

How does agonistic behaviour differ in albino and pigmented fish?

Ondřej Slavík, Pavel Horký, Marie Wackermannová

In addition to hypopigmentation of the skin and red iris colouration, albino animals also display distinct physiological and behavioural alterations. However, information on the social interactions of albino animals is rare and has mostly been limited to specially bred strains of albino rodents and animals from unique environments in caves. Differentiating between the effects of albinism and domestication on behaviour in rodents can be difficult, and social behaviour in cave fish changes according to species-specific adaptations to conditions of permanent darkness. The agonistic behaviours of albino offspring of pigmented parents have yet to be described. In this study, we observed agonistic behaviour in albino and pigmented juvenile *Silurus glanis* catfish. We found that the total number of aggressive interactions was lower in albinos than in pigmented catfish. The distance between conspecifics was also analysed, and albinos showed a tendency towards greater separation from their same-coloured conspecifics compared with pigmented catfish. These results demonstrate that albinism can be associated with lower aggressiveness and with reduced schooling behaviour preference, as demonstrated by a tendency towards greater separation of albinos from conspecifics.

1 How does agonistic behaviour differ in albino and pigmented fish?

2 Ondřej Slavík,¹ Pavel Horký and Marie Wackermannová

3 Department of Zoology and Fisheries, Faculty of Agrobiology, Food and Natural Resources, Czech

4 University of Life Sciences Prague, Kamýcká 129, Prague 6, Suchdol 165 21, Czech Republic

5 Abstract

6 In addition to hypopigmentation of the skin and red iris colouration, albino animals also display
7 distinct physiological and behavioural alterations. However, information on the social
8 interactions of albino animals is rare and has mostly been limited to specially bred strains of
9 albino rodents and animals from unique environments in caves. Differentiating between the
10 effects of albinism and domestication on behaviour in rodents can be difficult, and social
11 behaviour in cave fish changes according to species-specific adaptations to conditions of
12 permanent darkness. The agonistic behaviours of albino offspring of pigmented parents have yet
13 to be described. In this study, we observed agonistic behaviour in albino and pigmented juvenile
14 *Silurus glanis* catfish. We found that the total number of aggressive interactions was lower in
15 albinos than in pigmented catfish. The distance between conspecifics was also analysed, and
16 albinos showed a tendency towards greater separation from their same-coloured conspecifics
17 compared with pigmented catfish. These results demonstrate that albinism can be associated with
18 lower aggressiveness and with reduced schooling behaviour preference, as demonstrated by a
19 tendency towards greater separation of albinos from conspecifics.

20 Running title: Aggressive behaviour in catfish

¹ Corresponding author's e-mail address: oslavik@af.czu.cz

21

22

23 **Introduction**

24 Albinism is generally the result of combinations of homozygous recessive mutations from
25 pigmented parents, and in particular, albinos are often unable to synthesize tyrosine and
26 melatonin hormones (Carden et al., 1998). This disability is not only associated with red irises
27 and light skin colouring (oculocutaneous albinism, OCA; Carden et al., 1998) but also with
28 physiological, behavioural and social alterations. Some of vertebrate albinisms are indeed
29 associated with increased levels of tyrosine and catecholamine accompanying with physiological
30 and behavioural changes that occur during adaptation to specific conditions in caves (Bilandžija
31 et al., 2013).

32 Information on the prevalence of terrestrial albino animals in the wild is primarily based on
33 reports, and information on social interactions between albinos is mostly limited to studies of
34 specially bred strains of albino rats, whose behaviour is strongly influenced by domestication
35 (Himmler et al., 2014). The eyes of albino rodents show reduced adaptation to light, often
36 leading to photoreceptor degradation (Prusky et al., 2002; Refinetti, 2007; Marc et al., 2008),
37 which in turn can cause loss of vision (Buhusi, Perera & Meck, 2005) and movement perception
38 (Hupfeld & Hoffmann, 2006), eventually leading to acrophobia and/or photophobia (Abeelen &
39 Kroes, 1967; Owen, Thiessen & Lindzey, 1970). Albino rodents have a poorer sense of smell
40 (Keeler, 1942) and display lower activity levels compared with pigmented conspecifics (Fuller,
41 1967; DeFries, 1969). In particular, their activity is low during the day and increases during the
42 night (Stryjek et al., 2013). Albino rats also spend longer periods in deep sleep (rapid eye

43 movement, REM), especially during the dark phase (Benca, Gilliland & Obermeyer, 1998), and
44 during the night, they sleep more often out of the nests relative to pigmented conspecifics
45 (Stryjek et al., 2013). Albino rats are slower to inhibit the fear response and explore new objects
46 (Pisula et al., 2012), and they are less effective in completing spatial tasks (Harker & Whishaw,
47 2002). For example, albino rats displayed higher hoarding activity (Rebouças & Schmidek,
48 1997), and they burrowed more slowly and constructed less complex systems of tunnels
49 compared with wild conspecifics (Stryjek, Modlińska & Pisula, 2012).

50 Furthermore, albino vertebrates can be found in water environments, and compared with
51 pigmented conspecifics, they display physiological and behavioural differences. For example,
52 blind tetra *Astyanax mexicanus* (De Filippi 1853) living in caves (Jeffery, 2001), compared with
53 the pigmented surface-dwelling form, display physiological adaptations to permanent darkness
54 and limited food availability, such as greater number of taste buds (Yamamoto et al., 2009) and
55 highly sensitive sensors in the lateral line (Yoshizawa et al., 2010; 2013; 2014. Such
56 physiological adaptations appear to have resulted in a decrease in the length of sleep (Duboué,
57 Keene & Borowsky, 2011), loss of shoaling behaviour (Kowalko et al., 2013), and an
58 evolutionary shift from fighting to food source searching, leading to the loss of hierarchy
59 dominance and aggressiveness (Elipot et al., 2013). On the contrary, blind albino catfish in caves
60 displayed agonistic behaviour (Parzefall & Trajano, 2010) likely reflecting their relatively large
61 body size and bottom-dwelling form associated with stronger competition for resources. For
62 example, the catfish *Pimelodella kronei* (Ribeiro 1907) showed a similar level of aggressiveness
63 to its pigmented and sighted ancestor *Pimelodella transitoria* (Ribeiro 1907; Trajano, 1991).

64 Albinism in catfish often occurs in surface waters as well (Dingerkus, Seret & Guilbert, 1991;
65 Britton & Davies 2006; Wakida-Kusunoki & Amador-del-Angel, 2013; Leal et al., 2013).

66 Slavík, Horký & Maciak, (2015) described the separation of albino *Silurus glanis* (Linnaeus
67 1758) catfish from a group of pigmented conspecifics. Irregularity of albinos in a group of
68 pigmented conspecifics means a guiding target for predators (Landeau & Terborgh, 1986;
69 Theodorakis, 1989), facilitating their hunting (Ellegren et al., 1997), and may be a reason for
70 exclusion of albinos from a group (Slavík, Horký & Maciak, 2015). However, it is not yet clear
71 whether albinism in animals is associated with alternative social behaviour, resulting in for
72 example, ostracism. A possible alternative behavioural display is a shift in aggression altering
73 e.g. between domesticated albino rodents and their wild ancestors and/or between troglobites and
74 their pigmented surface-dwelling counterparts. In the present study, we observed aggressiveness
75 in albino and pigmented catfish *Silurus glanis* from surface waters. Considering the generally
76 lower level of aggression observed in albino animals, we assumed that agonistic behaviour
77 would be lower in albinos than in pigmented conspecifics.

78 Materials & Methods

79 Albinism in catfish *Silurus glanis* L. 1758 has been commonly recorded in the wild (Dingerkus,
80 Seret & Guilbert, 1991), where catfish usually occur in groups (Boulêtreau et al., 2011). Only
81 juvenile catfish were used to reflect the behaviour of wild fish. These juveniles were spatially
82 separated from adults (Slavík et al., 2007), and showed complex social behaviours under the
83 experimental conditions (Slavík, Maciak & Horký, 2012; Slavík et al., 2016).

84 Experimental animals

85 The fish used in this experiment were hatchery-reared juvenile catfish. One shoal of pigmented
86 and one shoal of albino catfish that were unfamiliar to each other were obtained from local fish
87 suppliers (Czech Fishery Ltd., Rybářství Hluboká and Rybářství Třeboň, Czech Republic,

88 respectively). A total of 400 approximately equally sized fish (200 from each shoal) were
89 transported from the hatcheries to the laboratory at 4 months of age. The fish were transported
90 under stable conditions in oxygenated tanks in an air-conditioned loading space. Transport lasted
91 approximately 2 hours, and there were no observable effects on the health or mortality of the
92 fish.

93 The fish were maintained in 2 separate holding tanks (380 L each, initial density 1.9 kg m^{-3} ;
94 one shoal or 200 individuals per tank) for 8 weeks prior to the start of the experiment. The fish
95 were fed food pellets ad libitum (Biomar Group, Denmark,www.biomar.com) that were
96 distributed throughout the entire tank, providing free access to food to all individuals twice a
97 day. The fish were maintaining under a natural photoperiod, which was the same regime they
98 had become accustomed to in the hatchery. The water was purified using biological filters with
99 an integrated UV sterilizer (Pressure-Flo 5000, Rolf C. Hagen Inc., www.lagunaponds.com). The
100 water temperature and dissolved oxygen were controlled automatically (HOBO data logger;
101 Onset Computer Corporation, Bourne, Massachusetts, USA). Fish were measured (mean 103
102 mm; range 90 - 117 mm) and weighed (mean 10 g, range 6 - 15 g) at the end of the experiment
103 and removed to separate tanks to prevent mixing with unused conspecifics.

104 All experimental fish (400 individuals) survived. After the experiment, the fish were released
105 under the control of the Fish Management Authorities into fish ponds with extensive production
106 management.

107 Experimental design

108 The experiment was conducted in the laboratory between December 2013 and January 2014. A
109 pair of randomly selected individuals of the same colour was placed into a rectangular plastic
110 experimental arena (36 cm long, 18 cm wide, 20 cm high) at the beginning of each trial. The

111 arena was separated by a partition into two equal parts, and the individuals were placed on
112 opposite sides of the arena. After an acclimation period of 1 minute, the partition was removed
113 and the behaviour of the fish was recorded for 5 minutes using a digital camera (GoPro Hero,
114 GoPro, Inc., San Matteo, CA, USA). The arena was flushed out and filled with clean water after
115 every trial. In total, 40 trials (20 pairs of albinos and 20 pairs of pigmented individuals) were
116 conducted.

117 Data analysis

118 In the laboratory experiment, we tested two levels of aggressive interactions among juvenile
119 catfish, designated as aggressive or mobile displays (Lehtonen, 2014). Aggressive displays were
120 further subdivided into frontal and lateral displays, and mobile displays were further subdivided
121 into chasing and biting displays (Hsu & Wolf, 1999; Dijkstra et al., 2009). The sum of aggressive
122 interactions, referred to as ‘total aggression,’ was used in further analyses (Pauers et al., 2012).
123 The bottom of the experimental arena was divided into six equally sized squares (9×12 cm) that
124 were used in the analyses of ‘mutual distance.’ Mutual distance was set as a three level class
125 variable. A mutual distance equal to 1 meant that the individuals were in the ‘same zone,’
126 meaning that both conspecifics were in the same square. A mutual distance equal to 2 meant that
127 the individuals were in ‘adjacent zones,’ meaning that conspecifics were in adjacent squares. A
128 mutual distance equal to 3 meant that the individuals were in the ‘farthest zones,’ meaning that
129 there was one square between conspecifics. Variable ‘size difference’ was defined as the
130 difference between the weights of two interacting conspecifics in an experimental arena (mean
131 1.9 g; range 0 - 6 g). For the purpose of analysing the probability of occurrence of different types
132 of agonistic behaviour over time, a ‘time grid’ of 5 seconds was set. For every time grid value,
133 the probability of occurrence of a particular agonistic behaviour was recorded as 1 (behaviour

134 occurred) or 0 (behaviour did not occur). The EthoLog software program
135 (<http://www.ip.usp.br/docentes/ebuttoni/EthoLog/ethohome.html>) was used to assign the number
136 of particular agonistic behaviours as well as the ‘duration’ (in seconds) that conspecifics spent at
137 particular mutual distances.

138 Statistical analysis

139 Statistical analyses were performed using the SAS software package (version 9.2; SAS Institute
140 Inc., Cary, NC, USA). When necessary, the data were square root transformed to meet normality
141 requirements.

142 Total aggression and duration were analysed using mixed models with random factors (PROC
143 GLIMMIX with Poisson distribution for total aggression and PROC MIXED with normal
144 distribution for duration). Random factors were used to account for repeated measures collected
145 for the same experimental units (pair of conspecifics) across the duration of the experiment. The
146 significance of each exploratory variable (i.e., fixed effects, including their interactions) in the
147 particular model was assessed using an F-test in which we sequentially dropped the least
148 significant effect, beginning with the full model (backward selection procedure). Least-squares
149 means (LSM), henceforth referred to as “adjusted means,” were computed for class variables.
150 The differences between the classes were tested using a t-test, and a Tukey–Kramer adjustment
151 was used for multiple comparisons. The degrees of freedom were calculated using the Kenward–
152 Roger method (Kenward & Roger, 1997).

153 The probabilities of occurrence for particular agonistic behaviours were analysed using the
154 generalized estimating equation (GEE) approach (Liang & Zeger, 1986) for categorical, repeated
155 measurements using the GENMOD procedure with binomial distributions. This approach is an

156 extension of generalized linear models that provides a semi-parametric approach to longitudinal
157 data analysis. In this study, four separate GENMOD procedures were designed to estimate the
158 probability of occurrence of particular agonistic behaviours (i.e., chasing, biting, frontal and
159 lateral displays) across the duration of the experiment.

160 **Ethics statement**

161 All of the laboratory experimental procedures were in compliance with valid legislative
162 regulations (law no. 246/1992, §19, art. 1, letter c). The permit was granted to O. Slavík,
163 according to Law no. 246/1992, §17, art. 1; permit no. CZ00167. All laboratory samplings were
164 conducted with the permission of the Departmental Expert Committee for Authorization of
165 Experimental Projects of the Ministry of Education, Youth and Sports of the Czech Republic
166 (permit no. MSMT-31220/2014-6). This study did not involve endangered or protected species.

167

168 **Results**

169 In total, we observed 1208 aggressive interactions, 68% of which were classified as lateral
170 displays, 16% as frontal displays, 11% as chasing displays and 5% as biting. The total number of
171 aggressive interactions was lower in the albino group ($F_{1, 110.6}=14.51$, $P<0.0002$; Fig. 1). In
172 addition, the probability of chasing ($\chi^2=6.64$, d.f.=2; $P<0.0362$; Fig. 2a) and lateral display
173 ($\chi^2=6.04$, d.f.=2; $P<0.0488$; Fig. 2b) changed over time and differed between groups. In the
174 albino group, the probability of chasing decreased over time, whereas the probability of lateral
175 display did not show any significant trend. In the pigmented group, the probability of chasing
176 also decreased over time, whereas the probability of lateral display sharply increased. In neither
177 group did the probability of frontal display or biting vary significantly over time. The results

178 indicated that albinos were less aggressive compared with their pigmented conspecifics, which
179 was primarily due to a higher probability of lateral display behaviours in the pigmented group.

180 Furthermore, the time that conspecifics spent at a particular distance from other conspecifics
181 varied in both groups ($F_{5, 111}=29.43$, $P<0.0001$; Fig. 3). While the catfish (both albino and
182 pigmented) generally spent the least amount of time in the farthest zones (time spent in the
183 farthest zones did not differ between albino and pigmented catfish), albinos spent more time in
184 adjacent zones and less time in the same zones than pigmented conspecifics (Adj. $P<0.05$).
185 Taken together, we found that albino catfish showed a higher tendency to be spatially separated
186 from conspecifics, whereas pigmented catfish showed a tendency towards close contact.

187

188 **Discussion**

189 The assumption that albinism is associated with different levels of aggression is supported by
190 this study. In particular, our results support the theory that species with different levels of
191 colouration should display different levels of aggression (Pryke & Griffith, 2006) and that the
192 level of aggression should correspond to different colour morphs (Pryke, 2009; Dijkstra et al.,
193 2009). Indeed, one colour morph is often predicted to be more aggressive than others (Dijkstra et
194 al., 2010). Our results are also consistent with recent findings showing that albinism has
195 pleiotropic effects that are mediated through hormones that can affect both skin pigmentation
196 and aggressive behaviour (Gonzales, Varizi & Wilson, 1996; Ducrest, Keller & Roulin, 2008).
197 As reported by Horth (2003), increases in the aggression of the melanic form of mosquitofish
198 correlate with changes in melanin synthesis. Therefore, albinism, in contrast to melanism, may
199 be generally associated with lower aggression due to shared genetic control mechanisms.

200 Comparison of the pigmented and albino forms of *Silurus glanis* revealed lower aggressiveness
201 in albinos. Loss of aggressive behaviour has been reported for albinos living in caves (Eliot et
202 al., 2013), and this relationship tend to be related to species-specific adaptations to unique
203 environmental conditions. For example, most of the populations of the blind albino tetra *A.*
204 *mexicanus* have lost aggressiveness, whereas individuals of the pigmented surface-dwelling form
205 blinded in an early ontogenetic stage remain aggressive at the same level as their sighted parents
206 (Espinasa, Yamamoto & Jeffery, 2005). Blind albino catfish in caves displayed similar
207 aggressiveness to their sighted surface ancestors (Trajano, 1991). According to Espinasa,
208 Yamamoto & Jeffery (2005), aggressive behaviour is activated by non-optical releasers, and the
209 reduction of aggressiveness is not the exclusive evolutionary pathway for blind albino
210 troglobites. Loss of vision in albino cavefish *A. mexicanus* is accompanied by the development
211 of non-visual sensors, such as neuromasts along the lateral line (Yoshizawa et al., 2010; 2013;
212 2014). Similarly, catfish are not typical visual predators such as salmonids (Valdimarsson &
213 Metcalfe, 2001), but are adapted to prey detection in lowland rivers with a high level of turbidity,
214 where prey are often hunted during flash floods (Slavík et al., 2007). Six robust tactile bristles
215 are used for prey detection in these catfish, and with the aid of highly sensitive lateral line, the
216 species can detect hydrodynamic traces as long as 10 seconds after the passage of prey
217 (Pohlmann, Grasso & Breithaupt, 2001). Provided that the vision of pigmented catfish does not
218 represent the main tool for prey detection, it can be inferred that its role in the aggressive
219 behaviour of albino catfish *S. glanis* is also minor. Although it can be assumed that albino catfish
220 from surface waters are able to see, their vision may be impaired. Accordingly, albinism in mice
221 has been correlated with acrophobia, photophobia and lower visual acuity (Owen, Thiessen &
222 Lindzey, 1970; Prusky et al., 2002; Buhusi, Perera & Meck, 2005). Moreover, specially bred

223 strains of albino rats (Sprague-Dawley) displayed a higher probability of playful attacks
224 compared with wild-type pigmented strains (Himmler et al., 2014). The behaviour of this
225 Sprague-Dawley strain, however, was also different from other albino strains. Interestingly, the
226 authors attributed these differences to differing levels of domestication in each of the strains.
227 Playful attacks are associated not only with domestication (see review Himmler et al., 2014) but
228 also with reduced aggression, as albino rats are less aggressive than their wild-type pigmented
229 counterparts (Barnett, Dickson & Hocking, 1979; Barnett, 1981). Although a direct comparison
230 between aggressiveness in catfish and rats is not possible, we speculate that albinism may be
231 generally associated with lower aggression compared with normally pigmented conspecifics.

232 Aggression is also associated with social position or rank (Mazur & Booth, 1998; Staffan,
233 Magnhagen & Alanärä, 2002). For example, an albino female vampire bat *Desmodus rotundus*
234 bred with pigmented individuals hold the lowest social position (Uieda, 2001). Hence, albinism
235 may be associated with not only lower aggressiveness but also lower dominance, as these
236 characteristics are often correlated (Dijkstra, Seehausen & Groothuis, 2005; Pryke & Griffith,
237 2006). Indeed, consistent with this idea, ostracism of albino catfish by a group of pigmented
238 conspecifics has been described (Slavík, Horký & Maciak, 2015), and the low ability of albinos
239 to remain within a group may be another reason for the high predation risk in albinos (Ellegren et
240 al., 1997).

241 Albino catfish also showed a greater tendency towards spatial separation compared with their
242 pigmented conspecifics, which preferred to be nearer to one another. This finding differs from
243 what was observed in domesticated albino rats, which were found to be more tolerant of
244 conspecifics compared with wild-type strains (Himmler et al., 2013; 2014). Indeed, colour-
245 assortative shoaling is often observed (McRobert & Bradner, 1998; Spence & Smith, 2006;

246 Goméz-Laplaza, 2009; Rodgers, Kelley & Morell, 2010). Considering the fact that albino catfish
247 are unable to darken their body colour to avoid aggressive interactions with dominant
248 conspecifics (O'Connor, Metcalfe & Taylor, 1999; Höglund, Balm & Winberg, 2000), spatial
249 separation may be a strategy for avoiding the escalation of aggressive behaviours. On the other
250 hand, if albino catfish have poor vision, then their low tendency towards grouping may be a
251 result of this weakened physiological condition. Accordingly, blind cave fish displayed loss of
252 schooling behaviour (Parzefall & Trajano, 2010; Kowalko et al., 2013). In the case of troglobites,
253 however, a low tendency towards grouping is considered to represent an evolutionary adaptation
254 to sparse prey and low food availability, conditions where life in a group is not beneficial to
255 better foraging activity such as it is in surface waters (Griffith et al., 2004; Ward & Hart, 2005).
256 Large numbers of albinos existing together in the wild has only been reported in insects (Hoste et
257 al., 2003), and whether albinos are mutually attracted to each other and form larger groups in
258 nature remains unknown.

259

260 **Conclusions**

261 Similarities to the shift in the behaviour of albino catfish towards lower aggressiveness can be
262 found in domesticated albino rodents and their wild pigmented counterparts as well as between
263 blind cave fish and their sighted ancestors from surface waters. Therefore, loss of pigmentation
264 may not only be linked to aggression in albinos, but also have other pleiotropic effects that can
265 be observed, for example, as impaired eyesight in surface environments and/or specie-specific
266 evolutionary adaptations to conditions of permanent darkness. In addition, albinos were found to

267 maintain greater distances between themselves compared with pigmented individuals in the
268 present study, corresponding to the loss of schooling behaviour in blind cave fish.

269

270 **Acknowledgements**

271 The authors sincerely thank Sergio Pellis, Tobias Backström and the anonymous referee for
272 critical evaluation and valuable comments on the manuscript. In addition, the authors wish to
273 thank A. Slavikova for the help with earlier versions of the manuscript.

274

275 **References**

- 276 **Abeelen van JHF, Kroes WH. 1967.** Albinism and mouse behaviour. *Genetica* **38**:419-429.
- 277 **Barnett SA, Hocking WE. 1981.** Further experiments on the social interactions of domestic
278 „Norway“ rats. *Aggressive Behavior* **7**:259-263.
- 279 **Barnett S A, Dickson RG, Hocking WE. 1979.** Genotype and environment in the social
280 interactions of wild and domestic „Norway“ rats. *Aggressive Behaviour* **5**:105-119.
- 281 **Benca RM, Gilliland MA, Obermeyer WH. 1998.** Effects of lighting conditions on sleep and
282 wakefulness in albino Lewis and pigmented Brown Norway rats. *Sleep* **21**:451-460.
- 283 **Bilandžija H, Ma L; Parkhurst A, Jeffery WR. 2013.** A potential benefit of albinism in
284 *Astyanax* cavefish: Downregulation of the *oca2* gene increases tyrosine and
285 catecholamine levels as an alternative to melanin synthesis. *PloS ONE* **8**: e80823. DOI:
286 10.1371/journal.pone.0080823

- 287 **Boulêtreau S, Cucherousset J, Villéger S, Masson R, Santoul F. 2011.** Colossal aggregations
288 of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS ONE* **6**:
289 e25732.
- 290 **Britton JR, Davies GD. 2006.** First record of the white catfish *Ameiurus catus* in Great Britain.
291 *Journal of Fish Biology* **69**: 1236-1238, DOI: 10.1111/j.1095-8649.2006.01171.x
- 292 **Buhusi CV, Perera D, Meck WH. 2005.** Memory for timing and auditory signals in albino and
293 pigmented rats. *Journal of Experimental Psychology - Animal Behaviour* **31**:18-30, DOI:
294 10.1037/0097-7403.31.1.18
- 295 **Carden SM, Boissy RE, Schoettker PJ, Good WV. 1998.** Albinism: modern molecular
296 diagnosis. *British Journal of Ophthalmology* **82**:189–1995.
- 297 **DeFries JC. 1969.** Pleiotropic effects of albinism on open field behaviour in mice. *Nature*
298 **221**:65-66.
- 299 **Dijkstra PD, Seehausen O, Groothuis TGG. 2005.** Direct male-male competition can facilitate
300 invasion of new colour types in Lake Victoria cichlids. *Behaviour Ecology and Socio-*
301 *biology* **58**:136-143, DOI: 10.1007/s00265-005-0919-5
- 302 **Dijkstra PD, Hemelrijk CK, Seehausen O, Groothuis TGG. 2009.** Colour polymorphism
303 reduces intrasexual selection in assemblages of cichlid fish. *Behaviour Ecology* **20**:138-
304 144.
- 305 **Dijkstra PD, Lindström J, Metcalfe NB, Hemelrijk CK, Brendel M, Seehausen O,**
306 **Groothuis TGG. 2010.** Frequency-dependent social dominance in a color polymorphic
307 cichlid fish. *Evolution* **64**:2797-2807, DOI: 10.1111/j.1558-5646.2010.01046.x

- 308 **Dingerkus G, Seret B, Guilbert E.** 1991. The first albino wels, *Silurus glanis* Linnaeus, 1758,
309 from France, with a review of albinism in catfishes (Teleostei: Siluriformes). *Cybium*
310 **15:**185-188.
- 311 **Duboué ER, Keene AC, Borowsky RL.** 2011. Evolutionary convergence on sleep loss in
312 cavefish populations. *Current Biology* **21:** 671-676. DOI: 10.1016/j.cub.2011.03020
- 313 **Ducrest A-L, Keller L, Roulin A.** 2008. Pleiotropy in the melanocortin system, coloration and
314 behavioural syndromes. *Trends in Ecology and Evolution* **23:**502-510.
- 315 **Ellegren H, Lindgren G, Primmer RC, Møller PA.** 1997. Fitness loss and germline mutations
316 in barn swallows breeding in Chernobyl. *Nature* **389:** 593-596.
- 317 **Elipot Y, Hinaux H, Callebert J, Rétaux S.** 2013. Evolutionary shift from fighting to foraging
318 in blind cavefish through changes in the serotonin network. *Current Biology* **23:** 1-10,
319 DOI: 10.1016/j.cub.2012.10.044
- 320 **Espinasa L, Yamamoto Y, Jeffery RW.** 2005. Non-optical releasers for aggressive behaviour
321 in blind and blinded *Astyanax* (Teleostei, Characidae). *Behavioural Processes* **70:** 144-
322 148, DOI:10.1016/j.beproc.2005.06.003
- 323 **Fuller LJ.** 1967. Effects of the albino gene upon behaviour of mice. *Animal Behaviour* **15:**467-
324 470. [http://dx.doi.org/10.1016/0003-3472\(67\)90045-0](http://dx.doi.org/10.1016/0003-3472(67)90045-0)
- 325 **Goméz-Laplaza ML.** 2009. Recent social environment affects colour-assortative shoaling in
326 juvenile angelfish (*Pterophyllum scalare*). *Behavioural Processes* **82:**39–44.
- 327 **Gonzales MI, Varizi S, Wilson CA.** 1996. Behavioural effects of a -MSH and MCH after
328 central administration in female rat. *Peptides* **17:**171-177.

- 329 **Griffith SW, Brockmark S, Höjesjö J, Johnsson IJ.** 2004. Coping with divided attention: the
330 advantage of familiarity. *Proceedings of the Royal Society of London B* **271**: 695-
331 699.**Harker KT, Whishaw IQ.** 2002. Place and matching-to-place spatial learning
332 affected by rat inbreeding (Dark-Agouti, Fischer 344) and albinism (Wistar, Sprague-
333 Dawley) but no domestication (wild rat vs. Long-Evans, Fischer-Norway). *Behavioural*
334 *Brain Resources* **134**:467-477.
- 335 **Harker KT, Whishaw IQ.** 2002. Place and matching-to-place spatial learning affected by rat
336 inbreeding (Dark-Agouti, Fischer 344) and albinism (Wistar, Sprague-Dawley) but no
337 domestication (wild rat vs. Long-Evans, Fischer-Norway). *Behavioural Brain Resources*
338 **134**:467-477.
- 339 **Himmler BT, Derksen SM, Stryjek R, Modlinska K, Pisula W, Pellis SM.** 2013. How
340 domestication modulates play behaviour: a comparative analysis between wild rats and a
341 laboratory strain of *Rattus norvegicus*. *Journal of Comparative Psychology* **127**:453-464.
- 342 **Himmler, SM, Modlinska K, Stryjek R, Himmler BT, Pisula W, Pellis SM.** 2014.
343 Domestication and diversification: a comparative analysis of the play fighting of the
344 Brown Norway, Sprague-Dawley, and Wistar Laboratory strains of (*Rattus norvegicus*).
345 *Journal of Comparative Psychology*, DOI:10.1037/a0036104.
- 346 **Höglund E, Balm PHM, Winberg S.** 2000. Skin darkening a potential social signal in
347 subordinate Arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and
348 pro-opiomelanocorticon-derived peptides. *Journal of Experimental Biology* **203**:1711-
349 1721.

- 350 **Horth L. 2003.** Melanic body-color and aggressive mating behaviour are correlated traits in
351 male mosquitofish, (*Gambusia holbrooki*). *Proceedings of the Royal Society of London*
352 *Series B* **270**:1033-1040.
- 353 **Hoste B, Simpson SJ, DeLoof A, Breuer M. 2003.** Behavioural differences in *Locusta*
354 *migratoria* associated with albinism and their relation to [His⁷]-corazonin. *Physiology &*
355 *Entomology* **28**:32-38.
- 356 **Hsu Y, Wolf LL. 1999.** The winner and looser effect: integrating multiple experiences. *Animal*
357 *Behaviour* **57**:903-910.
- 358 **Hupfeld D, Hoffmann K-P. 2006.** Motion perception in rats (*Rattus norvegicus* sp.): deficits in
359 albino Wistar rats compared to pigmented Long-Evans rats. *Behavioural Brain Resources*
360 **170**:29–33, DOI: 10.1016/j.bbr.2006.01.022
- 361 **Jeffery RW. 2001.** Cavefish as a model system in evolutionary developmental biology.
362 *Developmental Biology* **291**: 1-12.
- 363 **Keeler CA. 1942.** The association of the black (non-agouti) gene with behaviour in the Norway
364 rat. *Journal of Heredity* **33**:371-384.
- 365 **Kenward MG, Roger JH. 1997.** Small sample inference for fixed effects from restricted
366 maximum likelihood. *Biometrics* **53**:983–997.
- 367 **Kowalko EJ, Rohner N, Rompani BS, Peterson KB, Weber J, Hoekstra EH, Jeffery RW,**
368 **Borowsky R, Tabin JC. 2013.** Loss of schooling behaviour in cavefish through sight-
369 dependent and sight-independent mechanism. *Current Biology* **23**: 1874-1883, doi:
370 10.1016/j.cub.2013.07.056

- 371 **Landeau L, Terborgh J.** 1986. Oddity and the 'confusion effect' in predation. *Animal Behaviour*
- 372 **34:** 1372-1380.
- 373 **Leal ME, Schulz UH, Albornoz PL, Machado R, Ott PH.** 2013. First Record of Partial
- 374 Albinism in two Catfish Species of Genidens (Siluriformes: Ariidae) in an Estuary of
- 375 Southern Brazil. *Brazilian Archives of Biology and Technology* **56:** 237-240.
- 376 **Lehtonen TK.** 2014. Colour biases in territorial aggression in a Neotropical cichlid fish.
- 377 *Oecologia* **175:** 85-93, DOI: 10.1007/s00442-013-2879-1
- 378 **Liang KY, Zeger SL.** 1986. Longitudinal data analysis using generalized linear models.
- 379 *Biometrika* **73:**13–22.
- 380 **Marc RE, Jones BW, Watt CB, Vazquez-Chona F, Vaughan DK.** 2008. Extreme retinal
- 381 remodelling triggered by light damage: implications for age related macular
- 382 degeneration. *Molecular Vision* **14:**782-806.
- 383 **Mazur A, Booth A.** 1998. Testosterone and dominance in men. *Behavioural Brain. Science*
- 384 **21:**353-397.
- 385 **McRobert PS, Bradner J.** 1998. The influence of body coloration on shoaling preference in
- 386 fish. *Animal Behaviour* **56:**611–615.
- 387 **O'Connor KL, Metcalfe NB, Taylor AC.** 1999. Does darkening signal submission in territorial
- 388 contest between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour* **58:**1269–
- 389 1276.
- 390 **Owen K, Thiessen DD, Lindzey G.** 1970. Acrophobic and photophobic responses associated
- 391 with the albino locus in mice. *Behavior Genetics* **1:**249–255.

- 392 **Parzefall J, Trajano E.** 2010. *Behavioral Patterns in Subterranean Fishes*. pp 81-114, In:
393 Trajano E, Bichuette ME, Kapoor BG (Eds.) *Biology of Subterranean Fishes*. Science
394 Publishers, Enfield, NH.
- 395 **Pauers MJ, Kapfer JM, Doehler K, Lee TJ, Berg CS.** 2012. Gross colour pattern is used to
396 distinguish between opponents during aggressive encounters in a Lake Malawi cichlid.
397 *Ecology of Freshwater Fish* **21**:34–41, DOI: 10.1111/j.1600-0633.2011.00520.x
- 398 **Pisula W, Turlejski K, Stryjek R, Nalecy-Tolak A, Grabiec M, Djavadian RL.** 2012.
399 Response to novelty in the laboratory Wistar rat wild-captive WWCPS rat, and the grey
400 short-tailed opossum (*Monodelphis domestica*). *Behavioural Processes* **91**:145-151.
- 401 **Pohlmann K, Grasso FW, Breithaupt T.** 2001. Tracking wakes: the nocturnal predatory
402 strategy of piscivorous catfish. *Proceedings of the National Academy of Sciences of the*
403 *United States of America* **98**: 7371-7374.
- 404 **Prusky GT, Harker KT, Douglas MR, Whishaw IQ.** 2002. Variation in visual acuity within
405 pigmented, and between pigmented and albino rat strains. *Behavioural Brain Research*
406 **136**:339–348.
- 407 **Pryke SR.** 2009. Is red an innate or learned signal of aggression and intimidation? *Animal*
408 *Behaviour* **78**:393-398, DOI: 10.1016/j.anbehav.2009.05.013
- 409 **Pryke SR, Griffith SC.** 2006. Red dominants black: agonistic signalling among head morphs in
410 the colour polymorphic Gouldina finch. *Proceedings of the Royal Society of London*
411 *Series B* **273**:949-957, DOI: 10.1098/rspb.2005.3362.
- 412 **Rebouças RCR, Schmidek RW.** 1997. Handling and isolation in three strains of rats affect open
413 field, exploration, hoarding and predation. *Physiology & Behaviour* **62**:1159-1164.

- 414 **Refinetti R.** 2007. Enhanced circadian photoresponsiveness after prolonged dark adaptation in
415 seven species of diurnal and nocturnal rodents. *Physiology & Behaviour* **90**:431-437.
- 416 **Rodgers MG, Kelley LJ, Morell JL.** 2010. Colour change and assortment in the western
417 rainbowfish. *Animal Behaviour* **79**:1025–1030, DOI: 10.1016/j.anbehav.2010.01.017
- 418 **Slavík O, Horký P, Bartoš L, Kolářová J, Randák T.** 2007. Diurnal and seasonal behaviour of
419 adult and juvenile European catfish as determined by radio-telemetry in the River
420 Berounka, Czech Republic. *Journal of Fish Biology* **71**:104–114.
- 421 **Slavík O, Maciak M, Horký P.** 2012. Shelter use of familiar and unfamiliar groups of juvenile
422 European catfish *Silurus glanis*. *Applied Animal Behaviour Science* **142**:116–123.
- 423 **Slavík O, Horký P, Maciak M.** 2015. Ostracism of an albino individual by a group of
424 pigmented catfish. *PLoS ONE*, DOI:10.1371/journal.pone.0128279
- 425 **Slavík O, Horký P, Maciak M, Wackermannová M.** 2016. Familiarity, prior residency,
426 resource availability and body mass as predictors of the movement activity of the
427 European catfish. *Journal of Ethology* **34**: 23-30, DOI 10.1007/s10164-015-0441-9
- 428 **Spence R, Smith C.** 2006. The role of early learning in determining shoaling preferences based
429 on visual cues in the Zebrafish, *Danio rerio*. *Ethology* **113**:62–67, DOI: 10.1111/j.1439-
430 0310.2006.01295.x
- 431 **Staffan F, Magnhagen C, Alanärä A.** 2002. Variation in food intake within groups of juvenile
432 perch. *Journal of Fish Biology* **60**:606–614.
- 433 **Stryjek R, Modlińska K, Pisula W.** 2012. Species specific behavioural patterns (digging and
434 swimming) and reaction to novel objects in wild type, Wistar, Sprague-Dawley and
435 Brown Norway rats. *PLoS ONE* **7**:e40642, DOI: 10.1371/journal.pone.0040642

- 436 **Stryjek R, Modlińska K, Turlejski K, Pisula W.** 2013. Circadian rhythm of outside-nest
437 activity in wild (WWCPS), albino and pigmented laboratory rats. *PLoS ONE* **8**:
438 e66055.doi:10.1371/journal.pone.0066055
- 439 **Theodorakis ChW, 1989.** Size segregation and effects of oddity on predation risk in minnow
440 schools. *Animal Behaviour* **38**: 496-502.
- 441 **Trajano E. 1991.** The agonistic behaviour of *Pimelodella kronei*, a troglobitic catfish from
442 Southeastern Brazil (Siluriformes, Pimelodidae). *Behavioural Processes* **23**:113-124.
- 443 **Uieda W. 2001.** Behavior of an albino vampire bat, *Desmodus rotundus* (E. Geoffroy)
444 (Chiroptera, Phyllostomatidae), in captivity. *Revista Brasiliera de Zoologica* **18**:641–
445 644. <http://dx.doi.org/10.1590/S0101-81752001000200031>
- 446 **Valdimarsson SK, Metcalfe NB. 2001.** Is the level of aggression and dispersion in territorial
447 fish dependent on light intensity? *Animal Behaviour* **61**:1143-1149, DOI:
448 10.1006/anbe.2001.1071
- 449 **Wakida-Kusunoki AT, Amador-del-Angel LE. 2013.** First record of albinism in gafftopsail
450 catfish *Barge marinus* (Pisces: Ariidae) from southeast Mexico. *Revista de Biologia
451 Marina Y Oceanografia* **48**: 203-206.
- 452 **Ward AJW, Hart P JB. 2005.** Foraging benefits of shoaling with familiars may be exploited by
453 outsiders. *Animal Behaviour* **69**: 329–335.
- 454 **Yamamoto Y, Byerly MS, Jackman WR, Jeffery WR. 2009.** Pleiotropic function of
455 embryonic sonic hedgehog expression link jaw and taste bud amplification with eye loss
456 during cavefish evolution. *Developmental Biology* **330**:200-211

457 **Yoshizawa M, Gorički Š, Soares D, Jeffery RW. 2010.** Evolution of a behavioural shift
458 mediated by superficial neuromasts helps cavefish find food in darkness. *Current Biology*
459 **20:** 1631-1636 doi: 10.1016/j.cub.2010:07.017

460 **Yoshizawa M, O'Quin EK, Jeffery RW. 2013.** Evolution of an adaptive behaviour and its
461 sensory receptors promotes eye regression in blind cavefish: response to Borowsky
462 (2013). *BMS Biology* **11**:82.

463 **Yoshizawa M, Jeffery RW, Netten van MS, McHenry JM. 2014.** The sensitivity of lateral line
464 receptors and their role in the behaviour of Mexican blind cavefish (*Astyanax*
465 *mexicanus*). *Journal of Experimental Biology* **217**:886-895 DOI: 10.1242/jeb.094599

466

467 **Figure legends**

468 Fig. 1: Total number of aggressive interactions (adjusted means \pm SE) across albino and
469 pigmented treatments. Significant differences are indicated (*; Tukey–Kramer adjusted
470 $P<0\cdot0002$).

471 Fig. 2: Probability of chasing (a) and lateral display (b) as a function of time across the two
472 treatments. Dotted line = albino catfish; black line = pigmented catfish.

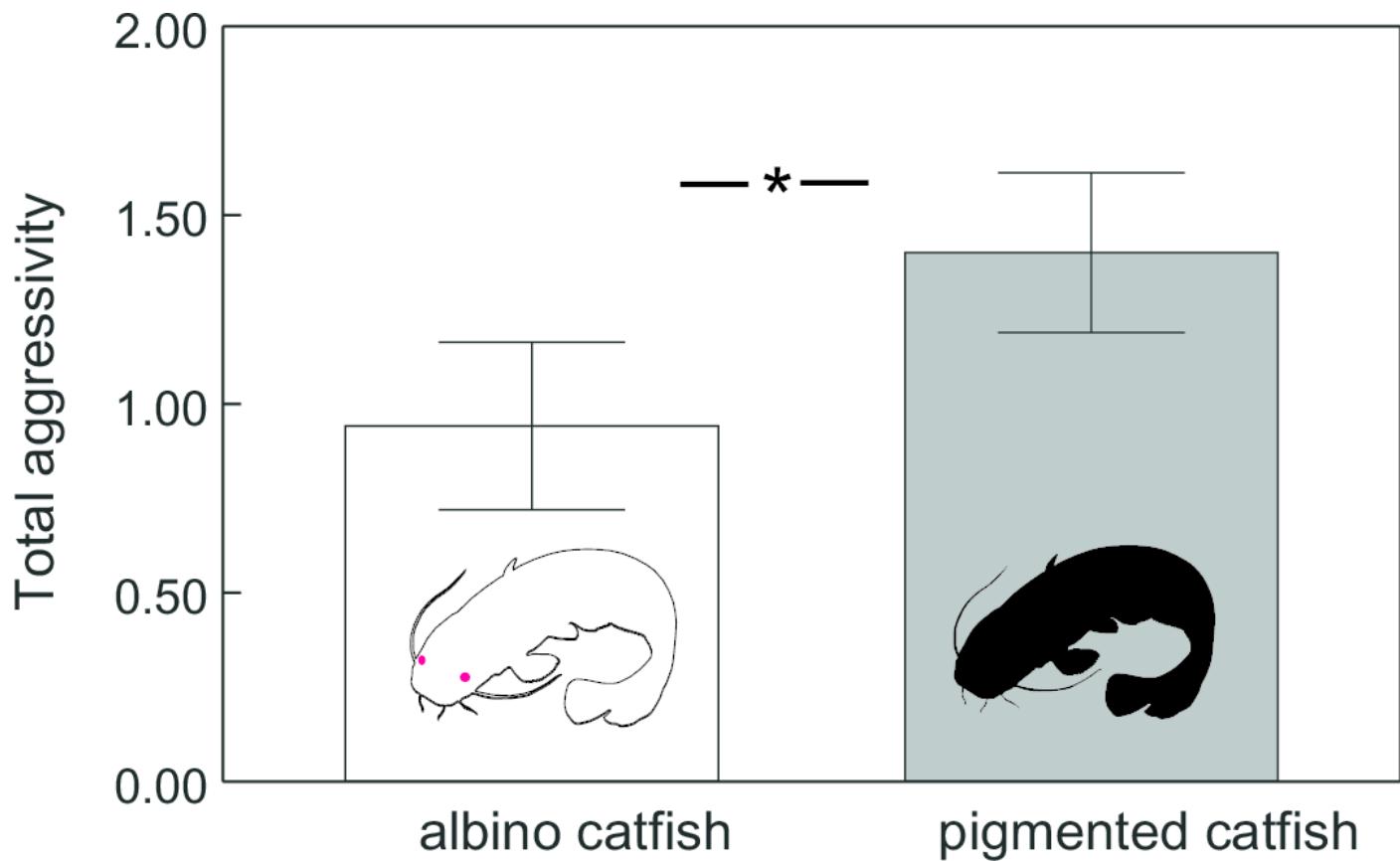
473 Fig. 3: Duration (adjusted means \pm SE of square root data) of time that conspecifics spent at
474 particular mutual distances across albino and pigmented treatments. Significant
475 differences are indicated (*; Tukey–Kramer adjusted $P<0\cdot05$).

476

477

1

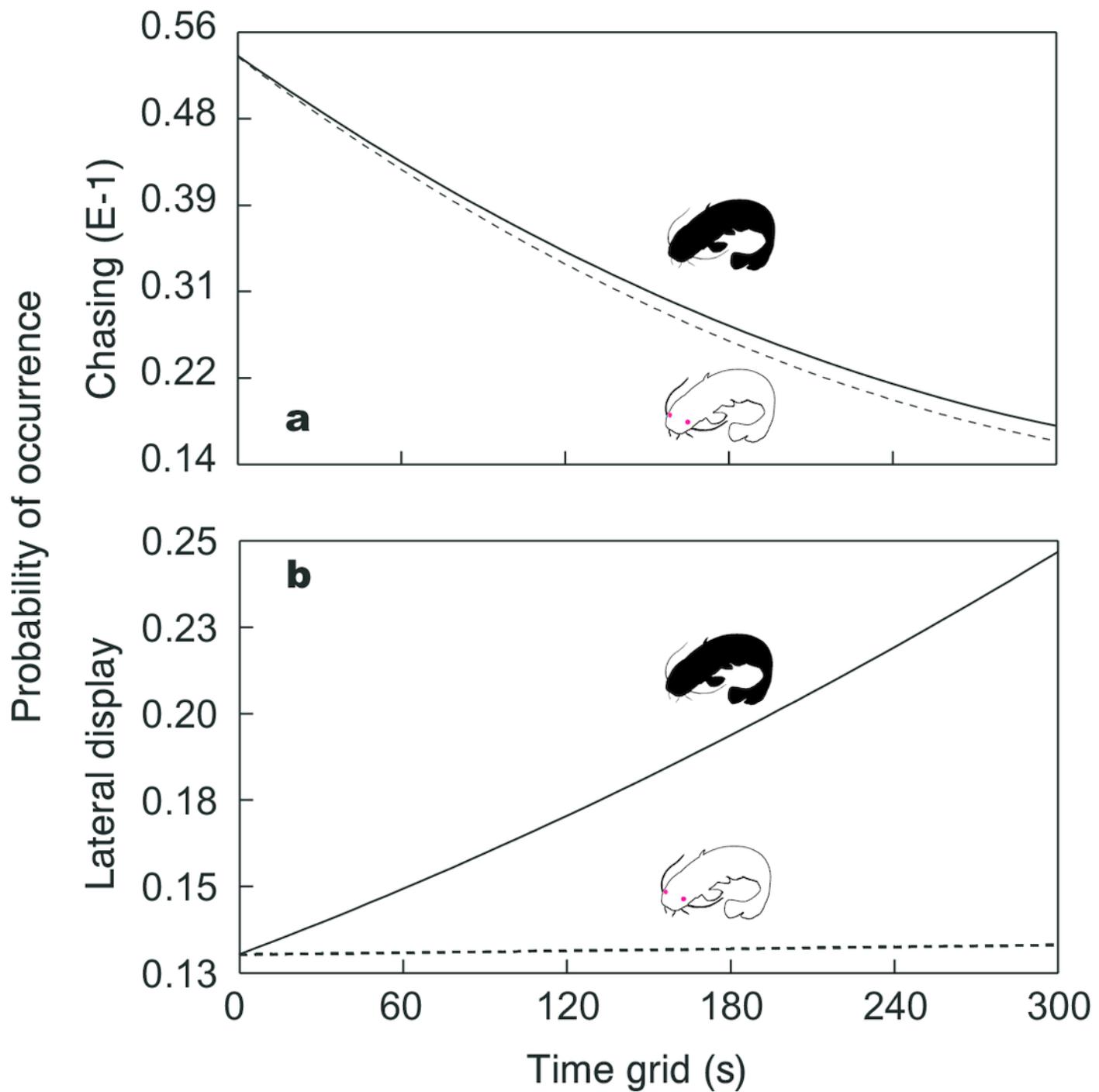
Total number of aggressive interactions (adjusted means \pm SE) across albino and pigmented treatments.



2

Probability of chasing (a) and lateral display (b) as a function of time across the two treatments.

Dotted line = albino catfish; black line = pigmented catfish.



3

Duration (adjusted means \pm SE of square root data) of time that conspecifics spent at particular mutual distances across albino and pigmented treatments.

