Title: Social network node-based metrics can function as proxies for animal personality traits

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Abstract: Behavioural traits are considered animal personality traits when individuals differ consistently in trait expression across time and context. Previous research has primarily focused on the shy-bold continuum, with research on sociability as potential proxy for animal personality traits only recently being considered. Here, we test the hypothesis that three node-based metrics derived from social association networks between individuals (strength, betweenness, closeness) can be considered proxies for animal personality traits in a passerine bird. Using experimental data from house sparrows in captive populations, and observational data from house sparrows in a wild population, we show that all three traits exhibit repeatability. The highest repeatability values were estimated in male-only captive groups, while repeatabilities estimated in single-sex networks subsets from mixed-sex groups showed no sex-specificity. We also show that changes in social group composition led to a decrease in repeatability for up to six months. Concluding, this work provides substantial and generalizable support for the notion that social network node-based traits map animal personalities.

Introduction:

Behaviour is considered to be flexible over time and context, allowing animals to respond to variation in the environment, and in particular, the social conditions (Réale & Dingemanse 2010). Also, individuals differ consistently in their behavioural phenotypes over both time and context, such as differing social or physical environments (Montiglio, Ferrari & Réale 2013). In cases where individuals consistently differ in their behavior across time and context, such individual differences have been termed animal personality (Réale *et al.* 2007) and have attracted extensive research (Wolf *et al.* 2007; van Oers & Mueller 2010, Wolf & Weissing 2012) .

Previous research on animal personality has primarily focused on the shy-bold continuum in captive populations which quantifies behaviours based on the individual's tendency to explore novel environments (Dingemanse *et al.* 2004; Dingemanse & Réale 2004; Smith & Blumstein 2007; Abbey-Lee & Dingemanse 2019). This research has shown that not only do animals differ consistently in their mean behavioural expression across time and context, but also these personality types have a heritable component (Dochtermann *et al*. 2019; van Oers *et al.* 2004; Montiglio *et al.* 2013; Winney *et al.* 2018). Different animal personality types have associated advantages and disadvantages, such as predator avoidance, access to social information and disease transmission (Wilson *et al.* 2013; Abbey-Lee & Dingemanse 2019, Moiron *et al.* 2019) suggesting a trade-off. Comparatively little attention has been dedicated to the study of animal personality in the context of sociability, defined as the tendency of individuals to interact with other conspecifics (Dingemanse & Réale 2004; Krause, James & Croft 2010). However, the sociable component has received less attention. More social individuals are likely to obtain essential information from others that will benefit their fitness, such as potential threats or the location of resources (Bergmüller & Taborsky 2010; Brent 2015; St Clair *et al.* 2015). Contrary, less social individuals – those that take part in fewer interactions – may obtain benefits by avoiding costs of being social, such as conflict, competition and disease transmission (Corner, Pfeiffer & Morris 2003; Atton *et al.* 2014; Silk *et al.* 2017).

The social environment, namely the group of individuals that interact with a focal individual, is crucial in shaping personality as social factors and interactions can both affect and be influenced by others, creating feed-back loops (Krause *et al.* 2010; Bergmüller & Taborsky 2010). However, data testing the underlying hypothesis – that social interactions can be considered animal personality traits – is still relatively limited. The inherent complexity of social interactions requires the integration of social network methodology (Krause et al., 2010).

Social interactions can be characterized through social network analysis (Krause *et al.* 2015). These node-based social network metrics are intricately based on interactions between individuals, so we think that the concept of animal personality cannot be directly applied. However, node-based metrics can function as proxies for underlying personality traits such as extraversion, or sociability. Indeed, it has been shown that individuals differ consistently in their node-based metrics in wild populations across long time scales in great tits *Parus major* (Aplin *et al.* 2015), wild ringtailed lemurs *Lemur catta* (Kulahci, Ghazanfar & Rubenstein 2018), wild eastern water dragons *Intellagama leseurii* (Strickland & Frere 2018), wild vervet monkeys *Chlorocebus pygerthrus* (Blaszczyk 2018), yellowbellied marmots *Marmota flaviventris* (Blumstein et al., 2012), and on shorter time scales in wild guppies *Poecilia reticulata* (Krause *et al.* 2017). This consistent among-individual variation have been shown to be maintained in different habitats including various social environments such as in captive sharks like the small-spotted catshark *Scyliorhinus canicula* (Jacoby *et al.* 2014), the lemon shark *Negaprion brevirostris*, (Finger *et al.* 2018) and captive forked fungus beetles like *Bolitotherus cornutus* (Formica *et al.* 2017). In some species like the eastern water dragon, sex-specific effects have been found (Strickland & Frere 2018), however studies in other species did not show such sex differences in the social traits (Kulahci *et al.* 2018). Furthermore, it remains unclear whether, and if so, in which circumstances, behaviors measured in captivity can be translated into the wild (Bell et al., 2009; Fisher *et al.* 2015, Osborn and Briffa, 2017).

Thus, we hypothesize that social network node-based metrics can be used as proxies for animal personality traits describing social interactions if they show non-zero repeatability across time and context. We present a comprehensive test for sex-specific effects and consistent between-individual differences across different timespans and social environments. We test our hypotheses in the house sparrow *Passer domesticus* (hereafter sparrow), a gregarious passerine, in two study systems: a wild insular population and a captive population kept in semi-natural conditions. We aim to offer a new perspective on the application of social network methods and fill the gap on how social networks dynamics may change over time and across contexts.

Methods:

Social associations across time

The wild sparrows of Lundy

We have been systematically collecting data on the Lundy sparrows since 2000. This population can be considered as closed because Lundy Island is at 19km from the closest mainland, so migration is approximately zero (Schroeder *et al.* 2015). Due to the isolated nature of the population, we are able to catch, visually identify and automatically record the birds using video cameras and/or RFID antennas (radio frequency antennas) logging data from passive-integrated transponders (hereafter PIT tag) that all sparrows carry (Schroeder *et al.* 2011; Sánchez-Tójar *et al.* 2017). Doing so throughout the year allowed us to acquire comparably precise knowledge of which bird is present at any time, and to minimize catching bias (Simons *et al.* 2015). To collect behavioral data, we recorded videos between November 2013 and December 2016 from 5:16 am to 17:55 pm of the individual behavior of sparrows at a feeder. The feeder was placed at the same location over the study period and consisted of a bowl of 15.5cm in diameter, filled *ad libitum* with dry mealworms or sunflower seeds. We performed ten discrete sampling events: five during the non-breeding season (between mid-November and mid-February) and five during the breeding season (between mid-March to mid-July). We collected 20 days of video footage from, on average, 5h per day (range: 2.4-13h per day, total of 99.3 h). From video transcription, all dyadic agonistic interactions (physical [i.e. pecks and fights] and not physical [i.e. threats and displacements]) were noted, and the identity of the two interacting individuals was recorded. Visual identification was possible as most birds on Lundy Island are ringed with a unique color ring combination. With this data we created ten social networks, one per sampling event, with weighted edgelists using the R package 'iGraph' v.1.2.4.1 (Csardi & Nepusz 2006). We then reduced the interaction dataset to those interactions between same-sex individuals only, and, for the sex-specific analyses, split these into two datasets, one for females, and one for males.

The captive sparrows of Seewiesen

We collected data from a population of male sparrows held at the Max Planck Institute for Ornithology in Seewiesen, Germany, between 14 October 2014 and 16 December 2014. Most of the sparrows tested were captively bred progeny of wild-caught sparrows in 2005 and 2006, with a few wild caught males still alive (see Girndt *et al.* 2018 for more information on animal husbandry). The group of 95 male sparrows was separated into four captive male-only groups. There were originally 96 individuals corresponding to 24 per group but one male died at the beginning of the experiment, and was therefore excluded from the analyses. We recorded videos similarly to the set-up used in the wild population (described above). We took 3h videos of dyadic interactions once per week, over ten weeks on 10 sampling events. From this data, we created 4 x 10 graphs (i.e. 40 graphs, one per population and sampling event) with weighted edgelists, exactly as we did for the data from the wild. The group compositions were kept stable throughout, and thus, the social environment did not change across the 10 sampling events.

The captive sparrows of Silwood

The Silwood dataset was collected over a period of ten weeks, between 26 December 2017 and 5 March 2018 in four aviaries with mixed-sex sparrow populations. This protocol matches the experiment conducted in Seewiesen, and as such serves as a control for the new method. From the Silwood experiment, we collected data from four aviaries and across five sampling events, hence 20 social networks.

Here, we collected data with the help of automated antennas and data loggers. Each sparrow was PIT tagged, and those PITs were read by antennas flanking a caged-in feeding area (30x50 cm, 25cm high). Two entrances allowed sparrows the access to the feeding area at their leisure and allowed them to leave when they did not choose to interact with a newly arriving individual. Each entrance had two sequential antennas connected to a data logger that recorded the 10-digit number provided by the PIT, allowing us to determine the direction of a sparrow entering or leaving the feeding area. We considered an interaction to be dyadic when two individuals remained together in the feeding area for more than three seconds using the coexistence as a proxy of interaction (Farine, 2015).

Across social environments – long term

We re-distributed Silwood sparrows after 5 March 2018 and split up the social groups into eight mixed sex groups (populations) to generate new social environments. The sparrows were allowed to breed in these groups during the summer of 2018. In the following winter, between 13 November and 31 December 2018 we re-assessed behaviour in these eight groups. This means the birds had roughly six months to adjust to their new social groups. We used data from the previous winter (as described above) as the first sampling event.

Across social environments – short term

Then, sparrows were re-distributed again, and sampled for a third event in March 2019, to test for short-term change in social environment. The winter 2018 sampling events were used as the reference for this test. We only created 7 populations to keep population sizes equivalent, due to natural mortality (Simons *et al.* 2019). We created 15 social networks from this dataset, one per population and sampling event, using weighted edgelists.

The captive population sizes ranged between 8 and 31 sparrows, with an average of 17 sparrows per population. We aimed for equal sex ratios in each population.

Statistical analysis

We extracted the node-based estimates for strength, betweenness, and closeness from each social network (Csardi & Nepusz 2006). Strength describes the number of individuals that a focal individual interacts with and is weighted to the total number of interactions. Betweenness describes the number of shortest paths between a pair of individuals that 'pass through' the focal individual, thus describing how well an individual is connected. Closeness describes how many edges are needed to link every other individual from a focal individual, thus it quantifies how central an individual is (Csardi & Nepusz 2006). Before all analyses, we log-transformed all measurements to approach normality, and then z-standardized all three measures by graph to compare node-based metrics between social networks (Schielzeth, 2010).

We then estimated the repeatability – the proportion of variance explained by between-individual differences, in all three datasets for all three variables. We did this by running linear mixed-effects models, one for each variable for each dataset, with the individual identity of a bird as a random effect on the intercept. We then extracted the random effects and calculated the repeatability as the proportion of variance explained among birds over the total phenotypic variance (Nakagawa & Schielzeth 2010).

In the analysis of association data, no individual is independent from the other individuals interacting with the focal individual. Hence, the network structure by itself might – by chance – produce a background level of repeatability, which needs to be considered the baseline calculated with the null hypothesis instead of a repeatability of zero (Farine 2017). This is expected to be less of a problem in closed populations as ours where all individuals are potentially observed – as interactions were always measured at the only feeder in each of the enclosures. However, to quantify that effect just in case, we ran 1000 iterations of the observed data for every model. In each iteration, we permuted the identity of the individuals (nodes) interacting with each other, and the number of times an association was observed (weights), while keeping the total number of associations, individuals, and the distribution of the weights the same. On each of these iterations, we conducted the same repeatability analyses as described above for the observed data. We consider the observed repeatabilities as statistically significant when the 95% confidence intervals (CI) did not include the mean of the respective permuted repeatabilities.

We used the R package 'MCMCglmm' v.2.25 (Hadfield 2010) in the R environment v.3.5.2 (CRAN R Team 2018) for statistical analysis. The Bayesian estimation allowed us to compute 95 credible intervals for the variance components.

Results:

For the wild Lundy sparrows, we collected 13085 dyadic interactions, including 471 individual birds, of which 49 birds had been seen only once, and 28 birds had been seen twice. 68 birds had been seen between three and 10 times. 95 birds had been observed between 11 and 29 times. Thus, a total of 231 birds had been seen 30 times and more. Of these, 74 individuals had been seen 100 times and more.

In the Seewiesen sparrows, we collected a total of 4432 observations of dyadic associations between 95 sparrows. One individual was only seen once, 22 individuals were seen 29 times or fewer. Thus, 73 individuals were recorded 30 times or more. Of these, 36 individuals were observed 100 times or more often. The dataset of the Silwood sparrows testing for between-individual differences across time contained of 3775 dyadic interactions between 95 individuals. Of these, 80 birds were observed interacting 30 times or more. The dataset of the Silwood sparrows to test for long-term changes included 4244 dyadic interactions of 150 individuals. Of these, 86 individuals were recorded having 30 interactions or more. The Silwood dataset testing for short-term changes included 3826 dyadic interactions of 105 individuals, of which 33 were observed 30 times and more often.

Table 1: Descriptions of the four datasets, and the repeatabilities of strength, betweenness, and closeness, of house sparrows interacting at a feeder. Note that the estimate for males in Seewiesen were quantified from a male-only group, with the sex-specific estimates for Lundy were quantified from a social network constrained to same-sex interactions only, while birds did interact with both sexes on Lundy.

Population		Lundy			Seewiesen	Silwood	Silwood	Silwood
Sampling events		10			40	20	13	15
Sex		mixed	Female	male	Male	mixed	mixed	mixed
Social environment between sampling events		Changing naturally through birth and death			Constant		Experimentally manipulated	
Habituation period		na			na	na	6 months	4 weeks
Sample size	Birds	471	218	249	95	95	150	105
	Interactions	13,085	3151	3727	4432	3775	4244	3826
Repeatability	Strength	0.25	0.21	0.23	0.65	0.45	0.25	0.02
95CI		0.15 – 0.36	0.04 – 0.30	0.07 – 0.39	0.56 – 0.73	0.33 – 0.56	0.00 – 0.57	0.00 – 0.18
	Betweenness	0.28	0.23	0.20	0.53	0.24	0.03	0.01
		0.17 – 0.39	0.04 – 0.40	0.01 – 0.37	0.44 – 0.63	0.12 – 0.36	0.00 – 0.20	0.00 – 0.16
	Closeness	0.22	0.27	0.11	0.39	0.21	0.10	0.00
		0.12 – 0.32	0.10 – 0.42	0.01 – 0.27	0.29 – 0.50	0.10 – 0.33	0.00 – 0.53	0.00 – 0.05

In the wild population, and in both captive experiments across time where the social environment was not changed, the repeatabilities were statistically significant (Fig. 1), and ranged between 10% - 65% (Table 1). Repeatabilities were highest in the male-only captive set-up (Fig. 1). Interestingly, the repeatabilities only including single-sex interactions from the wild population were similar to those from mixed sex groups, and their 95CI overlapped with the mean permuted repeatability (but for female closeness, Fig. 1A). In captivity, repeatabilities in the mixed sex groups were lower than in male-only groups but did not differ much from mixed-sex repeatabilities in the wild (Table 1, Fig. 1A, C). In addition, when sparrows had six months to habituate to a new social environment, strength and closeness still showed non-zero repeatability, whereas betweenness showed no repeatability (Table 1). After the social environment was changed, the 95CI overlapped with the 95CI of the permutations (Figure 1C, D). Note that for the short-term measurements, we did not get as many observations as we wanted, which may have contributed to a lower statistical power. However, the short-term repeatabilities differed from those calculated from long-term habituation experiment (Fig 1D). When sparrows had less than a month to habituate to a new social environment, repeatability was practically non-detectable (Fig 1D).

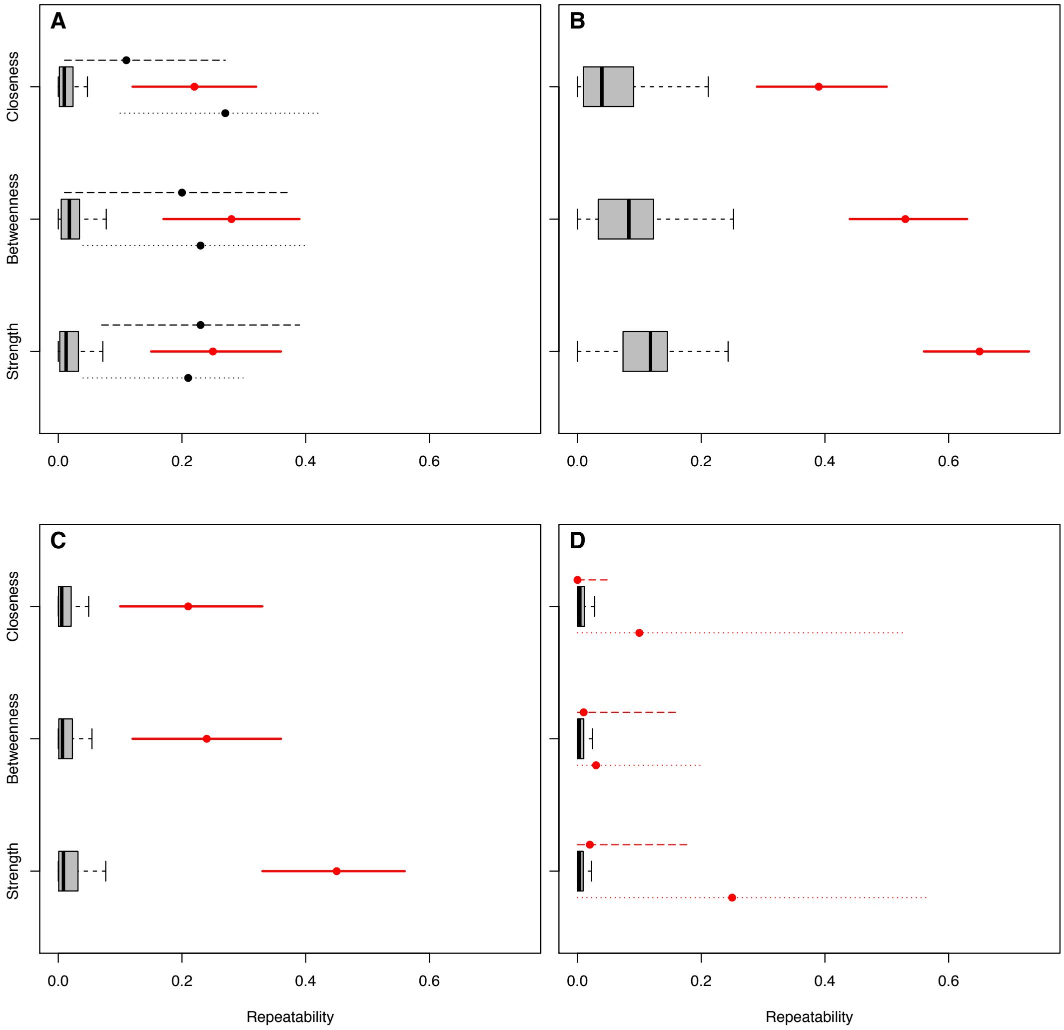

Fig. 1: Repeatabilities (filled circles) and 95CI (lines) of individual social network variables in comparison to results from permutations (boxplots, whiskers: 95%CI of permutation results). **A**: Lundy island sparrows across time. Red = all, black dotted lines = female-female interactions only, black dashed line = male-male interactions only. **B:** Seewiesen male sparrows across time. **C:** Silwood sparrows over time. **D:** Silwood

sparrows after the social environment was changed. Red dashed lines: short-term habituation, red dotted lines: long-term habituation.

Discussion:

Our results show that node-based metrics can be used as proxies for animal personalities. We also showed that sparrows' node-based metrics from social networks show repeatability across time and social environments. This was true for birds from the wild, and from captivity, and in mixed, and single-sex groups. Our results thus corroborate previous findings in passerines showing that there are consistent between-individual differences in social traits across years (Aplin *et al.* 2015). We have also shown that video recordings and automated assays are adequate methods to collect individual interactions, and to characterize the sociality of individuals.

Interestingly, we showed that between-individual differences across social contexts are dependent on the time frame. This is maybe partially to be expected, as our concept of sociability, especially in the context of personality, may depend on a certain amount of familiarity between individuals. If individual birds need time to habituate to each other, and adjust their behavior accordingly, a certain amount of time before social relationships is to be expected. However, the concept of individual familiarity has to our best knowledge, not been tested outside of family group structures (Lattore *et al.* 2019). Another consideration we must take into account is that because we did not measure continuously, a shorter experimental time span meant fewer data points, thus leading to a less precise statistic, which may have exacerbated the effect (Edwards *et al.* 2013). However, it suggests the importance of considering habituation time for any social experiments, and it may be that the time needed is longer than the expected.

Recently, it has been suggested that male sociability may show higher repeatability than female sociability due to the different drivers on the social behavior between sexes (Strickland & Frere 2018). Our data might be interpreted as supporting this notion, but with an important caveat: the social environment in which interactions are measured seems important. When we measured interactions in male-only environments, repeatabilities were surprisingly high. However, when we only used data of male-male interactions from mixed-sex environments, repeatability was nearly zero. Females did tend to have lower and bordering non-statistically significant repeatabilities in the wild comparing with captivity values, suggesting a biological effect. It may be possible that male-male competition increases in male-only environments, and hence future research differentiating between single sex groups, and single sex graphs, is required. This also highlights that we should not discuss node-based metrics as direct measures for individual behavior, but instead as proxies for a latent trait.

To conclude, our comprehensive analysis across time and context, both in the wild and in captivity, using video analysis and automated data collection, suggests that, node-based metrics from social networks can indeed be considered as proxies for personality traits in passerines.

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