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Original Article

Dominance rank and boldness predict social attraction in great tits

Lysanne Snijders,[a,b] Marc Naguib,[a] and Kees van Oers[b]
[a]Department of Animal Sciences, Behavioural Ecology Group, Wageningen University & Research, PO Box 338, 6700 AH Wageningen, The Netherlands and [b]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

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Social relationships can have important fitness consequences, and how well an individual is socially connected often correlates with other behavioral traits. Whether such correlations are caused by underlying individual differences in social attraction usually remains unclear, because to identify effects of individual traits on social attraction, it is essential to experimentally exclude the influence of the social partner. Using standardized high-definition video playback on captive great tits (*Parus major*), we effectively demonstrate the influence of individual traits on the motivation to be near a conspecific. We show that social attraction varied contrastingly with boldness and stimulus novelty. Shyer birds tended to show stronger social attraction when they were confronted with the stimulus bird for the first time. Lower ranked birds showed the overall strongest social attraction. This rank effect remained after experimentally changing dominance ranks by altering group compositions. Moreover, preference for social association tended to increase with a decrease in dominance rank, suggesting that birds plastically change their social preference in relation to their within-group dominance status. Our results provide insight into how social relations can form and change, processes that are key for understanding the long-term consequences of the social environment, and the role individuals might play in influencing this environment themselves.

Key words: **boldness, dominance, exploration, great tits, social attraction, video playback**

INTRODUCTION

In many animal populations, social associations are an essential part of an individual's ecology. Social connectivity modulates exposure to social information about where to forage and settle (Stamps 1988; Kurvers et al. 2010; Aplin et al. 2012; Templeton et al. 2012), but may at the same time increase social stress and aggression (Rowell 1974; Verbeek et al. 1996; Carere et al. 2003), indicating that an individual's social connectivity can have important fitness consequences (McDonald 2007; Oh and Badyaev 2010; Formica et al. 2012).

Many individual animals are not passive actors simply responding to the social environment, they also regularly influence the social environment themselves. Some individuals can even be disproportionally influential in the structuring and dynamics of the social environment (Modlmeier et al. 2014). Specific "policing" individuals were essential for maintaining stability in groups of pigtailed macaques (*Macaca nemestrina*) (Flack et al. 2006), and the presence of some hyperaggressive males decreased the average mating success for whole groups of water striders (*Aquarius remiges*) (Sih and Watters 2005). The influence individuals can exert on their social environment is especially interesting in relation to dominance structures. Dominance is a relative measure that depends on the other individuals in a group and, most importantly, is reversible (Rowell 1974; Drews 1993). Lower ranked individuals could thus influence the social environment to create better opportunities for themselves. For example, lower-ranked individuals in some species can increase their likelihood of rising in rank by social association and forming coalitions (McDonald 2007; Schülke et al. 2010; Gilby et al. 2013).

Social associations entail costs as well as benefits. Individuals in a more central position might experience more aggression (Rowell 1974; Carere et al. 2001; Colléter and Brown 2011), yet, being on the edge might leave an individual more vulnerable to predation (Romey and Galbraith 2008). When the costs and benefits of social associations differ between individuals, it is likely that their attraction to conspecifics will also vary. Previous studies have revealed intriguing correlations between the social associations and the dominance rank as well as the behavioral characteristics of individuals (Rushmore et al. 2013; Snijders et al. 2014). Higher ranked chimpanzees (*Pan troglodytes*) had more unique social associations (Rushmore et al. 2013), similar to more "exploratory" great tits

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Address correspondence to L. Snijders. E-mail: lysanne.snijders@wur.nl.

(*Parus major*) (Aplin et al. 2013; Snijders et al. 2014) and "bolder" three-spined sticklebacks (*Gasterosteus aculeatus*) (Pike et al. 2008). Yet slow exploring great tits showed more stable relationships and more collective behavior (Aplin et al. 2013, 2014) and shyer three-spined sticklebacks showed stronger unique associations (Pike et al. 2008) and stronger social attraction (Jolles et al. 2015). Also, a study on social networks in guppies revealed shyer guppies (*Poecilia reticulata*) to have more unique and stronger social associations (Croft et al. 2009). These findings suggest that individuals indeed could vary in social attraction in relation to their behavioral traits, yet the direction of these relationships may depend strongly on the specific context or the specific association measures (number vs. strength) used.

One of the challenges of studying social association behavior is that the formation of social associations can often be the consequence of the behavior of the focal individual, their social partner, and their interaction. Several studies indeed have revealed that social associations can strongly depend on the combination of the specific behavioral types of both individuals (Harcourt et al. 2009; Jolles et al. 2015; Keiser et al. 2016). When such interactions occur, it is difficult to reveal the underlying mechanism, because next to active approach or avoidance behavior of the focal individual, the social partner might also give subtle cues that promote or discourage a social association (Snijders and Naguib 2017).

These cues are certainly relevant in relation to dominance interactions, with subordinates providing signals that can elicit agonistic approaches by the dominants (Rowell 1974) or reduce the likelihood of a dominance interaction to take place (Drews 1993). Likewise, also dominants can show subtle behaviors that elicit or discourage associations (Drews 1993). Because it is difficult to detect or control for such signals, it usually remains unclear whether associations were actively initiated, elicited, or both. The role of social attraction, the tendency to initiate social associations independent of the social partner's (subtle) behavior, in such cases thus remains unresolved (Webster and Ward 2011; Wolf and Krause 2014). In human social structures, the tendency to initiate social associations is regarded vital for social relationships to form and maintain but is also not equal among individuals (Mollgaard and Mathiesen 2016). Insight into the individual factors driving variation in social attraction therefore represents an important next step toward understanding the mechanisms underlying the formation and stability of social structures (Flack et al. 2006; Shizuka et al. 2014).

To tease apart the effect of variation in social attraction from the response of a social partner, it is necessary to perform experimental manipulations that exclude the influence of the social partner. Hence, in this study, we conducted a standardized high-definition video playback experiment to study social attraction in great tits, an important model species for studying social connectivity (Aplin et al. 2013, 2014; Snijders et al. 2014, 2017). Video playback is now more realistic as a consequence of modern developments in recording devices and monitors, such as high-definition and LCD technology that circumvent previous challenges of conducting video playback with species with high flicker fusion frequencies, like birds (Oliveira et al. 2000; Bird and Emery 2008). Successful video playback studies have been conducted to study the social behavior of a variety of species, such as gloomy octopuses (*Octopus tetricus*), nutmeg manakins (*Lonchura punctulata*), and rooks (*Corvus frugilegus*) (Bird and Emery 2008; Rieucau and Giraldeau 2009a, 2009b; Pronk et al. 2010).

During our experiment, we provided subjects with a choice between a video of an empty cage and a video with an unfamiliar same-sex conspecific. Additionally, we conducted control trials to assure that our subjects were not merely responding to the movement on the screen. We expected lower ranked birds to show less social attraction, as we assumed that lower ranked birds would anticipate to be displaced by an unfamiliar conspecific. To subsequently illuminate a potential causal effect of dominance rank, we experimentally altered the dominance ranks by changing the group compositions and then repeated the experiment. Additionally, based on one of our own recent studies, revealing male fast explorers to spent relatively more time near any other male conspecific (Snijders et al. 2014), we expected fast explorers to show a stronger social attraction. Although we also expected an effect of boldness, given the previous mentioned contrasting findings in literature, we had no specific prediction regarding the direction of this effect.

METHODS

Experimental subjects

We used captive hand-reared first year great tits hatched in the spring of 2014, both as video playback stimuli (N = 38) and as experimental subjects (N = 36). These birds were offspring of captive parents but were raised by wild birds during the first 10 days after hatching and subsequently hand-reared under standard conditions (van Oers et al. 2005). Each bird was fitted with a unique aluminum leg ring and three color leg rings for individual recognition. Birds (12 females and 24 males) were sexed using molecular markers (Griffiths et al. 1998). For each bird, the tarsus (0.01 cm) was measured before the experiment and weight was monitored before and after the experiment (0.1 g) using a digital balance. Birds experienced natural daylight and temperature conditions (daily average: 3–10 °C) in semi-open aviaries (2 × 4 × 2.5 m). The indoor rooms with individual cages (0.9 × 0.4 × 0.5 m) were kept on a light regime similar to the natural day–night cycle and temperature maintained between 15 °C and 17 °C. Birds had auditory contact with each other at all times. All food and water was provided ad libitum, with the exception of mealworms, which were only provided in the aviaries and during experimental trials. See van Oers et al. (2005), for more details on housing conditions. Work was carried out under permit no. 14.12 granted to K.V.O. and M.N. by the Dutch legal entity: KNAW Dier Experimenten Commissie (DEC).

Experimental design

We conducted behavioral tests (novel environment and novel object tests) approximately 3 months before the start of the experiment. Next, all 38 birds (36 subjects) were recorded to become video stimuli, 3 weeks before the start of the experiment. Before the experiment, birds were always housed in individual cages and had not been in physical contact with each other since the hand-rearing period (3–4 months earlier). At the start of the experiment, 36 birds were randomly assigned to single-sex groups of six birds (two female and four male groups) and subsequently housed in six aviaries. We conducted dominance observations from 6 days to 9 days after the birds were grouped together, as dominance ranks in great tit groups stay relatively stable from the sixth day after group formation (Verbeek et al. 1999). After a minimum of 12 days in a group, birds were again individually housed for the onset of the video playback trials. An acclimatization period of at least 3 days was given before the onset of the experiment. After we conducted four video playbacks trials with each individual from all six groups, the birds were reassigned to six new groups based on their dominance ranks as measured in their original groups. In these new groups, we placed birds with similar dominance ranks together. The previous protocol was then repeated, after which one final video playback trial was conducted with each bird. See Supplementary Figure S1 for the exact timeline of the complete experimental setup.

Dominance

We assessed dominance ranks by observing interactions between birds in the aviaries from behind a one-way window. Groups were directly observed six times for half an hour directly and for two to three times half an hour by video. We conducted direct observations for each group on four consecutive mornings (07:30–13:00) and two afternoons (13:00–16:45), whereas video recordings were made only on mornings. During observations, we documented 1) displacement, 2) waiting, defined as an individual waiting for another bird to finish before feeding itself, and 3) aggressive behavior between two individuals (chasing and attacking). For each interaction, we noted the identity of the actor and the identity of the receiver. During the first round of dominance observations, 98–165 interactions were recorded per group, whereas the second round (after group compositions were changed) resulted in 166–236 interactions. We assigned dominance ranks based on the number of birds with whom an individual had lost the majority of its interactions. Group members could have the same dominance rank, as more than half of the groups did not have a significant linear hierarchy based on the linearity index h' (de Vries 1995). When it was unclear from how many birds exactly an individual had lost the majority of its interactions, due to unknown or tied relationships, we assigned the average of the minimum and maximum possible rank (6 of the 36 during the first round and 5 of the 36 during the second round).

We formed the six single-sex groups during the second round by grouping the three highest ranked birds of one group from the first round together with the three highest ranked birds of another group. This was likewise done, in a randomly paired fashion, for the three lowest ranked birds of each group. We used this specific procedure to force a number of the previously dominant individuals to adopt more submissive roles, and vice versa. The number of interactions in dominant groups ranged from 166 to 200 and in the subordinate groups from 172 to 236.

Boldness

Individual boldness was assessed for all, except one bird, using two standardized novel object tests as described in detail by Carere and van Oers (2004), approximately 3 months before the start of the experiment (at 50 days of age). These tests were based on the assay designed by Verbeek et al. (1994), in which the individual differences in novel object approach in juvenile great tits were strongly consistent for a duration of at least 9 weeks ($r_S = 0.81$).

Briefly, a novel object was presented in the home-cage on the furthest right of the three perches. Tests lasted 2 min and behavior was observed from behind a curtain. The boldness score was calculated following Drent et al. (2003), thereby incorporating the activity of the subject. Individuals not reaching the perch with the novel object within 2 min were given a score of 0–5 depending on the number of movements within these 2 min. Scores from 6 to 17 were given to animals that visited the perch, taking into account the latency to reach the perch and how close they approached the novel object. This score was then transformed to a score from 0 to 1, with 0 meaning that a bird did not move at all in the test and 1 indicating the bird touched the novel object repeatedly within 1 min. This measure was highly repeatable between the two novel object tests ($r = 0.44$, SE = 0.13, $N = 37$, $P = 0.003$). We used the average score for our analysis.

Exploratory behavior

The exploratory behavior of a bird (with exception of two individuals with temporary flight problems) was assessed with a standardized novel environment test following Drent et al. (2003) approximately 3.5 months before the start of this experiment (at 30–40 days of age). This test is conducted in a standard observation room that contains five artificial trees. After the bird enters the room, we quantify how it explores the new environment. The exploration score was calculated as the number of movements in the first 2 min (Dingemanse et al. 2002; Snijders et al. 2014). Exploratory behavior of wild juvenile and adult great tits recaptured and tested at least two times following this protocol from 1998 until 2001 (>200 birds) was repeatable for both sexes and for two different study areas (range $r = 0.27$–0.66, $P < 0.01$) (Dingemanse et al. 2002).

Exploratory behavior is a partially heritable behavioral trait in great tits (van Oers and Mueller 2010) but is also effected by the early social environment (Naguib et al 2011) and explains variation in various social behaviors, such as aggression (Verbeek et al. 1996), territory defense (Amy et al. 2010; Snijders et al. 2015b), approach of conspecifics (Groothuis and Carere 2005), social foraging (Aplin et al. 2014), and social network position (Aplin et al. 2013; Snijders et al. 2014).

Stimulus videos

Stimulus videos were constructed by recording a great tit from a fixed distance (40 cm) for 8–10 min in a white cage (0.67 × 0.37 × 0.38 m) including two perches and a Plexiglas front. Videos were recorded with a Full HD Panasonic HC-V550 (AVCHD, W 1920 × H 1080, 25 frames/s). In total, 29 of the 38 recorded videos were used in the experiment, only including videos of birds that were life size on full screen. We removed the sound of the videos to avoid potential influences of calls and songs and excluded the first 2 min of the original video. Using Adobe Premiere Pro (Adobe Systems, San Jose, CA), we selected an approximately 2-min time frame (Min: 1:46, Max: 2:05), in which the bird occupied the same location and body position at the start and end. This procedure allowed us to make realistic uninterrupted loops of the videos. Movement control videos were constructed by blurring a rectangle concealing the great tit in the stimulus video with Gaussian blurr (75.0) and Mosaic (250) frame by frame using Adobe Premiere Pro.

To test for the potential influence of stimulus bird activity, the stimulus videos were tracked with Ethovision XT (Noldus, static subtraction, sample rate: 25 s^{-1}). We checked the tracks manually afterward for incorrect detections and adjusted them if necessary. We used the total distance moved by center point (cm) as a proxy for stimulus activity.

Video playback protocol

All individual cages connected to the same experimental room (4.0 × 2.4 × 2.5 m) through sliding doors. The experimental room (Supplementary Figure S2), the same as the one used for the novel environment test, contained two wooden cages (0.85 × 0.40 × 1.0 m) with wire mesh on the front and attached on a rolling base (Reparaz et al. 2014), which we positioned against the back wall. Each of the two cages contained a black LCD computer monitor

(HP Compaq LA2306x, 60 Hz) allowing the birds a visual of the stimulus videos up to 20 cm. Additionally, the room contained three artificial "trees", with one tree in the middle of the room providing a view of both screens simultaneously and one tree in front of each screen that only allowed the bird to view one screen. We made observations through a one-way window situated at the opposite site of the room. Each stimulus video started before a subject entered the room and a trial lasted 15 min starting from the time a bird had entered the experimental room. Birds freely moved into the room by themselves. We turned off the lights after 15 min (birds stay perched then) and the subject was put back into its individual cage.

During the first round, each individual received four video playback trials. Per unique video stimulus bird (two for each subject), each subject received both an experimental trial and a movement control (video playback validation) trial in a random order. The experimental trial included a screen showing a bird in a cage and a screen showing the same cage empty (Supplementary Figure S2 and Supplementary Video S1). The movement control trial was similar to the experimental trial except that the video showing the empty cage was replaced by a great tit stimulus video, in which the bird in the video was "blurred" using video editing software. Subjects only received stimulus videos of birds that were unfamiliar to them (no previous or current group mates) and that were of the same sex. Movement control trials always showed the identical video stimulus bird (both blurred and original) as the subject would receive or had received during the accompanying experimental trial.

We randomized and balanced the screens (left or right) from which a video was shown. Trials per individual bird were 1 day apart, and the order between birds was kept constant. During the first two trials (video stimulus bird A), food was present in the form of four small cups attached to the trees in front of the screens. Each cup contained one mealworm. During the next two trials (video stimulus bird B), no food cups were present. We initially provided the mealworms to motivate the birds to come closer to the screens. However, to test whether the presence of food was not biasing the observed social attraction we removed the food during the following two trials. After group compositions changed, subjects received one experimental trial with a third unique video stimulus bird (video stimulus bird C; food was present). The experimental design thus included three experimental trials (social attraction tests) and two control trials (movement controls) for each of the 36 subjects (Table 1).

Table 1

Overview of the experimental design that included three experimental trials (social attraction test) and two control trials (movement control) for each of the 36 subjects

Before group composition change		**After**
Video stimulus bird A Two trials for each subject	**Video stimulus bird B** Two trials for each subject	**Video stimulus bird C** One trial for each subject
Experimental trial **following** Control trial	Experimental trial **following** Control trial	Experimental trial
OR	***OR***	
Control trial **following** Experimental trial	Control trial **following** Experimental trial	

Data analysis

All 180 trials were recorded (with the exception of three movement control trials due to video recording problems) using a broad angle camera from a fixed position (Observer, Noldus, Wageningen, The Netherlands). We used the program EthoVision XT version 9 (Noldus) to manually score the total duration and the frequency of visits 1) in the middle tree, 2) in front of the left cage, 3) in front of the right cage, or 4) in the rest of the experimental room. Sample sizes differ as a consequence of three failed data video recordings (only movement control trials) and of four birds that for a total of 13 times did not make a decision within 15 min (movement control and experimental trials). We calculated general interest in the videos as the total time spent in front of one of the videos divided by the total experiment duration (15 min). Our key metric, "social preference" was calculated as the proportion of time spent in front of the great tit video divided by the total time spent in front of the great tit video and the other video (empty cage or blurred great tit video). This measure has been used as a reliable indicator in mate-choice experiments (Schielzeth et al. 2008; Reparaz et al. 2014) and has been successfully used in captive great tits to quantify personality differences in social exploration in response to social defeat (Carere et al. 2001).

To analyze whether the subjects distinguished the great tit video stimuli from mere movement, we tested whether average social preference was significantly higher than random (Mean = 0.5). Indeed, the subjects spent a significantly higher proportion of time near the unmanipulated great tit video than would be expected if birds were randomly dividing their time over the great tit video and the identical blurred version of the video (two of the four trials $P < 0.05$; Figure 1).

Interestingly, birds only spent more time than expected at random near the social stimulus when they had received the control trial before the experimental trial, thus when they had not seen the specific stimulus video bird before (one sample *t*-test social preference against Mean = 0.5; video stimulus bird A: 1st encounter, Mean = 0.64, SD = 0.17, Range = 0.40–0.89, $t_{(14)} = 3.11$, $P = 0.008$ and 2nd encounter, Mean = 0.55, SD = 0.17, Range = 0.31–0.94, $t_{(16)} = 1.36$, $P = 0.19$; video stimulus bird B: 1st encounter, Mean = 0.62, SD = 0.20, Range = 0.27–0.95, $t_{(15)} = 2.42$, $P = 0.03$ and 2nd encounter, Mean = 0.52, SD = 0.32, Range = 0.03–0.94, $t_{(15)} = 0.30$, $P = 0.77$; Figure 1). Interest (the total time the great tits spent in front of either screen) was overall high with 71% (SD = 20%) when the first unique video stimulus was presented (stimulus A) and 64% (SD = 24%) when the second unique stimulus video was presented (stimulus B). That the birds showed a significant preference during the first and again in the third trial (when they received a novel video stimulus bird) but not during the second and the fourth trial (when they had already encountered the video stimulus bird before during the experimental trial) strongly suggest that neither habituation to the experimental setup nor difference in clarity or contrast between the social stimulus videos and the movement control videos explains the preference for the social stimulus. In summary, the subjects distinguished the great tit video stimuli from mere movement, responding with significant social preference when a new video stimulus bird was shown.

Also in the experimental trials, the birds spent on average more than 50% of the time with the social stimulus (video stimulus bird A: Mean = 0.57, SD = 0.24, Range = 0.11–1.00, $N = 34$; video stimulus bird B: Mean = 0.63, SD = 0.20, Range = 0.23–0.97, $N = 34$; video stimulus bird C (after group rearrangement): Mean = 0.57, SD = 0.22, Range = 0.01–0.92, $N = 34$).

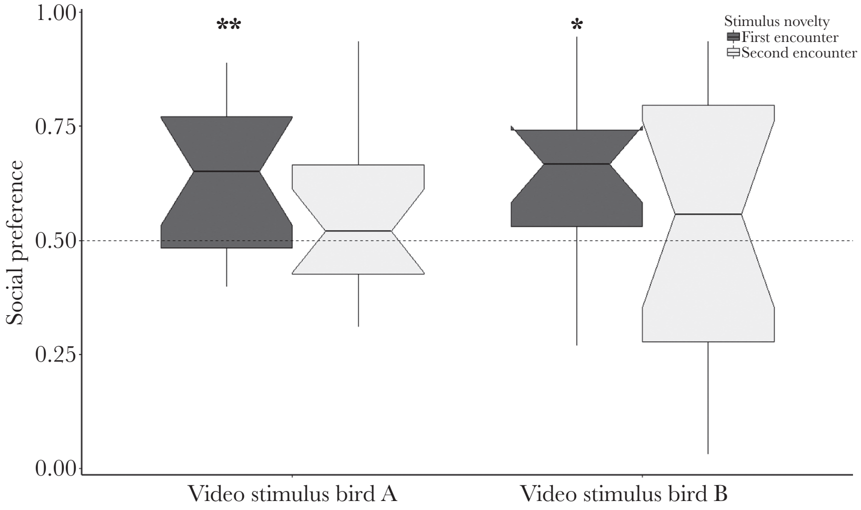

Figure 1

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 gray: stimulus novelty = first encounter, light gray: stimulus novelty = second encounter). This was true for the first (bird A) as well as for the second video stimulus presented (bird B). Notches not overlapping the chance line (0.5) visualize a significant divergence from chance. * $P < 0.01$, ** $P < 0.05$.

Next to *social preference*, *social choice* was calculated by dividing the total number of times the subjects moved to the great tit video from the neutral, middle tree by the total number of times the subject moved to either of the two screens. For analysis of the experimental trials (control trials were excluded from this analysis), we extracted the principal component (PC-social attraction) of *social preference* and *social choice* (arcsine transformed for normality) for stimulus bird A, B, and C (loadings on component > 0.9, eigenvalue > 1.6; percentage variance explained > 81%). Preference and choice were strongly correlated (weighted regression of *social choice* against *social preference*; $\beta > 0.59$, $P < 0.001$, for movement control trials; $\beta > 0.64$, $P < 0.0001$, for experimental trials). We calculated the repeatability for these measures before the change in group composition, following Lessells and Boag (1987). For this, we only included individuals that made at least one active choice in both trials, excluding one bird. Increasing the threshold of the number of active choices up to 10 did not significantly change our results.

To analyze social attraction, we conducted a mixed-model analysis (restricted maximum likelihood [REML]) with residuals weighted for the number of active choices made (from the tree in the middle) per individual per trial. We considered the observed social attraction of individuals that made more choices to be more reliable than of individuals that only made a small number of choices, because with fewer choices there is a higher risk of extreme chance effects. The starting model analyzing the first round of video playback experiments included PC-social attraction (dependent), boldness (covariate), exploratory behavior (covariate), dominance rank (covariate), stimulus novelty (first or second time encounter with the specific great tit stimulus; factor), food present (factor), and individual nested in aviary group (random factor). Additionally, based on our results, with the movement control trials, the model included the two-way interactions between dominance rank and stimulus novelty, boldness and stimulus novelty, and exploratory behavior and stimulus novelty. In our dataset, boldness was not correlated with exploratory behavior (Spearman correlation test; $r_S = -0.22$, $P = 0.21$, $N = 34$) or dominance rank (Spearman correlation test; $r_S = -0.01$, $P = 0.94$, $N = 35$). Also, exploratory behavior was not correlated with dominance rank (Spearman correlation test; $r_S = 0.00$, $P = 0.98$, $N = 34$). A back-wise model selection procedure was conducted by removing the least significant terms from the model stepwise ($0.1 < P < 1.0$), starting with the highest level interactions.

To further investigate whether the effects of dominance rank and behavioral characteristics changed over the course of the trial, we analyzed whether the likelihood of choosing the social stimulus differed between the last and the first choice a bird made. We conducted an analysis with social stimulus choice (yes/no) as the binary dependent variable. Our starting model was based on the final model for the analysis of social attraction but now included interactions with first/last choice. Model simplification was based on a stepwise backward selection procedure. We only considered active choices made from the tree in the middle of the room (*social choice*). Additionally, we only considered trials in which the bird made at least two choices and in which a bird made its first visit to one of the screens while having first perched on the tree in the middle. In this way, we could assure that each bird would have had an equal good view of both of the screens while making the first choice.

To test for potential effects of sex and body condition on social attraction, physical characteristics were added as control variables to the final model for social attraction. We calculated body condition as the residual of weight over tarsus for each sex separately. Neither sex ($F_{1,21.43} = 0.21$, $P = 0.65$) nor body condition ($F_{1,20.02} = 2.23$, $P = 0.15$) had a significant effect. Moreover, activity of the video stimulus bird did not influence the PC-social attraction (Spearman correlation test; video stimulus bird A: $r_S = 0.20$, $P = 0.25$, $N = 34$; video stimulus bird B: $r_S = 0.02$, $P = 0.92$, $N = 33$). Similarly, there was no effect of stimulus activity when solely analyzing the first and third trial ($r_S < 0.24$, $P > 0.35$). Stimulus activity as a control variable in the final model also did not have a significant effect ($F_{1,42.09} = 1.11$, $P = 0.30$). Finally, there was no main effect of food presence during the experiments ($F_{1,49.47} = 1.985$, $P = 0.17$).

To test whether the newly acquired dominance rank had an effect on social attraction, we again used a mixed-model analysis (REML) with the residuals weighted by the number of choices made per individual per trial. The starting model included PC-social attraction (dependent), dominance rank (covariate), any significant behavioral traits from the first model (covariate), and aviary group (random factor). One bird made twice as many choices as the bird with the second highest number of choices. Reducing the number of choices (weight) of this individual to the value of the second highest bird resulted in a trend effect of new dominance rank in the same direction as in the original model (see Results).

All statistical analyses were conducted in IBM SPSS Statistics for Windows, Version 22.0 (IBM Corp, Armonk, NY). We used nonparametric tests if the data were not normally distributed according to the Shapiro–Wilk test.

RESULTS

Dominance rank, boldness, and exploratory behavior in relation to social attraction

Great tits spent over 60% of the total time in front of the screens, and this did not decrease with the total number of trials received (60.8%, 69.7%, 66.3%, and 67.6% respectively). There was a tendency for the proportion of time spent near the social stimulus (*social preference*) to be moderately repeatable when comparing the first two experimental trials ($r = 0.26$, SE = 0.16, $P = 0.07$) but the proportion of times an individual actively chose to sit near the social stimulus (*social choice*: $r = -0.01$. SE = 0.18, $P = 0.53$) and the combined measure for social attraction (*PC-social attraction*) were not ($r = 0.13$, SE = 0.17, $P = 0.24$).

Lower ranking individuals showed a stronger social attraction (PC-social attraction) compared with higher ranked birds (Rank: $F_{1,\ 26.80} = 5.58$, $P = 0.03$; Figure 2). Shyer birds showed the strongest social attraction when they encountered a unique video stimulus for the first time, whereas bolder birds showed a relatively stronger social attraction when they encountered a unique video stimulus bird for the second time (Boldness × Stimulus novelty: $F_{1,\ 58.88} = 4.27$. $P = 0.04$; Figure 3). When solely considering novel video stimuli birds, shy birds still tended to show a higher social attraction (mixed model: $F_{1,21.58} = 3.38$, $P = 0.08$), whereas there was no effect of boldness when only considering video stimuli birds that were presented for the second time (mixed model: $F_{1,15.42} = 1.24$, $P = 0.28$). However, when the boldest individual (Figure 3) was left out of the analysis, there was no longer a significant interaction between boldness and novelty but an overall significant effect of boldness, with shyer individuals showing more social attraction (boldness: $F_{1,60} = 6.38$, $P = 0.01$; rank: $F_{1,60} = 4.43$, $P = 0.04$). Finally, exploratory behavior did not predict social attraction either as main effect (mixed model: $F_{1,28.98} = 0.01$, $P = 0.94$) or in interaction with stimulus novelty (mixed model: $F_{1,49.96} = 0.85$, $P = 0.36$).

To examine whether the effects of dominance rank and boldness changed over the course of the trial, we analyzed whether the likelihood of choosing the social stimulus differed between the first and the last choice in a trial. Birds overall tended to choose the social stimulus less during their last choice, but there was no significant interaction between the first or last choice and either dominance rank or boldness (Table 2).

Influence of dominance rank on social attraction after manipulation

The time spent in front of the screens during the final experimental trial, after the experimental change in dominance rank, was significantly higher (77%) when compared with the first experimental trial (paired *t*-test: $t_{(32)} = -2.83$, $P = 0.01$).

Even after the change in ranks, the birds with the lowest dominance rank showed again the strongest social attraction ($F_{1,26.99} = 4.54$, $P = 0.04$), whereas there was no significant correlation between old dominance rank and new dominance rank (Pearson correlation; $r = 0.21$, $P = 0.22$, $N = 36$). Adding the old rank as a control variable did not have a significant effect ($F_{1,10.30} = 0.42$, $P = 0.53$). Moreover, social preference tended to increase with a decrease in dominance rank (weighted regression, proportion of time spent with the great tit video stimulus weighted by minimum number of choices, $\beta = -0.34$, $P = 0.07$).

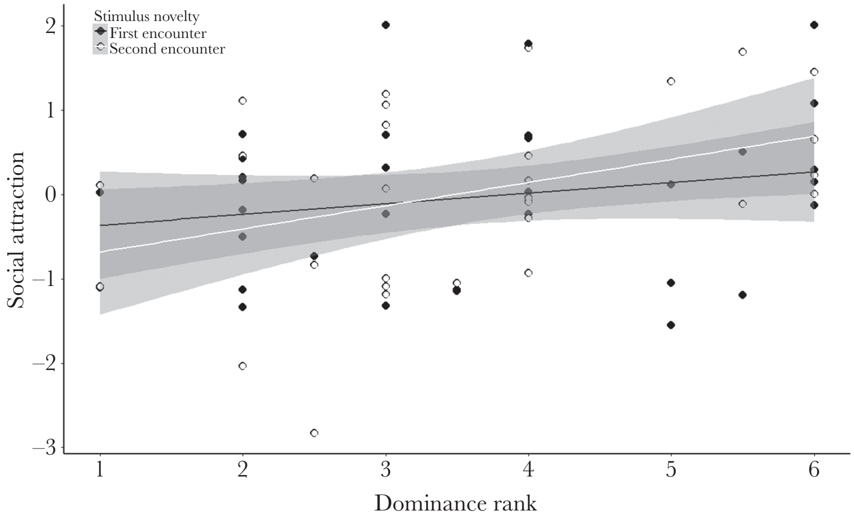

Figure 2

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, whereas the second time (stimulus novelty = second encounter) is represented in white. Gray areas represent 95% confidence intervals.

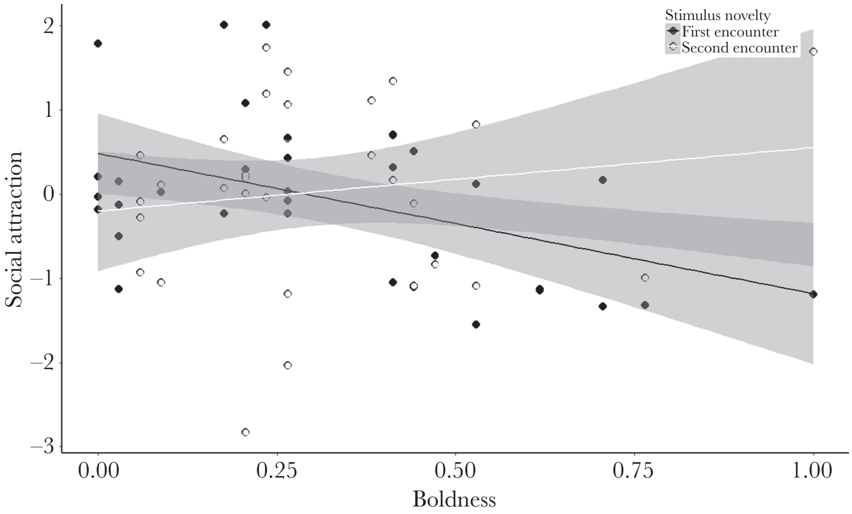

Figure 3

Shyer birds showed a stronger social attraction (PC-social attraction) compared with bolder birds, when confronted with a specific great tit video stimulus for the first time (stimulus novelty = first encounter), whereas bolder birds showed a relatively stronger social attraction than shyer 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. Gray areas represent 95% confidence interval.

Table 2

Mixed-model statistics for probability of choosing the social stimulus

Independent	Test statistic	DF residuals	*P* value
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 × First/Last choice	Z = 0.61	79	0.54

Statistics of main effects and interactions of interest are reported for the last occurrence of a variable or variable interaction in the model.

DISCUSSION

Using high-definition video playback, we uncovered a relationship between dominance and social attraction. More specifically, we here reveal a negative effect of dominance rank on the motivation to be in proximity of a simulated conspecific. Even after our manipulation of dominance rank by changing group compositions, low-ranking individuals showed the highest social attraction. Social attraction thus seems to be a relatively plastic behavior in these birds. Finally, we found evidence for a negative effect of boldness on social attraction, especially when the social stimulus was novel.

Responses of the subjects were unlikely to be driven by mere curiosity for movement on the screen, as we showed that the subjects could distinguish between the video stimulus and mere movement. Moreover, during the control trials, the birds showed significant social preference when a new video stimulus bird was encountered which they did not show when they had already seen a specific video stimulus bird before. Finally, we did not find evidence of any relationship between stimulus bird activity and observed social attraction. Indeed, several previous studies have revealed that video playback experiments can be effective tools to study social behavior in birds (Partan et al. 2005; Bird and Emery 2008; Rieucau and Giraldeau 2009a, 2009b; Boogert et al. 2013; Zoratto et al. 2014).

We reveal that lower ranked birds showed a significant higher social attraction, when offered the choice between a video of an unfamiliar great tit and a video of an empty cage. This result is somewhat surprising as we expected subordinate birds to be more evasive of unfamiliar conspecifics. Moreover, the significant effect of the new rank, but not the old rank, after we changed group compositions, strongly suggests a causal relationship between rank and social attraction. Possibly, lower ranked individuals actively initiated social associations as soon as they realized that the stimulus bird was not a threat to them. Yet, this seems unlikely, since throughout a trial birds did not change in their likelihood of social association depending on their dominance rank. Alternatively, subordinate birds might in general have to be more socially aware to avoid confrontations and they might therefore be more inclined to investigate a social stimulus. Indeed, as it is the subordinate's behavior that often determines the outcome of a dominance interaction ("you cannot chase someone who doesn't flee") lower ranked individuals have been suggested to be more socially responsive (Rowell 1974).

Furthermore, subordinate birds might be seeking social association because it could increase the social status or dominance rank, as shown for long-tailed manakins (*Chiroxiphia linearis*) (McDonald 2007) and eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Gilby et al. 2013) but also for male great tits associating with females (Sandell and Smith 1991). Furthermore, in nature, social associations can lead to more social information on feeding locations (Aplin et al. 2012) and thereby increase survival chances, because subordinate birds are known to suffer higher mortality from starvation (Gosler 1996). Finally, it could be a mechanism that increases overall vigilance. It would benefit lower ranked individuals that have less time to spend on vigilance (Krams 1998) to have the additional vigilance of a social partner in addition to the increased safety in numbers. For example, shared vigilance during foraging has recently been revealed as a likely driver of same-sex pair formation in rabbitfish (*Siganus* spp.) (Brandl and Bellwood 2015).

We showed that shyer birds spent relatively more time near a novel stimulus bird, indicating a higher social attraction when confronted with an unfamiliar conspecific. A study looking at social exploration in male great tits, measured as the time spent close to the cage of a unfamiliar male conspecific, likewise revealed that slower explorers (exploration score is a combination of the novel environment score and the novel object score in this study) spent more time on social exploration (Carere et al. 2001). Combined with this study, these findings suggest that great tits with reactive personality types have a higher motivation to spend time near (unfamiliar) conspecifics, at least in a nonthreatening context. Shyer individuals have previously been revealed to be more sensitive to the social environment (Carere et al. 2001; Kurvers et al. 2010; Webster and Ward 2011; Jolles et al. 2014; Guillette et al. 2015, but see Marchetti and Drent 2000).

Bolder birds seemed to become more socially attracted the second time they saw a particular stimulus bird. This could be explained by them becoming more interested in a stimulus bird that appears to be "persistent" (Amy et al. 2010; Snijders et al. 2015b). However, this interaction effect hinged on one particular bold individual, and exclusion of this one individual revealed shy birds to show greater social attraction overall. The contrasting effects of boldness detected in this study might thus not be biologically meaningful.

Previous studies in the wild found a positive effect of exploratory behavior on the time spent close to conspecifics (Aplin et al. 2013; Snijders et al. 2014), but we did not find an effect in this study. Fast exploring great tits are more risk-prone (van Oers et al. 2004) and are often the more aggressive and stronger responders in social conflicts (Amy et al. 2010; Snijders et al. 2015b; Verbeek et al. 1996). Because we created a much less hostile environment by presenting unfamiliar social stimuli via (non-threatening) videos, this might explain why we did not find effects of exploratory behavior on social attraction. This also emphasizes the difficulty of drawing causal conclusions from unmanipulated social associations that are the consequence of both the focal individual and the social partner. Unmanipulated individuals could be sending out (subtle) signals promoting or discouraging social associations and this stresses the necessity to perform fully controlled social stimulus experiments.

In conclusion, using effective manipulation of social stimuli via high-definition video playback, we have experimentally demonstrated the causal effect of dominance rank on the strength of social association in a key model species for the study of social dynamics (Carere et al. 2003; van Oers et al. 2005; Aplin et al. 2013; Snijders et al. 2015a, 2017). It is important to understand whether and how individuals can adapt to socially imposed traits, such as dominance rank, which can have large fitness consequences (Gosler 1996; McDonald 2007; Colléter and Brown 2011; Gilby et al. 2013). Moreover, insight into how social relations and thus social structures form, are maintained, and change, is crucial for understanding the long-term consequences of the social environment, including group positioning and social network connectivity (McDonald,2007; Romey and Galbraith 2008; Oh and Badyaev 2010; Formica et al. 2012; Shizuka et al. 2014; Culina et al. 2015; Snijders and Naguib 2017). Furthermore, understanding the mechanisms of social structuring can be key for identifying keystone individuals (Modlmeier et al. 2014) and their influence on the social environment. We therefore aim to stimulate the future use of such novel technologies to advance our understanding of the mechanisms of social structuring in ecology and evolution.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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