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Correcting for the impact of gregariousness in social network analyses

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The social network approach provides a set of statistical tools to analyse associations between individuals. The 'half-weight index' (HWI), the association index most commonly used in social network analyses, does not take into account differences between the gregariousness of individuals. Thus, the HWI may not be a good measure of relationships between individuals: it could indicate strong affinities that do not exist and vice versa. Here we present a new index, the HWIG, that corrects the association index between two individuals for their respective levels of gregariousness. We compared the HWIG to the HWI by simulating populations in which individuals varied in their gregariousness and their affinities for each other. Unlike the HWIG, the estimation of associations made by the HWI was strongly influenced by the gregariousness of individuals: the HWI was systematically less strongly correlated with the true (input) affinity than the HWIG and this discrepancy increased when variation in individual gregariousness increased. We recommend using the HWIG, or similar variants of other common association indices, as unbiased measures of association between individuals.

Social network analysis is a common tool used to characterize the social structure of a population. It describes how individuals differ in their relationships (using data on associations and/or interactions) in a population (Whitehead 1997). Social network analysis can help us understand the spread of information, diseases and genes through populations, and provides a powerful tool for the study of the evolution of cooperation (Croft et al. 2006; Wey et al. 2008). For example, many studies have used this method to highlight strong associations between kin (Gero et al. 2008) or between individuals of the same age or sex (Lusseau & Newman 2004), whereas others have used it to investigate the spread of diseases (Corner et al. 2003; Hamede et al. 2009). For instance, Croft et al. (2009) showed that social structure could be influenced by personality for Trinidadian guppies, *Poecilia reticulata*. Indeed, bolder individuals had weaker bonds than shy ones. Another example of the broad utility of social network analyses is the study of Flack et al. (2006), who showed that dominant pigtailed macaques, *Macaca nemestrina*, played a key role in group cohesion.

The first step in the construction of a social network is usually to estimate the strength of relationship between pairs of individuals using an association index. One of the most commonly used indices is the half-weight index (HWI). HWI estimates the proportion of time that two individuals spend together. This may in turn reflect an affinity between the two individuals, an affinity of one individual for another individual, some shared preference for a particular habitat, or the gregariousness of the individuals. In the absence of information on interactions among individuals, it is, usually tacitly, assumed that interactions occur among associated individuals (Whitehead & Dufault 1999). The HWI minimizes some commonly present biases linked to the sampling method (Cairns & Schwager 1987), but does not take into account differences in individuals' gregariousness, where gregariousness is a measure of the individual's tendency to associate. In this paper we address the impact of gregariousness on association indices.

Animal populations can show variation in individual gregariousness, with some individuals being found mainly in small groups, or having few associates, and others generally in larger groups, or having many associates. The overall gregariousness of a population can also change during a season or across seasons (chitals, *Axis axis*: Raman 1997; chamois, *Rupicapra rupicapra*: Loison et al. 1999; mountain goats, *Oreamnos americanus*: Festa-Bianchet & Côté 2008), or over other time periods. For example, mean HWI may vary if seasonal changes in population density are accompanied by changes in group size or association rates (Vital & Martins 2009). More important though is variation in gregariousness among individuals within a population. Although we know of no published estimates of variation in gregariousness among individuals, we examined it for three published matrices of association indices (Whitehead 2008a, Tables 2.5, 4.16, 4.17): a sperm whale, *Physeter*

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macrocephalus, social unit ($N = 7$; CV (gregariousness) $= 0.38$; range 0.76–2.35), disk-winged bat, *Thyroptera tricolor* ($N = 18$; CV (gregariousness) $= 0.85$; range 0–3.28), male northern bottlenose whale, *Hyperoodon ampullatus* ($N = 30$; CV (gregariousness) $=$ 0.68; range 0.08–1.24). Although some of this variation will be due to sampling, there are clearly major differences in gregariousness among individuals in these populations.

This individual variation in gregariousness has consequence for association indices. Highly gregarious individuals will associate more often with other highly gregarious individuals just by chance, even if there is no mutual affiliation. When sociality is expressed by grouping, the most gregarious individuals will tend to occur together in large groups whereas weakly gregarious individuals will be seen more often in separate small groups. In such a case, HWI may reflect variation in gregariousness of dyads and not real strong association between pairs of individuals.

It is important to note that there is nothing intrinsically wrong with association measures, such as the HWI, or network analyses using them, being functions of differences in gregariousness among the members of different dyads. The HWI is an efficient estimator of the proportion of time that two individuals spend together, and network analyses using it should indicate the mode of spread of disease or information through the population. However, as we will show, if there is major variation in gregariousness among individuals, then neither the HWIs and the network analysis using them will accurately reflect social preferences between individuals (i.e. who preferentially associates with whom, what we shall call affinity (following Pepper et al. 1999)). To remedy this problem, Pepper et al. (1999) proposed using the ratio of estimated over expected association index, the 'social affinity index', and developed it for the situation where classes of individuals, for instance males or females, differ in gregariousness.

Following Pepper et al.'s (1999) suggestion, we propose the HWIG, which represents the strength of relationship of a dyad after correcting for the gregariousness of the two individuals, or the ratio of observed over expected association indices. This new index corrects for the gregariousness of each individual in a dyad whereas Pepper et al.'s index corrected for the gregariousness of classes of individuals. We first describe how to calculate the HWIG and then compare the performance of the HWI and the HWIG in representing the patterns in the data using simulated populations in which individuals may differ in gregariousness.

METHODS

The association between two individuals could happen for different reasons (see Introduction). However, to simplify the situation, in the current model, we assume that the association between two individuals is essentially caused by their reciprocal affinity. Although we are conscious that other factors can affect association indices in a dyad, our goal here is to show that differences in gregariousness among individuals change the link between true affinity and association.

Calculating Indices

HWI between two individuals a and b ($\mathrm{HWI_{ab}}$) can be calculated as follows:

$$\mathrm{HWI_{ab}} = \frac{x}{\frac{1}{2}(y_\mathrm{a} + y_\mathrm{b})} \tag{1}$$

where x is the number of sampling periods in which individuals a and b were seen associated and y_a and y_b correspond to the total number of sampling periods that a and b were seen, respectively (Cairns & Schwager 1987).

We propose to calculate HWIG between a and b ($\mathrm{HWIG_{ab}}$) using the following equation, which is a direct transcription of that suggested by Pepper et al. (1999) for examining relationships between classes of individuals:

$$\mathrm{HWIG_{ab}} = \mathrm{HWI_{ab}}\frac{\sum \mathrm{HWI}}{\sum \mathrm{HWI_a} \sum \mathrm{HWI_b}} \tag{2}$$

where $\sum \mathrm{HWI_a}$ and $\sum \mathrm{HWI_b}$ are the sums of all the HWIs for individuals a and b, respectively (i.e. a measure of the gregariousness of individuals a and b; Whitehead 2008a), and $\sum \mathrm{HWI}$ is the sum of all the HWIs for all dyads. HWIG is the calculated HWI divided by its expected value if individuals associate at random, but based on their own calculated gregariousness.

HWIG equals one when the association between two individuals is random given their gregariousness; a HWIG lower than one indicates that the two individuals associate less often than expected considering their gregariousness, and a HWIG higher than one indicates that the two individuals associate more often than expected considering their gregariousness.

Comparing HWI and HWIG When Differences in Individual Gregariousness and Association Occur

We constructed populations of n individuals in which each individual, a possessed a gregariousness, g_a, and each pair of individuals, a and b, a true affinity, $\alpha_{\mathrm{a,b}}$. During each of 100 sampling periods, $\frac{n^2}{10}$ dyads were sampled randomly, with replacement. The probability that the dyad ab was chosen as associated in any sample was proportional to $g_\mathrm{a} \times g_\mathrm{b} \times g_\mathrm{ab}$. HWIs were then calculated between all pairs of individuals as in equation (1), and HWIGs were calculated as in equation (2). Then, to assess how well the indices represented true affinity (following Whitehead 2008b), we correlated $\mathrm{HWI_{ab}}$ with $\alpha_{\mathrm{a,b}}$, and $\mathrm{HWIG_{ab}}$ with $\alpha_{\mathrm{a,b}}$. The gregariousness values, $\{g_\mathrm{a}\}$, were chosen from a normal distribution with mean $= 1$ and SD $= s_\mathrm{g}$ while the true affinity values, $\{\alpha_\mathrm{ab}\}$, were chosen from a normal distribution with mean $= 1$ and SD $= s_\alpha$ (negative values were set to zero). We ran 10 simulated populations with all combinations of: $n = 10$, 40, 100; $s_\alpha = 0.1$, 0.3; $s_\mathrm{g} = 0.0$, $0.1 \times \mathrm{s_a}$, $0.2 \times \mathrm{s_a}$, …, $1.9 \times \mathrm{s_a}$, $2.0 \times \mathrm{s_a}$. So, here we test how the indices reflect the associations created from the combination of true affinity and gregariousness. Simulations were run using Matlab (v.R2008b, Mathworks, Natick, MA, U.S.A.).

We also ran simulations to investigate whether HWI overestimated or underestimated the true affinity between two individuals when the association was completely random in the population (i.e. no variation in true affinity among pairs of individuals). We assigned some individuals to a subcategory representing 10% of the population that was more gregarious than the rest of the population, but no dyad in the population showed any affiliation preferences (i.e. random association between all individuals). Each simulated population was composed of 100 individuals. A run was composed of 1000 observation periods. Observation periods could represent, for example, days of observation in a population. Preliminary analyses showed that 300 populations of 100 individuals, with 1000 observation periods, provided stable results. During the simulations, groups were sorted from the largest to the smallest prior to placing individuals in the groups. Groups were filled up one by one with individuals from the population. We increased the probability that the gregarious individuals were picked up so that they were more often in the first (big) groups than the rest of the population. For each simulated population, we assessed whether the HWI and HWIG detected any difference in the associations between highly gregarious individuals compared to the rest of the population. To do that, we computed a Mantel test (Mantel 1967; following implementation by Legendre & Legendre 1998) between binary matrices of identical size filled with one for dyads composed of two highly gregarious individuals and zero for other dyads and both the HWI and HWIG matrices. These simulations and Mantel tests were carried out using R statistical software (v.2.11.1, CRAN 2010, R Foundation for Statistical Computing, Vienna, Austria).

We ran a third set of simulations to examine how variation in gregariousness could affect the ability of HWI and HWIG to detect variation in affinity among pairs of individuals. In these simulations a subcategory of individuals (hereafter referred to as companions), representing 10% or 30% of the population, had higher true affinity with each other than with the rest of the population. We varied the strength of the true affinity between companions, from weak affinity to very strong affinity. We simulated situations where companions were more gregarious, less gregarious, or did not differ in their gregariousness compared to the rest of the population. Finally, we verified whether the two indices were able to detect the companions in each of these situations. As in the previous simulations, the simulated population was composed of 100 individuals. A run was composed of 1000 observation periods. For each observation period, groups were filled up one by one with individuals from the population. Picking a companion increased the probability that other companions were picked to complete the group, so that companions were more often in the same groups than the rest of the population. We varied the true affinity strength between companions, relative to other dyads in the population, by changing this probability. We chose to implement four classes of true affinity strength, ranging from low (category A) to very strong (category D; Table 1). True affinity strengths were chosen to provide a wide scope in true affinity among companions and to check for a potential threshold value in the detection of companions by HWI and HWIG.

To test the effect of gregariousness on the detection of the association between companions by the two association indices, we simulated three scenarios: one where the gregariousness of the companions did not differ from the rest of the population, one where companions were more gregarious and one where they were less gregarious than the rest of the population. We simulated two types of populations with 10% and 30% of companions. This allowed us to test whether the proportion of companions affected the ability to detect nonrandom associations using the two indices. For each simulated population, we assessed whether the HWI and HWIG detected the association between companions in the same manner as for the previous simulations (i.e. with Mantel tests). These simulations and Mantel tests were carried out using R statistical software (v.2.11.1, CRAN 2010).

Table 1
Definitions of the different classes of association strength used to create the subcategory of companions (i.e. individuals actually showing a higher affinity between each other than the rest of the population)

Association strength classes	Probability added to companions in the model	Resulting probability for two percentages of companions	
		10%	30%
A	0.01	0.09	0.26
B	0.05	0.22	0.5
C	0.2	0.47	0.76
D	0.9	0.74	0.91

The first column indicates the different classes of association strength used in the simulations, and the second the probability of association for companions that is added to the initial probability of association (the initial probability that two individuals would be in the same group comes from a normal distribution (mean = 0.01, SD = 0.005)). The next two columns show the resulting probabilities (i.e. the probability of assigning a companion to a group when another companion has just been placed in this group, and estimated from 100 000 iterations with replacement) for companions according to their percentage in the population (i.e. 10 or 30%): the higher these probabilities, the higher the likelihood that the companions would be assigned to the same group.

RESULTS

For each population size (n) and level of variation in social affinity (s_a), we plotted in Fig. 1 the measure of how well the indices represented the true affinities (correlation between HWI_{ab} or $HWIG_{ab}$ and the affinity, α_{ab}) against the variation in gregariousness as a proportion of the variation of affinity ($\frac{CV(g_a)}{CV(\alpha_{ab})}$, which approximates $\frac{s_g}{s_a}$). While the HWI gave a slightly better representation of the associations based on affinities when variation in gregariousness was low compared to variation in affinity $\left(\frac{CV(g_a)}{CV(\alpha_{ab})} < \sim 0.4\right)$, its performance fell quickly as the variation in gregariousness approached, and then exceeded the variation in affinity. In contrast, the HWIG's ability to represent associations based on affinities was little affected by large variations in gregariousness. The increase in the variation in affinity (which led to an increase in variation in association indices) within the population improved our ability to detect this variation in association among dyads: with a CV (affinity) = 0.1 the correlation between the HWIs and true affinity was only 0.6 whereas it rose to 0.9 when CV (affinity) = 0.3. Increasing sample size improved the precision of the results as shown by the less scattered results between simulations with $n = 100$ than with $n = 40$ and $n = 10$.

In the second set of simulations, when there was no variation in affinity (and thus in association), HWI detected a significantly higher average association between the most gregarious individuals than between individuals from the rest of the population in 48% of the simulated populations, whereas HWIG detected a significant difference in association in only 7% of the populations.

Both HWI and HWIG detected affinity between companions when they did not differ in gregariousness compared to the rest of the population, and the stronger the true affinity between companions was, the better both indices detected affinities between them (Fig. 2a). When companions were more gregarious than the rest of the population (Fig. 2b), the indices showed the same pattern: they both detected that companions were often in the same groups even when real affinity between companions was weak. In the third scenario (Fig. 2c), where companions were less gregarious than the rest of the population, HWI detected no affinity between the companions, whereas HWIG did almost as well as in the control situation (Fig. 2a). Increasing the percentage of companions in the population increased the detection capacity of both indices (cf. panels on the left with those on the right, Fig. 2).

DISCUSSION

Differences in gregariousness between individuals can strongly affect association indices commonly used in social network analyses of nonhumans, including the often used HWI. HWI provides an estimate of the proportion of time that two individuals spend together. The issue with such an index is that several factors other than the strict affinity (i.e. who likes whom) between two individuals can affect their association, and therefore the association index can overestimate or underestimate their true affinity. For example, two individuals may have a high HWI because they are

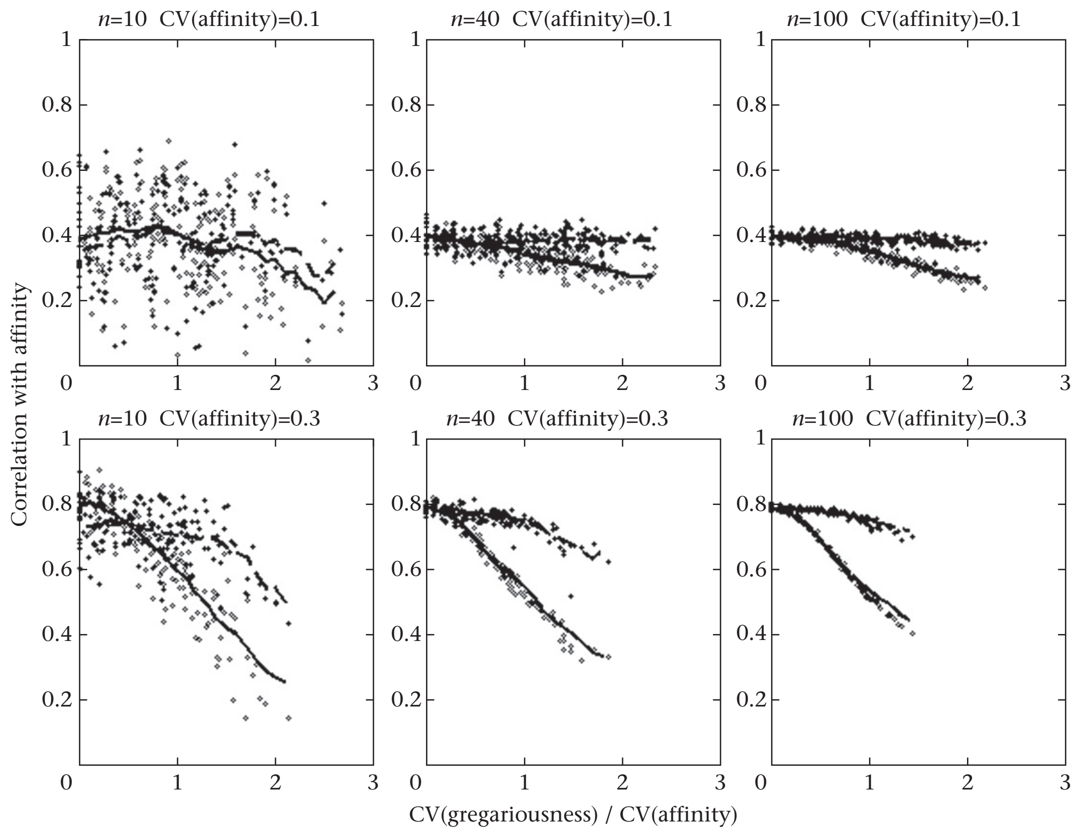

Figure 1. From simulations, correlations between HWIs and the true affinities of dyads (grey circles, solid lines), and HWIGs and the true affinities of dyads (black circles, slashed lines), plotted against the coefficient of variation in gregariousness as a proportion of the coefficient of variation of affinity $\left(\frac{CV(g_a)}{CV(\alpha_{ab})}\right)$, for three population sizes and two levels of variation in affinity. Lines represent moving averages (over 0.5 units on the X axis).

both highly gregarious and thus are often found in the same large groups, even though they do not seek each other's presence. They could also show preference for the same type of habitat or both share affinities with other individuals. Some effects such as habitat preference or affinities with a third party are difficult to correct when using group composition data, and other types of information such as locations or the types of social interaction may be needed to isolate the true affinity between individuals, and these effects are not controlled by the HWIG. However, as we show in this paper, the effect of gregariousness on association indices can be controlled for quite easily using the HWIG index.

We compared HWI with HWIG, an association index based upon a suggestion by Pepper et al. (1999) and which takes into account individual gregariousness; Pepper's index corrects for the gregariousness of classes of individuals but not for individual gregariousness, and thus cannot be used to compare individual association values in network analyses. Simulations (Fig. 1) revealed that HWI reflects only poorly the association based on the true affinity between two individuals when the variation in gregariousness increases. In comparison, HWIG is much less affected by variation in gregariousness. With our second series of simulations, we also showed that HWI was more likely than HWIG to detect a significant association in dyads of highly gregarious individuals even if these individuals did not show any true affinity. It means that, with variation in gregariousness, HWI can overestimate the associations based on the true affinity between two individuals. In contrast HWIG is more robust to gregariousness differences and does not detect an association between two individuals when they do not show any affinity.

In the last set of simulations (Fig. 2), companions (i.e. individuals actually showing a higher affinity between each other than the rest of the population) could be more gregarious, less gregarious or as gregarious as the rest of the population. Here again, HWI was strongly influenced by the gregariousness of individuals, especially when companions were not gregarious. In this case HWI underestimated the affinity between companions. In contrast HWIG reflected the true affinity between individuals independent of their gregariousness. For example, HWI did not detect affinities between less gregarious companions even when real affinity between companions was strong (Fig. 2c), whereas HWIG detected associations and it did so even better when real affinity became stronger.

In group-forming animals, large variation in group sizes allows individuals to vary in their gregariousness, some generally being part of small groups and others being part of large ones. This has been observed in many different taxa (e.g. ungulates: Côté et al. 1997; fishes: Krause et al. 2000; Pépin & Gerard 2008). Furthermore, situations where individuals showing strong associations prefer to be in small groups can exist in nature. For example, Pépin & Gerard (2008) noticed that the strongest relationships among Pyrenean chamois, *Rupicapra pyrenaica*, tended to occur among animals found in small groups.

We have concentrated on the half-weight index as it is perhaps the association index most often used in studies of animal societies. However, we carried out analyses like those shown in Fig. 1, and found nearly identical results, for three other often-used indices, the simple ratio, twice weight and square root (Cairns & Schwager 1987; Whitehead 2008a), when they were modified as in equation (2) (see Supplementary Materials for more details). A similar method could be used with interaction data, so that the rate of interactions (e.g. grooming or fighting) between two animals is corrected (using an analogy of equation (2)) for the overall rates at which the animals

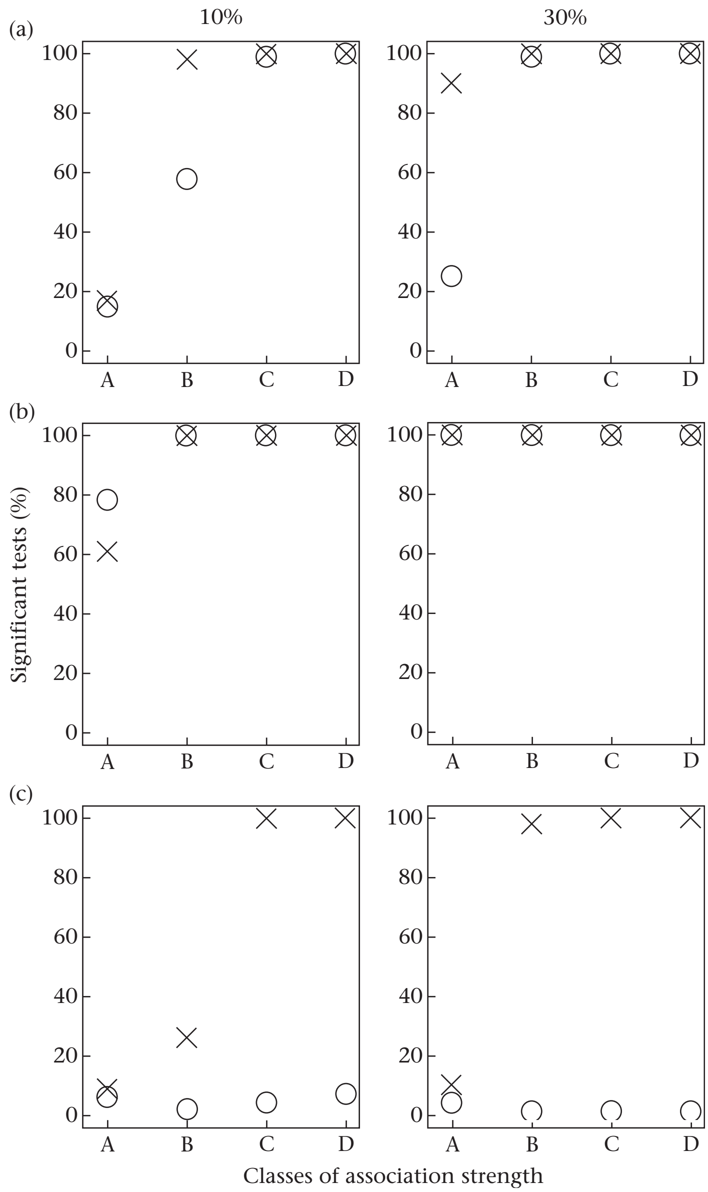

Figure 2. Detection of an association by HWI (circles) and HWIG (crosses) for dyads of individuals showing increasing affinities with each other (i.e. companions; A, B, C, D, with D being the highest association strength) for different scenarios of gregariousness: (a) no gregariousness difference between companions and the rest of the population; (b) companions more gregarious than the rest of the population; (c) companions less gregarious than the rest of the population. Companions represented 10% (left) or 30% (right) of the population size. The *Y* axis reports the percentage of simulations where the association index detected an association between the companions. Number of simulations = 300 populations; maximum group size = 100.

perform such interactions, indicating whether a pair interacts more or less than would be expected given the animals propensities to interact in this way. Thus, the corrected interaction rate between a and b would be the basal rate between the two individuals multiplied by the overall rate in the population, divided by the rate of interaction of a with anyone else multiplied by the interaction rate of b with anyone else. This formulation would be a little more complex for asymmetric interactions such as grooming.

The HWIG, even if not totally unaffected by gregariousness, is much more suitable than the HWI for identifying patterns of associations based on affinities, when variation in gregariousness is substantial compared with variation in affinity. Therefore, if the aim of the study is to map associations within a population, then, when variation in gregariousness is substantial, HWI may be misleading. In these conditions we thus recommend the use of HWIG over HWI. Note, that correction for gregariousness is not necessary if one wishes to estimate rates of association as in studies of disease or information transmission. Thus, the choice of an association index ultimately depends on the objective of the study.

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Supplementary Material

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