dominance; [2, 19]). Pairing with the same partner did occur over the course of the experiment, but we ensured that at least 3 weeks elapsed between any previous pairing of the same individuals (which only happened in 9 out of 120 pairings). Each week, our experimental individuals were placed into a new experimental tank [to remove any prior residence effects, e.g. 19, 20] where they stayed for the entirety of the week.

In total 12 fish were assigned to each treatment (total $n = 36$). During the early social experience treatment period (8 weeks i.e., 8 pairings, figure 1), all fish were kept in pairs in 3 l tanks outfitted with a piece of green PVC-tube which provided a refuge. All experimental tanks were on the same flow-through water system (water replacement ~10% per day) with ambient light conditions similar to the local conditions (~14:10 light:dark). Each pair was fed with standard flake fish food several times daily.

After pairing, we immediately observed each pair to determine which individual achieved dominance. We counted the number of bites, chases and tail beats each individual performed for five minutes An individual was assigned as dominant if by the end of the observation period they were the individual performing, but not receiving, any aggressive interactions (i.e. bites, chases, tail beats). Pairs were then observed again on the next two days. In all pairings, there was a clear dominant individual within the first five minute observation, and in all pairings except one, the dominant individual was the larger individual. (Supplemental figure 1 shows the average aggression exhibited by individuals in the larger and smaller roles toward their partners over the course of the experiment). In no pairing did this dominance relationship appear to reverse on the second or third day. Therefore, at the end of the early social experience treatment period we feel confident that individuals in the winning treatment only experienced the winning (dominant) social position; individuals in the losing treatment only experienced the losing (subordinate) social position, and individuals in the variable treatment experienced the same number of winning positions (total of 4 pairings) and losing positions (4 pairings).

Individual isolation after early social experience

After 8 weeks in the early social experience treatments, each individual was isolated into a separate 3 l tank maintained on the same flow-through system. Each tank was equipped with a green PVC-tube for refuge and individuals were in visual contact with each other. Individuals were isolated for 20 weeks to allow all individuals to reach sexual maturity. Females of the Atlantic molly, which is one of the proposed parental species of the Amazon molly [16], reach sexual maturity after ca. 200 days (=27 Weeks) post partum [21] and it is thus likely that Amazon mollies reach maturity within a similar timeframe. After 18 weeks in isolation, each fish was marked with a permanent subcutaneous UV elastomer tag (Northwest Marine Technologies, Inc., Shaw Island, USA) which was necessary for individual identification as we could no longer use body size differences among individuals. For marking, the fish were first anesthetized in 1ml L^{-1} 9:1 clove oil:ethanol solution in water. Fish were then given a unique combination of 4 colours at up to 3 locations on their dorsal side. Fish recovered in a dark, well-aerated tank until they resumed normal swimming activity (see [22] for a similar protocol in *P.mexicana*). Fish were then placed back in their individual tanks. Total handling time was quick (<45 seconds) and all individuals recovered normal swimming activity within several minutes with no apparent long-term detrimental effects.

Dominance hierarchy formation in triads as adults

After 20 weeks in isolation, one individual from each treatment (winning, losing, variable) were simultaneously placed into a larger 35 l tank equipped with a gravel bottom and plastic plant for refuge. While body size differences among all individuals were small (range: 44.7-50.5mm), groupings were made in such a way to minimize body size differences within a triad (<3mm among individuals within triad). The triads were maintained together for one week (7 days) after which we observed the aggressive interactions among the fish for 5 minutes. We recorded the number of bites each individual made towards each other individual. These measures allowed us to compute an ‘average dominance index’ (ADI) score for each fish [23]. Briefly, ADI scores represent the average proportion with which an individual performs aggressive behaviours towards each of its group mates. ADI scores fall between 0-1 with individuals that performed, but did not receive any aggressive interactions receiving a higher score thus indicating a higher dominance rank [23]. Previous work has shown that in a comparison of five different ranking methods on simulated hierarchy data, ADI scores were best at re-creating the true hierarchy [23], which is why we chose this method here.

Over the course of the entire 28 week experiment, 6 fish died (2 from each treatment) so in total 30 individuals (n = 10 per treatment) completed the entire experiment resulting in a 10 dominance triads.

Statistical analyses

We used the ADI rankings to assign each individual to its dominance rank within its triad. Individuals with the highest ADI (generally 1 which meant they only performed aggression and received no aggression) were assigned the top dominance rank, and those with the lowest ADI (generally 0 which meant they did not perform any aggression and only received aggression) were given the lowest rank; individuals with the middle ADI score were then assigned as the middle rank. In two triads, two individuals both had ADI scores of 0 and so we assigned them both to the lowest rank.

Because of the categorical nature of the response variable (dominance rankings) and the categorical nature of the predictor (early social experience), we used Fisher's exact test to test for an association between early social experience and dominance rank. We used a contingency table with 3 levels for each of the factors (3 early social experience treatments x 3 dominance ranks). If early social experience had no influence on later dominance rank then the highest, middle and lowest dominance ranks should be equally distributed among the treatments.

Finally, because even small differences in body size might benefit an individual within a triad, we also ranked each individual with the triad as 'smallest', 'largest', and 'middle' (regardless of their early social experience treatment). We then used a Fisher's exact test to test whether dominance ranks were unequally distributed across body sizes.

RESULTS

We generated three groups of individuals that had either only experienced winning dominance interactions, losing dominance interactions, or a combination of both winning and losing for the first two months of their lives.

We found that this early social experience dramatically affected the individual's behaviour and thus their ability to achieve dominance in a triad 20 weeks later (table 1, figures 2 & 3). In particular, individuals in the winning treatment exhibited high levels of aggression towards both variable and losing individuals (figure 2). Losing individuals exhibited moderate aggression towards variable individuals and were only rarely aggressive towards winning individuals (figure 2). Individuals in the variable treatment exhibited low levels of aggression towards both the winning and losing individuals (figure 2). These patterns of aggression resulted in winning individuals being over-represented in the top dominance rank whereas individuals from the variable treatment were over-represented in the bottom dominance rank (table 1, Fisher's exact test: $p < 0.001$). Individuals that experienced the losing treatment generally acquired the middle dominance rank. In total, 8 out of 10 triads exhibited this pattern of the winning individual achieving the top dominance rank and the variable individual being the bottom dominance rank (figure 3). Importantly, the aggression directed towards the winning individual by the variable individual only occurred in the two remaining triads where the variable individual was able to achieve the top dominance rank (groups I & J, figure 3). None of these differences in dominance rank appear to be driven by body size differences within each triad (table 2; Fisher's exact test: $p = 0.261$).

DISCUSSION

By pairing clonal Amazon mollies of differing sizes, we were able to manipulate an individual's success during dominance interactions early in life while controlling for variation in individual genetic background. We found that this experience with winning, losing or both roles had a significant impact on that individual's behaviour and its ability to achieve dominance in a triad five months later after sexual maturity, a major life-history transition.

Our results demonstrate that winner and loser effects can persist much longer than previously thought especially if they are reinforced. While the majority of literature suggests that winner-loser effects may only persist for a few hours, or days [3], one study did find evidence that these effects could last for up to 30 days [7]. However, this last study was also conducted in adult animals, making the persistence of winner-loser effects beyond sexual maturity found here even more consequential. Most previous work however has investigated the effect of a single winning or losing event making it unclear whether their effects would be stronger if these experiences were repeated. The clonal mollies used here experienced persistent and repeated bouts of dominance interactions with different partners for the first two months of their lives. Given that these are highly social animals, constant interactions with conspecifics during early life are likely, and as shown in our results, can have long-lasting consequences on later behaviour and social structure.

As predicted, individuals that only experienced winning dominance interactions early in life were more likely to achieve the top dominance rank in adulthood. Even though genetically identical to the other experimental individuals, as a result of the repeated dominance interactions in early life, these winning individuals accumulated more (successful) fighting experience than the other two treatments, likely increasing their own assessment of their fighting ability [3]. However, contrary to our initial prediction, individuals with half as much cumulative winning experience (i.e. those in the variable treatment) did not achieve the middle rank, but were rather consistently found at the bottom of the hierarchy. To our knowledge, only one other study has investigated how previous winning or losing experience influenced hierarchy formation in triads but, in sharp contrast to our study, the experimental individuals were only given one previous contest [8]. In that study, similar to our results, the authors found that previous winners emerged with a top dominance rank, but losers achieved the bottom rank and so-called 'neutral' individuals were in the middle. Importantly, these neutral individuals had no previous fighting experience at all. There are a number of studies demonstrating that just previous experience with fighting, regardless of the outcome, can improve an individual's later chance at success [24-26]. This was part of the motivation for generating individuals with variable winning and losing experiences; these individuals provide a control for the total amount of fighting experience that the winning and losing individuals experienced.

Counter our initial predictions, the variable individuals consistently ended up at the bottom of the hierarchy in most triads. Interestingly however, when the variable individual was not at the bottom, it instead switched positions with the winning individual and achieved the top rank. Across all 10 triads we saw this pattern: the winning and variable individuals occupied the top and bottom ranks, but never the middle rank. Previous research on dominance establishment in groups of three naïve individuals found that two individuals generally fought first and whichever individual won this encounter achieved the top rank, and whichever individual lost this initial encounter was subsequently unable to achieve dominance over the third individual and thus fell to the bottom of the hierarchy [27]. And while our experiment was unable to capture the series of fights that likely occurred during the establishment of the hierarchies as we only observed the triads after one week when the hierarchy was presumably well established, a similar pattern of interactions as above would be one potential explanation for our results. Winner/loser effects are thought to arise mainly be increasing (or decreasing) an individual's assessment of their own fighting ability [reviewed in 3, e.g., 9]. Based on the fact that the winning and variable individuals were the only individuals to have any experience with winning, we speculate that they may have been the first two fish to engage in a fight when the triads were first formed. While, the winning individuals were still able to achieve dominance most of the time, probably based on their higher accumulated winning experience, occasionally the variable ones were able to achieve the top rank instead. We suspect then that whichever individual did not achieve the top rank then fell to the very bottom of the hierarchy, and this would demonstrate a potentially high cost to seeking dominance, if this were the case. Future experiments that more closely follow the behavioural interactions immediately after triad formation are needed to elucidate the process of how hierarchies are established among the individuals with differing previous winning experiences.

By simultaneously controlling for differences in genetic background and maternal provisioning (i.e. by using a split-brood design) our experiment was able to demonstrate that differing social experiences early in life are sufficient to have long-lasting consequences on adult behavior. Alterations to epigenetic patterns or hormonal pathways are likely mechanisms through which these long-term changes to behaviour might occur [28]. Changes in androgen levels, specifically testosterone (11-ketotestosterone in fish) have been implicated as causing winner effects: higher circulating testosterone is associated with previous winning and increased fighting behaviour in California mice [11] and specifically blocking 11-KT eliminates any evidence of a winner effect in cichlid fish [29]. Similarly, it is known from green swordtails (*X. hellerii*), another member of the family Poeciliidae, that males increase testosterone levels after winning a contest [30]. These transient changes in circulating hormone levels therefore caused related transient changes in behaviour. Another possible mechanism that may be involved in these long-term carryover effects are alterations to epigenetic patterns [e.g. 28]. Clonal animals, such as the mollies used here, provide excellent model systems in which to investigate these questions given that they remove the complicating factor of differing genetic backgrounds among experimental individuals.

Using genetically identical individuals, we demonstrated that repeated experience with winning and/or losing early in life can impact an individual's behaviour and its dominance interactions later in life. The ability to achieve a high dominance rank is of paramount importance in many species as this will determine access to resources, mates and therefore impact individual fitness. Importantly, we further found that higher cumulative winning experience early in life does not necessarily lead to higher social ranks later in life. Differential social experiences with dominance interactions early in life may therefore have long-lasting and unexpected consequences for behavioural trajectories and the emerging social structure.

ACKNOWLEDGEMENTS

We are very grateful to Richard Benthin and Linda Sartoris who helped with animal care and behavioural observations and Manfred Schartl who provided the molly stock populations. We would like to thank two anonymous referees and Barbara Taborsky for their valuable comments on an earlier version of the manuscript. This work was supported through the Leibniz Competition ("B-types" SAW-2013-IGB-2).

ETHICS STATEMENT

All animals were handled in accordance with state and national laws. Experimental procedures were approved by the Landesamt für Umwelt, Gesundheit und Verbraucherschutz of Berlin Germany (project number: G-0124/14).

COMPETING INTERESTS

We have no competing interests.

AUTHOR CONTRIBUTIONS

All authors designed the experiment, KLL and DB collected the data, KLL analysed the data, KLL wrote the manuscript and all authors contributed substantially to revisions.

DATA ACCESSABILITY

The datasets supporting this article are deposited on Dryad (doi:10.5061/dryad.qj8t3).

REFERENCES

[1] Parker, G.A. 1974 Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* **47**, 223-243.

[2] Beacham, J.L. 1988 The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish, *Lepomis gibbosus*. *Animal Behaviour* **36**, 621-623.

[3] Hsu, Y., Earley, R.L. & Wolf, L.L. 2006 Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews* **81**, 33-74.

[4] Rutte, C., Taborsky, M. & Brinkhof, M.W.G. 2006 What sets the odds of winning and losing? *Trends in Ecology & Evolution* **21**, 16-21. (doi:http://dx.doi.org/10.1016/j.tree.2005.10.014).

[5] Johnsson, J.I. 1997 Individual recognition affects aggression and dominance relations in rainbow rrout, *Oncorhynchus mykiss*. *Ethology* **103**, 267-282. (doi:10.1111/j.1439-0310.1997.tb00017.x).

[6] Miklósi, Á., Haller, J. & Csányi, V. 1997 Learning about the opponent during aggressive encounters in paradise fish (Macropodus opercularis L.): when it takes place? *Behavioural Processes* **40**, 97-105. (doi:http://dx.doi.org/10.1016/S0376-6357(96)00755-3).

[7] Lan, Y.-T. & Hsu, Y. 2011 Prior contest experience exerts a long-term influence on subsequent winner and loser effects. *Frontiers in zoology* **8**, 1-12.

[8] Dugatkin, L.A. & Druen, M. 2004 The social implications of winner and loser effects. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, S488-S489.

[9] Goessmann, C., Hemelrijk, C. & Huber, R. 2000 The formation and maintenance of crayfish hierarchies: behavioral and self-structuring

properties. *Behavioral Ecology and Sociobiology* **48**, 418-428. (doi:10.1007/s002650000222).

[10] Hsu, Y. & Wolf, L.L. 1999 The winner and loser effect: integrating multiple experiences. *Animal Behaviour* **57**, 903-910. (doi:http://dx.doi.org/10.1006/anbe.1998.1049).

[11] Oyegbile, T.O. & Marler, C.A. 2005 Winning fights elevates testosterone levels in California mice and enhances future ability to win fights. *Hormones and behavior* **48**, 259-267.

[12] Zaharia, M.D., Kulczycki, J., Shanks, N., Meaney, M.J. & Anisman, H. 1996 The effects of early postnatal stimulation on Morris water-maze acquisition in adult mice: genetic and maternal factors. *Psychopharmacology* **128**, 227-239.

[13] Chase, I.D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. 2002 Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences* **99**, 5744-5749.

[14] Schlupp, I. 2009 Behavior of fishes in the sexual/unisexual mating system of the Amazon molly (Poecilia formosa). *Advances in the Study of Behavior* **39**, 153-183.

[15] Makowicz, A.M. & Schlupp, I. 2015 Effects of Female-Female Aggression in a Sexual/Unisexual Species Complex. *Ethology* **121**, 903-914.

[16] Stoeck, M., Lampert, K.P., Moeller, D., Schlupp, I. & Schartl, M. 2010 Monophyletic origin of multiple clonal lineages in an asexual fish (Poecilia formosa). *Molecular Ecology* **19**, 5204-5215.

[17] Schlupp, I. 2005 The evolutionary ecology of gynogenesis. *Annual review of ecology, evolution, and systematics*, 399-417.

[18] Bierbach, D., Klein, M., Sassmannshausen, V., Schlupp, I., Riesch, R., Parzefall, J. & Plath, M. 2012 Divergent evolution of male aggressive behaviour: another reproductive isolation barrier in extremophile poeciliid fishes? *International Journal of Evolutionary Biology* **2012**, 148745. (doi:http://dx.doi.org/10.1155/2012/148745).

[19] 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.

[20] Huntingford, F. & Leaniz, C.G. 1997 Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology* **51**, 1009-1014.

[21] Riesch, R., Reznick, D.N., Plath, M. & Schlupp, I. in revision Sex-specific local life-history adaptation in surface- and cave-dwelling Atlantic mollies (*Poecilia mexicana*). *Scientific Reports*.

[22] Bierbach, D., Oster, S., Jourdan, J., Arias-Rodriguez, L., Krause, J., Wilson, A.D. & Plath, M. 2014 Social network analysis resolves temporal dynamics of male dominance relationships. *Behavioral Ecology and Sociobiology* **68**, 935-945.

[23] Hemelrijk, C., Wantia, J. & Gygax, L. 2005 The construction of dominance order: comparing performance of five methods using an individual-based model. *Behaviour* **142**, 1037-1058.

[24] Dugatkin, L.A. & Ohlsen, S.R. 1990 Contrasting asymmetries in value expectation and resource holding power: effects on attack behaviour and dominance in the pumpkinseed sunfish, *Lepomis gibbosus*. *Animal Behaviour* **39**, 802-804.

[25] Stamps, J.A. & Krishnan, V. 1997 Functions of fights in territory establishment. *The American Naturalist* **150**, 393-405.

[26] Kim, T. & Zuk, M. 2000 The effects of age and previous experience on social rank in female red junglefowl, *Gallus gallus spadiceus*. *Animal Behaviour* **60**, 239-244.

[27] Chase, I.D. 1982 Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour* **80**, 218-239.

[28] Champagne, F.A. & Curley, J.P. 2009 Epigenetic mechanisms mediating the long-term effects of maternal care on development. *Neuroscience & Biobehavioral Reviews* **33**, 593-600.

[29] Oliveira, R.F., Silva, A. & Canário, A.V. 2009 Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish. *Proceedings of the Royal Society of London B: Biological Sciences* **276**, 2249-2256.

[30] 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). *Zeitschrift für Tierpsychologie* **65**, 53-65.

Table 1. Individuals from different early social experience treatments differed systematically in their ability to achieve dominance during adulthood (Fisher's exact test $p < 0.001$). Individuals with winning early social experience were over-represented in the highest dominance rank, individuals with losing social experience were over-represented in the middle dominance rank, and individuals with variable social experience were over-represented in the lower dominance rank.

	Dominance rank in triad		
Early social experience treatment	**Highest**	**Middle**	**Lowest**
Winning	8	0	2
Losing	0	8	2
Variable	2	0	8

Table 2. Individuals that were the largest or smallest within their triads were not more or less likely to achieve a particular dominance rank, difference in adult dominance rank thus do not appear to be driven by body size differences within each triad (Fisher's exact test $p = 0.261$).

	Dominance rank in triad		
Body size in triad	**Highest**	**Middle**	**Lowest**
Largest	4	3	3
Middle	2	6	2
Smallest	4	1	5

FIGURE CAPTIONS

Figure 1. Schematic of experimental design. Fish were placed into either of three early social experience treatments two weeks after birth (“Winning”, “Losing”, “Variable”). In this treatment, every week, for eight weeks, two individuals from different treatments were paired together to experience a dominance interaction. After one week in this pair, each individual was then paired with a new partner. In order to create different early social experiences, we tightly controlled whether individuals were paired with a larger or a smaller individual. In particular, individuals in the winning treatment were always the larger of the pair (black fish), individuals in the losing treatment were always smaller (white fish), and individuals in the variable treatment were larger one week and smaller the next week (gray fish). All fish were then isolated for a total of 20 weeks. Following isolation, we placed one individual from each treatment together in a triad and allowed them one week to establish a dominance hierarchy (n = 10 triads).

Figure 2. Average number of bites between individuals of each treatment group in the 10 dominance triads. Arrows point to the individual that is receiving the aggression and the size of the arrow is proportional to the number of bites.

Figure 3. Average dominance index (ADI) of each individual within each dominance triad. In eight out of ten triads, individuals that had only winning interactions early in life achieved the top dominance rank. Interestingly individuals with half as much cumulative winning experience (i.e. those in the variable treatment) tended to be found at the bottom of the hierarchy, whereas individuals with only losing experience tended to achieve the middle dominance rank. In the remaining two triads, variable individuals were able to achieve the top dominance rank.

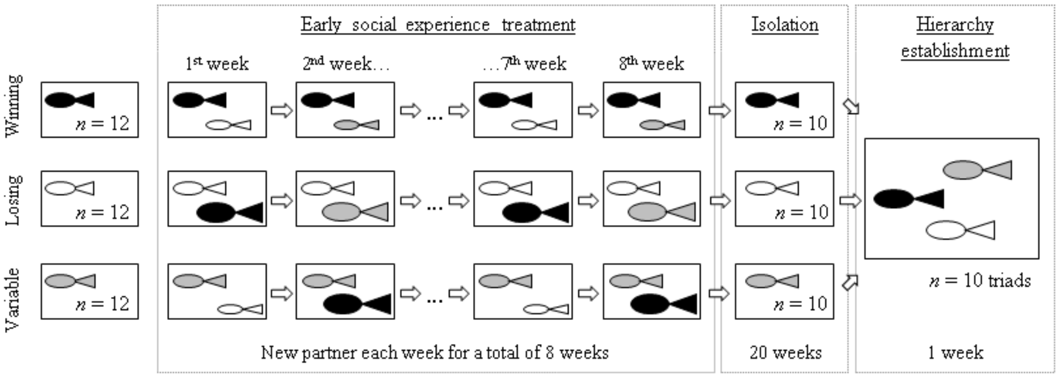
Early social experience treatment
Isolation
Hierarchy establishment
1st week
2nd week…
…7th week
8th week
Winning
Losing
Variable
n = 12
n = 12
n = 12
n = 10
n = 10
n = 10
n = 10 triads
New partner each week for a total of 8 weeks
20 weeks
1 week

Figure 1.

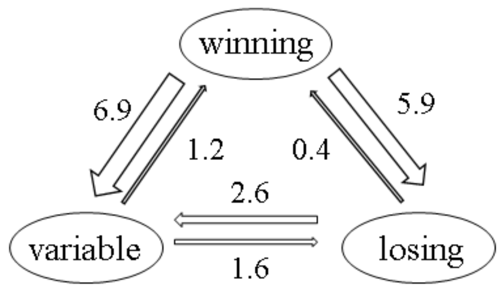

Figure 2.

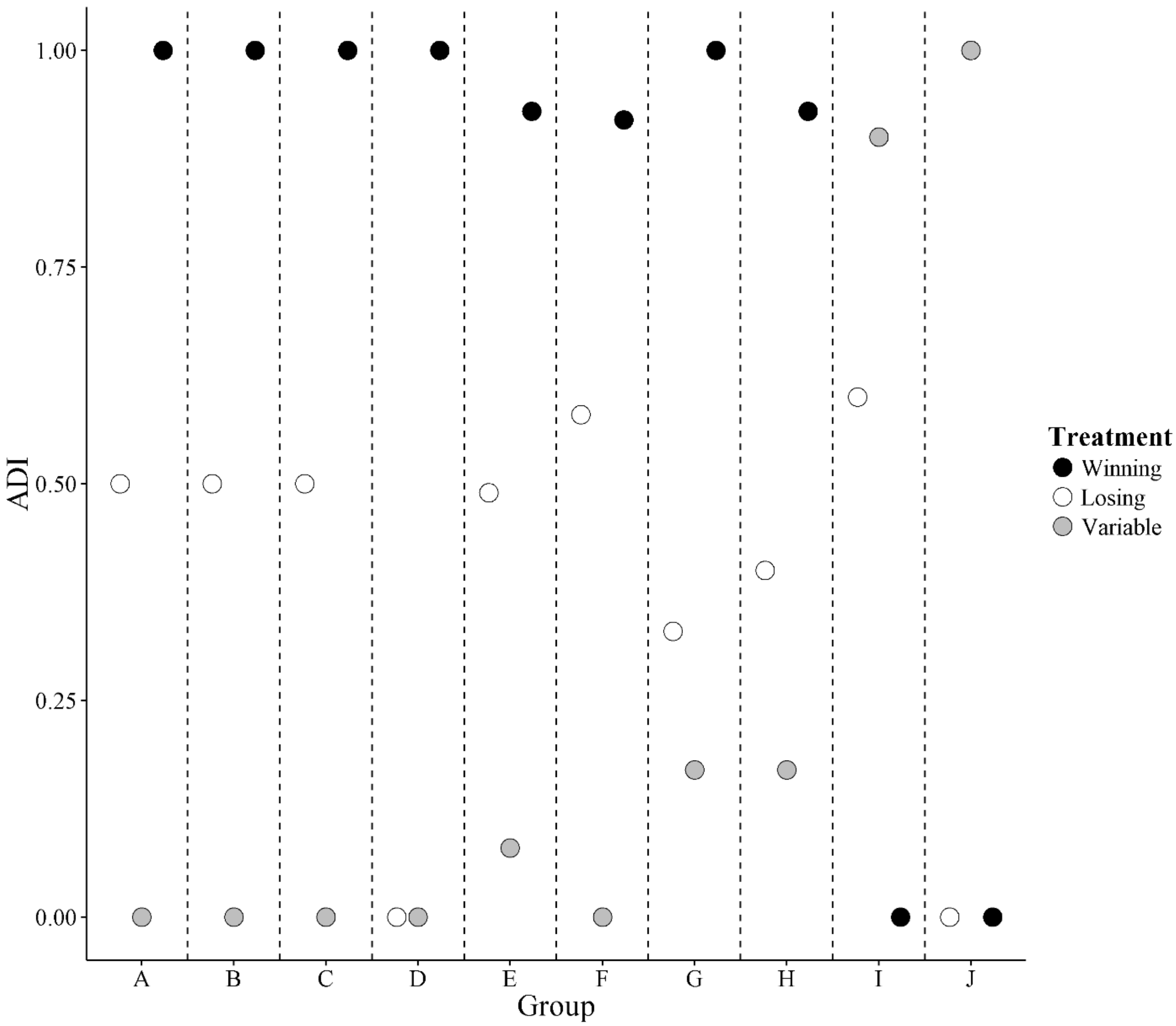
1.00
0.75
0.50
0.25
0.00
ADI
A
B
C
D
E
F
G
H
I
J
Group
Treatment
Winning
Losing
Variable

Figure 3.