Dominance rank and boldness predict social attraction in great tits

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Lay summary

Social bonds can have important fitness consequences. Yet individuals often differ in how well they are socially bonded in relation to certain individual traits. We examined if such traits relate to differences in social attraction. Using video playback in great tits, we demonstrate a causal effect of dominance and a contrasting relationship between boldness and social attraction, depending on stimulus novelty. Our findings suggest that individuals change their social behavior depending on dominance rank.

Title: Dominance rank and boldness predict social attraction in great tits

Short title: Dominance predicts social attraction in great tits

Abstract

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 on individuals and the consequences certain individuals can have on the social environment.

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 connectivity with its social environment can have important fitness consequences (McDonald, 2007; Oh and Badyaev, 2010; Formica et al., 2012).

Yet, 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 disproportionately 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 hyper-aggressive 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, which 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, however, entail costs as well as benefits. Being in a more central position might result in receiving more aggression and experiencing more social stress (Rowell, 1974; Careere et al., 2001; Colléter and Brown, 2011). Yet, being on the edge, especially from a group positioning perspective, 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 the 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 (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; Aplin et al., 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 versus 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 usually 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.
These cues are certainly relevant in relation to dominance interactions, with subordinates giving off signals that can illicit agonistic approaches by the dominants (Rowell, 1974) or actually remove the need for a dominance interaction to take place (Drews, 1993). Likewise, also dominants can show subtle behaviors that illicit or discourage associations (Drews, 1993). Because it is difficult to detect or control for such signals, it usually remains unclear if 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 between individuals (Mollgaard and Mathiesen, 2016). Insight into the individual factors driving variation in social attraction therefore represents an important next step towards understanding the mechanisms behind 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; Aplin et al., 2014; Snijders et al., 2014). Video playback is now more realistic than ever before as a consequence of modern developments in recording devices and monitors, such as high definition and LCD technology which circumvent previous challenges to 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, 2009b, a; 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 for the stimulus bird, 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 we conducted the experiment again. Additionally, based on one of our own recent studies, revealing male fast explorers to spent relatively more time near any other male great tit (Snijders et al., 2014), we expected fast explorers to also here show a stronger social attraction. Yet, 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 the 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 experimental subjects (N = 36). These birds were chicks of captive parents, but were raised by wild birds during the first ten 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, 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, during
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 x 4 x 2.5 m). The indoor rooms with individual cages
(0.9 x 0.4 x 0.5 m) were kept on a light regime similar to the natural day-
night cycle, and temperature maintained between 15 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 KVO and MN by the Dutch legal entity: KNAW
Dier Experimenten Commissie (DEC).

**Experimental Design**

We conducted behavioral tests (novel environment and novel object tests)
approximately three months before the start of the experiment. Next, all 38
birds (36 subjects) were recorded to be video stimuli, three weeks before
the start of the experiment. Before the experiment birds were always
housed in individual cages and so had not been in physical contact with
each other since the hand-rearing period (three to four 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 six to nine 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 twelve days in a group, birds were again individually housed for the onset of the video playback trials. An acclimatization period of at least three 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), while video recordings were made only on mornings. During observations we documented displacement, waiting, defined as an individual waiting for another bird to finish before feeding itself, and 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, while 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 exactly how many birds an individual had lost the majority of its interactions with due to unknown or tied relationships, we assigned the average of the minimum and maximum possible rank (six out of 36 during the first round; five out of 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 three 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 minutes 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
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min were given a score of 0-5 depending on the number of movements within these 2 min. Scores from 6–17 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 one minute. This measure was highly repeatable between the two novel object tests ($r = 0.44$, $SE = 0.13$, $N = 37$). 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 which 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 minutes (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) 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 eight to ten minutes in a white cage (0.67 x 0.37 x 0.38 m) including two perches and a Plexiglas front. Videos were recorded with a Full HD Panasonic HC-V550 (AVCHD, W 1920 x H 1080, 25 fps). 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 two minutes of the original video. Using Adobe Premiere Pro (Adobe Systems, San Jose, US) we selected an approximately two-minute 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 blur (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/sec). We checked the tracks manually afterwards 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 x 2.4 x 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 x 0.40 x 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’ (as described by Dingemanse et al. (2002)) 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 lasted fifteen minutes 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 fifteen minutes (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 video 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 which 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 one day apart and the order between birds was kept constant. During the first two trials (first video stimulus bird) 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 following two trials (second video stimulus bird) no food cups were present. We initially provided the mealworms to motivate the birds to come closer to the screens. However, to test if the presence of food was not biasing the observed social attraction we removed the food during the following two trials. During the second round (after group compositions changed), subjects received one experimental trial with a third unique video stimulus bird (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).

Data analysis
All 180 trials were recorded (with 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, Wageningen, The Netherlands) to manually score the total duration and the frequency of visits on (1) 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) or of four birds that for a total of thirteen times did not make a decision within fifteen minutes (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 great tits distinguished the great tit video stimuli from mere movement, we tested if average social preference was significantly higher than random (Mean = 0.5). The subjects spent a significantly higher proportion of time near the un-manipulated 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 out of four trials $P < 0.05$).

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 (figure 1), thus when they had not seen the specific stimulus video bird before (One sample T-Test Social preference against $Mean = 0.5$; First stimulus video: 1st encounter; $Mean = 0.64$, $SD = 0.17$, $Range = 0.40 - 0.89$, $t_{(14)} = 3.11$, $P = 0.008$; 2nd encounter; $Mean = 0.55$, $SD = 0.17$, $Range = 0.31 - 0.94$, $t_{(16)} = 1.36$, $P = 0.19$; Second stimulus video: 1st encounter; $Mean = 0.62$, $SD = 0.20$, $Range = 0.27 - 0.95$, $t_{(15)} = 2.42$, $P = 0.03$; 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 the videos) was overall high with 71% ($SD = 20\%$) when the first unique video stimulus was presented and 64% ($SD = 24\%$) when the second unique stimulus video was presented. 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 set-up nor differences 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 (first video stimulus: Mean = 0.57, SD = 0.24, Range = 0.11 – 1.00, N = 34; Second video stimulus: Mean = 0.63, SD = 0.20, Range = 0.23 - 0.97, N = 34; Third video stimulus (after group rearrangement): Mean = 0.57, SD = 0.22, Range = 0.01 - 0.92, N = 34).

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 videos. For analysis of the experimental trials (control trial were excluded from this analysis), we extracted the principal component (PC-
Social attraction) of social preference and social choice (arcsine transformed for normality) for each unique stimulus bird (Loadings on component > 0.9, Eigen value > 1.6; Percentage variance explained > 81%). Both measures were strongly correlated (Weighted Regression of social choice against social preference; β > 0.59, P < 0.001 for movement control trials; β > 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 (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, since 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 step-wise ($0.1 < P < 1.0$), starting with the highest-level
interactions.

To further investigate if effects of 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 has 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; First video stimulus bird: $r_S$
$= 0.20, P = 0.25, N = 34$; Second video stimulus bird: $r_S = 0.02, P = 0.92, N =
33$). 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 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 non-parametric
tests if the data was 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 videos, 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) between the first two
experimental trials to be moderately repeatable ($r = 0.26, SE = 0.16, P =
0.07$), 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 to 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, while 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: $F_{1,21.58} = 3.38, P = 0.08$), while 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 if 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 videos during the final experimental trial,
after the experimental change in dominance rank, was significantly higher
(77%) when compared to 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 ($F_{1.26.99} = 4.54, P = 0.04$),
while 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, \( \beta = -0.34, \ P = 0.07 \)).

**Discussion**

Using High Definition video playback, we uncovered effects of individual behavioral characteristics on 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, 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, b; 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, because 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 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, since 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, who 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 an unfamiliar male conspecific, also 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 non-threatening context. Intriguingly, 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) (Jolles et al., 2014; Guillette et al., 2015), but see (Marchetti and Drent, 2000).

Bolder birds seem to become more socially attracted the second time they see 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.

Lastly, 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), while 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 (Verbeek et al., 1996; Amy et al., 2010; Snijders et al., 2015b). Because we created a much less hostile environment by presenting unfamiliar social stimuli via (none-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 un-manipulated social associations that are the consequence of both the focal individual and the social partner. Un-manipulated 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, by 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). It is important to understand if 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). 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.

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Figure legends

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 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 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 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.

Grey areas represent 95% CI.
Tables and table legends

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

<table>
<thead>
<tr>
<th>Before group composition change</th>
<th>After</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>First video stimulus</strong></td>
<td><strong>Second video stimulus</strong></td>
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<tr>
<td>Two trials for each subject</td>
<td>Two trials for each subject</td>
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<tr>
<td>Experimental trial</td>
<td>Experimental trial</td>
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<tr>
<td>AND</td>
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<tr>
<td>Control trial</td>
<td>Control trial</td>
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<td>OR</td>
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<td>Control trial</td>
<td>Control trial</td>
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<td>AND</td>
<td>AND</td>
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<tr>
<td>Experimental trial</td>
<td>Experimental trial</td>
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</tbody>
</table>
Table 2. Mixed model statistics for probability of choosing the social stimulus. Statistics of main effects and interactions of interest are reported for the last occurrence of a variable or variable interaction in the model.

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

First/Last choice
Supplementary data legends

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 playbacks 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, again in two batches of three groups following the same protocol as before.

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 video S1. The experimental set-up. A male great tit in the experimental trial can choose sitting close to a screen showing a cage containing an unfamiliar male conspecific or a screen showing an empty cage.
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