

1
2
3 **1 Frequency-dependent social dominance in a color polymorphic cichlid fish**
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1 Peter D. Dijkstra^{1,2}, Jan Lindström¹, Neil B. Metcalfe¹, Charlotte K. Hemelrijk³,
2 Mischa Brendel¹, Ole Seehausen^{4,5}, and Ton G.G. Groothuis²

3
4
5
6
7 1. Division of Ecology and Evolutionary Biology. Graham Kerr Building, Faculty of
8 Biomedical and Life Sciences, University of Glasgow, Glasgow, G12 8QQ, UK.

9 2. Behavioural Biology, Institute for Behaviour and Neuroscience, University of
10 Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

11 3. Theoretical Biology, Centre for Ecological and Evolutionary Studies, University of
12 Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

13 4. Institute of Zoology – Aquatic Ecology and Macroevolution, University of Bern,
14 Baltzerstr.6, CH-3012 Bern, Switzerland.

15 5. Centre of Ecology, Evolution and Biogeochemistry, Swiss Federal Institute for
16 Aquatic Sciences, EAWAG, CH-6047 Kastanienbaum, Switzerland.

17
18 Words

19 Maintext: 5417

20 Abstract: 202

21 Figures: 4

22 Tables: 0

23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

24 Keywords: male-male competition, sexual selection, color polymorphism, frequency-
25 dependent selection, cichlid fish, Lake Victoria

26
27 Corresponding author: Peter D. Dijkstra, The University of Texas at Austin, Section
28 of Integrative Biology, Institute for Cellular and Molecular Biology, 1 University
29 Station–C0930, Austin, TX 78712. Phone: (1) 512-475-7318, Email:
30 pddijkstra@gmail.com

This document is the accepted manuscript version of the following article:
Dijkstra, P. D., Lindström, J., Metcalfe, N. B., Hemelrijk, C. K., Brendel,
M., Seehausen, O., & Groothuis, T. G. G. (2010). Frequency-dependent social
dominance in a color polymorphic cichlid fish. *Evolution, International
Journal of Organic Evolution*, 64(10), 2797–2807.
<https://doi.org/10.1111/j.1558-5646.2010.01046.x>

1
2
3 33 **Abstract**
4
5
6 34
7
8 35 A mechanism commonly suggested to explain the persistence of color polymorphisms
9
10 36 in animals is negative frequency-dependent selection. It could result from a social
11
12 37 dominance advantage to rare morphs. We tested for this in males of red and blue color
13
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
17
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
25
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
35
36 49 selection acting on social dominance, suggesting that additional fitness costs to the red
37
38 50 morph must explain their co-existence.
39
40
41
42
43
44
45
46 51
47
48
49
50
51
52
53
54
55
56
57
58
59
60

52

53 Introduction

54

55 Understanding the forces that maintain genetic and phenotypic variation within
56 populations is a major challenge in evolutionary ecology, because both selection and
57 drift tend to remove variation from populations (Ricklefs and Schluter 1993; Coyne
58 and Orr 2004). Negative frequency-dependent selection (where rare types are favored
59 by selection) can serve as a general mechanism maintaining variation (Fisher 1930;
60 Heino et al. 1998; Sinervo and Calsbeek 2006). Many animal species display discrete
61 variation in color, such as fish (Seehausen 2000; Hughes et al. 2005), lizards
62 (Calsbeek and Sinervo 2002a), frogs (Hoffman and Blouin 2000) and birds (Roulin
63 2004). Several types of advantages to rare types have been implicated in explaining
64 the maintenance of such variability in color, such as a rare-morph survival advantage
65 due to a decreased probability of predators detecting rare prey types (Olendorf et al.
66 2006; Fitzpatrick et al. 2009), a rare-male mating advantage due to a female
67 preference for males bearing rare or novel color patterns (Hughes et al. 1999; Royle et
68 al. 2008) or benefits of a rare-male mating strategy (Sinervo and Lively 1996; Bleay
69 et al. 2007).

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

1
2
3 77 al. 1996; Wong and Candolin 2005). When males preferentially direct aggression
4
5 78 towards phenotypically similar rival males, rare male phenotypes would receive less
6
7
8 79 aggression than common male phenotypes. This could generate frequency-dependent
9
10 80 selection in several ways, such as rare morphs being more likely to gain higher
11
12 81 dominance status as a result of reduced harassment from competing males (Seehausen
13
14 82 and Schluter 2004; Mikami et al. 2004; Van Doorn et al. 2004). However, conspecific
15
16 83 color phenotypes across a wide range of different taxonomic groups display
17
18 84 asymmetric social dominance relationships in which one morph is more likely to
19
20 85 defeat the other in dyadic interactions (e.g., Barlow 1983; Pryke and Griffith 2006;
21
22 86 Healey et al. 2007), but it is unknown how this would affect the dynamics of rare-
23
24 87 morph dominance advantages. The aim of this paper is to examine experimentally the
25
26 88 combined effect of own-morph aggression biases and different likelihoods of winning
27
28 89 dyadic contests on frequency-dependent social dominance between competing color
29
30 90 morphs in mixed group situations.
31
32
33
34
35

36 91 The haplochromine cichlid fishes of the Great African Lakes are famous for
37
38 92 their spectacular species diversity (for recent reviews see: Kocher 2004; Genner and
39
40 93 Turner 2005; Seehausen 2006). Within genera, there is large variation in male color
41
42 94 and this variation affects mate choice. Consequently, sexual selection by female mate
43
44 95 choice has been implicated in their color diversification (Seehausen and Van Alphen
45
46 96 1998; Knight and Turner 2004). Sexual selection is expected to be particularly strong
47
48 97 in haplochromines because their exclusively maternal brood care leads to an excess of
49
50 98 males competing for unmated females (Kokko and Jennions 2008). In addition, male
51
52 99 contest competition for access to females can exert selection on male color indirectly,
53
54 100 because social status and territory size are important in mate choice (Maan et al. 2004;
55
56
57
58
59
60

1
2
3 101 Dijkstra et al. 2008a), while color is used as a cue in intrasexual communication too
4
5
6 102 (Dijkstra et al. 2005; Pauers et al. 2008).

7
8 103 The cichlid genus *Pundamilia* is widespread in Lake Victoria, containing
9
10 104 many different sympatric color morphs and sibling species. Its Kissenda Island
11
12 105 (Mwanza Gulf, Tanzania) population comprises two genetically determined incipient
13
14 106 species or color morphs (red and blue; Seehausen 2009; Seehausen et al. 2008).
15
16
17 107 Females show color-based mating preferences and mating is largely assortative with
18
19 108 some gene-flow between red and blue as indicated by the occurrence of intermediate
20
21 109 morphs (Haesler and Seehausen 2005). *Pundamilia* males defend territories mainly
22
23 110 for mating purposes. Both morphs exhibit own-morph attack biases (Dijkstra et al.
24
25 111 2006; 2008b; 2009), but red males are more aggressive and tend to defeat blue in
26
27 112 dyadic contests between the two morphs (Dijkstra et al. 2005; 2006; 2009). We varied
28
29 113 the proportion of red and blue males in an assemblage situation and quantified
30
31 114 agonistic behavior and social dominance of the two color morphs. We show that red
32
33 115 males, but not blue males are dominant over the other morph when rare, in contrast to
34
35 116 the predictions of the usual model of negative frequency-dependent selection where
36
37 117 both rare types are favored. In addition, we confirmed the own-morph aggression bias
38
39 118 in both red and blue males and the higher rate of aggression in red males than in blue
40
41 119 males. We then constructed a simple model simulating the experimental situation in
42
43 120 order to better interpret these findings. In this simulation, we explored how two
44
45 121 different tendencies (own-morph aggression bias and different likelihoods of winning
46
47 122 dyadic contests) and their interaction would affect the expected social dominance of
48
49 123 the color morphs.
50
51
52
53
54
55
56
57
58
59

60 125 **Material and Methods**

1
2
3 126
4

5 127 *(a) Tests with life fish*
6
7

8 128
9

10 129 *Fish and housing conditions*
11

12 130
13

14
15 131 The Kissenda Island *Pundamilia* population consists of males expressing either blue
16

17 132 or red nuptial coloration (Witte-Maas and Witte 1985; Seehausen et al. 1998).
18

19
20 133 Laboratory crosses revealed that red and blue nuptial colors in *Pundamilia* are
21

22 134 genetically determined, with hybrid crosses resulting in intermediate phenotypes
23

24 135 (Haesler and Seehausen 2005; Van der Sluijs et al. 2008a). Red males at Kissenda
25

26 136 Island tend to occupy a range of different water depths from shallow to deep, whereas
27

28 137 blue males occur in the shallowest 3 m (Seehausen et al. 2008). Hence, their habitat is
29

30 138 fully overlapping in shallow waters, making it likely that males of the two color
31

32 139 morphs compete with one another over mating territories. More details on the study
33

34 140 species can be found elsewhere (Seehausen and Van Alphen 1998; Stelkens et al.
35

36 141 2008; Van der Sluijs et al. 2008b).
37
38

39
40 142 All experiments used lab-bred offspring obtained from a stock of 41 wild-
41

42 143 caught parental fish collected in June 2001 around Kissenda Island, Lake Victoria,
43

44 144 Tanzania. Fish were reared in sib groups until approximately 6 months of age, when
45

46 145 the first fish started to mature. They were then translocated into stock aquaria,
47

48 146 containing males and females of both color morphs. The sides and the back of all
49

50 147 aquaria were covered with black plastic. All aquaria were connected to a central
51

52 148 biological filter system and water circulated continuously. The water temperature was
53

54 149 kept at $25 \pm 2^\circ\text{C}$ and a 12:12 h light:dark cycle was maintained. All aquaria contained
55

56 150 a substrate of gravel. Fish were fed with flake food at least once per day, and a
57
58
59
60

1
2
3 151 mixture of ground shrimps and peas two times per week. Experimental males were
4
5 152 sexually mature and at least 11 months of age. To reduce possible effects of prior
6
7
8 153 experience, they were housed individually for at least one week before the experiment
9
10 154 in aquaria measuring 90 x 36 x 30 cm (l x w x h), divided into 8 compartments by
11
12 155 polyvinyl chloride (PVC) screens. Since the screens were transparent, all males were
13
14
15 156 able to see at least one other male of either color in an adjoining compartment, so
16
17 157 avoiding social deprivation. Each compartment contained an opaque PVC tube that
18
19
20 158 the fish used as a hiding place.
21

22 159

23
24
25 160 *Experimental protocol*
26

27 161

28
29 162 We used five experimental treatments, also referred to as ‘proportion of red males’,
30
31 163 which each had an assemblage of 8 males in a single aquarium tank but in different
32
33 164 ratios of red : blue as follows: i) 1/8 proportion of red males (7 replicates): 1 red and 7
34
35 165 blue males; (ii) 2/8 proportion of red males (7 replicates); (iii) 4/8 proportion of red
36
37 166 males (12 replicates); (iv) 6/8 proportion of red males (8 replicates): (v) 7/8
38
39 167 proportion of red males (8 replicates). The mean \pm standard error (SE) weight of the
40
41 168 fish was 15.94 ± 0.20 gram. To avoid effects of size asymmetry on dominance, fish in
42
43 169 all five treatments were size-matched within groups (difference in weight between any
44
45 170 male in an assemblage relative to the largest male, expressed as percentage of the
46
47 171 lighter male (mean across assemblages \pm SE) = $8.390 \pm 0.095\%$; coefficient of
48
49 172 variation mean \pm SE = 0.054 ± 0.043 , $n = 42$). The experimental aquaria, measuring
50
51 173 250 x 66 x 46 cm (l x w x h), contained three opaque PVC tubes in the middle of the
52
53 174 left, central and right part of the aquarium, standing upright on one end (diameter 15
54
55
56
57
58
59
60

1
2
3 175 cm, length 21 cm); these tubes mimic the type of rocky crevice that *Pundamilia* males
4
5
6 176 in the wild use as the focal point for territorial defence (Dijkstra et al. 2008a).

7
8 177 We used 15 *Melanotaenia lacustris* (rainbow fish) as background fish in each
9
10 178 experimental aquarium in order to disperse the aggression among experimental males,
11
12 179 as in previous work (Dijkstra et al. 2009). We employed 49 red males (out of a total of
13
14 180 104) and 45 blue males (out of a total of 100) in more than one treatment, but no fish
15
16 181 was used more than once within treatments (for a similar design, see Dijkstra et al.
17
18 182 2009). The interval between repeated use of the same male was a minimum of 7 days.
19
20 183 Prior to a test, we weighed all males to the nearest 0.01 g. We clipped males for
21
22 184 individual recognition on their dorsal (two positions) and caudal fin (three positions),
23
24 185 using scissors (Dijkstra et al. 2008a; 2009). These fin clips grow back in one week
25
26 186 and cause no long-lasting damage to the fish.

27
28
29 187 We observed each assemblage on the first three days following release of the
30
31 188 fish into the experimental aquarium. Each observation lasted 45 minutes, amounting
32
33 189 to a total observation time of 135 minutes per assemblage. The males displayed the
34
35 190 common aggressive behaviors of cichlids (Baerends and Baerends-Van Roon 1950).
36
37 191 We recorded (using a tape recorder) aggressive interactions that resulted in a
38
39 192 displacement, with the displaced fish being defined as the loser and the other as
40
41 193 winner. Displacements could come about via (1) attack (i.e. one fish charging or
42
43 194 chasing another fish) or (2) display (i.e. one or both fish showing lateral or frontal
44
45 195 display, followed by fleeing of one of them).

46
47
48 196 We also noted every 15 minutes (3 times per observation session) which males
49
50 197 were displaying vertical bars on their flanks, which is a strong indicator of
51
52 198 territoriality (Maan et al. 2004). Males that displayed these vertical bars during an
53
54 199 observation session were defined as having territorial status.
55
56
57
58
59
60

200

201 *Data analysis*

202

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

1
2
3 225 not shown). The number of males per assemblage that were able to attain territorial
4
5
6 226 status on at least one day of observation was on average 3.4 out of the 8.

7
8 227 To test whether the attacks by these territory holders were biased towards
9
10 228 own-morph rival males, we calculated the proportion of attacks by territorial males
11
12 229 towards their own morph, which is defined as the number of attacks against males of
13
14 230 their own morph divided by the sum of attacks to all males. If there was no attack bias
15
16 231 towards own color for the red territorial males, the proportion of attacks towards own
17
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
19
20 233 proportion of red males treatment; the equivalent expected proportions were
21
22 234 calculated for the blue territorial males. For each morph separately we tested for an
23
24 235 own-morph attack bias by testing the attack proportions (averaged at the assemblage
25
26 236 level, meaning that response(s) of male(s) of one color were averaged in each
27
28 237 assemblage) against the expected proportions if there were no attack bias using a
29
30 238 HLM (three daily scores nested within each assemblage). We included proportion of
31
32 239 red males as a covariate in the analysis.
33
34
35
36
37

38
39 240 We asked whether red and blue males differed in attack rate (per hour) given
40
41 241 their dominance rank (see below). Note that this is not a test of relative dominance
42
43 242 and that controlling for dominance rank enabled us to compare inherent aggression
44
45 243 levels between color morphs while accounting for the higher aggressiveness of more
46
47 244 socially dominant males. We calculated the dominance rank for each male and day
48
49 245 separately based on ranking the Win Ratios within assemblages, whereby the male
50
51 246 with dominance rank 1 had the highest Win Ratio and the male with dominance rank
52
53 247 8 the lowest Win Ratio. To eliminate variation in attack rates across days (Dijkstra et
54
55 248 al. 2009), we calculated z-scores of $\ln(x+1)$ transformed attack rates for all males in
56
57 249 each assemblage and day of observation separately. We used a HLM, comparing daily
58
59
60

1
2
3 250 aggression rates for each day of observation that a fish was territorial, for each
4
5 251 individual fish that at least once attained territorial status in an assemblage (i.e. up to 3
6
7
8 252 daily scores were nested within individuals, which were nested within replicate
9
10 253 assemblages). We included color morph as a factor and proportion of red males and
11
12 254 dominance rank as covariates in the analysis.

15 255 Proportions were arcsine square-root transformed and attack rates were
16
17 256 $\ln(x+1)$ transformed to meet assumptions of parametric testing. Statistical analyses
18
19 257 were carried out with SPSS 12.0.1, except for the hierarchical linear models (HLM),
20
21 258 which was carried out in MLwin 2.0 (Bryk and Raudenbush 1993). All reported
22
23 259 probabilities are for two-tailed tests of significance, unless stated otherwise. In all
24
25 260 analyses we also tested for possible effects of day of observation, but these are not
26
27 261 reported here because none were significant. Although analyses accommodated
28
29 262 possible variation in the response variable across days of observation, to simplify
30
31 263 graphical presentation we plotted the mean (\pm SE) based on the pooled data across the
32
33 264 three days of observation unless stated otherwise.
34
35
36
37
38
39
40

41 266 *(b) Simulation study*
42
43
44 267

45
46 268 In the experiment, we found that red males were socially dominant only when rare,
47
48 269 while blue males were not socially dominant when rare. In addition, we confirmed the
49
50 270 own-morph attack bias in both red and blue males and a higher attack rate by red than
51
52 271 blue (see below). As these results leave scope for different interpretations as to how
53
54 272 they can come about we decided to model the system in order to disentangle the
55
56 273 expected effects of (1) own-morph bias in aggression and (2) morph-specific
57
58 274 aggressiveness (which positively influences likelihood of winning a dyadic contest)
59
60

1
2
3 275 on social dominance. Several parameters were set in a way such that the model
4
5 276 closely *mimics* the study system, enabling us to vary the behavioral tendencies of
6
7
8 277 interest. These model parameters concern morph differences in the distribution of
9
10 278 aggressiveness and the dominance-rank dependent distribution in the number of fights
11
12
13 279 initiated. Parameter values are based on independent data sets of agonistic behavior of
14
15 280 *Pundamilia* and are specified below.

16
17 281 In the model, there are two different morphs, red and blue. For each individual
18
19
20 282 male, we drew a random number from a continuous normal distribution with mean μ
21
22 283 and standard deviation σ to represent his aggressiveness (or fighting ability), a_i . To
23
24
25 284 reflect the higher aggressiveness of red relative to blue (Dijkstra et al. 2005; 2006),
26
27 285 which determines who wins a contest dyadic contests (see below), these parameters
28
29
30 286 were set to $\mu + \tau$ and σ for red males, and μ and 0.5σ for blue males (the standard
31
32 287 deviation of aggressiveness of blue males has been found to be lower than that of the
33
34 288 red males in a range of different experimental settings, see e.g., Dijkstra et al. 2006).
35
36
37 289 To mimic the observation that a small fraction of individuals are generally more
38
39 290 aggressive than the others, these distributions, originally symmetric around μ , were
40
41 291 then made asymmetric by taking the absolute values of each a_i creating a skewed
42
43
44 292 distribution of aggressiveness scores, with a lower bound of 0. We varied τ in the
45
46
47 293 model to analyze the effect of a morph difference in the likelihood of winning dyadic
48
49 294 contest on social dominance.

50
51 295 Another key parameter in the model is the probability of an individual fighting
52
53 296 another individual belonging to the same morph, ρ . When $\rho = 0.5$, it corresponds to
54
55 297 no bias (fighting either morph is equally likely), while values $0 - 0.5$ or $0.5 - 1$
56
57
58 298 correspond to avoiding or preferring an individual of the same morph to fight with.
59
60

1
2
3 299 We varied ρ to analyze the influence of the own-morph aggression bias on social
4
5 300 dominance.

6
7
8 301 To imitate the experimental setting (see above), we simulated 8 individuals,
9
10 302 out of which 1, 2, 4, 6, or 7 were red. For each round of the simulation, i.e. when each
11
12 303 fish undergoes the pairwise agonistic interactions allocated to him, values of a_i were
13
14 304 drawn independently as described above, and each individual initiated a number of
15
16 305 fights against other individuals so that the most aggressive individual (i.e. with the
17
18 306 highest a_i value) had a number of fights F drawn from a gamma distribution with the
19
20 307 shape and scale parameters set to 5 and 20, respectively. These values were chosen
21
22 308 such that the resulting gamma distribution matches the real distribution of the number
23
24 309 of fights by the dominant individual in a group (Dijkstra et al. 2008a; 2009). The other
25
26 310 individuals initiated fights according to $F^{\frac{1}{2^{x-1}}}$ (rounded to the nearest integer) where x
27
28 311 = ranks 2 to 8 (according to a_i), resulting in a biased distribution of fights initiated,
29
30 312 and this number increasing with increasing dominance – a pattern typically observed
31
32 313 in haplochromine communities (Dijkstra et al. 2008a; 2009). Each fight initiated was
33
34 314 against a less aggressive individual with probability p and against an equally or more
35
36 315 aggressive individual with probability $1-p$ (and, as said earlier, against own morph
37
38 316 with probability ρ). 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
41
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
45
46 320 all the fights in a simulation round the Win Ratio of each morph was calculated (for
47
48 321 details on the Win Ratio, see Data analysis), and each parameter combination was
49
50 322 repeated 1,000 times.

51
52
53
54
55
56
57
58
59
60
323

1
2
3 324 **Results**
4

5 325
6

7 326 *(a) Tests with life fish*
8
9

10 327
11

12 328 *Own-morph attack bias and morph differences in attack rate*
13

14 329 For each morph we plotted the proportion of attacks initiated by males towards their
15
16

17 330 own morph as a function of the proportion of red males, and compared this to the no-
18

19 331 bias line (see fig. 1). Not surprisingly, the effect of proportion of red males was
20

21 332 significant, because the encounter rate and thus the opportunity of attack depends on
22
23

24 333 the ratio of red versus blue (HLM, proportion of red males for blue males: deviance =
25
26

27 334 44.54, $df = 1$, $P < 0.001$; for red males: deviance = 60.25, $df = 1$, $P < 0.001$). More
28

29 335 interestingly, males significantly biased their attacks towards their own morph in both
30

31 336 cases (HLM, observed against expected, $n = 72$ blue males, deviance 43.33, $df = 1$, P
32
33

34 337 < 0.001 ; $n = 71$ red males, deviance = 47.71, $df = 1$, $P < 0.001$).
35

36 338 After controlling for the effect of dominance rank (HLM, deviance = 101.03,
37

38 339 $df = 1$, $P < 0.001$), we found that red males were more aggressive than blue males
39

40 340 (fig. 2, color morph effect, deviance = 11.14, $df = 1$, $P < 0.001$, $n = 72$ blue; $n = 71$
41
42

43 341 red males.). However, proportion of red males did not have a significant effect on
44

45 342 attack rate (proportion of red males, deviance = 0.075, $df = 1$, $P = 0.78$).
46
47

48 343
49

50 344 *Frequency-dependent dominance*
51

52 345 Symmetric negative-frequency dependent dominance would predict a negative
53
54

55 346 relationship in both color morphs between their relative abundance in the population
56

57 347 and Win Ratio. Although there was a significant linear relationship between the Win
58

59 348 Ratios of red males and the proportion of red males in the predicted direction (fig. 3,
60

1
2
3
4 349 HLM, proportion of red males, deviance = 32.01, $df = 1$, $P < 0.001$, $n = 42$
5
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
9
10 352 function, which was supported by an improved fit of the model (as indicated by a
11
12 353 reduction in the deviance) when the quadratic term of proportion of red males was
13
14
15 354 added in the model for both red (HLM, quadratic term, deviance = 8.39, $df = 1$, $P <$
16
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
20
21 357 Win Ratio of red and blue males, it appears that red males show a tendency to be
22
23 358 more socially dominant when rare, but otherwise the dominance of red and blue males
24
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
28
29 361 the two extreme treatments, defining 1/8 and 2/8 as rare, 4/8 as intermediate, and 6/8
30
31 362 and 7/8 as abundant. The Win Ratio of red was significantly higher when rare (paired
32
33 363 t-test, $t_{13} = 2.41$, $P = 0.03$), but not when intermediate ($t_{11} = -0.42$, $P = 0.68$) or
34
35 364 abundant ($t_{15} = 0.65$, $P = 0.53$).

365

366 *(b) Simulation study*

367

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 τ (the
373 difference in aggressiveness that determines the strength of the tendency of red males

1
2
3
4 374 to socially dominate blue in dyadic contests) and ρ (the degree of own-morph fighting
5
6 375 bias) (fig. 4, see also figure caption). When red has a higher tendency to dominate
7
8 376 blue in dyadic contests ($\tau > 0$), then red is more dominant over the entire frequency
9
10 377 range of red in the population if there is no own-morph fighting bias (fig 4b).
11
12 378 Importantly, an own-morph fighting bias substantially reduced the Win Ratio of red
13
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
17
18 381 dyadic contest (τ), the Win Ratios become more strongly dependent on the proportion
19
20 382 of red males when males of both color morphs preferentially fight their own morph,
21
22 383 with red males being particularly socially dominant when rare (see figs. 4c and d).
23
24 384 The simulation suggests that when red and blue have equal tendencies to win dyadic
25
26 385 contests, an own-morph fighting bias can actually result in rare-morph social
27
28 386 dominance advantages to both color morphs (fig. 4c). However, curvilinear regression
29
30 387 fits of the relationships between Win Ratios and proportion of red males suggests that
31
32 388 expected patterns are not simply linear. In conclusion, it appears that a combination of
33
34 389 the tendency of red males to socially dominate blue males in dyadic contest and own-
35
36 390 morph fighting bias results in social dominance of red when they are rare, but not for
37
38 391 blue when they are rare (see fig. 4d). An interesting finding is that the model output in
39
40 392 fig 4d resembles the pattern in Win Ratio observed in our experiment (fig. 3), giving
41
42 393 support to the idea that the interaction between the difference in aggressiveness and
43
44 394 own-morph fighting bias is the key in understanding the experimental results.
45
46
47
48
49
50
51
52

53 395 Finally, it should be noted that the frequency-dependent pattern observed in
54
55 396 panel 4a disappears when the standard deviation in aggressiveness is set equal for the
56
57 397 two color morphs.
58
59
60

398

1
2
3 399 **Discussion**
4

5 400
6

7
8 401 In order to explain the coexistence of different color morphs we set out to test whether
9
10 402 symmetric negative frequency-dependent selection, i.e. rare advantages to both male
11
12 403 types, can arise from social dominance competition in two cichlid color morphs. As
13
14 404 expected, we found that red males were socially dominant over blue when rare, and
15
16 405 less so when more abundant. However, in contrast to expectation, blue males were not
17
18 406 socially dominant over red when rare. We then confirmed two important behavioral
19
20 407 properties of our study species that could help us understand the observed pattern in
21
22 408 frequency-dependent social dominance. First, red and blue males biased aggression
23
24 409 towards opponents of their own color morph, confirming previous findings (Dijkstra
25
26 410 et al. 2006; 2008b; 2009; Verzijden et al. 2009). Secondly, we found that for the same
27
28 411 dominance rank, red males had still a higher rate of attack than blue males, suggesting
29
30 412 that red males are inherently more aggressive than blue males, consistent with
31
32 413 previous studies in which red males were more aggressive and more likely to defeat
33
34 414 blue males in dyadic contests (Dijkstra et al. 2005; 2006; 2009).

35
36 415 The simulation study mimicked the experimental setting and explored how
37
38 416 two important behavioral properties or rules with regard to choice of opponent and
39
40 417 different likelihoods of winning dyadic contests could influence the dynamics of
41
42 418 frequency-dependent social dominance between two color morphs. When the red
43
44 419 morph has a higher tendency to dominate blue in dyadic contests then red is predicted
45
46 420 to dominate blue over the entire frequency range in the population. Notably, in the
47
48 421 simulation we found that when males show an own-morph attack bias, red males are
49
50 422 socially dominant over blue when they are rare, but considerably less so when red
51
52 423 increases in frequency. Additionally, the simulation shows that the social dominance
53
54
55
56
57
58
59
60

1
2
3 424 of red males in dyads prevents blue males from attaining a social dominance
4
5 425 advantage when rare, despite an own-morph attack bias. It appears that two simple
6
7
8 426 aspects of agonistic behavior (own-morph attack bias and different likelihoods of
9
10 427 winning dyadic contests) can help explain our experimental findings.
11
12 428 Male contest competition has been hypothesized to generate negative
13
14 429 frequency-dependent selection, explaining why differently colored congeners can
15
16 430 coexist (Seehausen and Schluter 2004; see also Partridge and Hill 1984; Grether et al.
17
18 431 2009). Previous studies proposed the possibility of negative frequency-dependent
19
20 432 social dominance between competing color morphs, whereby *both* color morphs
21
22 433 should enjoy higher dominance when rare (Dijkstra et al. 2006). Our experimental test
23
24 434 is inconsistent with such a symmetric rare-morph dominance advantage and rather
25
26 435 indicates that the rare-morph dominance advantage is one-sided and restricted to the
27
28 436 red, socially dominant morph in the species that we studied. Keeping the simulation
29
30 437 results in mind, we hypothesize that the higher aggressiveness of red males (which
31
32 438 determines the extent to which red males are socially dominant over blue in dyadic
33
34 439 contests) helped red males in our experiments to attain higher dominance status than
35
36 440 blue males when the red morph was rare. The reduced social dominance of red males
37
38 441 when occurring at higher proportions (4/8, 6/8, 7/8) is likely due to the own-morph
39
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
43
44 444 as winner-loser effects in the interpretation of our findings (see e.g., Hemelrijk and
45
46 445 Wantia 2005; Hsu et al. 2006), although it is likely these effects are relevant too. For
47
48 446 example, in a study on intersexual dominance in groups of primates, it was found that
49
50 447 in groups with a higher percentage of males, females become socially dominant over
51
52 448 males than in groups with fewer males (Hemelrijk et al. 2008). These findings could
53
54
55
56
57
58
59
60

1
2
3 449 be explained by self-reinforcing winner-loser effects, in particular the heavy losses
4
5 450 males suffered in groups with plenty of males. Studying how winner-loser effects
6
7
8 451 affects the social dominance dynamics in our cichlid study system would be an
9
10 452 interesting avenue for future research (e.g., Oliveira et al. 2009).

11
12 453 An important conclusion from our study is that despite a lack of evidence for
13
14 454 symmetric negative frequency-dependent social dominance, aggressive competition
15
16
17 455 can result in frequency-dependence in social dominance between color morphs and as
18
19
20 456 such it may *contribute* to coexistence of different morphs (Seehausen and Schluter
21
22 457 2004). Selection arising from male contest competition can be strong in
23
24 458 haplochromines since only territorial males have access to ripe females and territory
25
26
27 459 quality influences mate choice (Maan et al. 2004; Dijkstra et al. 2008a). The
28
29
30 460 restriction of the rare-male dominance advantage to red may indeed help explain field
31
32 461 data. Whereas *Pundamilia* populations are often entirely composed of blue males, red
33
34 462 *Pundamilia* males without exception occur sympatrically with blue ones (Seehausen
35
36 463 and Van Alphen, 1999). We hypothesized earlier that a social dominance advantage
37
38
39 464 of red may help them to invade blue populations (Dijkstra et al. 2005). However,
40
41 465 other factors are likely necessary to keep red males at bay. In the Gouldian finch,
42
43 466 Pryke et al. (2007) found that highly aggressive red-headed males were more
44
45
46 467 dominant socially, but had reduced immunocompetence compared with the less
47
48 468 aggressive black-headed males when red-headed males were frequent in the
49
50
51 469 population. It is possible that there is a physiological cost to the red *Pundamilia*
52
53 470 morph too (see also Clotfelter et al. 2007). In addition, in *Pundamilia*, red males
54
55
56 471 might be more easily detected by predators, although this remains untested (Maan et
57
58 472 al. 2008).

1
2
3 473 It is important to note that rare-male advantages arising from male contest
4
5
6 474 competition may also emerge in other ways (Seehausen and Schluter 2004; Hemelrijk
7
8 475 et al. 2008). For example, rare males may benefit from less costly competition by
9
10 476 being able to maintain above-average physical condition or to allocate more time and
11
12 477 energy to courtship displays (Seehausen and Schluter 2004). In one of our previous
13
14
15 478 studies, we also hypothesized that rare males are more likely to obtain high-quality
16
17 479 territories, which play a key role in mate-choice decisions (Dijkstra et al. 2008a).

18
19
20 480 Apart from the study on primates (Hemelrijk et al. 2008), frequency-
21
22 481 dependent social dominance has not been directly addressed before, although it could
23
24 482 be implicated in studies looking at frequency-dependent effects on fitness (Horth et al.
25
26 483 2003; Olendorf et al. 2006; Bleay et al. 2007; Fuller et al. 2009). Olendorf and co-
27
28 484 workers (2006) found frequency-dependent survival within highly variable guppy
29
30 485 populations. Although the authors mainly attribute this to a decreased probability of
31
32 486 predators detecting rare prey types, an alternative mechanism is that male guppies
33
34 487 with rare colors experience reduced intraspecific competition; more studies are
35
36 488 needed to elucidate the different factors that generate the frequency-dependent
37
38 489 selection within these guppy populations (Nosil 2006).

39
40
41 490 In this study we explored frequency-dependent effects of social interactions
42
43 491 emerging from own-morph attack biases and different likelihoods of winning dyadic
44
45 492 contests between two color morphs. Although our experiment was done with cichlids,
46
47 493 and is relevant to our understanding of the spectacular radiation of haplochromine
48
49 494 cichlid fish in the Great African Lakes, we believe that our findings have wider
50
51 495 implications. Many animal species preferentially direct agonistic behaviours towards
52
53 496 similarly colored rivals (fish: Losey 1982; Pauers et al. 2008; birds: Alatalo et al.
54
55 497 1994; insects: Tynkynnen et al. 2004; Anderson et al. 2009). Asymmetric dyadic

1
2
3 498 dominance relationships are also widespread (fish: Barlow 1983; Kingston 2003;
4
5 499 Horth 2003; Korzan and Fernald 2007; birds: Owen-Ashley and Butler 2004; Pryke
6
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.
13
14
15 503

17 504 **Acknowledgements**

19
20 505 We thank Dagmar Heidinga and Ruthy Fraterman for help with the experiment.
21
22 506 Mhoja Kayeba, Mohamed Haluna, John Mrosso and Martine Maan are acknowledged
23
24 507 for fish collection. The research was financed by the Netherlands Organisation for
25
26
27 508 Scientific Research, NWO (SLW) grant 810.64.013 to TGGG, a Rubicon grant
28
29 509 825.07.00, and a European Commission Marie Curie Outgoing International
30
31 510 Fellowship grant to PDD, and a grant from the Swiss Science Foundation to OS. The
32
33 511 research was carried out with an animal experiment license (DEC 2812) from
34
35
36 512 Groningen University and complied with current laws in The Netherlands.
37
38
39 513

41 514 **References**

42 515
43 516 Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1994. Male Coloration and Species
44 517 Recognition in Sympatric Flycatchers. *Proc. R. Soc. B* 256:113–118.
45 518
46 519 Anderson, C. N., and G. F. Grether. 2009. Interspecific aggression and character
47 520 displacement of competitor recognition in *Hetaerina* damselflies. *Proc. R. Soc. B* 277:
48 521 549-555.
49 522
50 523 Baerends, G. P., and J. M. Baerends-Van Roon. 1950. An introduction to the study of
51 524 the ethology of cichlid fishes. *Behaviour Supplement* 1:233–366.
52 525
53 526 Barlow, G. W. 1983. Do gold midas cichlid fish win fights because of their color, or
54 527 because they lack normal coloration? A logistic solution. *Behav. Ecol. Sociobiol.*
55 528 13:197–204.
56 529
57 530 Berglund, A., A. Bisazza, A. Pilastro. 1996. Armaments and ornaments: An
58 531 evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* 58:385–399

- 1
2
3 532
4 533 Bleay, C., T. Comendant, and B. Sinervo. 2007. An experimental test of frequency
5 534 dependent selection on male mating strategy in the field. *Proc. R. Soc. B* 274:2019–
6 535 2025.
7
8 536
9 537 Bryk, A. S., and S. W. Raudenbush. 1993. Hierarchical linear models: application and
10 538 data analysis method. Sage; Newbury Park.
11 539
12 540 Calsbeek, R., and B. Sinervo. 2002a. Uncoupling direct and indirect components of
13 541 female choice in the wild. *Proc. Natl. Acad. Sci. USA* 99:14897–14902.
14 542
15 543 Calsbeek, R., and B. Sinervo. 2002b. The ontogeny of territoriality during maturation.
16 544 *Oecologia* 132:468–477.
17 545
18 546 Clotfelter, E. D., D. R. Ardia, and K. J. McGraw. 2007. Red fish, blue fish: trade-offs
19 547 between pigmentation and immunity in *Betta splendens*. *Behav. Ecol.* 18:1139–1145.
20 548
21 549 Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Inc., Sunderland.
22 550
23 551 Dijkstra, P.D., O. Seehausen, and T. G. G. Groothuis. 2005. Direct male-male
24 552 competition can facilitate invasion of new colour types in Lake Victoria cichlids.
25 553 *Behav. Ecol. Sociobiol.* 58:136–143.
26 554
27 555 Dijkstra, P. D., O. Seehausen, B. L. A. Gricar, M. E. Maan, and T. G. G. Groothuis.
28 556 2006. Can male-male competition stabilize speciation? A test in Lake Victoria
29 557 haplochromine cichlid fish. *Behav. Ecol. Sociobiol.* 59:704–713.
30 558
31 559 Dijkstra, P.D., E. M. van der Zee, and T. G. G. Groothuis. 2008a. Territory quality
32 560 affects female preference in a Lake Victoria cichlid fish. *Behav. Ecol. Sociobiol.*
33 561 62:747–755.
34 562
35 563 Dijkstra, P.D., O. Seehausen, R. E. Fraterman, and T. G. G. Groothuis. 2008b.
36 564 Learned aggression biases in Lake Victoria cichlids. *Anim. Behav.* 76:649–655.
37 565
38 566 Dijkstra, P.D., C. K. Hemelrijk, O. Seehausen, and T. G. G. Groothuis. 2009. Colour
39 567 polymorphism and intrasexual selection in assemblages of cichlid fish. *Behav. Ecol.*
40 568 20:138–144.
41 569
42 570 Fisher, R. A. 1930. *The Genetical Theory of Natural selection*. Oxford Univ. Press,
43 571 Oxford.
44 572
45 573 Fitzpatrick, B. M., K. Shook, and R. Izally. 2009. Frequency-dependant selection by
46 574 wild birds promotes polymorphism in model salamanders. *BMC Ecology* 9:12.
47 575
48 576 Fuller, R. C., and A. M. Johnson. 2009 A test for negative frequency-dependent
49 577 mating success as a function of male colour pattern in the bluefin killifish. *Biol. J.*
50 578 *Linn. Soc.* 98:489-500.
51 579
52 580 Genner, M. J., and G. F. Turner. 2005. The Mbuna cichlids of Lake Malawi: a model
53 581 for rapid speciation and adaptive radiation. *Fish and Fisheries* 6:1–34.

- 1
2
3 582
4 583 Grether, G. F., N. Losin, C. N. Anderson and K. Okamoto. 2009. The role of
5 584 interspecific interference competition in character displacement and the evolution of
6 585 competitor recognition. *Biol. Rev.* 84:617–635.
7 586
8 587
9 588 Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within
10 589 sexes. *Trends Ecol. Evol.* 11:92–98.
11 590
12 591 Haesler, M. P., and O. Seehausen. 2005. Inheritance of female mating preference in a
13 592 sympatric sibling species pair of Lake Victoria cichlids: implications for speciation.
14 593 *Proc. R. Soc. B* 272:237–245.
15 594
16 595 Healey, M., T. O. Uller, and M. M. Olsson. 2007. Seeing red: morph-specific contest
17 596 success and survival rates in a colour-polymorphic agamid lizard. *Anim. Behav.*
18 597 74:337–341.
19 598
20 599 Heino M, J. A. J. Metz, and V. Kaitala. 1998. The enigma of frequency-dependent
21 600 selection. *Trends Ecol. Evol.* 13:367–370.
22 601
23 602 Hemelrijk, C. K., J. Wantia, L. Gyga. 2005. The construction of dominance order:
24 603 comparing performance of five methods using an individual-based model. *Behaviour*
25 604 142:1037–1058.
26 605
27 606 Hemelrijk, C. K., J. Wantia. 2005. Individual variation by self-organisation.
28 607 *Neuroscience and Biobehavioral Reviews* 29:125–136.
29 608
30 609 Hemelrijk, C. K., J. Wantia, and K. Isler. 2008. Female dominance over males in
31 610 primates: Self-organisation and sexual dimorphism. *PLoS ONE* 3:e2678.
32 611
33 612 Hoffman, E. A., and M. S. Blouin. 2000. A review of colour and pattern
34 613 polymorphisms in anurans. *Biol. J. Linn. Soc.* 70:633–665.
35 614
36 615 Horth, L., 2003. Melanic body-color and aggressive mating behavior are correlated
37 616 traits in male mosquitofish, (*Gambusia holbrooki*). *Proc. R. Soc. B* 270: 1033–1040.
38 617
39 618 Hughes, K. A., L. Du, F. H. Rodd, and D. N. Reznick. 1999. Familiarity leads to
40 619 female mate preference for novel males in the guppy, *Poecilia reticulata*. *Anim.*
41 620 *Behav.* 58:907–916.
42 621
43 622 Hughes, K. A., F. H. Rodd and D.N. Reznick. 2005. Genetic and environmental
44 623 effects on secondary sex traits in guppies (*Poecilia reticulata*). *J. Evol. Biol.* 18:35–45
45 624
46 625 Hsu, Y., R. L. Earley, and L. L. Wolf. 2006. Modulation of aggressive behaviour by
47 626 fighting experience: mechanisms and contest outcomes. *Biol. Rev.* 81:33–74.
48 627
49 628 Kingston, J. J., G. G. Rosenthal, and M. J. Ryan. 2003. The role of sexual selection in
50 629 maintaining a colour polymorphism in the pygmy swordtail, *Xiphophorus pygmaeus*.
51 630 *Anim. Behav.* 65:964–975.
52
53
54
55
56
57
58
59
60

- 1
2
3 631 Knight, M. E., and G. F. Turner. 2004. Laboratory mating trials indicate incipient
4 632 speciation by sexual selection among populations of the cichlid fish *Pseudotropheus*
5 633 *zebra* from Lake Malawi. *Proc. R. Soc. B* 271:675–680.
6 634
- 7
8 635 Kocher, T.D. 2004. Adaptive evolution and explosive speciation: the cichlid fish
9 636 model. *Nature Genetics* 5:289–298.
10 637
- 11 638 Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex
12 639 ratios. *J. Evol. Biol.* 21:919–948.
13 640
- 14
15 641 Korzan, W. J., and R. D. Fernald. 2007. Territorial male color predicts agonistic
16 642 behavior of conspecifics in a color polymorphic species. *Behav. Ecol.* 18:318–323.
17 643
- 18 644 Losey, G. S. 1982. Intra- and interspecific aggression by the Central American Midas
19 645 cichlid *Cichlasoma citrinellum*. *Behaviour* 79:9–80.
20 646
- 21
22 647 Maan, M. E., O. Seehausen, L. Soderberg, L. Johnson, A. P. Ripmeester, H. D. J.
23 648 Mrosso, M. I. Taylor, T. J. M. van Dooren, and J. J. M. van Alphen. 2004.
24 649 Intraspecific sexual selection on a speciation trait, male coloration, in the Lake
25 650 Victoria cichlid *Pundamilia nyererei*. *Proc. R. Soc. B* 271:2445–2452.
26 651
- 27
28 652 Maan, M. E., B. Eshuis, M. P. Haesler, M. V. Schneider, J. J. M. van Alphen, and O.
29 653 Seehausen. 2008. Colour polymorphism and predation in a Lake Victoria cichlid fish.
30 654 *Copeia* 3:621–629.
31 655
- 32
33 656 Mikami, O. K., M. Kohda, and M. Kawata. 2004. A new hypothesis for species co-
34 657 existence: male-male repulsion promotes co-existence of competing species. *Pop.*
35 658 *Ecol.* 46:213–217.
36 659
- 37
38 660 Nosil, P. 2006. Frequency-dependent selection: when being different makes you not
39 661 stand out. *Curr. Biol.* 16:R806–808
40 662
- 41 663 Olendorf, R., F. H. Rodd, D. Punzalan, A. E. Houde, C. Hurt, D. N. Reznick, and K.
42 664 A. Hughes. 2006. Frequency-dependent survival in natural guppy populations. *Nature*
43 665 441:633–636.
44 666
- 45
46 667 Oliveira, R. F., A. Silva, and A. V. M. Canário. 2009. Why do winners keep winning?
47 668 Androgen mediation of winner but not loser effects in cichlid fish. *Proc. R. Soc. B*
48 669 276:2249–2256.
49 670
- 50
51 671 Owen-Ashley, N. T., and L. K. Butler. 2004. Androgens, interspecific competition
52 672 and species replacement in hybridizing warblers. *Proc. R. Soc. B* 271:S498–S500.
53 673
- 54 674 Partridge, W., and G. Hill. 1984. Mechanisms for frequency-dependent mating
55 675 success. *Biol. J. Linn. Soc.* 23:113–132.
56 676
- 57
58 677 Pauers, M. J., J. M. Kapfer, C. E. Fendos, and C. S. Berg. (2008). Aggressive biases
59 678 towards similarly coloured males in Lake Malawi cichlid fishes. *Biol. Lett.* 4:156–
60 679 159.
680

- 1
2
3 681 Pryke, S. R., and S. C. Griffith. 2006. Red dominates black: agonistic signalling
4 682 among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. B*
5 683 273:949–957.
6 684
- 7 685 Pryke, S. R., L. B. Astheimer, W. A. Buttemer, and S. C. Griffith. 2007. Frequency-
8 686 dependent physiological trade-offs between competing colour morphs. *Biol. Lett.*
9 687 3:494–497.
10 688
- 11 689 Ricklefs, R. E., and D. Schluter. 1993. *Species diversity in ecological communities:*
12 690 *historical and geographical perspectives.* University of Chicago Press, Chicago.
13 691
- 14 692 Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour
15 693 polymorphism in birds. *Biol. Rev.* 79:815–848.
16 694
- 17 695 Royle, N. J., J. Lindström, and N. B. Metcalfe. 2008. Context-dependent mate choice
18 696 in relation to social composition in green swordtails *Xiphophorus helleri*. *Behav.*
19 697 *Ecol.* 19:998–1005.
20 698
- 21 699 Seehausen, O. 2000. Explosive speciation rates and unusual species richness in
22 700 haplochromine cichlids effects of sexual selection. *Advances in Ecological Research*
23 701 31:237–274.
24 702
- 25 703 Seehausen, O. 2006. African cichlid fish: a model system in adaptive radiation
26 704 research. *Proc. R. Soc. B* 273:1987–1998.
27 705
- 28 706 Seehausen, O, 2009. The sequence of events along a "speciation transect" in the Lake
29 707 Victoria cichlid fish *Pundamilia*. Pages 155-176 in R. Butlin, D. Schluter and J. R.
30 708 Bridle, eds. *Speciation and Ecology.* Cambridge University Press, Cambridge.
31 709
- 32 710 Seehausen, O, and D. Schluter. 2004. Male-male competition and nuptial-colour
33 711 displacement as a diversifying force in Lake Victoria cichlid fishes. *Proc. R. Soc. B*
34 712 271:1345–1353.
35 713
- 36 714 Seehausen, O., and J. J. M. van Alphen. 1998. The effect of male coloration on female
37 715 mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei*
38 716 complex). *Behav. Ecol. Sociobiol.* 42:1–8.
39 717
- 40 718 Seehausen, O., and J. J. M. van Alphen. 1999. Can sympatric speciation by disruptive
41 719 sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecol.*
42 720 *Lett.* 2:262–271.
43 721
- 44 722 Seehausen, O., E. Lippitsch, N. Bouton, and H. Zwennes. 1998. *Mbipi*, the rock-
45 723 dwelling cichlids of Lake Victoria: description of three new genera and fifteen new
46 724 species (*Teleostei*). *Ichthyological Exploration Freshwaters* 9:129–228.
47 725
- 48 726 Seehausen O., Y. Terai, I. S. Magalhaes, K. L. Carleton, H. Mrosso, R. Miyagi, I. van
49 727 der Sluijs, M. V. Schneider, M. E. Maan, H. Tachida, H. Imai, and N. Okada. 2008.
50 728 Speciation through sensory drive in cichlid fish. *Nature* 455:620–626.
51 729

- 1
2
3 730 Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution
4 731 of alternative male strategies. *Nature* 380:240–243.
5 732
6
7 733 Sinervo, B., and R. Calsbeek. 2006. The development, physiological, neural and
8 734 genetic causes and consequences of frequency-dependent selection in the wild.
9 735 *Annual Review of Ecology, Evolution and Systematics* 37:581–610.
10 736
11 737 Smith, R. D., and N. B. Metcalfe. 1997. Why does dominance decline with age in
12 738 wintering snow buntings? *Anim. Behav.* 53:313–322.
13 739
14 740 Stelkens, R. B., M. E. R. Pierotti, D. A. Joyce, A. M. Smith, I. van der Sluijs, and O.
15 741 Seehausen. 2008. Disruptive sexual selection on male nuptial coloration through
16 742 female mate choice in an experimental hybrid population of cichlid fish. *Philos.*
17 743 *Trans. R. Soc. B* 363:2861–2870.
18 744
19 745 Tynkkynen, K., M. J. Rantala, and J. Suhonen. 2004. Interspecific aggression and
20 746 character displacement in the damselfly *Calopteryx splendens*. *J. Evol. Biol.* 17:759–
21 747 767.
22 748
23 749 Van Doorn, G. S., U. Dieckmann, F. J. Weissing. 2004. Sympatric speciation by
24 750 sexual selection: a critical re-evaluation. *Am. Nat.* 163:709–725.
25 751
26 752 Van der Sluijs, I., T. J. M. van Dooren, K. D. Hofker, J. J. M. van Alphen, R. B.
27 753 Stelkens, and O. Seehausen. 2008a. Female mating preference functions predict
28 754 sexual selection against hybrids between sibling species of cichlid fish. *Philos. Trans.*
29 755 *R. Soc. B* 363:2871–2877.
30 756
31 757 Van der Sluijs, I., T. J. M. van Dooren, O. Seehausen, and J. J. M. van Alphen. 2008b.
32 758 A test of fitness consequences of hybridization in sibling species of Lake Victoria
33 759 cichlid fish. *J. Evol. Biol.* 21:480–491.
34 760
35 761 Verzijden, M.N., J. Zwinkels, and C. ten Cate. 2009. Cross-fostering does not
36 762 influence the mate preferences and territorial behaviour of males in Lake Victoria
37 763 Cichlids. *Ethology* 115:39–48.
38 764
39 765 West-Eberhard, M. J. 1979. Sexual selection, social competition, and evolution. *Proc.*
40 766 *Amer. Philos. Soc.* 51:222–234.
41 767
42 768 Witte-Maas, E., and F. Witte. 1985. *Haplochromis nyererei*, a new cichlid fish from
43 769 Lake Victoria named in honour of Mwalimu Julius Nyerere, president of Tanzania.
44 770 Brill, Leiden.
45 771
46 772 Wong, B. B. M, and U. Candolin. 2005. How is female mate choice affected by male
47 773 competition? *Biol. Rev.* 80:559–571.
48 774
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 775

4 776 Figure captions

5
6
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.

28 797

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

1
2
3 801 of red males (out of a population size of 8). The data are based on the median Win
4
5 802 Ratio of blue and red males of each assemblage per day, because the Win Ratios
6
7
8 803 within assemblages were skewed. The figure is based on the average of the three daily
9
10 804 scores. Note that the mean of the Win Ratio is lower than 0.5, because the average
11
12 805 Win Ratio for both colors is influenced by interactions with males of both own and
13
14
15 806 opposite color.
16
17
18 807

19
20 808 Figure 4

21
22 809 Results from the simulation study showing variation in the Win Ratios of blue (empty
23
24 810 symbols) and red males (filled symbols) in relation to the proportion of red males in
25
26
27 811 the population (out of a population size of 8). The four different panels show the
28
29 812 simulation results for differing parameters values of τ (difference in aggressiveness
30
31 813 which determines the extent to which red males are socially dominant over blue in
32
33 814 dyadic contests) and ρ (the degree of own-morph attack bias). Dots show the means of
34
35
36 815 1,000 simulation rounds for the red and blue males. The other parameter values used
37
38
39 816 here were: $\mu = 0.0001$ (mean aggressiveness), $p = 0.9$ (probability that the fight was
40
41 817 initiated against a less aggressive individual) and $w = 0.9$ (probability that the more
42
43 818 aggressive individual wins the fight). Curvilinear regression fits for red (solid line)
44
45
46 819 and blue males (dashed line) are also shown in each panel. It should be noted that the
47
48 820 small difference in Win Ratios between red and blue in panel 4a disappears when the
49
50
51 821 standard deviation in aggressiveness is set equal for the two color morphs. See text for
52
53
54 822 further explanation.
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure 1

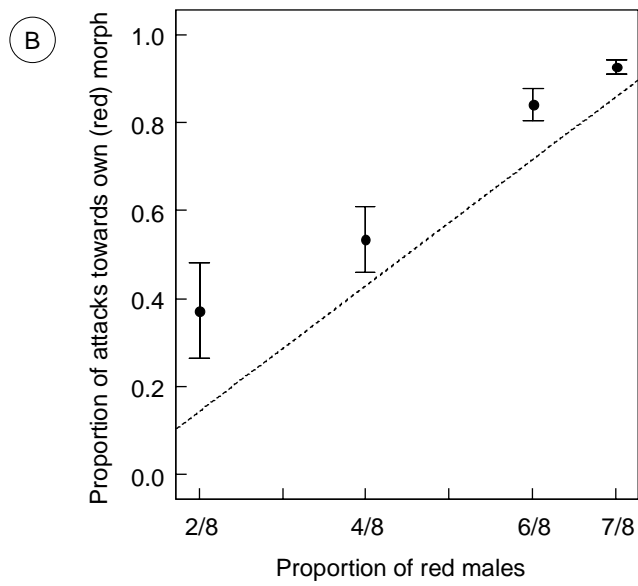
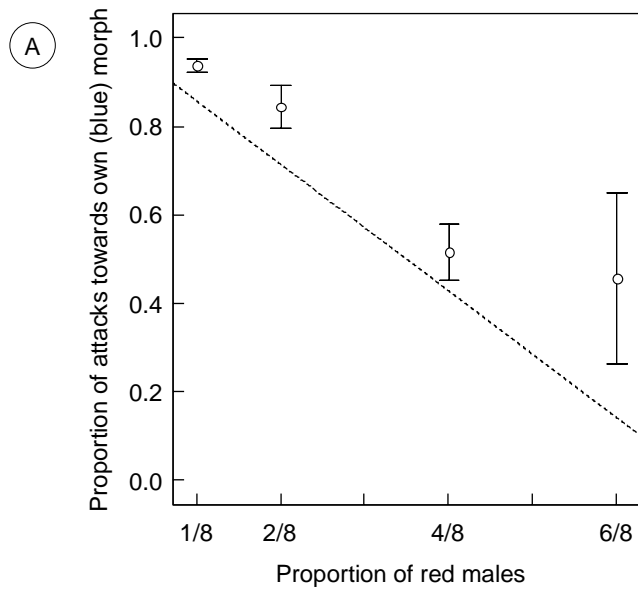
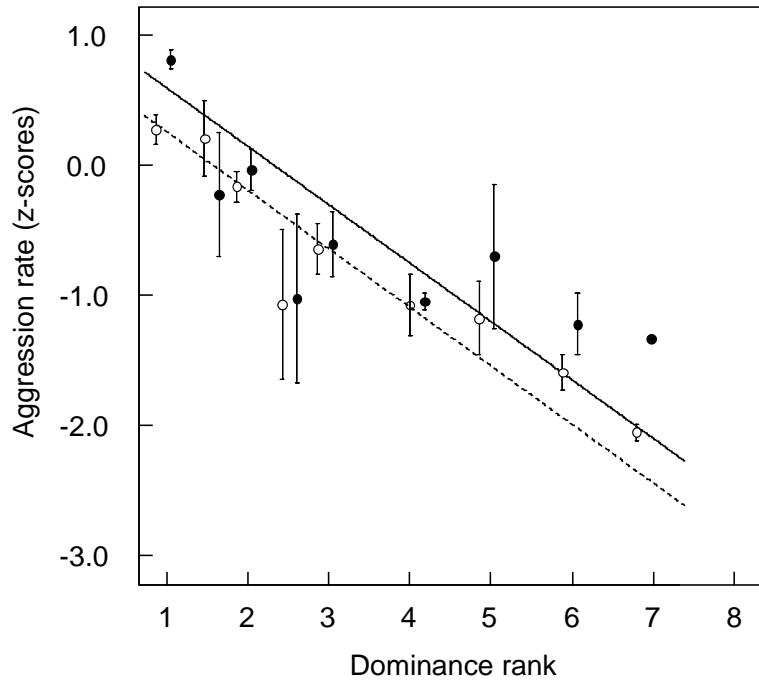


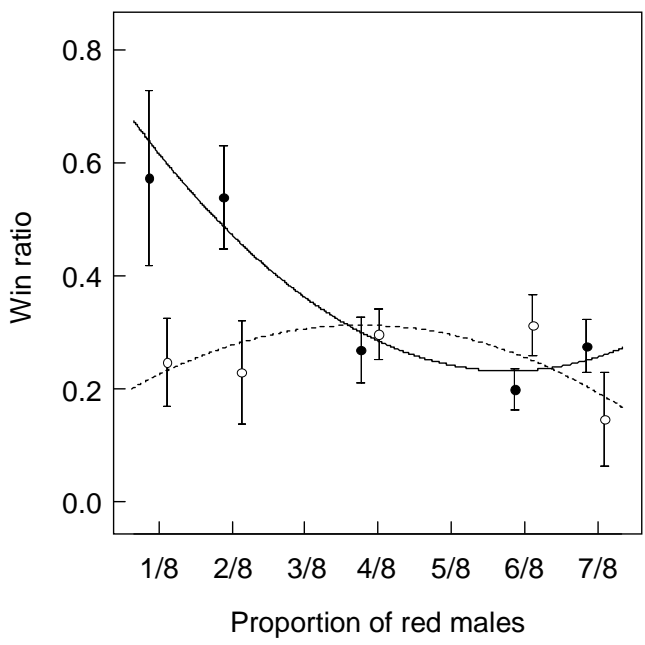
Figure 2



www Only

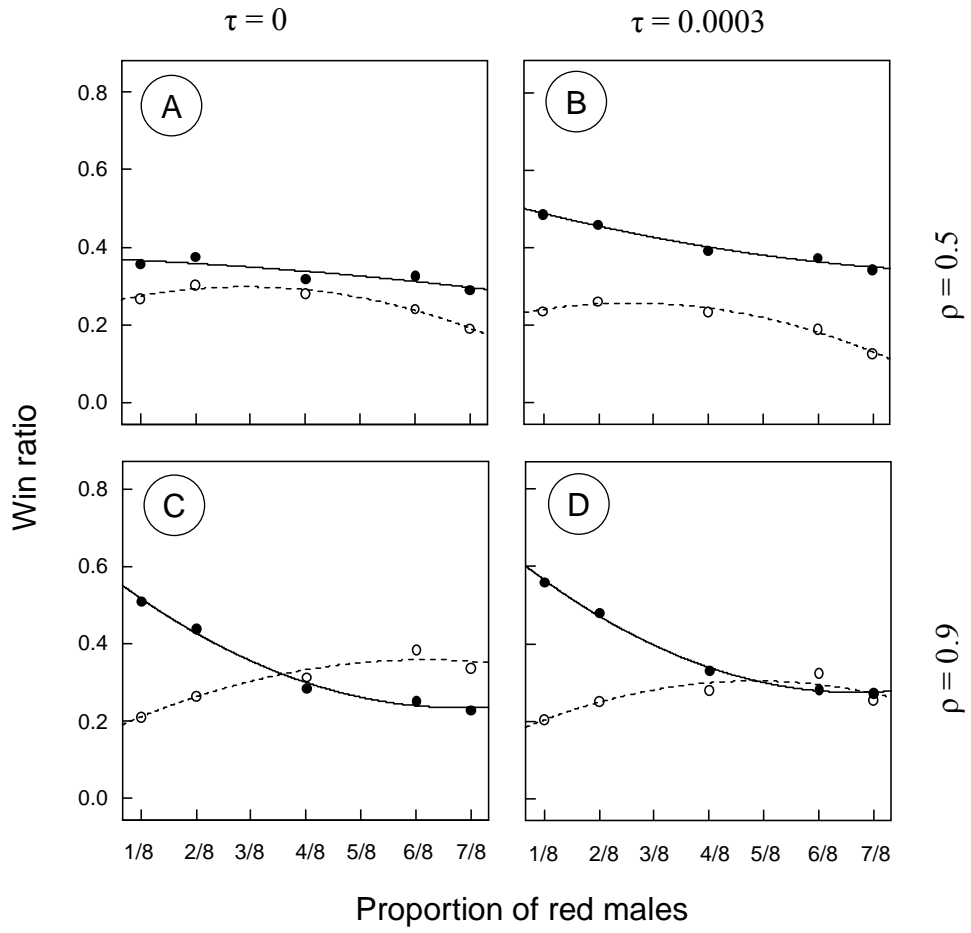
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure 3



W Only

Figure 4



Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 **1 Supplementary material**
4
5
6

7
8 3 An alternative method of estimating relative dominance is based on individual dyadic
9
10 4 relationships and is called the Average Dominance Index (Hemelrijk et al., 2005).
11
12 5 Here we show that we obtain similar results as compared to using the Win Ratio. We
13
14 6 calculated the Average Dominance Index for each individual and each day. To this
15
16 7 end we calculated for each male his Dominance Index (defined as the number of times
17
18 8 the individual won against a specific opponent, divided by the total number of fights
19
20 9 they engaged in) in relation to each community member he interacted with (maximum
21
22 10 7 opponents). We then took for that male the average of these values (Hemelrijk et al.
23
24 11 2005).
25
26
27
28

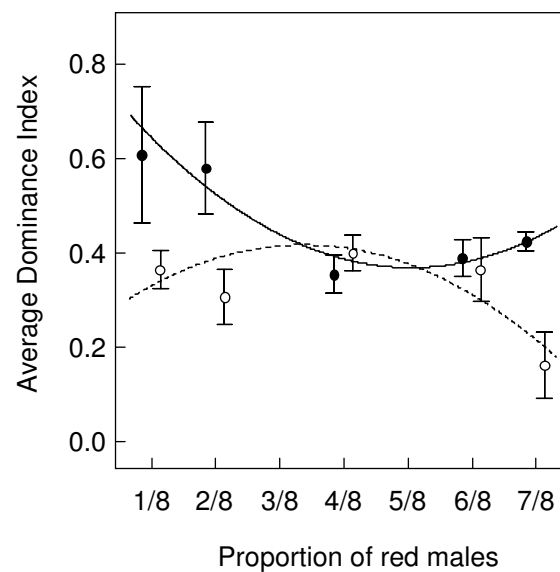
29 12 Following the analysis of the Win Ratio, we took the median Average
30
31 13 Dominance Index of blue and red males of each assemblage (the median because the
32
33 14 Average Dominance Index within assemblages were skewed). Figure S1 shows the
34
35 15 Average Dominance Index as a function of the proportion of red males and is very
36
37 16 similar to the pattern observed when using the Win Ratio (see figure 4 in main paper).
38
39 17 One exception is the 7/8 treatment where red males are doing far more better than
40
41 18 blue males, more so than in the analysis based on Win Ratios. This does however not
42
43 19 compromise our conclusions, but rather reinforces our main conclusion that the rare-
44
45 20 morph advantage is not symmetric but restricted to the red males.
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

22

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).

31



32