

A Practical Guide to the Study of Social Relationships

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Behavioral ecologists have devoted considerable effort to identifying the sources of variation in individual reproductive success.^{1–5} Much of this work has focused on the characteristics of individuals, such as their sex and rank. However, many animals live in stable social groups and the fitness of individuals depends at least in part on the outcome of their interactions with other group members. For example, in many primate species, high dominance rank enhances access to resources and reproductive success.^{4,5} The ability to acquire and maintain high rank often depends on the availability and effectiveness of coalitionary support.⁶ Allies may be cultivated and coalitions may be reinforced by affiliative interactions such as grooming, food sharing, and tolerance.^{7,8} These findings suggest that if we want to understand the selective pressures that shape the social behavior of primates, it will be profitable to broaden our focus from the characteristics of individuals to the properties of the relationships that they form with others. The goal of this paper is to discuss a set of methods that can be used to quantify the properties of social relationships.

Although primatologists have long emphasized the importance of social relationships, in most studies of social behavior the individual, not the dyad, is the unit of analysis. Researchers have focused primarily

on individuals for several reasons. First, we are used to thinking about how natural selection shapes behavioral traits, and natural selection acts on individuals, not dyads. Second, dyadic data present a statistical headache because dyads are not independent. Although powerful new statistical procedures enable us to deal with this problem, not all of us are up to speed on these methods. Third, behavioral data are not always dense enough to support dyadic analyses; in these cases, researchers may prefer to combine information across individuals within specified categories such as close kin and peers. Moreover, there is no established consensus about how measure the properties of social relationships.

The goal of this paper is to provide a practical guide to the study of social relationships. We begin with a brief discussion of the conceptual foundations for the study of relationships that was originally developed by Robert Hinde and subsequently expanded by Hans Kummer. Hinde and Kummer

raised several related questions: How are relationships among individuals patterned? What are the proximate mechanisms that mediate the impact of social interactions on individuals? What are the long-term adaptive consequences of social relationships for individuals? What do primates know about their own relationships and the relationships of others?

The absence of an established toolkit for describing the properties of social relationships complicates efforts to answer the first question, and this inevitably affects our ability to answer the others. Thus, our primary goal is to present a set of procedures for quantifying the properties of social relationships. Our efforts are strongly influenced by Jeanne Altmann's influential efforts to provide a rigorous foundation for behavioral data collection. We also discuss experimental methods that have been developed for probing primates' perception of their relationships, as well as noninvasive procedures that have begun to illuminate the proximate physiological mechanisms linking behavior to adaptive outcomes. We then explore the association between the structure of social relationships and fitness outcomes. We end with a discussion of questions that may direct future work.

CONCEPTUAL FOUNDATIONS

Current interest in social relationships builds on conceptual foundations established by Robert Hinde, who pioneered the study of relationships in primates.^{9,10} Hinde considered relationships to be the outcome of a contingent series of interactions between two individuals, and emphasized the importance of constructing

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descriptions of relationships from observational data on social interactions.

In studies of mother-infant relationships among rhesus macaques, Hinde and his colleagues showed how changes in the behavior of both mother and infant influenced the amount of time they spent in close proximity during the infant's maturation.^{11–13} Hinde's work showed that in many cases the behavior of an individual was best predicted by the properties of its relationship with others, not by its own properties. For example, the behavioral consequences of a brief separation of mother and infant were best predicted by the characteristics of the relationship before separation occurred rather than by individual attributes such as the infant's age, sex, or the mother's experience. Infants who showed the greatest distress were those who, before the separation, had been relatively more active than their mothers in maintaining physical contact. Jeanne Altmann's classic monograph, *Baboon Mothers and Infants*, took Hinde's approach to the field.¹⁰

Hans Kummer integrated Hinde's conceptual formulation with the functional perspectives of behavioral ecology. Kummer¹⁴ proposed that relationships are long-term investments that generate benefits for the members of the dyad. Kummer reasoned that the value of relationships would depend on the intrinsic qualities of the members of the dyad, such as rank and sex; their tendency to act in ways that increased or decreased each other's fitness; and their availability to one another, which would affect their ability to act on their behavioral tendencies. He proposed that individuals use social interactions to shape particular aspects of their relationships. For example, one monkey might groom another to enhance the likelihood that the recipient would be motivated to maintain proximity and thus be available to provide coalitionary support. Kummer assumed that individuals selectively invested in relationships that ultimately enhanced their fitness.

QUANTITATIVE DESCRIPTIONS OF SOCIAL RELATIONSHIPS

Hinde emphasized the importance of constructing systematic descrip-

tions of relationships from observations of social interactions. Such descriptions would include information about the content, quality, and temporal sequence of interactions.¹⁰ Researchers have spent thousands of hours conducting focal observations¹⁵ that generate high-quality data about who does what to whom, how often, for how long, and in what sequence. However, we do not have a well-developed consensus about how to quantify the characteristics of dyadic relationships.¹⁶

Any two animals that recognize one another as individuals and meet repeatedly have some kind of relationship; the empirical task is to describe its characteristics. We suggest that relationships or social bonds occupy a multidimensional space, and that we can use behavioral data to map the contours within that space. There are various dimensions along which relationships may differ.¹⁷ For example, two individuals may rarely interact or interact often (frequency); they may interact in a limited number or in a diverse range of behavioral contexts (diversity); their directional interactions may be highly one-sided or evenly balanced (symmetry); their interactions may range from mostly hostile to mainly friendly (tenor); they may be tense or relaxed when they are together (tension); they may behave toward one another in a consistent or inconsistent manner (predictability); and they may interact at high rates for short periods or consistently at high rates over long periods (stability). This is a preliminary, probably incomplete, list of the dimensions of social relationships that can be assessed with behavioral data.

The distribution of relationships along these types of continua can help us to characterize relationship quality. Relationships that fall toward the right side of the continua in Figure 1 could reasonably be categorized as close social bonds, roughly similar to what most people would think of as friendships. Relationships that show high levels on some dimensions but not others might be characterized in different ways. For example, there might be

dyads in which one partner becomes attractive to the other for a limited period (for example, a female in estrus), and such relationships might be characterized as opportunistic or instrumental.

Some researchers have used the rate of affiliative behavior or the absence of agonistic behavior as a proxy for relationship quality.¹⁸ In general, dyads with high rates of affiliation and/or low rates of aggression are categorized as having good, strong, or intense social relationships. Rates of affiliation may be an important component of social relationships, but they may not fully capture their complex dynamics.

Our multi-dimensional view of social relationships is similar in some ways to Cords and Aureli's¹⁹ proposition that relationships can be characterized by three components: compatibility, security, and value. They defined compatibility as the degree of tolerance within a dyad, it is therefore similar to what we have termed the tenor of social relationships. Secure relationships are those that are predictable and consistent over time, and thus partially overlap with the dimension that we have labeled consistency. Cords and Aureli define relationship value in terms of the benefits that individuals derive from their relationships. Our scheme has no direct analog for relationship value, partly because the value of social interactions is so difficult to quantify.

The procedures that we describe below provide a starting point for efforts to quantify the dimensions of dyadic relationships. Many of these methods were developed for analyses of baboon behavior, but ought to be appropriate for a range of species. We have not attempted to provide an exhaustive review of all methods that have been used for assessing social behavior, but focus on ones that seem to be particularly useful for characterizing the quality of social relationships in sizable groups. For some dimensions of relationships, we currently lack appropriate methods. We fully expect that the procedures that we describe will be modified, improved, and expanded by others over time.

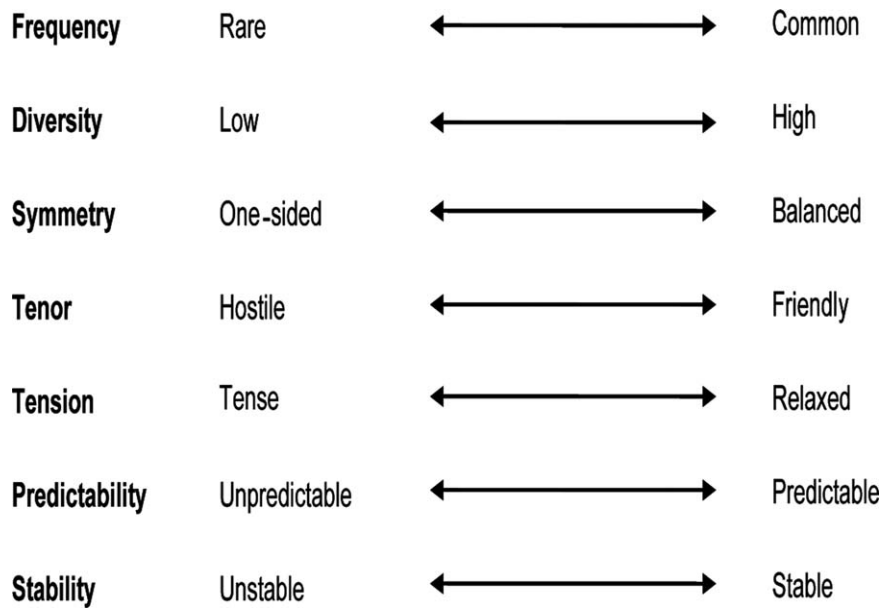


Figure 1. The dimensions of social relationships.

Observational Methods

Analyses of social relationships are constructed from raw behavioral data. The advantages and disadvantages of various data collection schemes were first laid out in Jeanne Altmann’s classic paper,¹⁵ which remains the primary reference on this topic. Altmann distinguished between behavioral events, which are instantaneous, and behavioral states, which have a measurable duration.

Focal sampling, in which a single individual is observed for a predetermined length of time and behavior is continuously monitored, is particularly useful for the study of dyadic relationships because focal data can provide information about the form, frequency, and sequence of social events, such as approaches and vocalizations and the duration of social states, such as grooming or proximity. Observers can keep track of which individual initiated social events or states and which individual was responsible for ending them. Continuous monitoring of activity state and location during focal samples can also provide useful information about the context in which interactions occur.

Despite its many problems, including biases due to differences in the observability of individuals and the

conspicuousness of behaviors, *ad libitum* sampling remains an important part of the observational toolkit because it provides information about important social interactions that are uncommon or unpredictable. For example, most observers rely on *ad lib* observations of conflict and competition to assess dominance relationships and to provide information about the patterning of coalitionary support.

DIMENSIONS OF DYADIC SOCIAL RELATIONSHIPS

Frequency of Events and Duration of States

The frequency of interaction is often used to evaluate relationship quality. It is straightforward to tabulate the frequency of events from focal data. However, it is often important to correct for differences in observation time, which can arise if individuals die or disappear, or are not sampled on the same schedule. Frequencies of event variables are often converted to rates for this reason.¹⁵ Rates are computed by dividing the number of events in which an individual participated by the amount of time that individual was observed. When information about

the duration of state variables is available, the proportion of time devoted to the activity can be computed by dividing the summed durations by the amount of time observed.

It is slightly more complicated to measure the frequency and duration of social interactions and proximity for species like chimpanzees, that live in fission-fusion groups, where opportunities to interact are influenced by both observation time and party composition. Thus, the number of interactions between two individuals, A and B, would be divided by the amount of time that A was observed when B was present in the same party and the amount of time that B was observed when A was present in the same party.

For animals that live in fission-fusion groups, the decision to join or leave a particular subgroup may be based on general preferences for being with others (gregariousness) or preferences for particular individuals within the subgroup. Pepper, Mitani, and Watts²⁰ devised a procedure to distinguish between associations that arise from general gregariousness and those that arise from preferences for particular partners. The pairwise affinity index can be expressed as:

$$\frac{I_{AB} * \sum_1^n s_i(s_i - 1)}{\sum A_i(s_i - 1) * \sum B_i(s_i - 1)}$$

where I_{AB} equals the number of times that individuals A and B were present in the same party, n represents the number of parties observed, and s represents party size. The summation term in the numerator represents the total number of “neighbors” that individuals had in all parties that were formed. In a party of size s , the number of possible neighbors is equal to $s(s-1)$. This value is computed for each party and summed across all parties observed. The first term in the denominator represents the total number of neighbors that A had in all of the parties that A was observed in. This is equal to the product of the number of times that A was in a party of size s and the number of neighbors in a

party of size s , or $s-1$. The second term in the denominator represents the same calculation for B. Observed values of the pairwise affinity index can be compared against values that would be obtained if individuals were randomly assigned to parties. The randomization procedure retains information about the observed distribution of party sizes and the number of times that particular individuals were observed in parties, but reshuffles the composition of parties to generate values expected on the basis of chance.

Composite Sociality Index

There are often positive correlations in the frequency with which particular dyads participate in different types of interactions. For example, dyads that have high rates of association may also have high rates of grooming. It is problematic to analyze inter-correlated behaviors separately because multiple tests increase the risk of committing Type 1 errors and the interactions are not independent.²¹ One solution is to combine different types of interactions together into a single variable, but this is not a useful solution if the absolute rates of behaviors differ (for example, approaches are much more common than grooming initiations). Under these conditions, aggregate measures will be strongly biased by the most common types of behaviors.

To address this problem, Sapolsky, Alberts, and Altmann²¹ created a composite measure based on the relative frequencies of positively correlated nonaggressive social interactions. This measure was originally developed to measure the degree of social integration of individuals. It was subsequently modified to measure the strength of dyadic affiliative relationships.²² This measure, which we label the Dyadic Composite Sociality Index to distinguish it from the individual-based measure, is computed with the following formula:

$$DSI_{xy} = \frac{\sum_{i=1}^d \frac{f_{ixy}}{\bar{f}_i}}{d}$$

Here, d is the number of behaviors that contribute to the index; f_{ixy} is

the rate of behavior i for dyad xy ; and \bar{f}_i is the mean rate of behavior i across all dyads in the subset of interest (for example, all group members or all adult females). The values of this index range from $0 \rightarrow \infty$. High values of the Composite Sociality Index (CSI) represent dyads that have more frequent and/or longer lasting affiliative interactions than the average dyad in their group. Low values represent dyads that have less frequent and/or shorter affiliative interactions than the average dyad.

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This basic procedure has been used to characterize dyadic relationships among baboons,²²⁻²⁴ several species of macaques,²⁵⁻²⁸ and wild horses.²⁹

One potential shortcoming of the CSI is that it does not account for differences in the amount of variation in behavioral variables (R. Mundry, personal communication). The contribution of variables to the composite measure will be correlated with their coefficient of variation. For all behavioral variables to contribute equally, they must be standardized. However, it is not clear whether composite measures based on standardized or unstandardized variables are more biologically meaningful. It is possible that behaviors with very uneven frequencies

across dyads, such as grooming, have a particularly important impact on relationship quality. If so, it would not be useful to standardize the behavioral variables. At this point, we suggest that users compute both versions of the CSI and compare their predictive power.

Exploratory Principal Components Analysis

Another approach is to use principal components analysis (PCA) to reduce a set of correlated behavioral variables to a smaller set of variables that vary orthogonally and are thus independent. For example, in a study of captive chimpanzees, Fraser, Schino, and Aureli³⁰ used exploratory PCA to analyze inter-relationships across nine behavioral variables. They found that these behaviors formed three distinct components, which they interpreted as relationship value, compatibility, and security.

This is an intuitively appealing approach, but may not be entirely suitable for some behavioral datasets. PCA is most reliable when the sample size is large and the ratio of observations to behavioral variables is high.³¹ However, there are no firm guidelines for sample size or the ratio of subjects to variables.

Another potential drawback of PCA is that it can be difficult to interpret the factors that emerge from the analysis. For example, four behavioral variables (grooming, proximity, support, and food sharing) loaded strongly on the first component in Fraser, Schino, and Aureli's analysis. They labeled this component as "value," but others might assign a different label, such as relationship strength or affiliativeness.

Diversity of Behaviors

Observational data also provide information about the types of interactions that dyads participate in and the kinds of vocalizations that they direct to one another. Some dyads might exchange many different kinds of interactions, while others might participate in a narrower range of

interactions. The fact that rates of various types of affiliative interactions are positively correlated across dyads suggests that variation in the range and diversity of interactions does exist.

Measures of the number of “behavioral diversity” factors are likely to be sensitive to observation time. Individuals observed often will have more opportunities to interact than individuals that are observed less often.³² This means that investigators need to assess how the diversity of interactions is related to observation time within their study groups and account for this in their analyses.

Symmetry

For directional social interactions, such as grooming, it is possible to measure the contributions of each member of a dyad, and this variation may be meaningful. For example, Seyfarth’s³³ hypothesis that females will trade grooming for support from higher ranking individuals predicts that low-ranking females will groom higher-ranking females more than they are groomed in return. To assess this kind of prediction, we need to assess the distribution of grooming within the dyad.

Grooming Equality Index

Grooming can be evenly balanced within a dyad or one member of the pair can contribute more grooming than the other. The extent of grooming equality within dyads can be assessed with the following formula:²²

$$1 - \left| \frac{(G_{ij} - G_{ji})}{(G_{ij} + G_{ji})} \right|$$

Here, G_{ij} is the amount of time that individual i groomed individual j and G_{ji} is the amount of time that j groomed i . The Grooming Equality Index ranges from 1, when grooming is evenly balanced within the dyad, to 0 when grooming is completely one-sided. This measure could also be used to assess other types of directional interactions, such as the distribution of food transfers or initiation of proximity.

This measure is similar to van Hoof and Wesling’s Directional Consistency Index (DCI),³⁴ which was originally designed to assess the directionality of interactions at the group level. The DCI, which has been adapted to assess consistency in the direction of interactions within dyads,³⁵ is computed as $(F_{ij} - F_{ji}) / (F_{ij} + F_{ji})$, where F_{ij} is equal to the frequency of interactions directed by i to j , F_{ji} equals the frequency of interactions directed by j to i , and $F_{ij} > F_{ji}$. The DCI ranges from 0 when behaviors are perfectly balanced within dyads to 1 when behaviors are unidirectional. One limitation of both these measures is that they are likely to be unreliable when samples are small.

Reciprocity Index

Skews in small samples are likely to occur by chance when the behaviors of interest occur infrequently or some pairs of individuals seldom interact. One solution to this problem is to limit the analysis to pairs of animals that interact more often than a threshold value, but it is not clear where this threshold should be set. An alternative method, first developed to analyze grooming among female baboons,³⁶ is based on the binomial probability of observing x events in a sample of $x + y$ events, in which x and y are the contributions of each member of a dyad. The directional reciprocity index is computed as the ratio between the cumulative binomial probability of the smaller of the two values and the cumulative binomial probability of the larger of the two values. When these values are equal, the probabilities are the same and the ratio is equal to 1. The reciprocity index ranges from 0 when interactions are highly skewed to 1 when interactions are perfectly balanced within dyads.

It is important to point out that it is more straightforward to interpret values of the reciprocity index that are near 0 than values that approach 1. Values near 0 occur only when there is a substantial difference in the binomial probabilities of the two events and thus provide strong evi-

dence that grooming is highly unbalanced within the dyad. Values may approach 1 if samples are large and grooming is evenly balanced within the dyad or if samples are small and binomial probabilities of events are therefore similar. It is possible to distinguish between these alternatives by computing the statistical power of the binomial probability estimate.

The reciprocity index can be rescaled to provide information about the pattern of skews in the distribution of events within dyads. If $d > s$, the adjusted reciprocity index, RI_{adj} , equals $1 - (0.5 \times RI)$. If $d \leq s$, $RI_{adj} = 0.5 \times RI$. RI_{adj} approaches 1 when d is much greater than s , and approaches 0 when s is much greater than d . If d and s represent contributions by the dominant and subordinate members of a dyad, then when RI_{adj} approaches 1, the dominant member of the dyad would be mainly responsible for grooming; when RI_{adj} approaches 0, the subordinate individual would be mainly responsible for grooming. Variables d and s could also represent older and younger members of dyads or males and females in mixed-sex dyads. As for the reciprocity index, extreme values of RI_{adj} are easier to interpret than intermediate values. Again, a power analysis can help to interpret the meaning of intermediate values.

Hinde Index

The Hinde Index, originally developed for assessing the nature of mother-infant relationships among rhesus macaques,³⁷ provides an alternative method for assessing the extent of symmetry in social interactions. The Hinde Index is calculated as:

$$100 \times \left(\frac{C_i}{C_i + C_m} - \frac{B_i}{B_i + B_m} \right)$$

In the case of physical contact between mothers and infants, C_i is the number of times the infant makes contact with the mother, C_m is the number of times the mother makes contact with the infant, B_i is

the number of times the infant breaks contact with the mother, and B_m is the number of times the mother makes contact with the infant. Values of the Hinde index range from -100 to $+100$. High values are generally interpreted to mean that i is mainly responsible for maintaining contact with m ; low values are interpreted to mean that m is mainly responsible for maintaining contact with i . The variables i and m could also represent male and female consort partners, high- and low-ranking members of a dyad, and so on. Similarly, in analyses of responsibility for proximity, C would represent approaches to within a given distance and B would represent leaves.

Brown³⁸ has pointed out that values of the Hinde Index are difficult to interpret because different proximity patterns can generate the same values. A value of 0 could occur because i was responsible for an equal number of makes and breaks of contact or because m was responsible for all makes and breaks of contact. To avoid this ambiguity, Brown devised an alternative measure, which is calculated as:

$$100 \times \left(\frac{C_i + B_i}{C_i + B_i + C_m + B_m} \right)$$

The values of Brown's index range from 0 to 100. High values of this index indicate that i is responsible most of the changes in contact and low values indicate that m is responsible for most of the changes in contact.

Relationship Tenor

It is common for pairs of individuals to exchange both affiliative and aggressive behaviors. One way to assess the general tenor of a relationship is to evaluate the relative frequency of affiliative and hostile behaviors within the dyad. Weaver and de Waal³⁹ devised a measure that is based on the ratio of the relative rate of affiliative to aggressive interactions. Their measure, which they referred to as relationship quality, is calculated as:

$$\left(\frac{F_{ij}}{\bar{F}} \right) \left(\frac{H_{ij}}{\bar{H}} \right)$$

where F_{ij} is the rate of friendly interactions between i and j , \bar{F} is the average rate of friendly interactions across dyads, H_{ij} is the rate of hostile interactions between i and j , and \bar{H} is the average rate of hostile interactions across dyads. One problem with this measure is that it is a ratio, and ratios are ungainly. In this case,

Analyses of the sequence of interactions and the conditional probability of particular outcomes could provide an index of predictability. For example, baboons and macaques sometimes grunt as they approach others, and these grunts seem to serve as a predictable signal that the caller will not behave aggressively.⁴⁶⁻⁴⁸ The use of these kinds of signals might vary across dyads and provide a measure of the predictability of aggression.

the measure is undefined if the denominator is zero. This means that it is possible to assess the quality of relationships in dyads that never engaged in affiliation (numerator equals 0) but did engage in conflict. However, it is not possible to assess the quality of relationships that engaged in affiliation but not conflict (denominator equals 0).

An alternative measure may be more useful. Perry, Barrett, and Manson⁴⁰ divided the number of focal samples that included friendly or cooperative behavior by the number of focal samples that contained friendly, cooperative, or agonistic behavior. This index ranges from 0 in dyads that have exclusively hostile interactions to 1 in dyads that have exclusively friendly or cooperative interactions. We used a very similar procedure, based on the rates of affiliative and aggressive interactions, to assess the tenor of relationships among female baboons.²³

Tension

Pairs of individuals may be relaxed or tense when they are together. In some primate species, the rate of self-directed behaviors (SDB), such as scratching, provides a reliable behavioral measure of stress and anxiety.⁴¹ While the rate of SDB has mainly been used to assess individuals' response to conflict and reconciliation,⁴² it can also be used to assess the quality of relationships. For example, Castles⁴³ found that female baboons displayed 40% higher rates of self-directed behaviors when their nearest neighbor was higher-ranking than themselves than when their nearest neighbor was lower-ranking, suggesting that proximity to higher-ranking individuals caused anxiety.

Predictability

One of the benefits that individuals derive from close relationships is greater predictability and sense of control.^{44,45} However, to our knowledge, no methods for assessing the predictability of social interactions have been developed. Analyses of the sequence of interactions and the conditional probability of particular outcomes could provide an index of predictability. For example, baboons and macaques sometimes grunt as they approach others, and these grunts seem to serve as a predictable signal that the caller will not behave aggressively.⁴⁶⁻⁴⁸ The use of these kinds of signals might vary across dyads and provide a measure of the predictability of aggression.

Temporal Stability

Methods for assessing the temporal stability of social relationships at the dyadic level are not well-developed. One procedure to assess this dimension of relationships focuses on relationships with preferred partners.²³ In a study of the duration of close social bonds among female baboons, values of the dyadic CSI were first used to rank each female's partners in each year. The partners with the three highest CSI values were then categorized as the female's "top partners." We tabulated the number of consecutive years in which particular females appeared among the focal females' three top partners. For example, if female A was observed over 5 years and female B was among her top three partners in years two, three, and four, their close social bond lasted 3 years. A 1-year gap between "consecutive" years was allowed. The rationale for allowing this gap was based on the arbitrariness of the threshold for identifying top partners and the realization that there might be temporary fluctuations in the nature of females' relationships from year to year. However, this decision has been criticized because it artificially inflates estimates of the temporal stability of social bonds.^{49,50} In such analyses, it is important to control for partner availability, as opportunities to form close social bonds are constrained by coresidence. Mitani⁵¹ used a similar procedure to assess the stability of social bonds among male chimpanzees.

AGGREGATING INFORMATION ABOUT THE PROPERTIES OF SOCIAL RELATIONSHIPS

Once we have measured the various dimensions of relationships, we can explore the correlations among them. For example, we have discovered that pairs of female baboons having high CSI values also tend to have well-balanced grooming relationships and to maintain their relationships over time.^{23,24} Similarly, Mitani⁵¹ documented correlations between the frequency of pairwise associations, the symmetry of

grooming, and the stability of social bonds among male chimpanzees. As more information about the properties of social relationships is accumulated, we will be able to determine whether there are consistent patterns in their collective properties.

Individual Measures of Sociality

Individuals may vary in the kinds of relationships they form with others. For example, some individuals may be more gregarious than others. Similarly, some individuals might allocate all of their grooming to a small number of partners, while others might distribute grooming across a larger number of partners. Thus, it is also useful to develop

In some cases, individual measures of sociality can be derived directly from dyadic data. For example, to determine whether females vary in how well-balanced their grooming relationships are, we could compute the average value of the grooming equality index for each female with all of her partners. In some cases, however, different methods are appropriate.

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equality index for each female with all of her partners. In some cases, however, different methods are appropriate.

Sociality Index

Sapolsky, Alberts, and Altmann²¹ devised an individual measure of sociality, or social integration, which was subsequently modified to create the dyadic Composite Sociality Index. The individual Sociality Index, SI, is calculated as:

$$SI_x = \frac{\sum_{i=1}^d \frac{b_{ix}}{\bar{b}_i}}{d}$$

where b_{ix} is the rate of behavior i for individual x , and \bar{b}_i is the median rate of behavior x for all individuals in the subset of interest (for example, all group members or all adult females), and d is the number of different types of behavior measured. The values of this index range from $0 \rightarrow \infty$. High values of the index represent individuals who are more socially integrated than other are members of their group; low values represent individuals who are less socially integrated than other members of their group.

Duration

There are several ways to assess the temporal stability of relationships at the individual level. Correlations in partner rank orders between successive time periods can be computed using matrix correlation statistics.^{51,52} This procedure requires separate tests for each pair of successive years, which raises the likelihood of committing Type 1 errors. To evaluate the consistency of partner rank orderings over longer times or more time periods, a nonparametric Friedman's test⁵³ can be used. However, these methods cannot accommodate changes in group membership from one time period to the next, which limits their usefulness.

We devised two alternative procedures to assess variation in the stability of social bonds and to accommodate demographic changes.⁵⁴ For each individual in

each year, partners are rank ordered. For each individual, the number of different partners that the individual had within a given range of partner ranks (for example, rank orders 1–3, 4–6, 7–9) across time periods is tabulated. The following formula is computed:

$$\text{PSI} = \frac{NS - U}{NS - S}$$

where N is the number of years being considered, S is the number of partner-rank slots being evaluated, and U is the observed number of different (unique) partners that occupy positions within the S partner-rank slots across years. The value of the PSI varies from 1 for females who had the same S partners in each year to 0 for females who had a completely different set of partners in each year.

One useful feature of this procedure is that observed values of the PSI can be compared using simulation analysis against values that would be expected if females chose their partners. It is also possible to evaluate different possible ranges of rank orderings (for example, 1–2, 2–4...; 1–4, 5–8...), and to compare observed values of the PSI against simulated values. When we applied this method to female baboons, we found that females showed stable preferences for their top three partners but not for lower-ranked partners.⁵⁴

There are some limitations to this procedure. For instance, it does not deal well with multiple tied ranks, which often arose at the bottom of females' preference orders. In addition, this procedure may be less useful for species that live in small groups because it will be harder to demonstrate that observed patterns of preferences differ from patterns expected to occur by chance.

The PSI does not account for changes in partner rankings that were due to the death, disappearance, or dispersal of a partner from one time period to the next. To account for this, we created an alternative measure, the Partner Preference Index^{55,56}:

$$\text{PPI} = \frac{2S - U}{2S - S - X}$$

where S is the number of partner rank slots being evaluated, U is the number of different partners that the individual had in those years, and X is the number of top partners in the first time period who were not present in the next time period. Individuals with high values on the Partner Preference Index are ones that maintained the same partners from one time period to the next; individuals with low values on the Partner Preference Index are ones who switched partners from one time period to the next although their former partners were still present in the group.

Partner Diversity

If the amount of time and energy that animals can devote to socializing varies, then they can apportion social interactions evenly among potential partners or focus their attention on a subset of the group. Cheney⁵⁶ used the Shannon-Weiner Diversity Index, originally developed as an information theoretic measure, which has been widely used in ecology, to assess how evenly grooming is distributed across group members. The index is calculated as:

$$H = \sum_{i=1}^R p_i \log p_i$$

where p_i is the relative proportion of grooming directed toward individual i . H is maximized when a female interacts with all possible partners with equal frequency and minimized when a female focuses all of her interactions on one partner.

To standardize the measure for comparison with values obtained in studies of groups of different sizes, it is useful to compute the ratio between the observed diversity index, H , and the maximum possible value of the diversity index for a group of size N : $H_{\text{max}} = -\ln(N - 1)$.

One strong caution in using this method is that the distribution of grooming across dyads is sensitive to sampling effort and variation in the rate of interaction across individuals.⁵⁷ Alternative measures of partner diversity are needed.

EXPERIMENTAL STUDIES OF RELATIONSHIP QUALITY AND FUNCTION

Playback experiments using animals' natural vocalizations have mainly been designed to plumb primates' knowledge about their social world, but they can also provide valuable insights about the nature and function of social interactions and relationships. For example, we observed that female baboons sometimes grunted to their former opponents after conflicts. We hypothesized that the grunts served a reconciliatory function.⁴⁶ To test this hypothesis, a series of playback experiments were conducted in which victims of aggression heard the grunts of their former opponent (test condition) or another female (control condition) shortly after conflicts had ended.^{46,47} After hearing the grunts of their former opponents, females seemed to be less anxious about becoming the target of redirected aggression from their former opponents⁴⁶ and were also more likely to approach and interact with their former opponents.⁴⁷

Playback experiments are also useful because they can provide independent evidence that a particular kind of relationship exists between two individuals. For example, several playback studies have shown that adult male baboons respond more strongly to the distress calls of their female friends' infants than to the calls of other females' infants,^{58,59} suggesting that males have a special kind of relationship with the offspring of their female friends.

Playback experiments, using the calls of a single individual or a sequence of calls from several individuals, can be designed to simulate normal social interactions or to mimic an anomalous event such as an apparent rank reversal. Most playback experiments follow a within-subject design; all include a test and at least one control. Although some playback experiments can be done opportunistically, others are dependent on a prior event. For example, in a study designed to determine whether baboons treat vocal signals by an opponent's close relative as a form of alliance support, playbacks were conducted only after

naturally occurring agonistic interactions were observed.⁶⁰ If the critical prior events are uncommon, these kinds of experiments can take months to complete.

To retain their credibility, playback experiments must be done at very low rates. Ideally, experimenters should also use as dependent variables behaviors other than orienting responses, such as the subject's subsequent interactions with the caller, because orienting responses can be difficult to interpret.

Because they use natural stimuli that can be combined in novel ways and presented under controlled conditions, playback experiments can offer an independent test of hypotheses generated from observation. For more details about the design and execution of field playback experiments, see Zuberbühler and Wittig.⁶¹

METHODS FOR ASSESSING PROXIMATE MECHANISMS THAT MEDIATE THE EFFECTS OF SOCIAL BEHAVIOR

Just as playback experiments offer a means to 'interview' subjects about what they know about each other's relationships, new advances in the noninvasive extraction of hormones provide information about how individuals perceive the events they experience. Robert Sapolsky, who pioneered endocrinological studies of free-ranging primates, developed darting techniques that minimized anticipatory stress before the procedure and avoided loss of habituation.⁶² He showed that dominant male baboons generally had lower glucocorticoid metabolite (GC) levels than subordinate males, but that dominant males who rarely groomed females or interacted with infants had elevated GC levels.^{63,64} This work suggested that social relationships may buffer the effects of stress.

Darting is invasive and potentially dangerous, so researchers welcomed new methods for the extraction of hormone metabolites from feces. Feces can be collected without handling animals directly. Also, it is relatively straightforward to collect samples from known individuals on

a systematic basis. As a result, it is now possible to monitor with some precision how individuals respond to social and environmental events. For a more complete discussion of the methods of involved in collecting and processing hormone samples, see Beehner and Whitten,⁶⁵ Hodges and Heistermann,⁶⁶ and Anestis.⁶⁷

Information derived from hormonal analyses is beginning to provide insight about the impact of social relationships on individuals. For example, among chacma baboons, the presence of immigrant, potentially infanticidal males produces elevated GC levels among lactating females with vulnerable infants.^{68,69} However, lactating females who have

Hormone metabolites extracted from fecal samples generally reflect responses to events during the past 24-48 hours, whereas urine samples reflect responses to events during the previous 1-3 hours.⁶⁶ When there is a time lag, a urine sample is much more likely to be influenced by a single social event, such as a fight or a grooming interaction, than is a fecal sample.

established friendships with resident males have significantly lower GC levels than females who have not.⁶⁹ Similarly, females who lose a close relative to predation experience significant increases in GC levels compared with females who have not.⁷⁰

Developments in the extraction of hormones from urine promise to shed

additional light on how animals respond to social events. For example, it has been known for some time that the neuropeptide oxytocin is important in social bond formation and affiliation.⁷¹ Recently, it been shown that the peripheral release of oxytocin in urine also correlates with affiliative behaviors.^{72,73} Studying captive marmosets, Snowdon and coworkers⁷² found that elevated levels of oxytocin were correlated with different behaviors in males and females, but that the highest mean levels of oxytocin were found in the most strongly bonded male-female pairs. In other words, supporting Hinde's original observation, oxytocin levels were best predicted by properties of the pair's relationship, not by any single property of either individual. Similarly, Crockford and colleagues⁷⁴ found that in wild chimpanzees urinary concentrations of oxytocin were higher after individuals groomed with a closely bonded partner than after they groomed with a less closely bonded partner.

Hormone metabolites extracted from fecal samples generally reflect responses to events during the past 24-48 hours, whereas urine samples reflect responses to events during the previous 1-3 hours.⁶⁶ When there is a time lag, a urine sample is much more likely to be influenced by a single social event, such as a fight or a grooming interaction, than is a fecal sample. Thus, if observers are interested in hormonal responses to particular events, urine is more useful than feces. However, this also means that the observer must know what has happened to the animal over the last few hours. The observer will therefore have to have monitored the individual continuously for several hours before and after the collection of a urine sample in order to make use of it.

LONG-TERM CONSEQUENCES OF VARIATION IN THE QUALITY OF SOCIAL RELATIONSHIPS

Systematic descriptions of the properties of social relationships derived from behavioral data,

experiments, or physiological analyses, can be used to assess the adaptive value of social bonds. The first effort to address this possibility drew on long-term data on the social behavior and reproductive histories of female yellow baboons.⁷⁵ For each female, an individual-based sociality index (SI) was constructed. These data were matched against information about offspring survival to one year of age, an important component of variation in the lifetime fitness of females. Females with higher SI values had higher survivorship among their offspring than females with lower SI values. This effect was independent of the effects of female dominance rank and the presence of kin.

These data suggest that sociality enhances female reproductive success. But it is also possible that the causal arrow goes in the other direction: Females that have surviving infants may become more sociable.⁵⁴ Female baboons are strongly attracted to newborn infants,^{76,77} so it is possible that the relationship between female sociality and infant survival is an artifact of this “natal attraction.” Therefore, in a subsequent study of a different baboon population, we restricted the analyses to observations of adult females when they did not have young infants and computed dyad-specific Composite Sociality Index (CSI) values for females with each of their adult female partners. The offspring of females with higher CSI values lived significantly longer than did the offspring of females with lower CSI values. This pattern was independent of the effects of dominance rank.⁷⁸ Taken together, these analyses strongly suggest that the quality of females’ social bonds influences the survival of their offspring. Females that had the strongest and most stable bonds with their most preferred partners also lived longer than other females.⁷⁹

There is also some evidence that the strength of social bonds influences the reproductive success of primate males. For example, male chimpanzees form strong and enduring bonds with other males in their group.⁵¹ These relationships may affect male reproductive success

because males preferentially support preferred partners in agonistic interactions. Also, coalitionary support plays an important role in the acquisition of top-ranking positions and top-ranking males sire the majority of infants within their groups.⁸⁰ Moreover, top-ranking males may selectively tolerate their allies’ efforts to mate with receptive females.⁸¹ However, researchers have not yet directly linked the quality of social

We do not fully understand the mechanisms that underlie the relationship between sociality and fitness in primate groups. Data from female baboons suggest that the strength of social bonds enhances females’ ability to cope with stress and protects them and their offspring from the deleterious effects of chronic elevation of the stress response. It is also possible that females with stronger and more secure social bonds may be less vulnerable to predation.

bonds among male chimpanzees to male reproductive success. Such links have been established in one group of Assamese macaques: the strength of males’ social bonds was linked to coalitionary support, their ability to acquire and maintain high ranking positions, and paternity success.²⁵

We do not fully understand the mechanisms that underlie the relationship between sociality and fitness in primate groups. Data from female baboons suggest that the strength of social bonds enhances females’ ability to cope with stress and protects them and their offspring from the deleterious effects of chronic elevation of the stress response. It is also possible that females with stronger and more secure social bonds may be less vulnerable to predation. Crested macaques respond more strongly to alarm calls produced by individuals with whom they have a close social bond than to alarm calls produced by other group members.²⁸ The alarm calls alert others that a predator is nearby and prompt collective mobbing behavior. Social bonds may also buffer feeding competition and enhance foraging efficiency.⁸²

FUTURE DIRECTIONS

Primatologists have made considerable progress in addressing the fundamental questions raised by Hinde and Kummer often using the observational methods advocated by Jeanne Altmann. At the same time, however, this research has generated new questions that may guide future research. We outline a few of these questions below.

1. What mechanisms underlie the relationship between sociality and fitness outcomes? In humans, social support has important effects on health.⁸³ Social ties seem to buffer the short-term effects of stress and may enhance the efficacy of anabolic processes involved in somatic maintenance and repair. This may affect both females and their offspring. Maternal exposure to environmental and social stressors can have detrimental impacts on their offspring’s growth rates, longevity, physiology, and behavior.^{84–87} It is important to determine whether the same mechanisms operate in humans and other primates.

2. Why do levels of sociability differ among individuals? A growing body of evidence suggests that social bonds enhance the fitness of

individuals, but there is considerable variation in the levels of sociability among individuals. In baboons, some variation is linked to the presence of preferred categories of partners, such as close kin and peers, but a substantial amount of variation remains unexplained.

We have recently explored the linkage between sociality and personality dimensions among female baboons.⁸⁸ Females with the highest scores on the Composite Sociality Index were significantly more likely to be characterized as “nice,” which means that they had higher rates of friendly contact (excluding grooming), higher rates of grunting when they approached lower ranking females, and were less likely to be alone. In contrast, females that were characterized as “loners” (females that were often alone and grunted mainly when they approached higher ranking females with infants) had uniformly low Composite Sociality Index values and higher stress levels. These findings suggest that at least some of the variation in sociality may be caused by individual differences in personality. Further efforts to identify the linkage among personality, sociality, and fitness are clearly needed.

3. Is there meaningful structure in primate groups above the level of the dyad? There is growing interest in using social network analyses to describe social structure in primate groups.⁸⁹ Network analyses are particularly useful because they can reveal structure above the level of the dyad. There are good reasons to believe that indirect (nondyadic) connections can have important impacts on information transfer and disease transmission within groups, but it is less clear how indirect connections would influence the patterns or consequences of social behavior. Brent and colleagues⁹⁰ have shown that proximity reach, one measure of indirect connectedness, is associated with lower glucocorticoid levels among high-ranking female rhesus macaques. However, we do not believe that network analyses can replace dyadic analyses. As King, Clark, and Cowlishaw⁸² concluded, “our results show how network analyses can enable

researchers to describe and interpret complex social processes in primate groups. However, the full interpretation of our results would not have been possible if detailed analyses of ... behavior at the level of the dyad had not been conducted previously.”

4. How widespread and strong are the effects of sociality on fitness? A growing body of evidence from a wide range of taxa suggests that the correlation between social bonds and reproductive success is not limited to primates. Similar patterns have been also been detected in female horses,²⁹ bottlenose dolphins,⁹¹ wild house mice,⁹² laboratory rats,⁹³ and rock hyrax.⁹⁴ However, we know little about the properties of social bonds in these taxa, and it is not yet clear whether particular features of close bonds recur across taxa.

CONCLUSIONS

By collecting fine-grained data on the behavior, social knowledge, and physiology of known individuals over extended times, primatologists are in a position to ask detailed questions about the selective pressures that shape the evolution of social behavior and cognition in complex societies. To make the most of our data, we need systematic procedures for assessing and describing the behavior of individuals and the properties of their relationships with others. We can use the kinds of methods described here to test hypotheses about the selective forces that shape behavioral strategies and to construct comparisons across individuals, groups, or taxa. Additional methods for characterizing social relationships are clearly needed. We hope that this paper stimulates efforts to develop them.

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