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COMMENTARY

Disentangling association patterns in fission–fusion societies using African buffalo as an example

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A description of the social network of a population aids us in understanding dispersal, the spread of disease, and genetic structure in that population. Many animal populations can be classified as fission–fusion societies, whereby groups form and separate over time. Examples discussed in the literature include ungulates, primates and cetaceans (Lott & Minta 1983; Whitehead et al. 1991; Henzi et al. 1997; Christal et al. 1998; Chilvers & Corkeron 2002). In this study, we use a heuristic simulation model to illustrate potential problems in applying traditional techniques of association analysis to fission–fusion societies and propose a new index of association: the fission decision index (FDI). We compare the conclusions resulting from traditional methods with those of the FDI using data from African buffalo, *Syncerus caffer*, in the Kruger National Park. The traditional approach suggested that the buffalo population was spatially and temporally structured into four different 'herds' with adult males only peripherally associated with mixed herds. Our FDI method indicated that association decisions of adult males appeared random, but those of other sex and age categories were nonrandom, particularly when we included the fission events associated with adult males. Furthermore, the amount of time that individuals spent together was only weakly correlated with their propensity to remain together during fission events. We conclude with a discussion of the applicability of the FDI to other studies.

Researchers attempting to quantify individual association patterns in fission–fusion societies often use group membership as an indicator of association, calculating an index of association for all pairs of individuals (or dyads) based on the proportion of time spent in the same group (Cairns & Schwager 1987; Ginsberg & Young 1992; Whitehead & DuFault 1999). Traditional association indices that are based upon the proportion of time spent together, however, may be the product of two underlying processes: the fission and fusion of groups, and the choices of individuals as to which subgroup to join during a fission event. Most studies calculate association indices using the entire data set, without paying attention to the timing of fission events. While these indices represent the proportion of time that two individuals spend together, they may be poor estimates of the propensity for dyads to remain together during future fission events. Each fission event provides only one data point on a pair's likelihood of remaining together when the group separates, and additional samples within a fission–fusion event are autocorrelated with samples occurring during the same interval between fission and fusion events.

We defined a fission event as the separation of one group of individuals into two or more distinct subgroups. For our study system, distinct groups are readily identified spatially: in Kruger National Park, African buffalo exist in herds of ∼200–1200 individuals, and individuals within herds are usually separated by a few metres. Herds are typically separated by 1–40 km and are rarely within visual contact of one another. Thus, we defined a group as the set of individuals that were within ∼1 km of one another. This definition was only problematic when groups were relatively close (e.g. within a diameter of the group size itself), which occurred rarely. Furthermore, when groups were close to one another, they were either

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in the process of splitting apart or rejoining. More generally, researchers might define groups as distinct if they are sufficiently separated such that individuals within a group would be more likely to incur significant cost (e.g. greater exposure to predation) if they were to move between groups. Very mobile species, or those that can communicate over large distances, may perceive groups at larger spatial scales than species that use groups as a form of predator defence. Ultimately, the definition of a group will vary between study systems and the appropriate definition may depend on the questions being addressed.

The distinction between the fission–fusion of groups and individual decisions during fission events has not been made in traditional association analyses, and each measurement of group membership is assumed implicitly to be the result of independent individual choices. For many species, however, dispersal between fission groups may be limited by predation, reduced foraging efficiency, and/or hostility from conspecifics (e.g. Waser et al. 1994; Alberts & Altmann 1995; Isbell & Van Vauren 1996; Ferreras et al. 2004). Thus, an individual's association with other individuals may be constrained because it is unable to move independently between groups. Factors influencing the fission and fusion of groups are often not well understood. In the absence of information, one might assume either that individuals have no control over the timing of group fission events or that group fission events are the product of individuals' dissatisfaction with their associates.

Here, we consider the case in which the timing of fission and fusion events is beyond any individual's control. From this viewpoint, traditional association indices are a function of both individual choices during a fission event and the duration that a splinter group remains separate after the fission event. We propose a modified pairwise association index, the fission decision index (FDI), which is the proportion of fission events involving both individuals in which they choose the same post-fission subgroup. This limits sampling to only one point during the interval between fission and any subsequent fusion events. Let T_{ij} be the number of times individuals i and j were together after fission events, and A_{ij} be the number of times i and j separated during fission events. The FDI, which we denote by δ_{ij}, is given by the formula:

$$\delta_{ij} = \frac{T_{ij}}{T_{ij} + A_{ij}}.$$

Note that the symmetry in the roles of individuals i and j implies that $\delta_{ij} = \delta_{ji}$.

In this study, we use simulation models in two contexts. First, we use a heuristic model to illustrate some of the deficiencies of traditional analyses by generating simulated association data for particular fission–fusion processes and sampling regimes. In these simulations, individuals choose to join postfission subgroups at random. We analyse the simulated data using standard methods and show that autocorrelated data lead to statistically significant association patterns that do not reflect the random individual choices made during fission events. Repeating the analysis using the FDI reveals the random structure of the data. We then apply our FDI method to an empirical data set of 123 radiocollared buffalo, and use a simulation model to generate the expected distribution of FDI values for the observed fission–fusion history if all buffalo had chosen subgroups at random. We compare the conclusions that are drawn from the traditional and FDI approaches. We conclude with a discussion of scenarios where the FDI should be used in conjunction with traditional methods of analysis to gain a more comprehensive understanding of animal associations.

Methods

Heuristic simulation model

Our first simulation model is intended to clarify conceptually the need for, and utility of, the FDI. The model generates simulated association data for particular fission–fusion histories, subject to the rule that individuals choose subgroups at random. Using this model, we assessed how conclusions about social structure depend on the association index used and on sampling protocol and intensity. We analysed the simplest possible fission–fusion society: one group, which sometimes separates into two groups and later fuses back together. This simplification is intended to expose potential bias with a minimal level of complexity rather than quantify the bias present in more complicated field situations.

To make the model, we first generated fission–fusion histories (e.g. Fig. 1a) that described when the group splits apart and regroups. Fission and fusion were treated as Poisson processes, occurring randomly with a constant probability per unit time. This is a simple way of modelling the fission process, which agrees with the roughly negative exponential distribution of group lifetimes for African buffalo in the KNP (P. C. Cross, unpublished data; i.e. the probability of a group ceasing to exist remains constant and independent of how long it has existed in the past). Fission and fusion rates were set equal, so groups spent half of their time apart, on average. For a given fission–fusion history, we simulated the movements of 20 individuals as they randomly chose subgroups during fission events. We sampled group membership at different intensities to generate data from which association indices could be calculated for all dyads. Sampling events occurred at regular intervals (or once following each fission event, for the FDI; Fig. 1a), and all individuals were recorded during a sampling event.

African buffalo in the KNP: field methods

Field data were collected during an ongoing study of bovine tuberculosis in the Satara Region of the Kruger National Park from November 2000 to November 2003 (Caron et al. 2003). The study area contained 4–12 buffalo herds, depending upon the amount of herd fragmentation, and roughly 3000 buffalo. The majority of study individuals were fitted with radiocollars in four helicopter sessions: November 2000 ($N = 6$), April 2001 ($N = 27$), August ($N = 51$) and November 2001 ($N = 12$). The

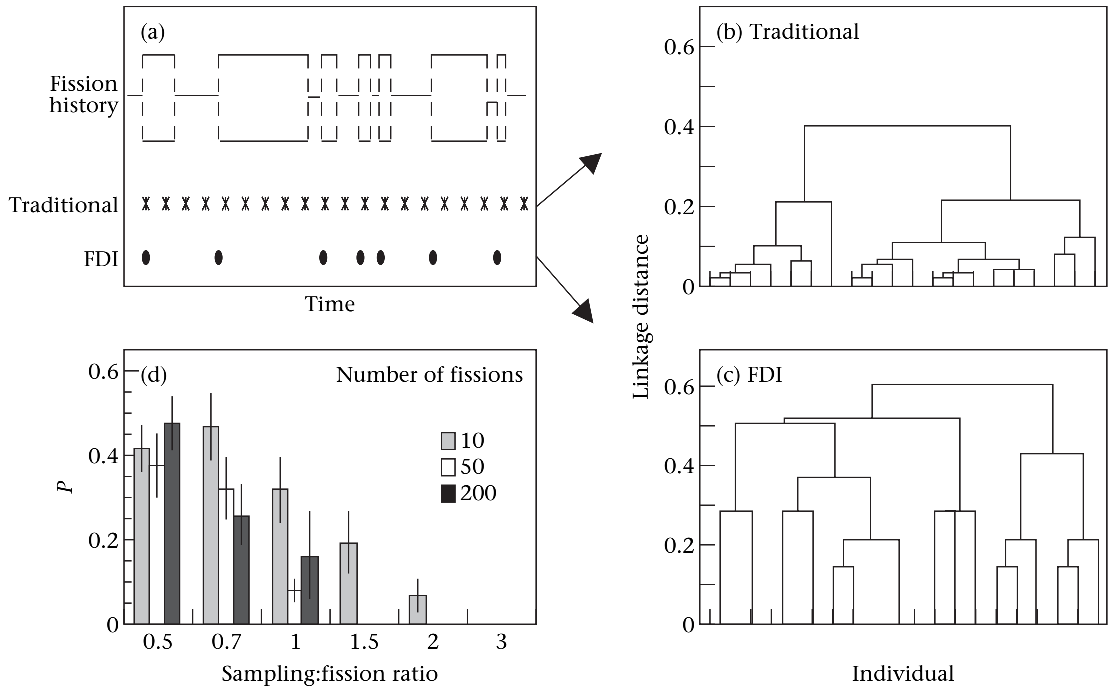

Figure 1. (a–d) We used a heuristic model of random individual choices to simulate different fission–fusion histories and sampling regimes. The fission–fusion history shown in Fig. 1a depicts one group separating into two groups seven times, subject to traditional sampling occurring at regular intervals, and to fission decision index (FDI) sampling after fission events. Simulated data were used to calculate the unpaired group averaging method (UPGMA) dendrogram for the traditional simple ratio association index (b, $P < 0.001$) and FDI (c, $P = 0.71$). The statistical significance of the traditional simple ratio index increases with sampling intensity regardless of the number of fission events. For Fig. 1d, each column represents 20 simulations of the heuristic model with a fixed number of fission and sampling events, and vertical lines represent the standard deviation of the P value.

remaining individuals were darted from ground vehicles throughout the study period. Animals were placed into age classes using incisor eruption patterns (Pienaar 1969; Grimsdell 1973; Sinclair 1977). All individuals over 5 years old were classified as adult. Although data for some individuals were available from November 2000, we restricted the data set to sightings of 123 radiocollared individuals that were seen more than five times during January 2002–October 2003. During this period, we had relatively complete information about the fission–fusion process. We monitored the buffalo herds approximately two to three times per week (917 herd sightings on 351 days) from distances ranging from 50 to 1000 m. If an individual was missing for over one month we located it from aircraft. Group membership was recorded only once per day per individual. Since all marked individuals had radiocollars and herds were usually separated by several kilometres, we could determine which individuals were in a herd without visually sighting all individuals.

Although fission events occurred when groups of individuals separated, we identified fission events in the buffalo data set as any time two radiocollared individuals were together on one sighting and then recorded in different groups, separated by several kilometres, in their next sighting. Individuals other than adult males only separated as a result of a larger group-level fission event. Adult males, however, often moved to smaller bachelor groups (~2–30 individuals) from mixed groups (Sinclair 1977; Prins 1996), and thus the definition of a fission event can be made dependent on the class of animals being considered (in our case adult males versus females and juveniles). By analysing data sets with or without adult males included we show how the FDI approach accurately captures this aspect of buffalo biology, whereby females are rarely seen moving with males into bachelor groups.

On some occasions, single radiocollared individuals were absent from the data set for a short period and then returned to the same herd where they were last seen. These data records may occur due to actual fission events that involved only one marked individual, or due to data entry errors. We required that an individual had to be absent during at least two successive observations of its last-known herd before we considered it a fission event. According to this definition, fission events involving only one marked individual occurred 16 times out of a total of 185 fission events for the data set excluding adult males, and 38 times out of 375 fission events when adult males were included. We analysed the FDI values for all dyads that were involved in two or more fission events together ($N = 1093$ and 834 with and without male fission events, respectively).

Buffalo data randomization

We compared the results of the buffalo FDI analysis to 1000 simulated random data sets. To generate these, we collected the following data from the real data set: identification of individuals involved in each fission event, the number of fragments sighted after the fission event, and the number of individuals in each fragment. To simulate random decisions, we conserved the number and size of postfission fragments but distributed the individuals at random between them. This eliminated the variability associated with different herd sizes and isolated the variability associated with individual fission decisions. We simulated fissions on an event-by-event basis, so that each simulated fission event was begun with the same individuals on-hand as in the buffalo data. This served to maintain the same number of fission events per dyad in the simulated and buffalo data sets, which has important implications for the distribution and variance of FDI values.

We encountered one problem when comparing the simulated and real FDI values. In real data sets, dyads will either separate from one another during their last shared fission event or the dyad will still be together when one animal dies or the study ends. Because fission events were frequent, the FDI values for dyads with only two events were either 0 or 0.5 (since their final event must have been a separation, or else they would have been involved in further fission events). However, the simulated FDI values could equal 0, 0.5 or 1 for dyads with only two events, because the individuals could randomly choose to remain together both times (and yet not undergo further shared fissions, since simulated fission events used the on-hand individuals from the real data). Taking this approach, simulated FDI values would be biased upward relative to the data-based FDI values for these two-event dyads. The same reasoning applies to dyads with greater numbers of fission events. To correct for this bias and to make the simulated and real data sets comparable, we did not include the last decision of each dyad in the analysis of either the buffalo or simulated data sets.

Statistical analysis

Following Whitehead & DuFault (1999), we considered two individuals to be associating if they were located in the same group. This one–zero metric of association was used to calculate the proportion of samples in which two individuals were seen together (i.e. the simple ratio index). For the case presented here, where all individuals had radiocollars, the probability of locating a pair of animals was unlikely to be related to whether they were together or apart, and as a result the simple ratio index yielded an unbiased estimate of the proportion of time they spent together (Cairns & Schwager 1987; Ginsberg & Young 1992). To test the statistical significance of the traditional simple ratio, we applied the permutation methods described by Bejder et al. (1998), using programs modified from the SOCPROG 1.3 package (http://is.dal.ca/~hwhitehe/social.htm) to shuffle individuals within samples to test the null hypothesis that no preferred companions exist between sampling periods. We considered the null hypothesis rejected if fewer than 5% of the permuted data sets had a standard deviation greater than that of the original data set. The standard deviation of the distribution of all pairwise association indices is expected to be higher when certain individuals preferentially associate with others (Whitehead 1999). For data sets generated by our heuristic simulations, we found that *P* values stabilized around 40 000 permutations. Statistical significance of the buffalo FDI values was determined using a chi-square goodness-of-fit test to compare the empirical distribution of FDI values to that of the mean of 1000 simulations (see Buffalo data randomization above). Dendrograms were generated using the unpaired group averaging method (UPGMA), which had the highest cophenetic correlation coefficient compared with other cluster analysis methods (Romesburg 1984). Simulations were coded in MATLAB 6.1, and cluster analyses were conducted using the MATLAB 6.1 Statistics Toolbox (MathWorks 2001).

Results

Heuristic simulations

To demonstrate how the method of analysis can affect conclusions about social structure, we analysed the data from the same fission–fusion history (shown in Fig. 1a) using standard methods and the FDI. With 50 regularly spaced sampling events, the simple ratio index appears to show nonrandom population structure (Fig. 1b) even though the model separated individuals at random during each fission event. This apparent structure arises because groupings that lasted longer were sampled more times. Specifically, the main division in the population (the top node of the dendrogram in Fig. 1b) is defined by the second fission event because it lasted for the longest period of time. The next two nodes of the dendrogram (at linkage distance ~0.2) are defined by the sixth fission event, which produced the next longest-lived subgroups. The Monte Carlo randomization procedure indicates that the association patterns shown in Fig. 1b are highly unlikely to occur at random ($P < 0.0001$), even though individual decisions were simulated to be random. In contrast, the FDI analysis did not show any spurious nonrandom structure (Fig. 1c, $P = 0.71$).

The above results show that association patterns derived from the traditional simple ratio index (or other association indices based on proportion of time spent together) can be biased towards nonrandomness, due to oversampling of longer-lived fission subgroups. To assess the effects of study design on this bias, we next simulated the model for a range of sampling and fission rates and analysed the results using the simple ratio index. For ratios of sampling rate to fission rate between 0.5 and 3, the reported nonrandom structure gains significance (i.e. the *P* value decreases) as the sampling to fission ratio increases (Fig. 1d). Thus, if sampling events occur more frequently than fission events, then the simple ratio index tends to be significantly nonrandom. The apparent nonrandom structure of the simple ratio indices is not influenced as much by the number of fission events observed as by the ratio of sampling to fission events (Fig. 1d).

Buffalo association patterns

Analysis using the simple ratio index indicated that the association patterns of buffalo in the Satara region were

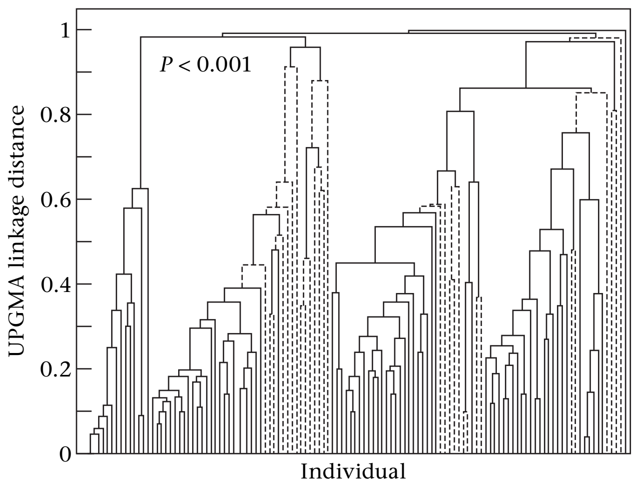

Figure 2. Unpaired group averaging method (UPGMA) cluster diagram of the traditional simple ratio index for 123 radiocollared buffalo using data collected during January 2002–October 2003. Adult males are represented by dotted lines. Statistical significance was determined using the randomization procedure described in the Methods.

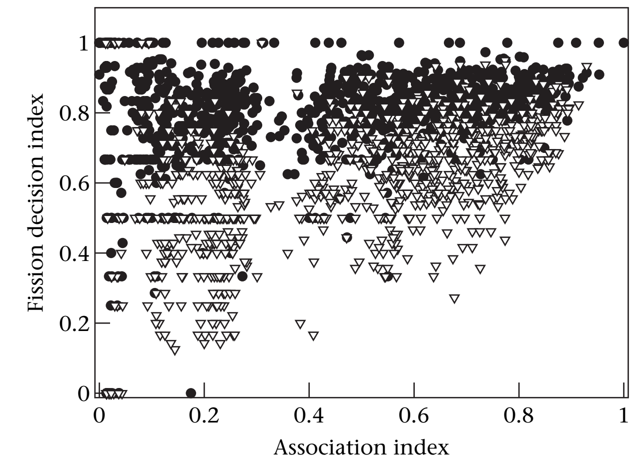

Figure 3. The relationship between the traditional simple ratio association index and the fission decision index (FDI) for all pairs of radiocollared buffalo that had two or more fission events together. Indices were calculated from data that included fission events involving only adult males (●; 1093 pairs) and excluded fission events involving adult males (▽; 834 pairs).

significantly nonrandom according to the permutation methods described by Bejder et al. (1998, $P < 0.001$). UPGMA cluster analysis (Fig. 2) suggests four main buffalo groups, with adult males being less tightly clustered than other sex–age categories. Cluster analyses of the FDI results did not show the same structuring of the sampled population into four groups as in Fig. 2 (data not shown).

For dyads involving females and juveniles, the FDI and the traditional association index were not closely correlated, indicating that the proportion of time spent together may not be a good predictor of the probability of remaining in the same group during a fission event (Fig. 3). The mean $\pm$ SE FDI score for females and juveniles was significantly higher when adult male fission events were included (0.805 ± 0.005) than when they were excluded (0.603 ± 0.006; Fig. 3). Furthermore, the distribution of FDI values was further from random with the inclusion of adult male fission events compared with when only those events associated with females and juveniles were used (chi-square test: $\chi^2_6 = 2040$, $P < 0.01$ and $\chi^2_6 = 151$, $P < 0.001$, respectively; Fig. 4a, b). The fission decisions of adult male dyads were not significantly different from what would be expected given random decisions ($\chi^2_6 = 10.5$, $P = 0.11$; Fig. 4c).

Discussion

Fission–fusion societies lie on a spectrum. At one end of the spectrum individuals are free to move between groups at any time. At the other end, individuals only move between groups when subgroups separate from one group and join another, and individuals do not control the fission–fusion process. Traditional association indices and the fission decision index apply best to opposite extremes of this spectrum, but in many situations they offer complementary information. Traditional association indices assume that the proportion of time that a pair of individuals spends together indicates the strength of their association. In some species or ecosystems, however, individuals may be reluctant to switch between groups on their own, and the proportion of time that individuals spend together may reflect aspects of the group-level fission–fusion history rather than individual-level preferences. Our results show that traditional association indices are poor descriptors of individual choices in such settings, and suggest that our FDI is a more appropriate index to study individual choices.

Our simulations illustrate that, if sampling occurs faster than fission and fusion events, the proportion of time that dyads spend together may show statistically significant clustering (Fig. 1b), even if individuals choose herds at random and independently of other individuals' decisions. This follows because multiple samples taken within the same interfission interval are autocorrelated with respect to individual choices. Furthermore, the statistical significance of this effect is dependent upon the ratio of sampling and fission events rather than the absolute number of fission events. The FDI eliminates autocorrelated data and presents an unbiased estimate of individual choices. In this study, we used the simple ratio index as the traditional metric of association. The potential biases shown in this study, however, apply to other association indices that are based upon the total number of samples taken (e.g. twice-weight, half-weight, simple ratio, square-root) rather than the number of fission events.

Traditional association analyses suggest that the buffalo population we studied was spatially and temporally structured into four different groups (Fig. 2). This result matches our intuition from collecting the field data, because (like the association indices) our intuition places greater weightage on group compositions with longer lifetimes. Since it is based on association indices that incorporate all observations from the entire study period, the cluster analysis shows the hierarchical structure of the population

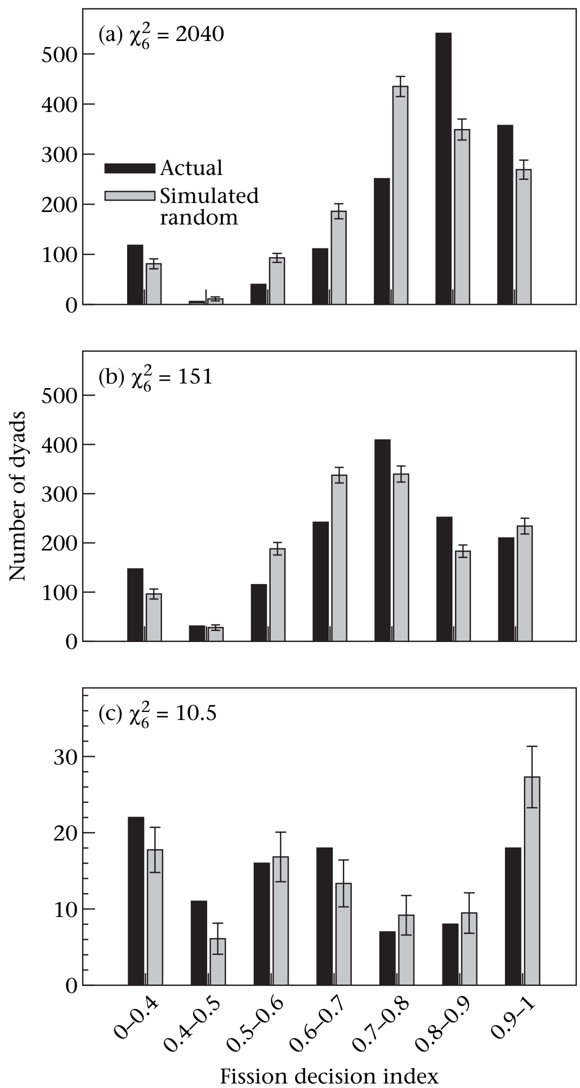

Figure 4. Fission decision index (FDI) values calculated from the buffalo data and from simulations assuming random fission decisions using (a) female and juvenile dyads with all fission events, (b) female and juvenile dyads without adult male fission events and (c) dyads involving adult males only. Bars represent the standard deviations from 1000 simulations of random decisions.

integrated over time. On the other hand, an aerial survey representing a snapshot in time typically would show 4–12 herds in our study area. As one would expect from previous research, adult males were less tightly clustered than other sex and age groups because they often moved between mixed herds and bachelor groups (Fig. 2).

Not surprisingly, dyads that had high association indices (e.g. >0.8) also had high FDI values because, in order for a pair to spend all of their time together, they would have to choose to remain in the same groups during fission events (Fig. 3). For dyads with lower association indices, however, the probability of a dyad remaining in the same group during a fission event was not closely correlated with the amount of time that they spent together (Fig. 3). Therefore, the nonrandom group structure apparent in the traditional association analysis (Fig. 2) is due in small part to nonrandom decisions made by individuals during all fission events (the weak effect in Fig. 3), but in greater part to the variable lifetimes of the resulting fission groups. Consideration of FDI scores has thus helped us to understand the mechanisms underlying results of traditional association analysis.

FDI scores reflected the qualitatively different fission–fusion behaviour of adult male buffalo versus females and juveniles. Mean FDI scores of dyads involving females and juveniles were significantly higher when fission events associated with adult males were included (Figs 3, 4a). This arises from the frequent occasions when a few adult males left a mixed group (constituting a fission event); all other pairs of individuals were counted as having stayed together, thus increasing their FDI. The distribution of FDI values of female and juvenile pairs was significantly different from what would be expected given random decisions (Fig. 4). This difference was magnified when adult male fission events were included in the analysis (Fig. 4a), compared with when they were excluded (Fig. 4b). Finally, the fission decisions of adult males were not statistically different from random decisions (Fig. 4c).

While this distinct behaviour of females and juveniles versus adult males confirms and elaborates earlier results, some of our findings differ from the previous studies of African buffalo by Sinclair (1977), Mloszewski (1983) and Prins (1996). First, fission events seem to happen frequently in the KNP (185 female and juvenile fission events over a 2-year period), whereas in previous studies it is not clear how often herds were splitting apart, perhaps due to the smaller number of marked individuals in those studies. During this study we saw only 36 groups in the study area that did not have radiocollars (compared with 917 sightings of collared groups) due to the high density of marked individuals (~90 radiocollars in 4–12 groups). Second, both Mloszewski (1983) and Prins (1996) suggested that certain individuals always remain together in fission events due to either dominance and intraherd competition (Prins 1996) or family group structure within herds (Mloszewski 1983). In this study, we showed that although there were some nonrandom patterns in the FDI of female and juvenile pairs (Fig. 4b), the pattern was not as strong as what might be expected from previous studies. Further work on how fission decisions may be affected by body condition, reproductive status and genetic relatedness would be enlightening.

Application of the FDI

The fission decision index may not be applicable to all studies. The FDI is best applied when individuals choose between subgroups only during fission events. This may be reasonable for species that incur high dispersal costs, perhaps due to high predation rates or lowered foraging efficiency, but if individuals are highly mobile and often move between subgroups, then traditional indices reflecting the proportion of time that dyads spend together are reasonable measures of association. The study of Szykman et al. (2001) on hyaenas is an example where individuals may be relatively unconstrained in their choice of subgroups: as top predators, the cost of dispersing short distances between subgroups within a clan may be minimal. The necessity of observing multiple fission events per dyad may also limit application of the FDI method. Finally, the lifetime of fission subgroups may reflect the degree of satisfaction with that group composition. In this case, our initial assumption that group fission and fusion dynamics are not controlled by individuals no longer applies, and thus the greater weight that is assigned to longer-lived groupings in traditional association indices may be more appropriate.

The FDI requires rich data regarding the underlying fission–fusion process, and the probability of detecting fission events is related to the proportion of individuals that are marked. Studies with fewer marked individuals will have downwardly biased FDI values because they are more likely to miss fission events when all the marked animals stay together, which would increase their FDI. This presents difficulties if individuals choose differently in short-duration fission events, as these are most likely to be missed. It also presents difficulties when comparing across studies. However, if a researcher has a random sample of fission events, then the FDI should represent an unbiased estimate of the probability that two individuals will remain together during a fission event. Furthermore, one could structure the data according to each splinter group's duration to investigate whether the FDI is more random during short-term splits (which may be unintentional and due to predation and/or lack of communication) than during long-term splits (which may be due to intragroup competition). Previous studies may not have had the data resolution necessary for our FDI approach. We believe, however, that this technique will become increasingly valuable as improved technology facilitates the tracking of more individuals with greater spatial and temporal resolution.

Analysis of an aggregate parameter (e.g. proportion of time spent together by a pair) that is the product of two underlying processes limits our ability to understand those underlying processes. We believe that separating the process of individual choice from the process of group fission or fusion leads to an improved understanding of the mechanisms of association. In addition, this separation helps to avoid apparently arbitrary definitions of classes of companionship based upon the amount of time that individuals spend together (e.g. Weinrich 1991; Whitehead et al. 1991). Analyses using traditional association indices implicitly combine the effects of the fission–fusion process and the choices made by individuals, and although their conclusions about the proportion of time that individuals spend with one another remain valid, they may not accurately reflect individual preferences.

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