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## Dominance rank and boldness predict social attraction in great tits

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**Dominance rank and boldness predict social attraction in great tits**

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3 **1 Lay summary**  
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5 2 Social bonds can have important fitness consequences. Yet individuals often  
6  
7 3 differ in how well they are socially bonded in relation to certain individual  
8  
9 4 traits. We examined if such traits relate to differences in social attraction.  
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11 5 Using video playback in great tits, we demonstrate a causal effect of  
12  
13 6 dominance and a contrasting relationship between boldness and social  
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15 7 attraction, depending on stimulus novelty. Our findings suggest that  
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17 8 individuals change their social behavior depending on dominance rank.  
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23  
24 **Title:** Dominance rank and boldness predict social attraction in great tits  
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26 **Short title:** Dominance predicts social attraction in great tits  
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31 **13 Abstract**  
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33 14 Social relationships can have important fitness consequences and how well  
34  
35 15 an individual is socially connected often correlates with other behavioral  
36  
37 16 traits. Whether such correlations are caused by underlying individual  
38  
39 17 differences in social attraction usually remains unclear, because to identify  
40  
41 18 effects of individual traits on social attraction it is essential to  
42  
43 19 experimentally exclude the influence of the social partner. Using  
44  
45 20 standardized high definition video playback on captive great tits (*Parus*  
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3 21 *major*), we effectively demonstrate the influence of individual traits on the  
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5 22 motivation to be near a conspecific. We show that social attraction varied  
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7 23 contrastingly with boldness and stimulus novelty. Shyer birds tended to  
8  
9 24 show stronger social attraction when they were confronted with the  
10  
11 25 stimulus bird for the first time. Lower ranked birds showed the overall  
12  
13 26 strongest social attraction. This rank effect remained after experimentally  
14  
15 27 changing dominance ranks by altering group compositions. Moreover,  
16  
17 28 preference for social association tended to increase with a decrease in  
18  
19 29 dominance rank, suggesting that birds plastically change their social  
20  
21 30 preference in relation to their within-group dominance status. Our results  
22  
23 31 provide insight into how social relations can form and change, processes  
24  
25 32 that are key for understanding the long-term consequences of the social  
26  
27 33 environment on individuals and the consequences certain individuals can  
28  
29 34 have on the social environment.  
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35 **Key words:** boldness, dominance, exploration, great tits, social attraction,  
36 video playback  
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3 **38 Introduction**  
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5  
6 39 In many animal populations social associations are an essential part of an  
7  
8 40 individual's ecology. Social connectivity modulates exposure to social  
9  
10 41 information about where to forage and settle (Stamps, 1988; Kurvers et al.,  
11  
12 42 2010; Aplin et al., 2012; Templeton et al., 2012), but may at the same time  
13  
14 43 increase social stress and aggression (Rowell, 1974; Verbeek et al., 1996;  
15  
16 44 Carere et al., 2003), indicating that an individual's connectivity with its  
17  
18 45 social environment can have important fitness consequences (McDonald,  
19  
20 46 2007; Oh and Badyaev, 2010; Formica et al., 2012).  
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24 47 Yet, many individual animals are not passive actors simply responding  
25  
26 48 to the social environment, they also regularly influence the social  
27  
28 49 environment themselves. Some individuals can even be disproportionately  
29  
30 50 influential in the structuring and dynamics of the social environment  
31  
32 51 (Modlmeier et al., 2014). Specific 'policing' individuals were essential for  
33  
34 52 maintaining stability in groups of pigtailed macaques (*Macaca nemestrina*)  
35  
36 53 (Flack et al., 2006) and the presence of some hyper-aggressive males  
37  
38 54 decreased the average mating success for whole groups of water striders  
39  
40 55 (*Aquarius remiges*) (Sih and Watters, 2005). The influence individuals can  
41  
42 56 exert on their social environment is especially interesting in relation to  
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44 57 dominance structures. Dominance is a relative measure, which depends on  
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3 58 the other individuals in a group and, most importantly, is reversible (Rowell,  
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5 59 1974; Drews, 1993). Lower-ranked individuals could thus influence the  
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8 60 social environment to create better opportunities for themselves. For  
9  
10 61 example, lower-ranked individuals in some species can increase their  
11  
12 62 likelihood of rising in rank by social association and forming coalitions  
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14  
15 63 (McDonald, 2007; Schülke et al., 2010; Gilby et al., 2013).

16  
17 64 Social associations, however, entail costs as well as benefits. Being in  
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19 65 a more central position might result in receiving more aggression and  
20  
21 66 experiencing more social stress (Rowell, 1974; Carere et al., 2001; Colléter  
22  
23 67 and Brown, 2011). Yet, being on the edge, especially from a group  
24  
25 68 positioning perspective, might leave an individual more vulnerable to  
26  
27 69 predation (Romey and Galbraith, 2008). When the costs and benefits of  
28  
29 70 social associations differ between individuals, it is likely that the attraction  
30  
31 71 to conspecifics, will also vary. Previous studies have revealed intriguing  
32  
33 72 correlations between the social associations and the dominance rank as  
34  
35 73 well as the behavioral characteristics of individuals (Rushmore et al., 2013;  
36  
37 74 Snijders et al., 2014). Higher ranked chimpanzees (*Pan troglodytes*) had  
38  
39 75 more unique social associations (Rushmore et al., 2013), similar to more  
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41 76 'exploratory' great tits (*Parus major*) (Aplin et al., 2013; Snijders et al.,  
42  
43 77 2014) and 'bolder' three-spined sticklebacks (*Gasterosteus aculeatus*) (Pike  
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3 78 et al., 2008). Yet, slow exploring great tits showed more stable relationships  
4  
5 79 and more collective behavior (Aplin et al., 2013; Aplin et al., 2014) and  
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7  
8 80 shyer three-spined sticklebacks showed stronger unique associations (Pike  
9  
10 81 et al., 2008) and stronger social attraction (Jolles et al., 2015). Also, a study  
11  
12 82 on social networks in guppies revealed shyer guppies (*Poecilia reticulata*) to  
13  
14 83 have more unique and stronger social associations (Croft et al., 2009).  
15  
16  
17 84 These findings suggest that individuals indeed could vary in social attraction  
18  
19 85 in relation to their behavioral traits, yet the direction of these relationships  
20  
21 86 may depend strongly on the specific context or the specific association  
22  
23 87 measures (number versus strength) used.  
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25

26 88         One of the challenges of studying social association behavior is that  
27  
28 89 the formation of social associations can often be the consequence of the  
29  
30 90 behavior of the focal individual, their social partner and their interaction.  
31  
32 91 Several studies indeed have revealed that social associations can strongly  
33  
34 92 depend on the combination of the specific behavioral types of both  
35  
36 93 individuals (Harcourt et al., 2009; Jolles et al., 2015; Keiser et al., 2016).  
37  
38 94 When such interactions occur, it is usually difficult to reveal the underlying  
39  
40 95 mechanism, because next to active approach or avoidance behavior of the  
41  
42 96 focal individual, the social partner might also give subtle cues that promote  
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44 97 or discourage a social association.  
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3 98           These cues are certainly relevant in relation to dominance  
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5 99           interactions, with subordinates giving off signals that can illicit agonistic  
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8 100          approaches by the dominants (Rowell, 1974) or actually remove the need  
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10 101          for a dominance interaction to take place (Drews, 1993). Likewise, also  
11  
12 102          dominants can show subtle behaviors that illicit or discourage associations  
13  
14 103          (Drews, 1993). Because it is difficult to detect or control for such signals, it  
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16 104          usually remains unclear if associations were actively initiated, elicited or  
17  
18 105          both. The role of social attraction, the tendency to initiate social  
19  
20 106          associations independent of the social partner's (subtle) behavior, in such  
21  
22 107          cases thus remains unresolved (Webster and Ward, 2011; Wolf and Krause,  
23  
24 108          2014). In human social structures the tendency to initiate social  
25  
26 109          associations is regarded vital for social relationships to form and maintain,  
27  
28 110          but is also not equal between individuals (Mollgaard and Mathiesen, 2016).  
29  
30 111          Insight into the individual factors driving variation in social attraction  
31  
32 112          therefore represents an important next step towards understanding the  
33  
34 113          mechanisms behind the formation and stability of social structures (Flack et  
35  
36 114          al., 2006; Shizuka et al., 2014).

37  
38 115                 To tease apart the effect of variation in social attraction from the  
39  
40 116          response of a social partner, it is necessary to perform experimental  
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42 117          manipulations that exclude the influence of the social partner. Hence, in



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3 118 this study we conducted a standardized high definition video playback  
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5 119 experiment to study social attraction, in great tits, an important model  
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8 120 species for studying social connectivity (Aplin et al., 2013; Aplin et al., 2014;  
9  
10 121 Snijders et al., 2014). Video playback is now more realistic than ever before  
11  
12 122 as a consequence of modern developments in recording devices and  
13  
14 123 monitors, such as high definition and LCD technology which circumvent  
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16  
17 124 previous challenges to conducting video playback with species with high  
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19 125 flicker fusion frequencies, like birds (Oliveira et al., 2000; Bird and Emery,  
20  
21 126 2008). Successful video playback studies have been conducted to study the  
22  
23 127 social behavior of a variety of species, such as gloomy octopuses (*Octopus*  
24  
25 128 *tetricus*), nutmeg manakins (*Lonchura punctulata*) and rooks (*Corvus*  
26  
27 129 *frugilegus*) (Bird and Emery, 2008; Rieucau and Giraldeau, 2009b, a; Pronk  
28  
29 et al., 2010).  
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33 131 During our experiment we provided subjects with a choice between a  
34  
35 132 video of an empty cage and a video with an unfamiliar same-sex  
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37 133 conspecific. Additionally, we conducted control trials to assure that our  
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39 134 subjects were not merely responding to the movement on the screen. We  
40  
41 135 expected lower-ranked birds to show less social attraction for the stimulus  
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43 136 bird, as we assumed that lower-ranked birds would anticipate to be  
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45 137 displaced by an unfamiliar conspecific. To subsequently illuminate a  
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3 138 potential causal effect of dominance rank, we experimentally altered the  
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5 139 dominance ranks by changing the group compositions and we conducted  
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8 140 the experiment again. Additionally, based on one of our own recent studies,  
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10 141 revealing male fast explorers to spent relatively more time near any other  
11  
12 142 male great tit (Snijders et al., 2014), we expected fast explorers to also here  
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14 143 show a stronger social attraction. Yet, although we also expected an effect  
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17 144 of boldness, given the previous mentioned contrasting findings in literature,  
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19 145 we had no specific prediction regarding the direction of the effect.  
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## 24 147 **Methods**

### 26 148 *Experimental Subjects*

27  
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29 149 We used captive hand-reared first year great tits hatched in the spring of  
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31 150 2014, both as video playback stimuli ( $N = 38$ ) and experimental subjects ( $N$   
32  
33 151 = 36). These birds were chicks of captive parents, but were raised by wild  
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36 152 birds during the first ten days after hatching and subsequently hand reared  
37  
38 153 under standard conditions (van Oers et al., 2005). Each bird was fitted with  
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40 154 a unique aluminum leg ring and three color leg rings for individual  
41  
42 155 recognition. Birds (12 females, 24 males) were sexed using molecular  
43  
44 156 markers (Griffiths et al., 1998). For each bird the tarsus (0.01 cm) was  
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47 157 measured before the experiment and weight was monitored before, during  
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3 158 and after the experiment (0.1 g) using a digital balance. Birds experienced  
4  
5 159 natural daylight and temperature conditions (daily average: 3 - 10 °C) in  
6  
7 160 semi-open aviaries (2 x 4 x 2.5 m). The indoor rooms with individual cages  
8  
9 161 (0.9 x 0.4 x 0.5 m) were kept on a light regime similar to the natural day-  
10  
11 162 night cycle, and temperature maintained between 15 and 17 °C. Birds had  
12  
13 163 auditory contact with each other at all times. All food and water was  
14  
15 164 provided ad libitum, with the exception of mealworms, which were only  
16  
17 165 provided in the aviaries and during experimental trials. See (van Oers et al.,  
18  
19 166 2005) for more details on housing conditions. Work was carried out under  
20  
21 167 permit no. 14.12 granted to KVO and MN by the Dutch legal entity: KNAW  
22  
23 168 Dier Experimenten Commissie (DEC).  
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### 31 *Experimental Design*

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33 171 We conducted behavioral tests (novel environment and novel object tests)  
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35 172 approximately three months before the start of the experiment. Next, all 38  
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37 173 birds (36 subjects) were recorded to be video stimuli, three weeks before  
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39 174 the start of the experiment. Before the experiment birds were always  
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41 175 housed in individual cages and so had not been in physical contact with  
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43 176 each other since the hand-rearing period (three to four months earlier). At  
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45 177 the start of the experiment 36 birds were randomly assigned to single-sex  
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3 178 groups of six birds (two female and four male groups) and subsequently  
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5 179 housed in six aviaries. We conducted dominance observations from six to  
6  
7 180 nine days after the birds were grouped together, as dominance ranks in  
8  
9 181 great tit groups stay relatively stable from the sixth day after group  
10  
11 182 formation (Verbeek et al., 1999). After a minimum of twelve days in a  
12  
13 183 group, birds were again individually housed for the onset of the video  
14  
15 184 playback trials. An acclimatization period of at least three days was given  
16  
17 185 before the onset of the experiment. After we conducted four video  
18  
19 186 playbacks trials with each individual from all six groups, the birds were  
20  
21 187 reassigned to six new groups based on their dominance ranks as measured  
22  
23 188 in their original groups. In these new groups we placed birds with similar  
24  
25 189 dominance ranks together. The previous protocol was then repeated, after  
26  
27 190 which one final video playback trial was conducted with each bird. See  
28  
29 191 supplementary figure S1 for the exact timeline of the complete  
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31 192 experimental setup.  
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#### 40 *Dominance*

41  
42 195 We assessed dominance ranks by observing interactions between birds in  
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44 196 the aviaries from behind a one-way window. Groups were directly observed  
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46 197 six times for half an hour directly and for two to three times half an hour by  
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3 198 video. We conducted direct observations for each group on four  
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5 199 consecutive mornings (07:30-13:00) and two afternoons (13:00-16:45),  
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8 200 while video recordings were made only on mornings. During observations  
9  
10 201 we documented displacement, waiting, defined as an individual waiting for  
11  
12 202 another bird to finish before feeding itself, and aggressive behavior  
13  
14 203 between two individuals (chasing and attacking). For each interaction we  
15  
16  
17 204 noted the identity of the actor and the identity of the receiver. During the  
18  
19 205 first round of dominance observations 98-165 interactions were recorded  
20  
21 206 per group, while the second round (after group compositions were  
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23  
24 207 changed) resulted in 166- 236 interactions. We assigned dominance ranks  
25  
26 208 based on the number of birds with whom an individual had lost the  
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28 209 majority of its interactions. Group members could have the same  
29  
30 210 dominance rank, as more than half of the groups did not have a significant  
31  
32 211 linear hierarchy based on the linearity index  $h'$  (De Vries, 1995). When it  
33  
34 212 was unclear exactly how many birds an individual had lost the majority of  
35  
36 213 its interactions with due to unknown or tied relationships, we assigned the  
37  
38 214 average of the minimum and maximum possible rank (six out of 36 during  
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40 215 the first round; five out of 36 during the second round).

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44 216 We formed the six single-sex groups during the second round by  
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46 217 grouping the three highest-ranked birds of one group from the first round  
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3 218 together with the three highest-ranked birds of another group. This was  
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5 219 likewise done, in a randomly paired fashion, for the three lowest-ranked  
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7 220 birds of each group. We used this specific procedure to force a number of  
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9 221 the previously dominant individuals to adopt more submissive roles and  
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11 222 vice versa. The number of interactions in dominant groups ranged from 166  
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13 223 to 200 and in the subordinate groups from 172 to 236.  
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19 224  
20 225 *Boldness*

21 226 Individual boldness was assessed for all except one bird, using two  
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23 227 standardized novel object tests as described in detail by (Carere and van  
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25 228 Oers, 2004), approximately three months before the start of the  
26  
27 229 experiment (at 50 days of age). These tests were based on the assay  
28  
29 230 designed by (Verbeek et al., 1994), in which the individual differences in  
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31 231 novel object approach in juvenile great tits were strongly consistent for a  
32  
33 232 duration of at least 9 weeks ( $r_s = 0.81$ ).  
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37 233 Briefly, a novel object was presented in the home-cage on the  
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39 234 furthest right of the three perches. Tests lasted 2 minutes and behavior was  
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41 235 observed from behind a curtain. The boldness score was calculated  
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43 236 following (Drent et al., 2003), thereby incorporating the activity of the  
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45 237 subject. Individuals not reaching the perch with the novel object within 2  
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3 238 min were given a score of 0-5 depending on the number of movements  
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5 239 within these 2 min. Scores from 6–17 were given to animals that visited the  
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7 240 perch, taking into account the latency to reach the perch and how close  
8  
9 241 they approached the novel object. This score was then transformed to a  
10  
11 242 score from 0 to 1, with 0 meaning that a bird did not move at all in the test  
12  
13 243 and 1 indicating the bird touched the novel object repeatedly within one  
14  
15 244 minute. This measure was highly repeatable between the two novel object  
16  
17 245 tests ( $r = 0.44$ ,  $SE = 0.13$ ,  $N = 37$ ). We used the average score for our  
18  
19 246 analysis.  
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#### 26 248 *Exploratory behavior*

27  
28 249 The exploratory behavior of a bird (with exception of two individuals with  
29  
30 250 temporary flight problems) was assessed with a standardized novel  
31  
32 251 environment test following Drent et al. (2003) approximately 3.5 months  
33  
34 252 before the start of this experiment (at 30-40 days of age). This test is  
35  
36 253 conducted in a standard observation room which contains five artificial  
37  
38 254 trees. After the bird enters the room we quantify how it explores the new  
39  
40 255 environment. The exploration score was calculated as the number of  
41  
42 256 movements in the first 2 minutes (Dingemanse et al., 2002; Snijders et al.,  
43  
44 257 2014). Exploratory behavior of wild juvenile and adult great tits recaptured  
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3 258 and tested at least two times following this protocol from 1998 until 2001  
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5 259 (>200 birds) was repeatable for both sexes and for two different study  
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7  
8 260 areas (range  $r = 0.27-0.66$ ,  $P < 0.01$ )(Dingemanse et al., 2002).  
9

10 261 Exploratory behavior is a partially heritable behavioral trait in great  
11  
12 262 tits (van Oers and Mueller, 2010) and explains variation in various social  
13  
14 263 behaviors, such as aggression (Verbeek et al., 1996), territory defense (Amy  
15  
16  
17 264 et al., 2010; Snijders et al., 2015b), approach of conspecifics (Groothuis and  
18  
19 265 Carere, 2005), social foraging (Aplin et al., 2014) and social network position  
20  
21 266 (Aplin et al., 2013; Snijders et al., 2014).  
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25  
26 268 *Stimulus videos*  
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28 269 Stimulus videos were constructed by recording a great tit from a fixed  
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30 270 distance (40 cm) for eight to ten minutes in a white cage (0.67 x 0.37 x 0.38  
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32 271 m) including two perches and a Plexiglas front. Videos were recorded with a  
33  
34 272 Full HD Panasonic HC-V550 (AVCHD, W 1920 x H 1080, 25 fps). In total 29 of  
35  
36 273 the 38 recorded videos were used in the experiment, only including videos  
37  
38 274 of birds that were life size on full screen. We removed the sound of the  
39  
40 275 videos to avoid potential influences of calls and songs, and excluded the  
41  
42 276 first two minutes of the original video. Using Adobe Premiere Pro (Adobe  
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44 277 Systems, San Jose, US) we selected an approximately two-minute time-  
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3 278 frame (Min: 1:46, Max: 2:05), in which the bird occupied the same location  
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5 279 and body position at the start and end. This procedure allowed us to make  
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7 280 realistic uninterrupted loops of the videos. Movement control videos were  
8  
9 281 constructed by blurring a rectangle concealing the great tit in the stimulus  
10  
11 282 video with Gaussian blurr (75.0) and Mosaic (250) frame by frame using  
12  
13 283 Adobe Premiere Pro.  
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16  
17 284 To test for the potential influence of stimulus bird activity, the  
18  
19 285 stimulus videos were tracked with Ethovision XT (Noldus, static subtraction,  
20  
21 286 sample rate: 25/sec). We checked the tracks manually afterwards for  
22  
23 287 incorrect detections and adjusted them if necessary. We used the total  
24  
25 288 distance moved by center point (cm) as a proxy for stimulus activity.  
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30  
31 290 *Video playback protocol*  
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33 291 All individual cages connected to the same experimental room (4.0 x 2.4 x  
34  
35 292 2.5 m) through sliding doors. The experimental room (supplementary figure  
36  
37 293 S2), the same as the one used for the novel environment test, contained  
38  
39 294 two wooden cages (0.85 x 0.40 x 1.0 m) with wire mesh on the front and  
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41 295 attached on a rolling base (Reparaz et al., 2014), which we positioned  
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43 296 against the back wall. Each of the two cages contained a black LCD  
44  
45 297 computer monitor (HP Compaq LA2306x, 60 Hz) allowing the birds a visual  
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3 298 of the stimulus videos up to 20 cm. Additionally the room contained three  
4  
5 299 artificial 'trees' (as described by Dingemanse et al. (2002)) with one tree in  
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7  
8 300 the middle of the room providing a view of both screens simultaneously  
9  
10 301 and one tree in front of each screen that only allowed the bird to view one  
11  
12 302 screen. We made observations through a one-way window situated at the  
13  
14  
15 303 opposite site of the room. Each stimulus video started before a subject  
16  
17 304 entered the room and lasted fifteen minutes starting from the time a bird  
18  
19 305 had entered the experimental room. Birds freely moved into the room by  
20  
21 306 themselves. We turned off the lights after fifteen minutes (birds stay  
22  
23 307 perched then) and the subject was put back into its individual cage.

24  
25  
26 308 During the first round, each individual received four video playback  
27  
28 309 trials. Per unique video stimulus bird (two for each subject) each subject  
29  
30 310 received both an experimental trial and a movement control (video  
31  
32 311 playback validation) trial in a random order. The experimental trial included  
33  
34 312 a screen showing a bird in a cage and a screen showing the same cage  
35  
36 313 empty (supplementary figure S2 and Supplementary video S1). The  
37  
38 314 movement control trial was similar to the experimental trial except that the  
39  
40 315 video showing the empty cage video was replaced by a great tit stimulus  
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42 316 video, in which the bird in the video was "blurred" using video-editing  
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47 317 software. Subjects only received stimulus videos of birds which were

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3 318 unfamiliar to them (no previous or current group mates) and that were of  
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5 319 the same sex. Movement control trials always showed the identical video  
6  
7 320 stimulus bird (both blurred and original) as the subject would receive or had  
8  
9 321 received during the accompanying experimental trial.  
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11  
12 322 We randomized and balanced the screens (left or right) from which a  
13  
14 323 video was shown. Trials per individual bird were one day apart and the  
15  
16 324 order between birds was kept constant. During the first two trials (first  
17  
18 325 video stimulus bird) food was present in the form of four small cups  
19  
20 326 attached to the trees in front of the screens. Each cup contained one  
21  
22 327 mealworm. During the following two trials (second video stimulus bird) no  
23  
24 328 food cups were present. We initially provided the mealworms to motivate  
25  
26 329 the birds to come closer to the screens. However, to test if the presence of  
27  
28 330 food was not biasing the observed social attraction we removed the food  
29  
30 331 during the following two trials. During the second round (after group  
31  
32 332 compositions changed), subjects received one experimental trial with a  
33  
34 333 third unique video stimulus bird (food was present). The experimental  
35  
36 334 design thus included three experimental trials (social attraction tests) and  
37  
38 335 two control trials (movement controls) for each of the 36 subjects (table 1).  
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47 337 *Data analysis*  
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3 338 All 180 trials were recorded (with exception of three movement control  
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5 339 trials due to video recording problems) using a broad angle camera from a  
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7 340 fixed position (Observer, Noldus, Wageningen, The Netherlands). We used  
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9  
10 341 the program EthoVision XT version 9 (Noldus, Wageningen, The  
11  
12 342 Netherlands) to manually score the total duration and the frequency of  
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14 343 visits on (1) the middle tree, (2) in front of the left cage, (3) in front of the  
15  
16 344 right cage or (4) in the rest of the experimental room. Sample sizes differ as  
17  
18 345 a consequence of three failed data video recordings (only movement  
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20 346 control trials) or of four birds that for a total of thirteen times did not make  
21  
22 347 a decision within fifteen minutes (movement control and experimental  
23  
24 348 trials). We calculated general interest in the videos as the total time spent  
25  
26 349 in front of one of the videos divided by the total experiment duration (15  
27  
28 350 min). Our key metric, 'social preference' was calculated as the proportion of  
29  
30 351 time spent in front of the great tit video divided by the total time spent in  
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32 352 front of the great tit video and the other video (empty cage or blurred great  
33  
34 353 tit video). This measure has been used as a reliable indicator in mate-choice  
35  
36 354 experiments (Schielzeth et al., 2008; Reparaz et al., 2014) and has been  
37  
38 355 successfully used in captive great tits to quantify personality differences in  
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40 356 social exploration in response to social defeat (Carere et al., 2001).  
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3 357 To analyze whether great tits distinguished the great tit video stimuli  
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5 358 from mere movement, we tested if average social preference was  
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8 359 significantly higher than random ( $Mean = 0.5$ ). The subjects spent a  
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10 360 significantly higher proportion of time near the un-manipulated great tit  
11  
12 361 video than would be expected if birds were randomly dividing their time  
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15 362 over the great tit video and the identical blurred version of the video (two  
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17 363 out of four trials  $P < 0.05$ ).

18  
19 364 Interestingly, birds only spent more time than expected at random  
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21 365 near the social stimulus when they had received the control trial before the  
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23 366 experimental trial (figure 1), thus when they had not seen the specific  
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25 367 stimulus video bird before (One sample T-Test Social preference against  
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27  
28 368  $Mean = 0.5$ ; First stimulus video: 1<sup>st</sup> encounter;  $Mean = 0.64$ ,  $SD = 0.17$ ,  
29  
30 369  $Range = 0.40 - 0.89$ ,  $t_{(14)} = 3.11$ ,  $P = 0.008$ ; 2<sup>nd</sup> encounter;  $Mean = 0.55$ ,  $SD =$   
31  
32 370  $0.17$ ,  $Range = 0.31 - 0.94$ ,  $t_{(16)} = 1.36$ ,  $P = 0.19$ ; Second stimulus video: 1<sup>st</sup>  
33  
34 371 encounter;  $Mean = 0.62$ ,  $SD = 0.20$ ,  $Range = 0.27 - 0.95$ ,  $t_{(15)} = 2.42$ ,  $P = 0.03$ ;  
35  
36 372 2<sup>nd</sup> encounter;  $Mean = 0.52$ ,  $SD = 0.32$ ,  $Range = 0.03 - 0.94$ ,  $t_{(15)} = 0.30$ ,  $P =$   
37  
38 373  $0.77$ ; figure 1). Interest (the total time the great tits spent in front of the  
39  
40 374 videos) was overall high with 71% ( $SD = 20\%$ ) when the first unique video  
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42 375 stimulus was presented and 64% ( $SD = 24\%$ ) when the second unique  
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44 376 stimulus video was presented. That the birds showed a significant  
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3 377 preference during the first and again in the third trial (when they received a  
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5 378 novel video stimulus bird) but not during the second and the fourth trial  
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8 379 (when they had already encountered the video stimulus bird before during  
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10 380 the experimental trial), strongly suggest that neither habituation to the  
11  
12 381 experimental set-up nor differences in clarity or contrast between the social  
13  
14 382 stimulus videos and the movement control videos explains the preference  
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16 383 for the social stimulus. In summary, the subjects distinguished the great tit  
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18 384 video stimuli from mere movement, responding with significant social  
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20 385 preference when a new video stimulus bird was shown.  
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24 386 Also in the experimental trials the birds spent on average more than  
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26 387 50% of the time with the social stimulus (first video stimulus: *Mean* = 0.57,  
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28 388 *SD* = 0.24, *Range* = 0.11 – 1.00, *N* = 34; Second video stimulus: *Mean* = 0.63,  
29  
30 389 *SD* = 0.20, *Range* = 0.23 - 0.97, *N* = 34; Third video stimulus (after group  
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32 390 rearrangement): *Mean* = 0.57, *SD* = 0.22, *Range* = 0.01 - 0.92, *N* = 34).  
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38 392 Next to *social preference*, *social choice* was calculated by dividing the total  
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40 393 number of times the subjects moved to the great tit video from the neutral,  
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42 394 middle tree by the total number of times the subject moved to either of the  
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44 395 two videos. For analysis of the experimental trials (control trial were  
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46 396 excluded from this analysis), we extracted the principal component (PC-  
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3 397 Social attraction) of *social preference* and *social choice* (arcsine transformed  
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5 398 for normality) for each unique stimulus bird (Loadings on component > 0.9,  
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7 399 *Eigen value* > 1.6; Percentage variance explained > 81%). Both measures  
8  
9 400 were strongly correlated (Weighted Regression of *social choice* against  
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11 401 *social preference*;  $\beta > 0.59$ ,  $P < 0.001$  for movement control trials;  $\beta > 0.64$ ,  
12  
13 402  $P < 0.0001$  for experimental trials). We calculated the repeatability for these  
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15 403 measures before the change in group composition, following (Lessells and  
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17 404 Boag, 1987). For this, we only included individuals that made at least one  
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19 405 active choice in both trials, excluding one bird. Increasing the threshold of  
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21 406 the number of active choices up to 10 did not significantly change our  
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23 407 results.

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28 408 To analyze social attraction, we conducted a mixed model analysis  
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30 409 (REML) with residuals weighted for the number of active choices made  
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32 410 (from the tree in the middle) per individual per trial. We considered the  
33  
34 411 observed social attraction of individuals that made more choices to be  
35  
36 412 more reliable than of individuals that only made a small number of choices,  
37  
38 413 since with fewer choices there is a higher risk of extreme chance effects.  
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40 414 The starting model analyzing the first round of video playback experiments  
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42 415 included PC-Social attraction (dependent), boldness (covariate), exploratory  
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44 416 behavior (covariate), dominance rank (covariate), stimulus novelty (first or  
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3 417 second time encounter with the specific great tit stimulus; factor), food  
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5 418 present (factor) and individual nested in aviary group (random factor).  
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8 419 Additionally, based on our results with the movement control trials, the  
9  
10 420 model included the two-way interactions between dominance rank and  
11  
12 421 stimulus novelty, boldness and stimulus novelty and exploratory behavior  
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14  
15 422 and stimulus novelty. In our dataset, boldness was not correlated with  
16  
17 423 exploratory behavior (Spearman correlation test;  $r_s = -0.22$ ,  $P = 0.21$ ,  $N = 34$ )  
18  
19 424 or dominance rank (Spearman correlation test;  $r_s = -0.01$ ,  $P = 0.94$ ,  $N = 35$ ).  
20  
21 425 Also, exploratory behavior was not correlated with dominance rank  
22  
23 426 (Spearman correlation test;  $r_s = 0.00$ ,  $P = 0.98$ ,  $N = 34$ ). A back-wise model  
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25 427 selection procedure was conducted by removing the least significant terms  
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27 428 from the model step-wise ( $0.1 < P < 1.0$ ), starting with the highest-level  
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29 429 interactions.  
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33 430 To further investigate if effects of behavioral characteristics changed  
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35 431 over the course of the trial, we analyzed whether the likelihood of choosing  
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37 432 the social stimulus differed between the last and the first choice a bird  
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39 433 made. We conducted an analysis with social stimulus choice (yes/no) as the  
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41 434 binary dependent variable. Our starting model was based on the final  
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43 435 model for the analysis of social attraction but now included interactions  
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45 436 with first/last choice. Model simplification was based on a stepwise  
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3 437 backward selection procedure. We only considered active choices made  
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5 438 from the tree in the middle of the room (*social choice*). Additionally, we  
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7 439 only considered trials in which the bird made at least two choices and in  
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9 440 which a bird made its first visit to one of the screens while having first  
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11 441 perched on the tree in the middle. In this way we could assure that each  
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13 442 bird has had an equal good view of both of the screens while making the  
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15 443 first choice.  
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19 444 To test for potential effects of sex and body condition on social  
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21 445 attraction, physical characteristics were added as control variables to the  
22  
23 446 final model for social attraction. We calculated body condition as the  
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25 447 residual of weight over tarsus for each sex separately. Neither sex ( $F_{1,21.43} =$   
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27 448 0.21,  $P = 0.65$ ) nor body condition ( $F_{1,20.02} = 2.23$ ,  $P = 0.15$ ) had a significant  
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29 449 effect. Moreover, activity of the video stimulus bird did not influence the  
30  
31 450 PC-Social attraction (Spearman correlation test; First video stimulus bird:  $r_s =$   
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33 451  $0.20$ ,  $P = 0.25$ ,  $N = 34$ ; Second video stimulus bird:  $r_s = 0.02$ ,  $P = 0.92$ ,  $N =$   
34  
35 452 33). Similarly, there was no effect of stimulus activity when solely analyzing  
36  
37 453 the first and third trial ( $r_s < 0.24$ ,  $P > 0.35$ ). Stimulus activity as a control  
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39 454 variable in the final model also did not have a significant effect ( $F_{1,42.09} =$   
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41 455 1.11,  $P = 0.30$ ). Finally, there was no effect of food presence during the  
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43 456 experiments ( $F_{1,49.47} = 1.985$ ,  $P = 0.17$ ).  
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3 457 To test whether the newly acquired dominance rank had an effect on  
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5 458 social attraction we again used a mixed model analysis (REML) with the  
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7 459 residuals weighted by the number of choices made per individual per trial.  
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10 460 The starting model included PC-Social attraction (dependent), dominance  
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12 461 rank (covariate), any significant behavioral traits from the first model  
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14 462 (covariate) and aviary group (random factor). One bird made twice as many  
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16 463 choices as the bird with the second highest number of choices. Reducing  
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18 464 the number of choices (weight) of this individual to the value of the second  
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20 465 highest bird resulted in a trend effect of new dominance rank in the same  
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22 466 direction as in the original model (see Results).  
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26 467 All statistical analyses were conducted in IBM SPSS Statistics for  
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28 468 Windows, Version 22.0 (IBM Corp, Armonk, NY). We used non-parametric  
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30 469 tests if the data was not normally distributed according to the Shapiro-Wilk  
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32 470 test.  
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## 37 472 **Results**

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40 473 *Dominance rank, boldness and exploratory behavior in relation to social*  
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42 474 *attraction*  
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45 475 Great tits spent over 60% of the total time in front of the videos, and this  
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47 476 did not decrease with the total number of trials received (60.8%, 69.7%,  
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3 477 66.3% and 67.6% respectively). There was a tendency for the proportion of  
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5 478 time spent near the social stimulus (*social preference*) between the first two  
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7 479 experimental trials to be moderately repeatable ( $r = 0.26$ ,  $SE = 0.16$ ,  $P =$   
8  
9 480  $0.07$ ), but the proportion of times an individual actively chose to sit near  
10  
11 481 the social stimulus (*social choice*:  $r = -0.01$ ,  $SE = 0.18$ ,  $P = 0.53$ ) and the  
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13 482 combined measure for social attraction (*PC-social attraction*) were not ( $r =$   
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15 483  $0.13$ ,  $SE = 0.17$ ,  $P = 0.24$ ).

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19 484 Lower-ranking individuals showed a stronger social attraction (PC-  
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21 485 Social attraction) compared to higher-ranked birds (Rank:  $F_{1, 26.80} = 5.58$ ,  $P =$   
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23 486  $0.03$ ; figure 2). Shyer birds showed the strongest social attraction when  
24  
25 487 they encountered a unique video stimulus for the first time, while bolder  
26  
27 488 birds showed a relatively stronger social attraction when they encountered  
28  
29 489 a unique video stimulus bird for the second time (Boldness\*Stimulus  
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31 490 novelty:  $F_{1, 58.88} = 4.27$ ,  $P = 0.04$ ; figure 3). When solely considering novel  
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33 491 video stimuli birds, shy birds still tended to show a higher social attraction  
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35 492 (Mixed model:  $F_{1, 21.58} = 3.38$ ,  $P = 0.08$ ), while there was no effect of boldness  
36  
37 493 when only considering video stimuli birds that were presented for the  
38  
39 494 second time (Mixed model:  $F_{1, 15.42} = 1.24$ ,  $P = 0.28$ ). However, when the  
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41 495 boldest individual (figure 3) was left out of the analysis there was no longer  
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43 496 a significant interaction between boldness and novelty, but an overall  
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3 497 significant effect of boldness, with shy individuals showing more social  
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5 498 attraction (Boldness:  $F_{1,60} = 6.38$ ,  $P = 0.01$ ; Rank:  $F_{1,60} = 4.43$ ,  $P = 0.04$ ).  
6  
7  
8 499 Finally, exploratory behavior did not predict social attraction either as main  
9  
10 500 effect (Mixed model:  $F_{1,28.98} = 0.01$ ,  $P = 0.94$ ) or in interaction with stimulus  
11  
12 501 novelty (Mixed model:  $F_{1,49.96} = 0.85$ ,  $P = 0.36$ ).

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15 502 To examine if effects of dominance rank and boldness changed over  
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17 503 the course of the trial, we analyzed whether the likelihood of choosing the  
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19 504 social stimulus differed between the first and the last choice in a trial. Birds  
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21 505 overall tended to choose the social stimulus less during their last choice,  
22  
23 506 but there was no significant interaction between the first or last choice and  
24  
25 507 either dominance rank or boldness (table 2).  
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31 509 *Influence of dominance rank on social attraction after manipulation*

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33 510 The time spent in front of the videos during the final experimental trial,  
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35 511 after the experimental change in dominance rank, was significantly higher  
36  
37 512 (77%) when compared to the first experimental trial (Paired T-Test:  $t_{(32)} =$   
38  
39 513  $2.83$ ,  $P = 0.01$ ).

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41  
42 514 Even after the change in ranks, the birds with the lowest dominance  
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44 515 rank showed again the strongest social attraction ( $F_{1,26.99} = 4.54$ ,  $P = 0.04$ ),  
45  
46 516 while there was no significant correlation between old dominance rank and  
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3 517 new dominance rank (Pearson correlation;  $r = 0.21$ ,  $P = 0.22$ ,  $N = 36$ ).  
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5 518 Adding the old rank as a control variable did not have a significant effect  
6  
7  
8 519 ( $F_{1,10.30} = 0.42$ ,  $P = 0.53$ ). Moreover, social preference tended to increase  
9  
10 520 with a decrease in dominance rank (Weighted Regression, proportion of  
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12 521 time spent with the great tit video stimulus weighted by minimum number  
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14 522 of choices,  $\beta = -0.34$ ,  $P = 0.07$ ).  
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## 19 524 **Discussion**

20 525 Using High Definition video playback, we uncovered effects of individual  
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22 526 behavioral characteristics on social attraction. More specifically, we here  
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24 527 reveal a negative effect of dominance rank on the motivation to be in  
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26 528 proximity of a simulated conspecific. Even after our manipulation of  
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28 529 dominance rank by changing group compositions, low ranking individuals  
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30 530 showed the highest social attraction. Social attraction thus seems to be a  
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32 531 relatively plastic behavior in these birds. Finally, we found evidence for a  
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34 532 negative effect of boldness, especially when the social stimulus was novel.  
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40 533 Responses of the subjects were unlikely to be driven by mere  
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42 534 curiosity for movement on the screen, as we showed that the subjects  
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44 535 could distinguish between the video stimulus and mere movement.  
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47 536 Moreover, during the control trials the birds showed significant social  
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3 537 preference when a new video stimulus bird was encountered which they  
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5 538 did not show when they had already seen a specific video stimulus bird  
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8 539 before. Finally, we did not find evidence of any relationship between  
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10 540 stimulus bird activity and observed social attraction. Indeed, several  
11  
12 541 previous studies have revealed that video-playback experiments can be  
13  
14 542 effective tools to study social behavior in birds (Partan et al., 2005; Bird and  
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16  
17 543 Emery, 2008; Rieucou and Giraldeau, 2009a, b; Boogert et al., 2013; Zoratto  
18  
19 544 et al., 2014).

20  
21  
22 545 We reveal that lower-ranked birds showed a significant higher social  
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24 546 attraction, when offered the choice between a video of an unfamiliar great  
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26 547 tit and a video of an empty cage. This result is somewhat surprising as we  
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28 548 expected subordinate birds to be more evasive of unfamiliar conspecifics.  
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31 549 Moreover, the significant effect of the new rank, but not the old rank, after  
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33 550 we changed group compositions, strongly suggests a causal relationship  
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35 551 between rank and social attraction. Possibly, lower ranked individuals  
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37 552 actively initiated social associations as soon as they realized that the  
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39 553 stimulus bird was not a threat to them. Yet, this seems unlikely, because  
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42 554 throughout a trial birds did not change in their likelihood of social  
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44 555 association depending on their dominance rank. Alternatively, subordinate  
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47 556 birds might in general have to be more socially aware to avoid

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3 557 confrontations and they might therefore be more inclined to investigate a  
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5 558 social stimulus. Indeed, as it is the subordinate's behavior that often  
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8 559 determines the outcome of a dominance interaction ("you cannot chase  
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10 560 someone who doesn't flee") lower ranked individuals have been suggested  
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12 561 to be more socially responsive (Rowell, 1974).

14 562 Furthermore, subordinate birds might be seeking social association  
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17 563 because it could increase social status or dominance rank, as shown for  
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19 564 long-tailed manakins (*Chiroxiphia linearis*) (McDonald, 2007) and eastern  
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21 565 chimpanzees (*Pan troglodytes schweinfurthii*) (Gilby et al., 2013), but also  
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23  
24 566 for male great tits associating with females (Sandell and Smith, 1991).  
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26 567 Furthermore, in nature, social associations can lead to more social  
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28 568 information on feeding locations (Aplin et al., 2012) and thereby increase  
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31 569 survival chances, since subordinate birds are known to suffer higher  
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33 570 mortality from starvation (Gosler, 1996). Finally, it could be a mechanism  
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35 571 that increases overall vigilance. It would benefit lower-ranked individuals,  
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38 572 who have less time to spend on vigilance (Krams, 1998), to have the  
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40 573 additional vigilance of a social partner in addition to the increased safety in  
41  
42 574 numbers. For example, shared vigilance during foraging has recently been  
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45 575 revealed as a likely driver of same-sex pair formation in rabbitfish (*Siganus*  
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47 576 spp.) (Brandl and Bellwood, 2015).

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3 577 We showed that shy birds spent relatively more time near a novel  
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5 578 stimulus bird, indicating a higher social attraction when confronted with an  
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7  
8 579 unfamiliar conspecific. A study looking at social exploration in male great  
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10 580 tits, measured as the time spent close to the cage of a unfamiliar male  
11  
12 581 conspecific, also revealed that slower explorers (exploration score is a  
13  
14 582 combination of the novel environment score and the novel object score in  
15  
16 583 this study) spent more time on social exploration (Carere et al., 2001).  
17  
18 584 Combined with this study, these findings suggest that great tits with re-  
19  
20 585 active personality types have a higher motivation to spent time near  
21  
22 586 (unfamiliar) conspecifics, at least in a non-threatening context. Intriguingly,  
23  
24 587 shy individuals have previously been revealed to be more sensitive to the  
25  
26 588 social environment (Carere et al., 2001; Kurvers et al., 2010; Webster and  
27  
28 589 Ward, 2011; Jolles et al., 2014) (Jolles et al., 2014; Guillette et al., 2015), but  
29  
30 590 see (Marchetti and Drent, 2000).  
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35 591 Bolder birds seem to become more socially attracted the second time  
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37 592 they see a particular stimulus bird. This could be explained by them  
38  
39 593 becoming more interested in a stimulus bird that appears to be “persistent”  
40  
41 594 (Amy et al., 2010; Snijders et al., 2015b). However, this interaction effect  
42  
43 595 hinged on one particular bold individual and exclusion of this one individual  
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45 596 revealed shy birds to show greater social attraction overall. The contrasting  
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3 597 effects of boldness detected in this study might thus not be biologically  
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5 598 meaningful.

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7 599 Lastly, previous studies in the wild found a positive effect of  
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9 600 exploratory behavior on the time spent close to conspecifics (Aplin et al.,  
10  
11 601 2013; Snijders et al., 2014), while we did not find an effect in this study.  
12  
13 602 Fast exploring great tits are more risk-prone (van Oers et al., 2004) and are  
14  
15 603 often the more aggressive and stronger responders in social conflicts  
16  
17 604 (Verbeek et al., 1996; Amy et al., 2010; Snijders et al., 2015b). Because we  
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19 605 created a much less hostile environment by presenting unfamiliar social  
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21 606 stimuli via (none-threatening) videos, this might explain why we did not  
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23 607 find effects of exploratory behavior on social attraction. This also  
24  
25 608 emphasizes the difficulty of drawing causal conclusions from un-  
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27 609 manipulated social associations that are the consequence of both the focal  
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29 610 individual and the social partner. Un-manipulated individuals could be  
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31 611 sending out (subtle) signals promoting or discouraging social associations  
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33 612 and this stresses the necessity to perform fully-controlled social stimulus  
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35 613 experiments.

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37 614 In conclusion, by using effective manipulation of social stimuli via  
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39 615 High Definition video playback, we have experimentally demonstrated the  
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41 616 causal effect of dominance rank on the strength of social association in a  
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3 617 key model species for the study of social dynamics (Carere et al., 2003; van  
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5 618 Oers et al., 2005; Aplin et al., 2013; Snijders et al., 2015a). It is important to  
6  
7 619 understand if and how individuals can adapt to socially imposed traits, such  
8  
9 620 as dominance rank, which can have large fitness consequences (Gosler,  
10  
11 621 1996; McDonald, 2007; Colléter and Brown, 2011; Gilby et al., 2013).  
12  
13 622 Moreover, insight into how social relations and thus social structures form,  
14  
15 623 are maintained, and change, is crucial for understanding the long-term  
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17 624 consequences of the social environment, including group positioning and  
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19 625 social network connectivity (McDonald, 2007; Romey and Galbraith, 2008;  
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21 626 Oh and Badyaev, 2010; Formica et al., 2012; Shizuka et al., 2014; Culina et  
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23 627 al., 2015). Furthermore, understanding the mechanisms of social  
24  
25 628 structuring can be key for identifying keystone individuals (Modlmeier et  
26  
27 629 al., 2014) and their influence on the social environment. We therefore aim  
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29 630 to stimulate the future use of such novel technologies to advance our  
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31 631 understanding of the mechanisms of social structuring in ecology and  
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33 632 evolution.  
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814 **Figure legends**

815

816 **Figure 1** The average proportion of time birds spent in front of the original  
817 great tit video stimulus relative to the time spent in front of the “blurred”,  
818 but otherwise identical, great tit video (movement control) was higher than  
819 expected by chance (0.5). However, this distinction from mere movement  
820 was only shown when a bird was confronted with a certain great tit video  
821 stimulus for the first time (dark grey: stimulus novelty = first encounter,  
822 light grey: stimulus novelty = second encounter). This was true for the first  
823 as well as for the second video stimulus bird presented. Notches not  
824 overlapping the chance line (0.5) visualize a significant divergence from  
825 chance.

826

827 **Figure 2** Birds with lower dominance ranks showed the strongest social  
828 attraction (PC- Social attraction). The first time a bird was confronted with a  
829 certain great tit video stimulus (stimulus novelty = first encounter) is  
830 represented in black while the second time (stimulus novelty = second  
831 encounter) is represented in white. Grey areas represent 95% confidence  
832 intervals.

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3 834 **Figure 3** Shyer birds showed a stronger social attraction (PC-Social  
4 attraction) compared to bolder birds, when confronted with a specific great  
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6 835  
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8 836 tit video stimulus for the first time (stimulus novelty = first encounter),  
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10 837 while bolder birds showed a relatively stronger social attraction than shyer  
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12 838 birds when they were confronted with a specific great tit stimulus for the  
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14 839 second time (stimulus novelty = second encounter). When excluding the  
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16 840 boldest bird, shy individuals showed the strongest social attraction overall.  
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18 841 Grey areas represent 95% CI.  
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843 **Tables and table legends**

844 **Table 1** Overview of the experimental design which included three  
 845 experimental trials (social attraction test) and two control trials (movement  
 846 control) for each of the 36 subjects.

Before group composition change		After
<b>First video stimulus</b>	<b>Second video stimulus</b>	<b>Third video stimulus</b>
Two trials for each subject	Two trials for each subject	One trial for each subject
Experimental trial	Experimental trial	Experimental trial
<b>AND</b>	<b>AND</b>	
Control trial	Control trial	
<b>OR</b>	<b>OR</b>	
Control trial	Control trial	
<b>AND</b>	<b>AND</b>	
Experimental trial	Experimental trial	

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849 **Table 2.** Mixed model statistics for probability of choosing the social  
 850 stimulus. Statistics of main effects and interactions of interest are reported  
 851 for the last occurrence of a variable or variable interaction in the model.

<b>Independent</b>	<b>Test statistic</b>	<b>DF- residuals</b>	<b>P-value</b>
First/Last choice	Z = -2.14	85	0.03
Rank	Z = 2.49	85	0.01
Boldness	Z = -2.71	85	0.01
Rank*First/Last choice	Z = 0.66	83	0.51
Boldness*First/Last choice	Z = 1.12	84	0.26
Novelty*Boldness*	Z = 0.61	79	0.54
First/Last choice			

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3 853 **Supplementary data legends**  
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7 855 **Supplementary figure S1. Time line of the experiment.** Stimulus video recording took place three  
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9 856 weeks before the start of the experiment. Subjects had not been in physical contact with each other  
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11 857 since the hand-rearing period. We assigned 36 birds to single-sex groups of six birds (two female and  
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13 858 four male groups) and housed them in six aviaries. We conducted dominance observations from the  
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15 859 6th until the 9th day birds were transferred to the aviaries, as dominance ranks in great tits stay  
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17 860 relatively stable from that moment onwards (Verbeek et al., 1999). After a minimum of twelve days  
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19 861 in the group, birds were individually housed in cages connected to the experimental room. Because  
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21 862 of space limitations, we conducted the first four video playback trials (one trial per day) with  
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23 863 individuals from only three groups. Subsequently, individuals from the first three groups were moved  
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25 864 to new individually cages and individuals from the other three groups were moved into the cages  
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27 865 adjacent to the experimental room. After we conducted all four playback trials also with these three  
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29 866 groups, all birds ( $N = 36$ ) were reassigned to six new groups based on their previous dominance  
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31 867 ranks. We placed birds with similar dominance ranks together. After a new round of dominance  
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33 868 recordings, one final video playback trial was conducted with each bird, again in two batches of three  
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35 869 groups following the same protocol as before.  
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42 871 **Supplementary figure S2. Schematic overview of the experimental room.** A wide-angle camera was  
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44 872 located on the left hand side in the door of the experimental room above the one-way window. The  
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46 873 observer was situated behind the one-way window (left hand side). A bird would enter from their  
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48 874 home cage either along the upper side or lower side. Three artificial trees were present, one in front  
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50 875 of each of the screens and one in the middle of the room. The bird could see both screens  
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52 876 simultaneously when perched on the middle tree, but only one screen when perched on either one  
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54 877 of the other two trees.  
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3 879 **Supplementary video S1. The experimental set-up.** A male great tit in the experimental trial can  
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5 880 choose sitting close to a screen showing a cage containing an unfamiliar male conspecific or a screen  
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7 881 showing an empty cage  
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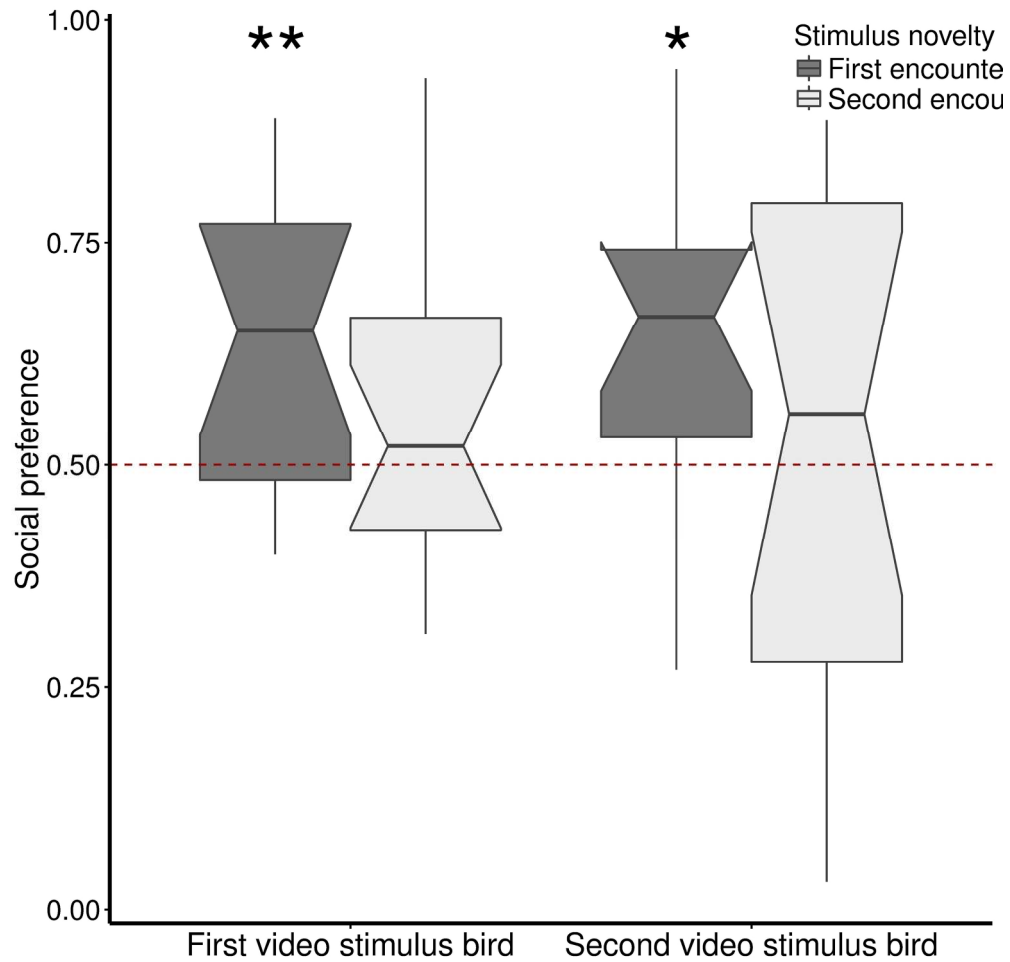


Figure 1 The average proportion of time birds spent in front of the original great tit video stimulus relative to the time spent in front of the "blurred", but otherwise identical, great tit video (movement control) was higher than expected by chance (0.5). However, this distinction from mere movement was only shown when a bird was confronted with a certain great tit video stimulus for the first time (dark grey: stimulus novelty = first encounter, light grey: stimulus novelty = second encounter). This was true for the first as well as for the second video stimulus bird presented. Notches not overlapping the chance line (0.5) visualize a significant divergence from chance.

figure 1

195x187mm (300 x 300 DPI)

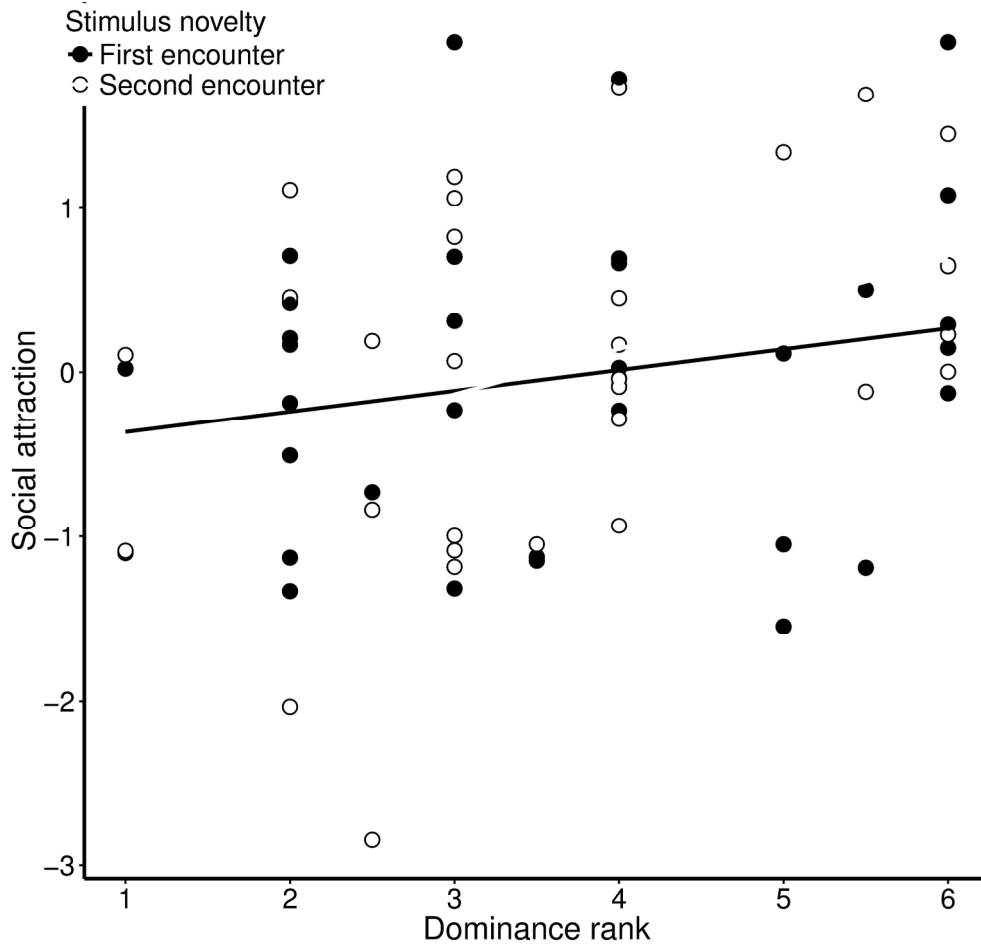


Figure 2 Birds with lower dominance ranks showed the strongest social attraction (PC- Social attraction). The first time a bird was confronted with a certain great tit video stimulus (stimulus novelty = first encounter) is represented in black while the second time (stimulus novelty = second encounter) is represented in white. Grey areas represent 95% confidence intervals.

figure 2  
 195x187mm (300 x 300 DPI)

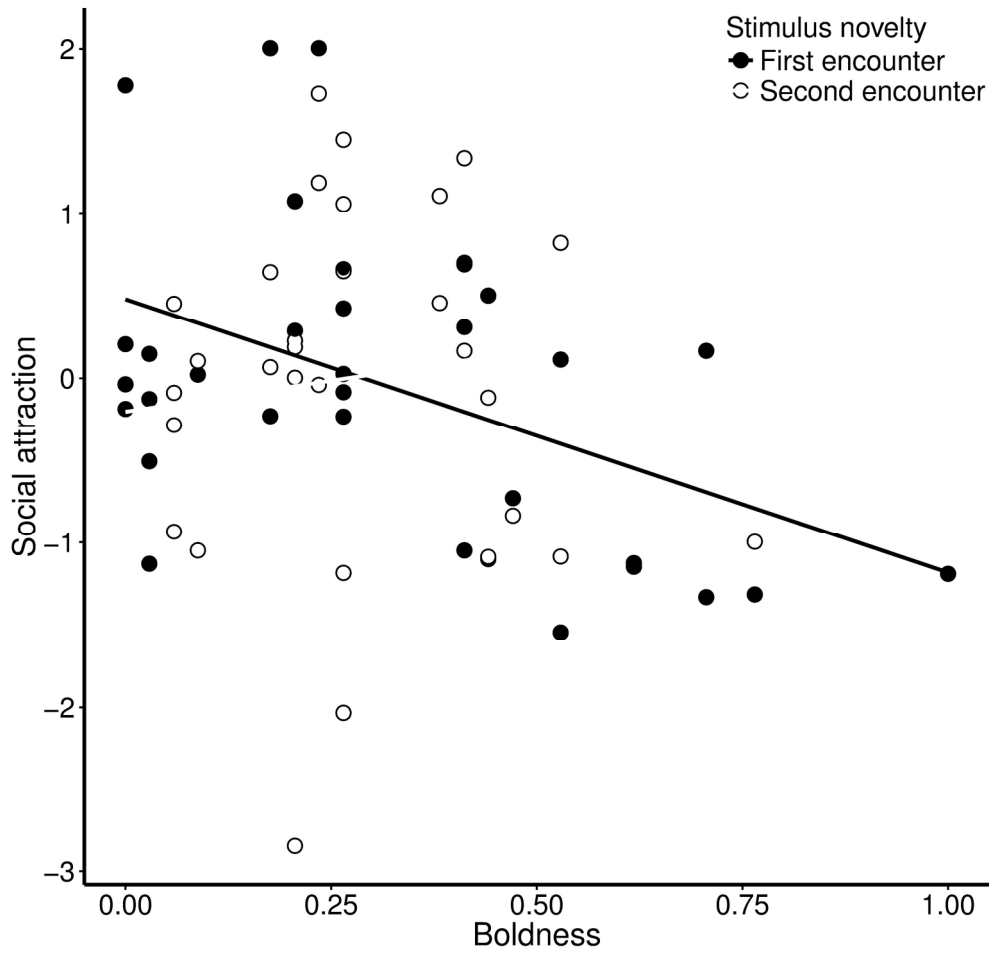
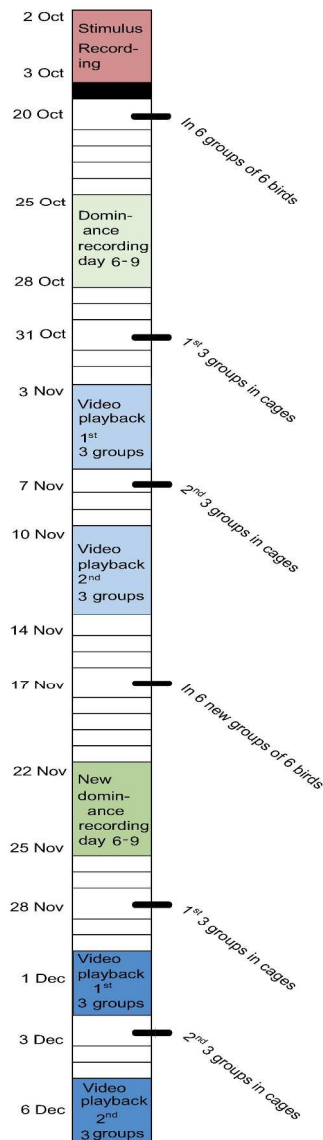


Figure 3 Shyer birds showed a stronger social attraction (PC-Social attraction) compared to bolder birds, when confronted with a specific great tit video stimulus for the first time (stimulus novelty = first encounter), while bolder birds showed a relatively stronger social attraction than shy birds when they were confronted with a specific great tit stimulus for the second time (stimulus novelty = second encounter). When excluding the boldest bird, shy individuals showed the strongest social attraction overall. Grey areas represent 95% CI.

figure 3  
195x187mm (300 x 300 DPI)

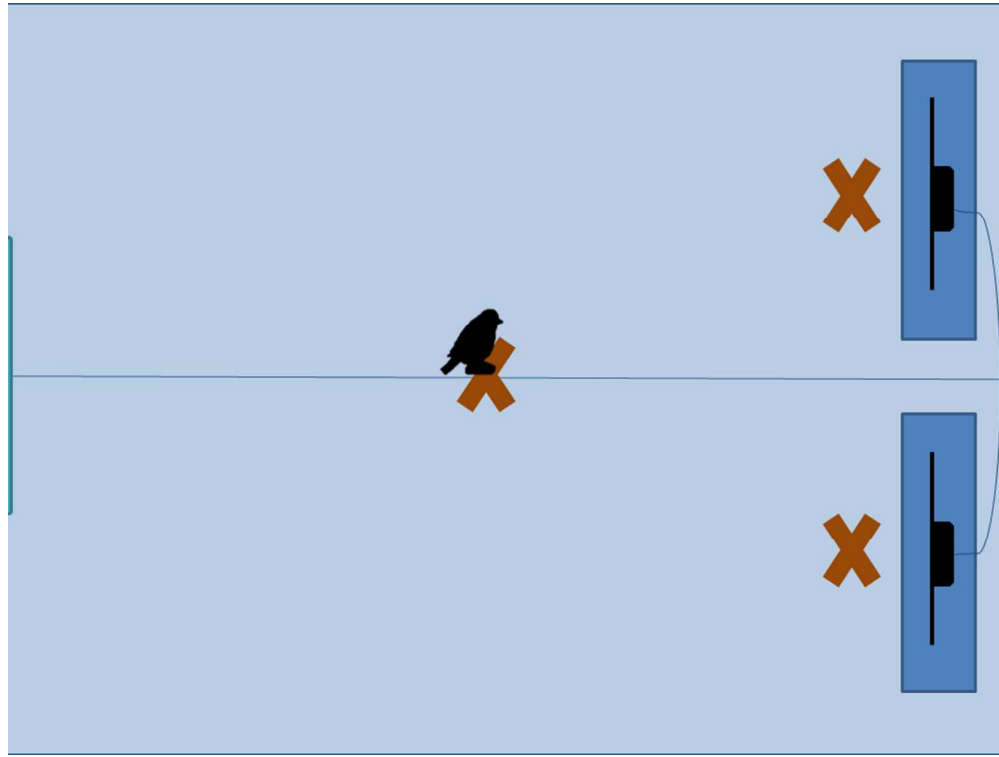


Supplementary figure S1. Time line of the experiment. Stimulus video recording took place three weeks before the start of the experiment. Subjects had not been in physical contact with each other since the hand-rearing period. We assigned 36 birds to single-sex groups of six birds (two female and four male groups) and housed them in six aviaries. We conducted dominance observations from the 6th until the 9th day birds were transferred to the aviaries, as dominance ranks in great tits stay relatively stable from that moment onwards (Verbeek et al., 1999). After a minimum of twelve days in the group, birds were individually housed in cages connected to the experimental room. Because of space limitations, we conducted the first four video playback trials (one trial per day) with individuals from only three groups. Subsequently, individuals from the first three groups were moved to new individually cages and individuals from the other three groups were moved into the cages adjacent to the experimental room. After we conducted all four playback trials also with these three groups, all birds (N = 36) were reassigned to six new groups based on their previous dominance ranks. We placed birds with similar dominance ranks together. After a new round of dominance recordings, one final video playback trial was conducted with each bird,

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again in two batches of three groups following the same protocol as before.  
supplementary figure S1  
203x634mm (300 x 300 DPI)

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Supplementary figure S2. Schematic overview of the experimental room. A wide-angle camera was located on the left hand side in the door of the experimental room above the one-way window. The observer was situated behind the one-way window (left hand side). A bird would enter from their home cage either along the upper side or lower side. Three artificial trees were present, one in front of each of the screens and one in the middle of the room. The bird could see both screens simultaneously when perched on the middle tree, but only one screen when perched on either one of the other two trees.

supplementary figure S2  
254x190mm (96 x 96 DPI)