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1 **Frequency-dependent social dominance in a color polymorphic cichlid fish**

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3 33 **Abstract**  
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8 35 A mechanism commonly suggested to explain the persistence of color polymorphisms  
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10 36 in animals is negative frequency-dependent selection. It could result from a social  
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12 37 dominance advantage to rare morphs. We tested for this in males of red and blue color  
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14 38 morphs of the Lake Victoria cichlid, *Pundamilia*. Earlier work has shown that males  
15  
16 39 preferentially attack the males of their own morph, while red males are more likely to  
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18 40 win dyadic contests with blue males. In order to study the potential contribution of  
19  
20 41 both factors to the morph co-existence, we manipulated the proportion of red and blue  
21  
22 42 males in experimental assemblages and studied its effect on social dominance. We  
23  
24 43 then tried to disentangle the effects of the own-morph attack bias and social  
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26 44 dominance of red using simulations. In the experiment, we found that red males were  
27  
28 45 indeed socially dominant to the blue ones, but only when rare. However, blue males  
29  
30 46 were not socially dominant when rare. The simulation results suggest that an own-  
31  
32 47 morph attack bias reduces the social dominance of red males when they are more  
33  
34 48 abundant. Thus, there is no evidence of symmetric negative frequency-dependent  
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36 49 selection acting on social dominance, suggesting that additional fitness costs to the red  
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38 50 morph must explain their co-existence.  
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6 53**Introduction**7  
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Understanding the forces that maintain genetic and phenotypic variation within populations is a major challenge in evolutionary ecology, because both selection and drift tend to remove variation from populations (Ricklefs and Schluter 1993; Coyne and Orr 2004). Negative frequency-dependent selection (where rare types are favored by selection) can serve as a general mechanism maintaining variation (Fisher 1930; Heino et al. 1998; Sinervo and Calsbeek 2006). Many animal species display discrete variation in color, such as fish (Seehausen 2000; Hughes et al. 2005), lizards (Calsbeek and Sinervo 2002a), frogs (Hoffman and Blouin 2000) and birds (Roulin 2004). Several types of advantages to rare types have been implicated in explaining the maintenance of such variability in color, such as a rare-morph survival advantage due to a decreased probability of predators detecting rare prey types (Olendorf et al. 2006; Fitzpatrick et al. 2009), a rare-male mating advantage due to a female preference for males bearing rare or novel color patterns (Hughes et al. 1999; Royle et al. 2008) or benefits of a rare-male mating strategy (Sinervo and Lively 1996; Bleay et al. 2007).

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Male color is often used as a cue in aggressive interactions between males (Alatalo et al. 1994; Tynkkynen et al. 2004) and consequently male contest has been proposed to exert selection on male color (Seehausen and Schluter 2004; for recent review see Grether et al. 2009). Selection arising from male contest competition or social hierarchy can be strong, because social dominance is often associated with priority of access to mates and resources and as a consequence dominant individuals are generally assumed to attain the highest fitness (West-Eberhard 1979; Berglund et

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3 77 al. 1996; Wong and Candolin 2005). When males preferentially direct aggression  
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5 78 towards phenotypically similar rival males, rare male phenotypes would receive less  
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8 79 aggression than common male phenotypes. This could generate frequency-dependent  
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10 80 selection in several ways, such as rare morphs being more likely to gain higher  
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12 81 dominance status as a result of reduced harassment from competing males (Seehausen  
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14 82 and Schluter 2004; Mikami et al. 2004; Van Doorn et al. 2004). However, conspecific  
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16 83 color phenotypes across a wide range of different taxonomic groups display  
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18 84 asymmetric social dominance relationships in which one morph is more likely to  
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20 85 defeat the other in dyadic interactions (e.g., Barlow 1983; Pryke and Griffith 2006;  
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22 86 Healey et al. 2007), but it is unknown how this would affect the dynamics of rare-  
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24 87 morph dominance advantages. The aim of this paper is to examine experimentally the  
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26 88 combined effect of own-morph aggression biases and different likelihoods of winning  
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28 89 dyadic contests on frequency-dependent social dominance between competing color  
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30 90 morphs in mixed group situations.  
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36 91 The haplochromine cichlid fishes of the Great African Lakes are famous for  
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38 92 their spectacular species diversity (for recent reviews see: Kocher 2004; Genner and  
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40 93 Turner 2005; Seehausen 2006). Within genera, there is large variation in male color  
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42 94 and this variation affects mate choice. Consequently, sexual selection by female mate  
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44 95 choice has been implicated in their color diversification (Seehausen and Van Alphen  
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46 96 1998; Knight and Turner 2004). Sexual selection is expected to be particularly strong  
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48 97 in haplochromines because their exclusively maternal brood care leads to an excess of  
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50 98 males competing for unmated females (Kokko and Jennions 2008). In addition, male  
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52 99 contest competition for access to females can exert selection on male color indirectly,  
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54 100 because social status and territory size are important in mate choice (Maan et al. 2004;  
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3 101 Dijkstra et al. 2008a), while color is used as a cue in intrasexual communication too  
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6 102 (Dijkstra et al. 2005; Pauers et al. 2008).

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8 103 The cichlid genus *Pundamilia* is widespread in Lake Victoria, containing  
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10 104 many different sympatric color morphs and sibling species. Its Kissenda Island  
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12 105 (Mwanza Gulf, Tanzania) population comprises two genetically determined incipient  
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14 106 species or color morphs (red and blue; Seehausen 2009; Seehausen et al. 2008).  
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17 107 Females show color-based mating preferences and mating is largely assortative with  
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19 108 some gene-flow between red and blue as indicated by the occurrence of intermediate  
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21 109 morphs (Haesler and Seehausen 2005). *Pundamilia* males defend territories mainly  
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23 110 for mating purposes. Both morphs exhibit own-morph attack biases (Dijkstra et al.  
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25 111 2006; 2008b; 2009), but red males are more aggressive and tend to defeat blue in  
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27 112 dyadic contests between the two morphs (Dijkstra et al. 2005; 2006; 2009). We varied  
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29 113 the proportion of red and blue males in an assemblage situation and quantified  
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31 114 agonistic behavior and social dominance of the two color morphs. We show that red  
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33 115 males, but not blue males are dominant over the other morph when rare, in contrast to  
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35 116 the predictions of the usual model of negative frequency-dependent selection where  
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37 117 both rare types are favored. In addition, we confirmed the own-morph aggression bias  
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39 118 in both red and blue males and the higher rate of aggression in red males than in blue  
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41 119 males. We then constructed a simple model simulating the experimental situation in  
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43 120 order to better interpret these findings. In this simulation, we explored how two  
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45 121 different tendencies (own-morph aggression bias and different likelihoods of winning  
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47 122 dyadic contests) and their interaction would affect the expected social dominance of  
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49 123 the color morphs.  
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60 125 **Material and Methods**

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6 127 (a) Tests with life fish  
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11 129 *Fish and housing conditions*  
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16 131 The Kissenda Island *Pundamilia* population consists of males expressing either blue  
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18 132 or red nuptial coloration (Witte-Maas and Witte 1985; Seehausen et al. 1998).  
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20 133 Laboratory crosses revealed that red and blue nuptial colors in *Pundamilia* are  
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22 134 genetically determined, with hybrid crosses resulting in intermediate phenotypes  
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24 135 (Haesler and Seehausen 2005; Van der Sluijs et al. 2008a). Red males at Kissenda  
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26 136 Island tend to occupy a range of different water depths from shallow to deep, whereas  
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28 137 blue males occur in the shallowest 3 m (Seehausen et al. 2008). Hence, their habitat is  
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30 138 fully overlapping in shallow waters, making it likely that males of the two color  
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32 139 morphs compete with one another over mating territories. More details on the study  
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34 140 species can be found elsewhere (Seehausen and Van Alphen 1998; Stelkens et al.  
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36 141 2008; Van der Sluijs et al. 2008b).  
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39 142 All experiments used lab-bred offspring obtained from a stock of 41 wild-  
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41 143 caught parental fish collected in June 2001 around Kissenda Island, Lake Victoria,  
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43 144 Tanzania. Fish were reared in sib groups until approximately 6 months of age, when  
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45 145 the first fish started to mature. They were then translocated into stock aquaria,  
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47 146 containing males and females of both color morphs. The sides and the back of all  
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49 147 aquaria were covered with black plastic. All aquaria were connected to a central  
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51 148 biological filter system and water circulated continuously. The water temperature was  
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53 149 kept at  $25 \pm 2^\circ\text{C}$  and a 12:12 h light:dark cycle was maintained. All aquaria contained  
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55 150 a substrate of gravel. Fish were fed with flake food at least once per day, and a  
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3 151 mixture of ground shrimps and peas two times per week. Experimental males were  
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5 152 sexually mature and at least 11 months of age. To reduce possible effects of prior  
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8 153 experience, they were housed individually for at least one week before the experiment  
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10 154 in aquaria measuring 90 x 36 x 30 cm (l x w x h), divided into 8 compartments by  
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12 155 polyvinyl chloride (PVC) screens. Since the screens were transparent, all males were  
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15 156 able to see at least one other male of either color in an adjoining compartment, so  
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17 157 avoiding social deprivation. Each compartment contained an opaque PVC tube that  
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20 158 the fish used as a hiding place.  
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25 160 *Experimental protocol*  
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29 162 We used five experimental treatments, also referred to as ‘proportion of red males’,  
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31 163 which each had an assemblage of 8 males in a single aquarium tank but in different  
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33 164 ratios of red : blue as follows: i) 1/8 proportion of red males (7 replicates): 1 red and 7  
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35 165 blue males; (ii) 2/8 proportion of red males (7 replicates); (iii) 4/8 proportion of red  
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37 166 males (12 replicates); (iv) 6/8 proportion of red males (8 replicates): (v) 7/8  
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39 167 proportion of red males (8 replicates). The mean  $\pm$  standard error (SE) weight of the  
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41 168 fish was  $15.94 \pm 0.20$  gram. To avoid effects of size asymmetry on dominance, fish in  
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43 169 all five treatments were size-matched within groups (difference in weight between any  
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45 170 male in an assemblage relative to the largest male, expressed as percentage of the  
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47 171 lighter male (mean across assemblages  $\pm$  SE) =  $8.390 \pm 0.095\%$ ; coefficient of  
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49 172 variation mean  $\pm$  SE =  $0.054 \pm 0.043$ ,  $n = 42$ ). The experimental aquaria, measuring  
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51 173 250 x 66 x 46 cm (l x w x h), contained three opaque PVC tubes in the middle of the  
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53 174 left, central and right part of the aquarium, standing upright on one end (diameter 15  
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3 175 cm, length 21 cm); these tubes mimic the type of rocky crevice that *Pundamilia* males  
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6 176 in the wild use as the focal point for territorial defence (Dijkstra et al. 2008a).

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8 177 We used 15 *Melanotaenia lacustris* (rainbow fish) as background fish in each  
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10 178 experimental aquarium in order to disperse the aggression among experimental males,  
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12 179 as in previous work (Dijkstra et al. 2009). We employed 49 red males (out of a total of  
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14 180 104) and 45 blue males (out of a total of 100) in more than one treatment, but no fish  
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16 181 was used more than once within treatments (for a similar design, see Dijkstra et al.  
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18 182 2009). The interval between repeated use of the same male was a minimum of 7 days.  
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20 183 Prior to a test, we weighed all males to the nearest 0.01 g. We clipped males for  
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22 184 individual recognition on their dorsal (two positions) and caudal fin (three positions),  
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24 185 using scissors (Dijkstra et al. 2008a; 2009). These fin clips grow back in one week  
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26 186 and cause no long-lasting damage to the fish.

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29 187 We observed each assemblage on the first three days following release of the  
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31 188 fish into the experimental aquarium. Each observation lasted 45 minutes, amounting  
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33 189 to a total observation time of 135 minutes per assemblage. The males displayed the  
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35 190 common aggressive behaviors of cichlids (Baerends and Baerends-Van Roon 1950).  
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37 191 We recorded (using a tape recorder) aggressive interactions that resulted in a  
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39 192 displacement, with the displaced fish being defined as the loser and the other as  
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41 193 winner. Displacements could come about via (1) attack (i.e. one fish charging or  
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43 194 chasing another fish) or (2) display (i.e. one or both fish showing lateral or frontal  
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45 195 display, followed by fleeing of one of them).

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48 196 We also noted every 15 minutes (3 times per observation session) which males  
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50 197 were displaying vertical bars on their flanks, which is a strong indicator of  
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52 198 territoriality (Maan et al. 2004). Males that displayed these vertical bars during an  
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54 199 observation session were defined as having territorial status.  
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201 *Data analysis*

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203 In order to obtain an estimate of the relative dominance of red over blue we calculated  
204 each individual's Win Ratio by counting the total number of wins relative to the total  
205 number of interactions for each day of observation separately (Smith and Metcalfe  
206 1997). We opted for this measure of dominance, since total win-defeat experience of  
207 an individual is probably more important in terms of achieving territorial status and  
208 fitness than when this measure is corrected for the identity of the partner with which it  
209 fought. As a check on this approach, we also used an alternative method of estimating  
210 relative dominance that is more dyadic-relationship-based and is based on the  
211 Average Dominance Index (Hemelrijk et al. 2005). This change in analysis had little  
212 effect on the results (supplementary material). Once we had calculated the Win  
213 Ratios, we took for each replicate assemblage the median Win Ratio, calculated for  
214 blue and red males separately (the median because the Win Ratios within assemblages  
215 were highly skewed) and used for red and blue males separately a hierarchical linear  
216 model (HLM) to test whether the Win Ratio was dependent on the proportion of red  
217 males, using the 3 daily scores nested within replicate assemblages and proportion of  
218 red males as covariate.

219 In analyzing the own-morph bias for aggression and the morph difference in  
220 rate of aggression we only used data on attacks from the territorial males to reduce  
221 possible effects of differences in social status on the results. Territorial males receive  
222 fewer attacks than nonterritorial males, thereby potentially compromising the  
223 estimates of attack biases when for example males of just one color morph were  
224 territorial. However, similar results were found using all males in the analysis (data

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3 225 not shown). The number of males per assemblage that were able to attain territorial  
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5 226 status on at least one day of observation was on average 3.4 out of the 8.  
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8 227 To test whether the attacks by these territory holders were biased towards  
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10 228 own-morph rival males, we calculated the proportion of attacks by territorial males  
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12 229 towards their own morph, which is defined as the number of attacks against males of  
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14 230 their own morph divided by the sum of attacks to all males. If there was no attack bias  
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16 231 towards own color for the red territorial males, the proportion of attacks towards own  
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18 232 morph should have been 1/7, 3/7, 5/7 and 6/7 in respectively the 2/8, 4/8, 6/8 and 7/8  
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20 233 proportion of red males treatment; the equivalent expected proportions were  
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22 234 calculated for the blue territorial males. For each morph separately we tested for an  
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24 235 own-morph attack bias by testing the attack proportions (averaged at the assemblage  
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26 236 level, meaning that response(s) of male(s) of one color were averaged in each  
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28 237 assemblage) against the expected proportions if there were no attack bias using a  
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30 238 HLM (three daily scores nested within each assemblage). We included proportion of  
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32 239 red males as a covariate in the analysis.  
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38 240 We asked whether red and blue males differed in attack rate (per hour) given  
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40 241 their dominance rank (see below). Note that this is not a test of relative dominance  
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42 242 and that controlling for dominance rank enabled us to compare inherent aggression  
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44 243 levels between color morphs while accounting for the higher aggressiveness of more  
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46 244 socially dominant males. We calculated the dominance rank for each male and day  
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48 245 separately based on ranking the Win Ratios within assemblages, whereby the male  
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50 246 with dominance rank 1 had the highest Win Ratio and the male with dominance rank  
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52 247 8 the lowest Win Ratio. To eliminate variation in attack rates across days (Dijkstra et  
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54 248 al. 2009), we calculated z-scores of  $\ln(x+1)$  transformed attack rates for all males in  
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56 249 each assemblage and day of observation separately. We used a HLM, comparing daily  
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3 250 aggression rates for each day of observation that a fish was territorial, for each  
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5 251 individual fish that at least once attained territorial status in an assemblage (i.e. up to 3  
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8 252 daily scores were nested within individuals, which were nested within replicate  
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10 253 assemblages). We included color morph as a factor and proportion of red males and  
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12 254 dominance rank as covariates in the analysis.

15 255 Proportions were arcsine square-root transformed and attack rates were  
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17 256  $\ln(x+1)$  transformed to meet assumptions of parametric testing. Statistical analyses  
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19 257 were carried out with SPSS 12.0.1, except for the hierarchical linear models (HLM),  
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21 258 which was carried out in MLwin 2.0 (Bryk and Raudenbush 1993). All reported  
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23 259 probabilities are for two-tailed tests of significance, unless stated otherwise. In all  
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25 260 analyses we also tested for possible effects of day of observation, but these are not  
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27 261 reported here because none were significant. Although analyses accommodated  
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29 262 possible variation in the response variable across days of observation, to simplify  
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31 263 graphical presentation we plotted the mean ( $\pm$ SE) based on the pooled data across the  
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33 264 three days of observation unless stated otherwise.  
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41 266 *(b) Simulation study*

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45 268 In the experiment, we found that red males were socially dominant only when rare,  
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47 269 while blue males were not socially dominant when rare. In addition, we confirmed the  
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49 270 own-morph attack bias in both red and blue males and a higher attack rate by red than  
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51 271 blue (see below). As these results leave scope for different interpretations as to how  
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53 272 they can come about we decided to model the system in order to disentangle the  
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55 273 expected effects of (1) own-morph bias in aggression and (2) morph-specific  
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57 274 aggressiveness (which positively influences likelihood of winning a dyadic contest)  
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3 275 on social dominance. Several parameters were set in a way such that the model  
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5 276 closely *mimics* the study system, enabling us to vary the behavioral tendencies of  
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8 277 interest. These model parameters concern morph differences in the distribution of  
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10 278 aggressiveness and the dominance-rank dependent distribution in the number of fights  
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13 279 initiated. Parameter values are based on independent data sets of agonistic behavior of  
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15 280 *Pundamilia* and are specified below.

17 281 In the model, there are two different morphs, red and blue. For each individual  
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20 282 male, we drew a random number from a continuous normal distribution with mean  $\mu$   
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22 283 and standard deviation  $\sigma$  to represent his aggressiveness (or fighting ability),  $a_i$ . To  
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25 284 reflect the higher aggressiveness of red relative to blue (Dijkstra et al. 2005; 2006),  
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27 285 which determines who wins a contest dyadic contests (see below), these parameters  
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30 286 were set to  $\mu + \tau$  and  $\sigma$  for red males, and  $\mu$  and  $0.5\sigma$  for blue males (the standard  
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32 287 deviation of aggressiveness of blue males has been found to be lower than that of the  
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34 288 red males in a range of different experimental settings, see e.g., Dijkstra et al. 2006).  
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37 289 To mimic the observation that a small fraction of individuals are generally more  
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39 290 aggressive than the others, these distributions, originally symmetric around  $\mu$ , were  
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41 291 then made asymmetric by taking the absolute values of each  $a_i$  creating a skewed  
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44 292 distribution of aggressiveness scores, with a lower bound of 0. We varied  $\tau$  in the  
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47 293 model to analyze the effect of a morph difference in the likelihood of winning dyadic  
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49 294 contest on social dominance.

51 295 Another key parameter in the model is the probability of an individual fighting  
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53 296 another individual belonging to the same morph,  $\rho$ . When  $\rho = 0.5$ , it corresponds to  
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55 297 no bias (fighting either morph is equally likely), while values  $0 - 0.5$  or  $0.5 - 1$   
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58 298 correspond to avoiding or preferring an individual of the same morph to fight with.  
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3 299 We varied  $\rho$  to analyze the influence of the own-morph aggression bias on social  
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5 300 dominance.

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8 301 To imitate the experimental setting (see above), we simulated 8 individuals,  
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10 302 out of which 1, 2, 4, 6, or 7 were red. For each round of the simulation, i.e. when each  
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12 303 fish undergoes the pairwise agonistic interactions allocated to him, values of  $a_i$  were  
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14 304 drawn independently as described above, and each individual initiated a number of  
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16 305 fights against other individuals so that the most aggressive individual (i.e. with the  
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18 306 highest  $a_i$  value) had a number of fights  $F$  drawn from a gamma distribution with the  
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20 307 shape and scale parameters set to 5 and 20, respectively. These values were chosen  
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22 308 such that the resulting gamma distribution matches the real distribution of the number  
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24 309 of fights by the dominant individual in a group (Dijkstra et al. 2008a; 2009). The other  
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26 310 individuals initiated fights according to  $F^{\frac{1}{2^{x-1}}}$  (rounded to the nearest integer) where  $x$   
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28 311 = ranks 2 to 8 (according to  $a_i$ ), resulting in a biased distribution of fights initiated,  
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30 312 and this number increasing with increasing dominance – a pattern typically observed  
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32 313 in haplochromine communities (Dijkstra et al. 2008a; 2009). Each fight initiated was  
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34 314 against a less aggressive individual with probability  $p$  and against an equally or more  
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36 315 aggressive individual with probability  $1-p$  (and, as said earlier, against own morph  
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38 316 with probability  $\rho$ ). Parameter  $p$  was set at 0.9, as we know that in social groups  
39  
40 317 cichlid males preferentially attack subordinate individuals (Dijkstra unpublished). The  
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42 318 more aggressive individual (with higher value of  $a_i$ ) had probability  $w$  (specified in  
43  
44 319 results section) to win the dyadic interaction regardless of which one initiated it. After  
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46 320 all the fights in a simulation round the Win Ratio of each morph was calculated (for  
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48 321 details on the Win Ratio, see Data analysis), and each parameter combination was  
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50 322 repeated 1,000 times.

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3 324 **Results**  
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7 326 *(a) Tests with life fish*  
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12 328 *Own-morph attack bias and morph differences in attack rate*  
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14 329 For each morph we plotted the proportion of attacks initiated by males towards their  
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16 330 own morph as a function of the proportion of red males, and compared this to the no-  
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18 331 bias line (see fig. 1). Not surprisingly, the effect of proportion of red males was  
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20 332 significant, because the encounter rate and thus the opportunity of attack depends on  
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22 333 the ratio of red versus blue (HLM, proportion of red males for blue males: deviance =  
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24 334 44.54,  $df = 1$ ,  $P < 0.001$ ; for red males: deviance = 60.25,  $df = 1$ ,  $P < 0.001$ ). More  
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26 335 interestingly, males significantly biased their attacks towards their own morph in both  
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28 336 cases (HLM, observed against expected,  $n = 72$  blue males, deviance 43.33,  $df = 1$ ,  $P$   
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30 337  $< 0.001$ ;  $n = 71$  red males, deviance = 47.71,  $df = 1$ ,  $P < 0.001$ ).  
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34 338 After controlling for the effect of dominance rank (HLM, deviance = 101.03,  
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36 339  $df = 1$ ,  $P < 0.001$ ), we found that red males were more aggressive than blue males  
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38 340 (fig. 2, color morph effect, deviance = 11.14,  $df = 1$ ,  $P < 0.001$ ,  $n = 72$  blue;  $n = 71$   
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40 341 red males.). However, proportion of red males did not have a significant effect on  
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42 342 attack rate (proportion of red males, deviance = 0.075,  $df = 1$ ,  $P = 0.78$ ).  
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48 344 *Frequency-dependent dominance*  
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50 345 Symmetric negative-frequency dependent dominance would predict a negative  
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52 346 relationship in both color morphs between their relative abundance in the population  
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54 347 and Win Ratio. Although there was a significant linear relationship between the Win  
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56 348 Ratios of red males and the proportion of red males in the predicted direction (fig. 3,  
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4 349 HLM, proportion of red males, deviance = 32.01,  $df = 1$ ,  $P < 0.001$ ,  $n = 42$   
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6 350 assemblages), this was not the case for blue males (proportion of red males, deviance  
7  
8 351 = 0.36,  $df = 1$ ,  $P = 0.55$ ). Rather, both curves apparently took the form of a curvilinear  
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10 352 function, which was supported by an improved fit of the model (as indicated by a  
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12 353 reduction in the deviance) when the quadratic term of proportion of red males was  
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15 354 added in the model for both red (HLM, quadratic term, deviance = 8.39,  $df = 1$ ,  $P <$   
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17 355 0.01) and blue males (quadratic term, deviance = 5.25,  $df = 1$ ,  $P = 0.02$ ). The curves  
18  
19 356 of red and blue have opposite shapes. When examining the difference between the  
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21 357 Win Ratio of red and blue males, it appears that red males show a tendency to be  
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23 358 more socially dominant when rare, but otherwise the dominance of red and blue males  
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25 359 are similar (fig. 3). This is also supported by comparing the median Win Ratios of red  
26  
27 360 and blue males; to increase power we averaged the three daily scores and combined  
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29 361 the two extreme treatments, defining 1/8 and 2/8 as rare, 4/8 as intermediate, and 6/8  
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31 362 and 7/8 as abundant. The Win Ratio of red was significantly higher when rare (paired  
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33 363 t-test,  $t_{13} = 2.41$ ,  $P = 0.03$ ), but not when intermediate ( $t_{11} = -0.42$ ,  $P = 0.68$ ) or  
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35 364 abundant ( $t_{15} = 0.65$ ,  $P = 0.53$ ).

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366 *(b) Simulation study*

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368 The simulation study was designed to mimic the experimental situation in order to  
369 determine whether we can interpret the observed pattern in terms of an own-morph  
370 aggression bias and different likelihoods of winning dyadic contests by both morphs.  
371 The output of the models show that the expected pattern of the Win Ratios of blue and  
372 red males against the proportion of red males depends on both parameters  $\tau$  (the  
373 difference in aggressiveness that determines the strength of the tendency of red males



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4 374 to socially dominate blue in dyadic contests) and  $\rho$  (the degree of own-morph fighting  
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6 375 bias) (fig. 4, see also figure caption). When red has a higher tendency to dominate  
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8 376 blue in dyadic contests ( $\tau > 0$ ), then red is more dominant over the entire frequency  
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10 377 range of red in the population if there is no own-morph fighting bias (fig 4b).  
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12 378 Importantly, an own-morph fighting bias substantially reduced the Win Ratio of red  
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14 379 when they become more abundant (compare fig. 4b, where  $\rho = 0.5$ , with 4d where  $\rho >$   
15  
16 380 0.5). Irrespective of the strength of the tendency of red males to dominate blue in  
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18 381 dyadic contest ( $\tau$ ), the Win Ratios become more strongly dependent on the proportion  
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20 382 of red males when males of both color morphs preferentially fight their own morph,  
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22 383 with red males being particularly socially dominant when rare (see figs. 4c and d).  
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24 384 The simulation suggests that when red and blue have equal tendencies to win dyadic  
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26 385 contests, an own-morph fighting bias can actually result in rare-morph social  
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28 386 dominance advantages to both color morphs (fig. 4c). However, curvilinear regression  
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30 387 fits of the relationships between Win Ratios and proportion of red males suggests that  
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32 388 expected patterns are not simply linear. In conclusion, it appears that a combination of  
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34 389 the tendency of red males to socially dominate blue males in dyadic contest and own-  
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36 390 morph fighting bias results in social dominance of red when they are rare, but not for  
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38 391 blue when they are rare (see fig. 4d). An interesting finding is that the model output in  
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40 392 fig 4d resembles the pattern in Win Ratio observed in our experiment (fig. 3), giving  
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42 393 support to the idea that the interaction between the difference in aggressiveness and  
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44 394 own-morph fighting bias is the key in understanding the experimental results.  
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53 395 Finally, it should be noted that the frequency-dependent pattern observed in  
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55 396 panel 4a disappears when the standard deviation in aggressiveness is set equal for the  
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57 397 two color morphs.  
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3 399 **Discussion**  
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8 401 In order to explain the coexistence of different color morphs we set out to test whether  
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10 402 symmetric negative frequency-dependent selection, i.e. rare advantages to both male  
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12 403 types, can arise from social dominance competition in two cichlid color morphs. As  
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14 404 expected, we found that red males were socially dominant over blue when rare, and  
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16 405 less so when more abundant. However, in contrast to expectation, blue males were not  
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18 406 socially dominant over red when rare. We then confirmed two important behavioral  
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20 407 properties of our study species that could help us understand the observed pattern in  
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22 408 frequency-dependent social dominance. First, red and blue males biased aggression  
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24 409 towards opponents of their own color morph, confirming previous findings (Dijkstra  
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26 410 et al. 2006; 2008b; 2009; Verzijden et al. 2009). Secondly, we found that for the same  
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28 411 dominance rank, red males had still a higher rate of attack than blue males, suggesting  
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30 412 that red males are inherently more aggressive than blue males, consistent with  
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32 413 previous studies in which red males were more aggressive and more likely to defeat  
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34 414 blue males in dyadic contests (Dijkstra et al. 2005; 2006; 2009).

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36 415 The simulation study mimicked the experimental setting and explored how  
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38 416 two important behavioral properties or rules with regard to choice of opponent and  
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40 417 different likelihoods of winning dyadic contests could influence the dynamics of  
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42 418 frequency-dependent social dominance between two color morphs. When the red  
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44 419 morph has a higher tendency to dominate blue in dyadic contests then red is predicted  
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46 420 to dominate blue over the entire frequency range in the population. Notably, in the  
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48 421 simulation we found that when males show an own-morph attack bias, red males are  
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50 422 socially dominant over blue when they are rare, but considerably less so when red  
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52 423 increases in frequency. Additionally, the simulation shows that the social dominance  
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3 424 of red males in dyads prevents blue males from attaining a social dominance  
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5 425 advantage when rare, despite an own-morph attack bias. It appears that two simple  
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8 426 aspects of agonistic behavior (own-morph attack bias and different likelihoods of  
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10 427 winning dyadic contests) can help explain our experimental findings.  
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12 428 Male contest competition has been hypothesized to generate negative  
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14 429 frequency-dependent selection, explaining why differently colored congeners can  
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16 430 coexist (Seehausen and Schluter 2004; see also Partridge and Hill 1984; Grether et al.  
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18 431 2009). Previous studies proposed the possibility of negative frequency-dependent  
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20 432 social dominance between competing color morphs, whereby *both* color morphs  
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22 433 should enjoy higher dominance when rare (Dijkstra et al. 2006). Our experimental test  
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24 434 is inconsistent with such a symmetric rare-morph dominance advantage and rather  
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26 435 indicates that the rare-morph dominance advantage is one-sided and restricted to the  
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28 436 red, socially dominant morph in the species that we studied. Keeping the simulation  
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30 437 results in mind, we hypothesize that the higher aggressiveness of red males (which  
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32 438 determines the extent to which red males are socially dominant over blue in dyadic  
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34 439 contests) helped red males in our experiments to attain higher dominance status than  
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36 440 blue males when the red morph was rare. The reduced social dominance of red males  
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38 441 when occurring at higher proportions (4/8, 6/8, 7/8) is likely due to the own-morph  
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40 442 attack bias leading to more competition among red males in which they obviously  
41  
42 443 lack the advantage of red-blue fights. We did not include self-reinforcing effects, such  
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44 444 as winner-loser effects in the interpretation of our findings (see e.g., Hemelrijk and  
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46 445 Wantia 2005; Hsu et al. 2006), although it is likely these effects are relevant too. For  
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48 446 example, in a study on intersexual dominance in groups of primates, it was found that  
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50 447 in groups with a higher percentage of males, females become socially dominant over  
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52 448 males than in groups with fewer males (Hemelrijk et al. 2008). These findings could  
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3 449 be explained by self-reinforcing winner-loser effects, in particular the heavy losses  
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5 450 males suffered in groups with plenty of males. Studying how winner-loser effects  
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8 451 affects the social dominance dynamics in our cichlid study system would be an  
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10 452 interesting avenue for future research (e.g., Oliveira et al. 2009).

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12 453 An important conclusion from our study is that despite a lack of evidence for  
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14 454 symmetric negative frequency-dependent social dominance, aggressive competition  
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17 455 can result in frequency-dependence in social dominance between color morphs and as  
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19 456 such it may *contribute* to coexistence of different morphs (Seehausen and Schluter  
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21 457 2004). Selection arising from male contest competition can be strong in  
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23 458 haplochromines since only territorial males have access to ripe females and territory  
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25 459 quality influences mate choice (Maan et al. 2004; Dijkstra et al. 2008a). The  
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27 460 restriction of the rare-male dominance advantage to red may indeed help explain field  
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29 461 data. Whereas *Pundamilia* populations are often entirely composed of blue males, red  
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31 462 *Pundamilia* males without exception occur sympatrically with blue ones (Seehausen  
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33 463 and Van Alphen, 1999). We hypothesized earlier that a social dominance advantage  
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35 464 of red may help them to invade blue populations (Dijkstra et al. 2005). However,  
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37 465 other factors are likely necessary to keep red males at bay. In the Gouldian finch,  
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39 466 Pryke et al. (2007) found that highly aggressive red-headed males were more  
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41 467 dominant socially, but had reduced immunocompetence compared with the less  
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43 468 aggressive black-headed males when red-headed males were frequent in the  
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45 469 population. It is possible that there is a physiological cost to the red *Pundamilia*  
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47 470 morph too (see also Clotfelter et al. 2007). In addition, in *Pundamilia*, red males  
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49 471 might be more easily detected by predators, although this remains untested (Maan et  
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51 472 al. 2008).

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3 473 It is important to note that rare-male advantages arising from male contest  
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6 474 competition may also emerge in other ways (Seehausen and Schluter 2004; Hemelrijk  
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8 475 et al. 2008). For example, rare males may benefit from less costly competition by  
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10 476 being able to maintain above-average physical condition or to allocate more time and  
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12 477 energy to courtship displays (Seehausen and Schluter 2004). In one of our previous  
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14 478 studies, we also hypothesized that rare males are more likely to obtain high-quality  
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16 479 territories, which play a key role in mate-choice decisions (Dijkstra et al. 2008a).

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19 480 Apart from the study on primates (Hemelrijk et al. 2008), frequency-  
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21 481 dependent social dominance has not been directly addressed before, although it could  
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23 482 be implicated in studies looking at frequency-dependent effects on fitness (Horth et al.  
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25 483 2003; Olendorf et al. 2006; Bleay et al. 2007; Fuller et al. 2009). Olendorf and co-  
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27 484 workers (2006) found frequency-dependent survival within highly variable guppy  
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29 485 populations. Although the authors mainly attribute this to a decreased probability of  
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31 486 predators detecting rare prey types, an alternative mechanism is that male guppies  
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33 487 with rare colors experience reduced intraspecific competition; more studies are  
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35 488 needed to elucidate the different factors that generate the frequency-dependent  
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37 489 selection within these guppy populations (Nosil 2006).

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39 490 In this study we explored frequency-dependent effects of social interactions  
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41 491 emerging from own-morph attack biases and different likelihoods of winning dyadic  
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43 492 contests between two color morphs. Although our experiment was done with cichlids,  
44  
45 493 and is relevant to our understanding of the spectacular radiation of haplochromine  
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47 494 cichlid fish in the Great African Lakes, we believe that our findings have wider  
48  
49 495 implications. Many animal species preferentially direct agonistic behaviours towards  
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51 496 similarly colored rivals (fish: Losey 1982; Pauers et al. 2008; birds: Alatalo et al.  
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53 497 1994; insects: Tynkynnen et al. 2004; Anderson et al. 2009). Asymmetric dyadic

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3 498 dominance relationships are also widespread (fish: Barlow 1983; Kingston 2003;  
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5 499 Horth 2003; Korzan and Fernald 2007; birds: Owen-Ashley and Butler 2004; Pryke  
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7  
8 500 and Griffith 2006; lizards: Calsbeek and Sinervo 2002b; Healey et al. 2007). We  
9  
10 501 therefore believe that our findings have general bearing on understanding the selective  
11  
12 502 forces that maintain phenotypic and genetic variation.  
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15 503

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4 776 Figure captions

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7 7778  
9 778 Figure 1

10 779 Results from the experimental data on cichlids showing the observed proportion of

11 780 attacks by territorial males towards their own morph (mean  $\pm$  SE) as a function of the

12 781 proportion of red males (out of a population size of 8). Data shown separately for (A)

13 782 blue and (B) red males, based on the average of the individual responses across the

14 783 three days of observation. Dashed line indicates the predicted ratio if there was no

15 784 bias. Males of both color morphs bias aggression towards their own color (for

16 785 statistics, see text).

17 786

18 787 Figure 2

19 788 Results from the experimental data on cichlids showing the observed rate of attacks

20 789 (z-scores) of territorial males as a function of their dominance rank (1 is most

21 790 dominant); regression is fitted for blue males (empty symbols) and red males (filled

22 791 symbols) separately. Red males (solid line) performed more attacks at a given

23 792 dominance rank than blue males (dashed line). Shown are the mean  $\pm$  SE, based on

24 793 scores of individual males. Note that in contrast to other figures we could not pool the

25 794 data of the three days of observation, because males could change dominance rank

26 795 and sometimes even status across days of observation. Although we accounted for this

27 796 in our analysis, for graphical purposes we show each daily observation individually.

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29 798 Figure 3

30 799 Results from the experimental data on cichlids showing the Win Ratio of blue (empty

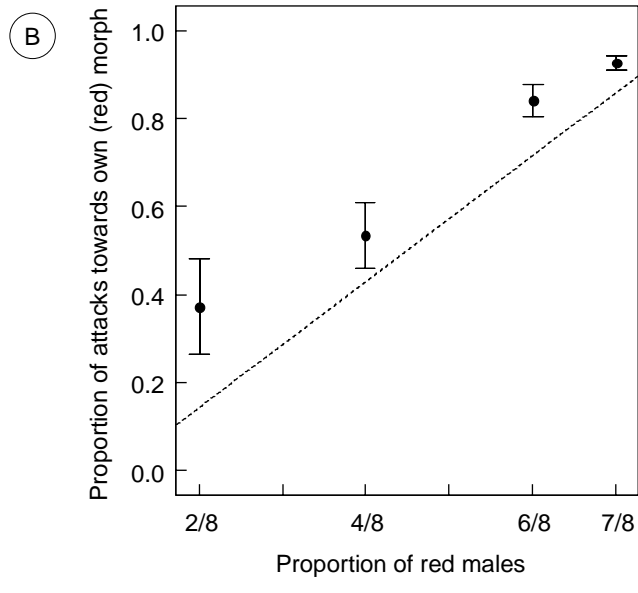
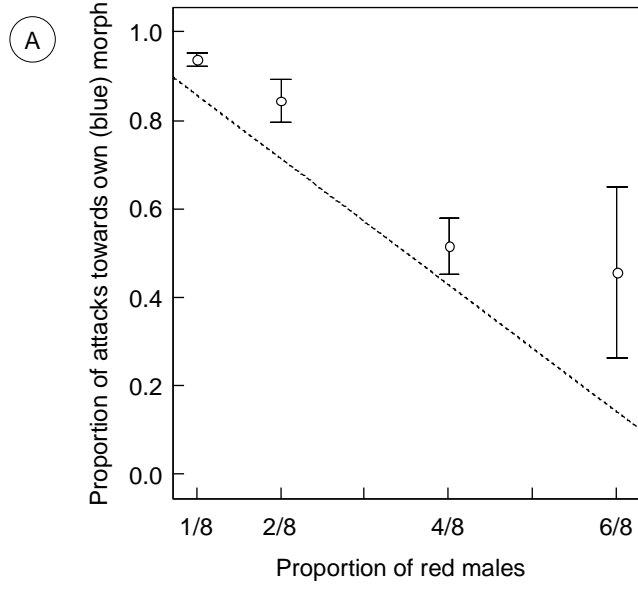
31 800 symbols) and red males (filled symbols) (mean  $\pm$  SE) as a function of the proportion

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3 801 of red males (out of a population size of 8). The data are based on the median Win  
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5 802 Ratio of blue and red males of each assemblage per day, because the Win Ratios  
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8 803 within assemblages were skewed. The figure is based on the average of the three daily  
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10 804 scores. Note that the mean of the Win Ratio is lower than 0.5, because the average  
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12 805 Win Ratio for both colors is influenced by interactions with males of both own and  
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15 806 opposite color.  
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20 808 Figure 4

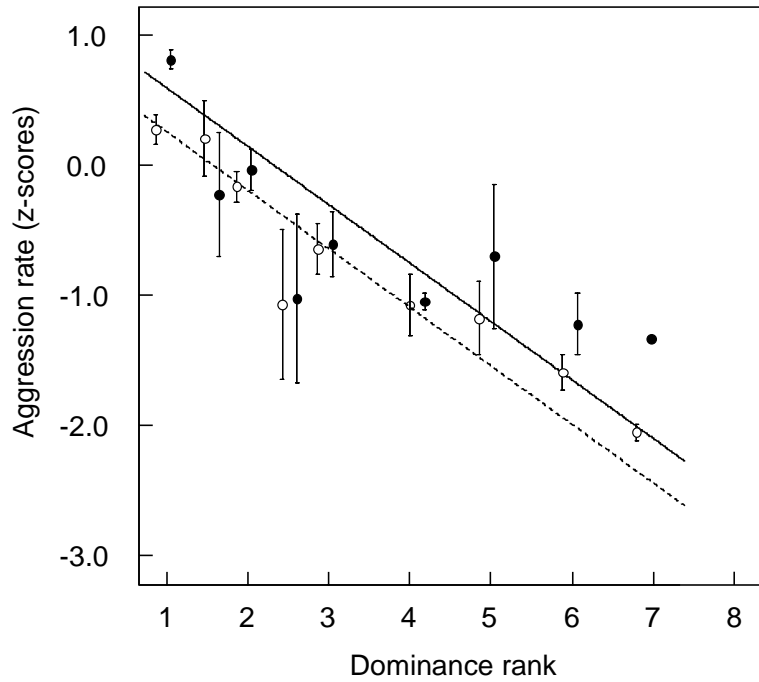
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22 809 Results from the simulation study showing variation in the Win Ratios of blue (empty  
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24 810 symbols) and red males (filled symbols) in relation to the proportion of red males in  
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27 811 the population (out of a population size of 8). The four different panels show the  
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29 812 simulation results for differing parameters values of  $\tau$  (difference in aggressiveness  
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31 813 which determines the extent to which red males are socially dominant over blue in  
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33 814 dyadic contests) and  $\rho$  (the degree of own-morph attack bias). Dots show the means of  
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36 815 1,000 simulation rounds for the red and blue males. The other parameter values used  
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39 816 here were:  $\mu = 0.0001$  (mean aggressiveness),  $p = 0.9$  (probability that the fight was  
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41 817 initiated against a less aggressive individual) and  $w = 0.9$  (probability that the more  
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43 818 aggressive individual wins the fight). Curvilinear regression fits for red (solid line)  
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46 819 and blue males (dashed line) are also shown in each panel. It should be noted that the  
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48 820 small difference in Win Ratios between red and blue in panel 4a disappears when the  
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51 821 standard deviation in aggressiveness is set equal for the two color morphs. See text for  
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54 822 further explanation.  
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Figure 1



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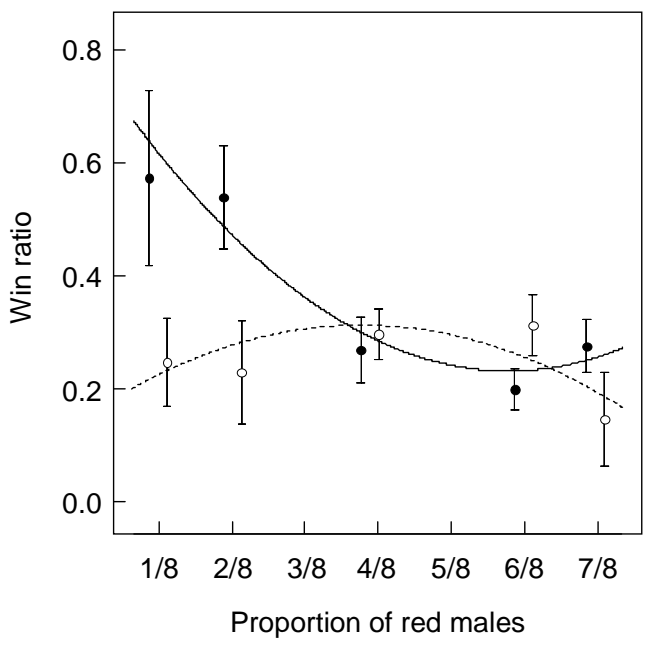
Figure 2



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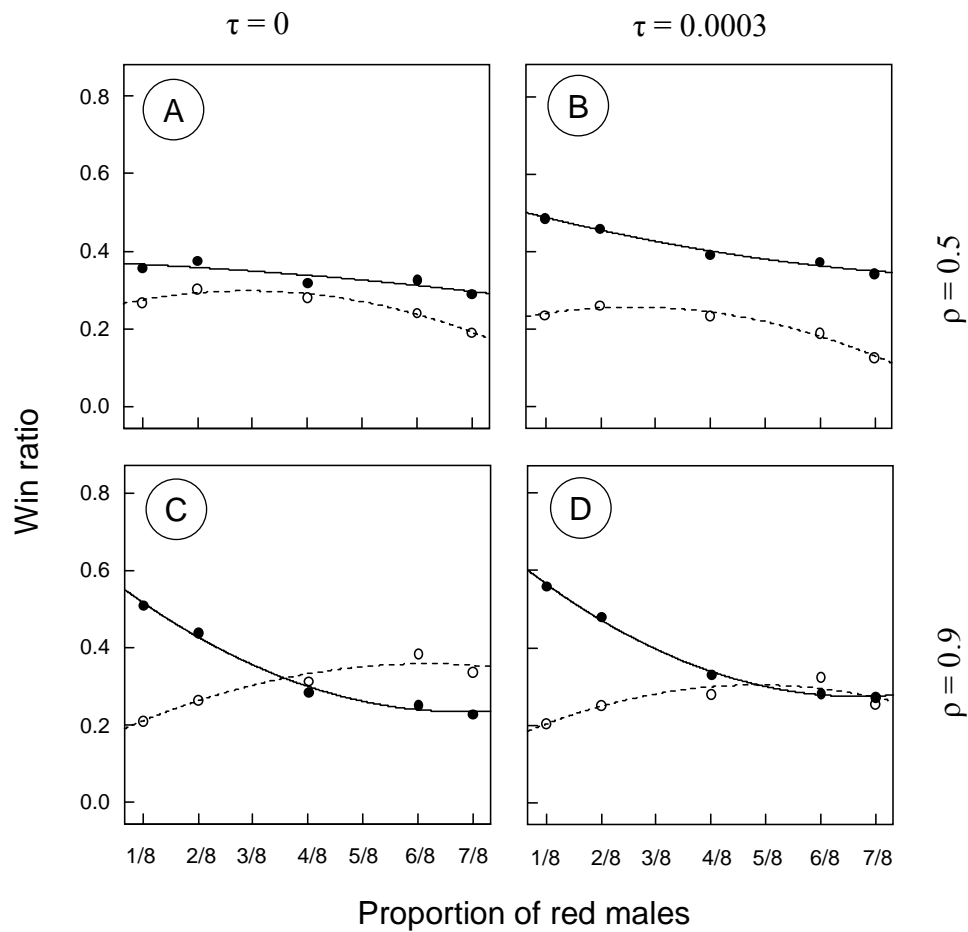
Figure 3



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Figure 4



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3 **1 Supplementary material**  
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8 3 An alternative method of estimating relative dominance is based on individual dyadic  
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10 4 relationships and is called the Average Dominance Index (Hemelrijk et al., 2005).

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12 5 Here we show that we obtain similar results as compared to using the Win Ratio. We  
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14 6 calculated the Average Dominance Index for each individual and each day. To this  
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16 7 end we calculated for each male his Dominance Index (defined as the number of times  
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18 8 the individual won against a specific opponent, divided by the total number of fights  
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20 9 they engaged in) in relation to each community member he interacted with (maximum  
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22 10 7 opponents). We then took for that male the average of these values (Hemelrijk et al.  
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24 11 2005).  
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29 12 Following the analysis of the Win Ratio, we took the median Average  
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31 13 Dominance Index of blue and red males of each assemblage (the median because the  
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33 14 Average Dominance Index within assemblages were skewed). Figure S1 shows the  
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35 15 Average Dominance Index as a function of the proportion of red males and is very  
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37 16 similar to the pattern observed when using the Win Ratio (see figure 4 in main paper).  
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39 17 One exception is the 7/8 treatment where red males are doing far more better than  
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41 18 blue males, more so than in the analysis based on Win Ratios. This does however not  
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43 19 compromise our conclusions, but rather reinforces our main conclusion that the rare-  
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45 20 morph advantage is not symmetric but restricted to the red males.  
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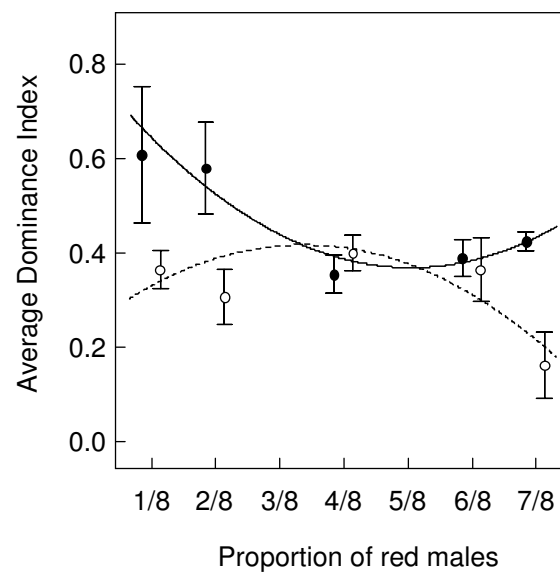
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23 Figure S1

24 Empirical results showing the Average Dominance Index of blue (empty symbols)  
25 and red males (filled symbols) (mean  $\pm$  SE) as a function of the proportion of red  
26 males (out of a population size of 8). The data are based on the median Average  
27 Dominance Index of blue and red males of each assemblage per day, because the  
28 Average Dominance Indexes within assemblages were skewed. The figure is based on  
29 the average of the three daily scores. The resulting patterns resembles the one based  
30 on the Win Ratio (see figure 4).

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