ARTICLES

Recent Developments in the Study of Wild Chimpanzee Behavior

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Chimpanzees have always been of special interest to anthropologists. As our closest living relatives,[1–3] they provide the standard against which to assess human uniqueness and information regarding the changes that must have occurred during the course of human evolution. Given these circumstances, it is not surprising that chimpanzees have been studied intensively in the wild. Jane Goodall[4,5] initiated the first long-term field study of chimpanzee behavior at the Gombe National Park, Tanzania. Her observations of tool manufacture and use, hunting, and meat-eating forever changed the way we define humans. Field research on chimpanzee behavior by Toshisada Nishida and colleagues[6] at the nearby Mahale Mountains National Park has had an equally significant impact. It was Nishida[7,8] who first provided a comprehensive picture of the chimpanzee social system, including group structure and dispersal.

Two generations of researchers have followed Goodall and Nishida into the field. As a result, chimpanzees are now one of the best and most widely studied of nonhuman primates. Long-term field research has been conducted at six sites by several researchers spanning 42 years (Fig. 1). Shorter field studies have also been carried out in some areas.[9–11] With this extensive body of research, one might think that we have learned everything about the behavior of these apes in nature. But this is not the case. In fact, we are entering a new and extremely exciting era in the study of wild chimpanzee behavior. The purpose of this review is to highlight some intriguing findings that have emerged through recent study. We focus specifically on results from our own field research conducted in the Kibale National Park, Uganda, giving special emphasis to five areas: social organization, genetics and behavior, hunting and meat-eating, inter-group relationships, and behavioral endocrinology. Our treatment is selective, and we explicitly avoid comment on inter-population variation in behavior as it relates to the question of chimpanzee cultures. Excellent reviews of this topic, of central concern to anthropologists, can be found elsewhere.[12–14]

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SOCIAL ORGANIZATION

No single issue in the study of wild chimpanzee behavior has seen more debate than the nature of their social system. We now know that chimpanzees live in a "fission-fusion" society. Individuals form socially and geographically circumscribed "unit-groups" or "communities," within which they associate in temporary subgroups or "parties" that vary in size, composition, and duration. Males are philopatric, whereas females typically disperse. This seemingly clear-cut picture of chimpanzee society did not emerge easily. Given the fluid nature of chimpanzee society, it took exceedingly long for field observers to discern regularities in grouping, dispersal, associations, and range use.

Kortlandt[15] was the first to report temporary associations among wild chimpanzees based on early observations in the Belgian Congo. Here he described groups of 1–30 individuals that either contained members of both sexes or consisted of "nursery" groups of females and their young. Kortlandt was prescient in his descriptions of the temporary and fluid nature of chimpanzee aggregations and laid the groundwork for further study. Subsequent reports by Good-

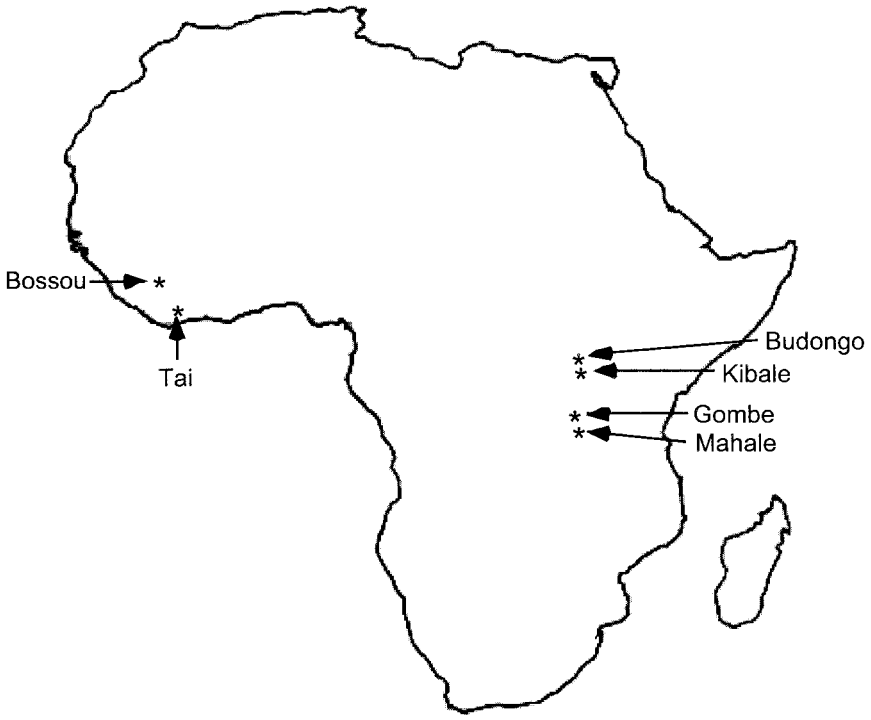

Figure 1. Chimpanzee study sites.

all[16] and the Reynolds[17] tended to blur distinctions between communities. After five years of field observations at Gombe, Gooodall[16] wrote: "Since chimpanzee groups in the reserve freely unite from time to time without signs of aggression, they cannot be divided into separate communities. It seems likely that only a geographic barrier would constitute a limiting factor on the size of a community, although individuals living at opposite ends of the range might never come into contact."

Nishida[7] altered this picture by defining the social group of wild chimpanzees at Mahale. In contrast to Goodall and the Reynolds, Nishida emphasized the stable nature of chimpanzee communities. Although he never recorded all community members together at a single place and time, his longitudinal observations of association between individuals revealed an unambiguous social network and structure (Fig. 2). From these observations, Nishida[7] concluded that, "The chimpanzees live a clear-cut social unit which consists of adult males, adult females, and immature animals." Subsequent field work indicated that chimpanzee communities are not closed. While males typically spend their entire lives in their natal communities, females commonly transfer to neighboring ones during adolescence.[8,18,19]

While effectively laying to rest persistent questions regarding the existence of chimpanzee communities, Nishida[7] simultaneously described sex differences in association. He noted that males associated more frequently with each other than females did with other females. From this he concluded that strong bonds form between males and that males compose the core of chimpanzee society. Subsequent field research at Gombe,[20,21] Mahale,[22,23] and the Kanyawara study area of Kibale National Park, Uganda,[24] validated and expanded Nishida's picture of chimpanzee society. Male chimpanzees in these populations are more gregarious and distribute their activities more widely and evenly over their territories than do females. Goodall[25] aptly summarized the standard picture of chimpanzee society to emerge from these studies: "The most deep-seated principles underlying chimpanzee community structure are those concerned with sex differences in sociability and in the choice of companions. Males are more gregarious than females and prefer each other's company, except when females are in oestrus. Females are less sociable and spend most of their time with their own offspring—except when cycling, at which time they become very sociable."

Consideration of sex differences in reproductive strategies and the costs of feeding competition provide a theoretical rationale to explain observed sex differences in chimpanzee association patterns. Females forage alone because the potential reproductive costs of scramble and contest feeding competition are higher for them than they are for males.[21,26,27] Males may be more willing to assume the costs of feeding competition to gain mating opportunities and to derive social benefits from associating with other males.[21,26,27] Part of the power of this model lies in its ability to accommodate intraspecific variation in association patterns. The theoretical prediction is that such variation will occur between study sites because for females the costs of grouping are expected to vary with differences in local resource abundance and distribution.[28,29]

In keeping with this model, considerable intraspecific variation exists in chimpanzee association patterns. As far back as 1979, Sugiyama and Koman[30] reported that females were as sociable as males in a small, isolated community at Bossou, Guinea. Ghiglieri[31] found no evidence of sex bias in grouping tendencies in the unprovisioned and largely unhabituated Ngogo community at Kibale. More recently, Boesch[32] and Boesch-Achermann,[33] working in the Taï National Park, Ivory Coast, observed that most parties contained adults of both sexes, while parties consisting of only males or only females were rare. This led them to conclude that members of this population are "bisexually bonded." Given a lack of information regarding feeding behavior and food availability across study sites, we are not presently capable of evaluating whether sex differences in the costs of competition account for these reported intraspecific differences. Temporal variation in association patterns at Taï appears to be consistent with

Figure 2. Early observations at the Mahale Mountains established the fission-fusion nature of chimpanzee society. Here a temporary subgroup or "party," consisting of individuals of all ages and sexes, is shown.

this hypothesis,[34] but again firm conclusions are elusive due to an absence of measures of food availability. Using such measures, our own observations conform to expectation by showing that anestrous and lactating females at Ngogo become more sociable during periods of food abundance.[35]

Problems in recording, measuring, and analyzing associations among chimpanzees, a species with a fluid social system, have plagued field researchers for years. Accordingly, some of the reported intraspecific variation may be more illusory than real. For example, some of the differences may simply reflect differences in how observers record party membership.[36] Other differences can be attributed to the different ways that field researchers have defined age-sex categories.[37] More serious problems ensue from attempts to assay and analyze association patterns to make inferences about social affinities and bonds.[38,39] Standard methods, pioneered by Nishida[7] in his original research, typically involve the use of dyadic association indices.[40] Inferring social affinities from these indices, however, is problematic because they are subject to biases due to variations in individual gregariousness and group demography.[39] For example, high indices between males may indicate genuine social preferences or may simply result from either a tendency to aggregate or a male-biased community sex ratio.

In keeping with past studies, we have found that males at Ngogo are more gregarious than are anestrous females. After controlling for the overall general gregariousness of males, however, we found that males do not associate with other males more often than would be expected by chance.

To overcome these problems, we have used recently developed association indices and randomization techniques to analyze associations among chimpanzees living in an unusually large community at Ngogo, Kibale National Park, Uganda. In keeping with past studies, we have found that males at Ngogo are more gregarious than are anestrous females.[39] After controlling for the overall general gregariousness of males, however, we found that males do not associate with other males more often than would be expected by chance.[39] Alternatively, anestrous females associate with each other more frequently than chance expectation after taking their relatively low levels of sociability into account.[39] We note that even these results are vulnerable to methodological

criticism. As in other studies, our observations of female behavior were unlikely to compose a random sample. Given their relatively asocial nature, female chimpanzees are elusive and difficult to observe. Our randomization procedures nonetheless provide the kind of unbiased analytical method necessary to determine whether intraspecific variations in association can be attributed to methodological differences and the degree of concordance in patterns across study sites.

While considerable intraspecific variations in associations appear to exist, differences in dispersal patterns have also emerged. Observations from Gombe reveal that female dispersal is the norm there, but that only 60% of females disperse from their natal communities, with 10% doing so only after giving birth for the first time.[19] Although all females have been previously described as dispersing at Mahale,[41] new observations indicate that a few remain and give birth in their natal communities (T. Nishida, personal communication). Recently compiled data from Taï show that only a single female failed to disperse from the main study community during 16 years of observation.[33]

Research at Bossou provides a contrast to the results from Gombe, Mahale, and Taï. Observations over 21 years suggest one successful immigration by an adult male, along with visits by two extra-community males.[42] Moreover, 86% of all adolescent males have disappeared from the Bossou community. Based on these observations, Sugiyama[42] has argued that male dispersal occurs regularly at Bossou because the community has no immediate neighbors and no need for territorial defense. Consequently, selection for male cooperation has been relaxed, and young males disperse to reduce within-group competition for mates. Male transfer between communities is rare or absent at Gombe, Mahale, and Taï. We require more studies across a broader range of habitats to evaluate whether variation in the costs and benefits of territoriality leads to systematic differences in the frequency of male dispersal. Irrespective of resolving this question, dispersal is likely to have important effects on the genetic structure of chimpanzee populations.[43–45]

GENETICS AND BEHAVIOR

Recent advances in extracting, amplifying, and sequencing DNA from hair and fecal samples collected noninvasively in the wild are beginning to revolutionize our understanding of the behavior of animals.[46,47] The study of chimpanzees has contributed to this revolution.[43] Two particularly informative areas of recent investigation have involved the integration of genetic and behavioral data. Recent findings have now produced clearer pictures of the chimpanzee mating system and the role of maternal kinship in structuring aspects of male social behavior.

Tutin originally described both males and females as equally interested and involved in maintaining consortships. While this clearly is true in some cases, we now know that males often display considerable aggression toward females before "persuading" them to follow.

It took 20 years of field study for the mating habits of wild chimpanzees to come into focus. Working at Gombe, Caroline Tutin[48] was the first to describe the alternative mating tactics employed by male chimpanzees. At Gombe and elsewhere,[33,49,50] the vast majority of observed copulations occur in a group context. Here chimpanzees gather in relatively large parties containing members of both sexes, and estrous females mate repeatedly with multiple males. All adult males present typically share in such opportunistic matings; adolescent males also frequently mate in this context. Males additionally mate in three restrictive situations. In one, high-ranking males attempt to control mating access to females, while mate-guarding them against others in a group setting. This "possessive" pattern differs from consortships, in which male-female pairs move away from other community members and engage in a nearly exclusive mating relationship over the course of a single estrous cycle. Tutin[48] originally described both males and females as equally interested and involved in maintaining consortships. While this clearly is true in some cases, we now know that males often display considerable aggression toward females before "persuading" them to follow.[25,51] Based on our observations of the Ngogo chimpanzees,[50] we can add a third restrictive tactic to the two already described. When the Ngogo chimpanzees form extremely large parties, high-ranking duos and trios begin to mate-guard estrous females. These mating-guarding coalitions appear to form, both successfully and unsuccessfully, when male party sizes become so large that it becomes prohibitive for a single male to mate-guard successfully (Fig. 3).

Early on, Tutin[48] speculated that although the vast majority of all copulations occur opportunistically in a group context, most conceptions actually take place during consortships. Using more recent behavioral observations from Gombe, Wallis[52] has suggested that most conceptions can be attributed to matings that occur in multi-male parties, a finding that concurs with behavioral reports from Mahale.[49,53] In chimpanzees, as with other primates, multiple mating and internal fertilization make it difficult to determine paternity using behavioral observations alone. Recent studies employing genetic markers assayed through noninvasive sampling regimes have permitted more reliable paternity assignments, which, in turn, allow more definitive statements about the payoffs of different male mating tactics.

Perhaps the most startling claim made in recent studies of wild chimpanzees involves paternity determinations among the Taï chimpanzees.[54,55]

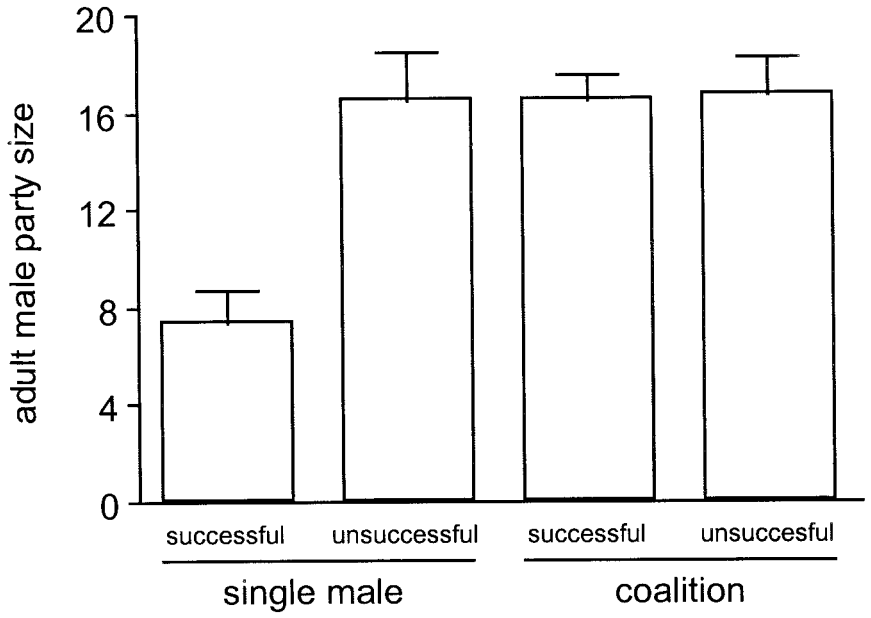

Figure 3. Mate-guarding form and success vary with male party size. Mean (± 1 SE) values are shown for single male and coalitionary mate-guarding episodes at Ngogo, Kibale National Park, Uganda.

Using genetic data derived from 11 microsatellite markers, Gagneux and colleagues assigned the paternity of 13 offspring born into the Taï chimpanzee community between 1990 and 1995. Their surprising results suggested that 7 of the 13 young chimpanzees did not have fathers residing in the community. The clear implication drawn from this analysis was that females actively seek matings with males who live outside their own social group.[33,54,55]

Given the apparently unassailable nature of the genetic data, this astonishing result has been widely reported in major scientific publications,[56] monographs,[33] and textbooks,[57] as well as the popular[58] and news[59] media. As a result, belief that extra-group paternity is a common feature of wild chimpanzee behavior is now widespread both inside and outside the academic community. Reconciling behavioral observations and life history information with the high frequency of extra-group paternity reported at Taï has nevertheless been difficult. We would not be surprised to find that, as in many species of birds and mammals,[60–63] female chimpanzees occasionally conceive offspring with nonresident males. Despite hints that this might be the case,[25,64,65] however, long-term observations in the wild gave no reason to think that extra-group matings and conceptions were so common. The Taï result has also been perplexing because females who engage in such behavior would run the risk of receiving severe aggression from males in their own communities, and if discovered, of having those males kill their infants. Because reproductive opportunities are so rare, with interbirth intervals typically averaging five to six years in the wild,[33,41,52] we expect males to be especially wary, to guard against extra-group matings, and to punish females who engage in them. In principle, the benefits of mate choice might outweigh these risks,[33] but females could gain these same benefits by simply transferring to another group. Alternatively, extra-group paternity may provide insurance against between-community infanticide.[33] Any benefits derived here, however, would be offset by increased costs of aggression by males living within communities.

Two recent and independent studies promise to put these questions to rest. Constable and colleagues[66] determined the paternity of 14 infants born into the Kasekela community at Gombe. Their analyses indicate that all 14 infants were sired by resident males. Vigilant and colleagues[67] have reported similar results in a sample of 41 infants from three communities at Taï. Here paternity could be assigned with a probability greater than 99% for 34 of these infants. All 34 infants had probable fathers who resided within the infant's community, although complete sampling of potential fathers was achieved in only 13 cases. Of the seven remaining infants for which fathers could not be ascribed, extra-group paternity was implicated in one for whom all potential fathers were sampled and excluded. Taken together, these new data indicate that extra-group paternity in chimpanzees occurs only rarely in the two populations investigated thus far. Additional research at other sites will be required to evaluate the generality of this finding.

The discrepant results between these two studies and the earlier Taï analysis have been attributed to multiple sources of error.[67] Some samples used in the original Taï paternity study may have been handled improperly, leading to contamination and sample mix-up.[67] Genotyping errors due to amplification artifacts during polymerase chain reaction[68] and allelic dropout[69,70] may have exacerbated these problems. The acknowledgment that imperfect laboratory procedures and analyses led to an erroneous conclusion regarding the importance of extra-group paternity among wild chimpanzees[67] will undoubtedly result in more careful studies in the future. This should also promote critical evaluation of additional claims that are not easily accommodated by theory or empirical observation.

Besides helping to resolve some outstanding questions regarding chimpanzee paternity, Constable and colleagues[66] study is notable for providing additional information regarding the effectiveness of alternative mating tactics employed by male chimpanzees and the relationship between male rank and reproduction. Data regarding the mating tactic employed by fathers was documented for 12 conceptions. Offspring were conceived during opportunistic mat-

ings five times (42%), possessive matings four times (33%) and consortships three times (25%). High-ranking males produced half of the infants. The alpha male sired 36% of all offspring (5/14), four times via possessive mating and once through mating the mother opportunistically. Another high-ranking male used opportunistic matings to father two offspring (14%). Interestingly, he conceived one of these infants with his mother. Middle-ranking males were responsible for an additional 36% of all offspring, using opportunistic matings twice and consortships twice; the mating tactic employed by one middle-ranking male to produce another infant was unknown. Finally, two low-ranking males fathered two infants (14%), once during a consortship.

This study may additionally provide an explanation for the higher frequency of consortships that has been reported at Gombe than at other sites. Constable and colleagues[66] note that females tended to consort with low-ranking males when they had high-ranking male relatives in the community. For such females, consortships may be a tactic to avoid inbreeding because male chimpanzees sometimes attempt to force copulations with their unwilling mothers or maternal sisters.[25] Two predictions follow. First, between communities, consortships should be more common in cases where females disperse less often. Second, within communities, natal females should show higher rates of consortship than immigrant females. Additional study will be needed to evaluate these predictions.

While genetic data have furnished novel insights into the chimpanzee mating system, similar information has begun to clarify the effects of maternal kinship on male chimpanzee behavior. Kinship plays a large and important role in the lives of humans as well as other primates,[71] and chimpanzees are frequently used to illustrate the effects of kinship on primate social behavior. Among chimpanzees, enduring and long-lasting bonds form between mothers and their offspring,[5,25] while genetically related males living within the same social group cooperate together in competition with males from other communities.[25,44,72,73]

Male chimpanzees develop strong social bonds with other males in their own community (Fig. 4). These bonds are manifest in several contexts, including association, grooming, proximity, coalitions, meat-sharing, and territorial boundary patrols.[7,21,33,51,73–81] Given the well-known effects of kinship on primate behavior, chimpanzee male bonds have often been assumed to form between close genetic relatives.[25,82] Two independent field studies have recently questioned this assumption. In observations of the Kanyawara community in Kibale, Goldberg and Wrangham[83] showed that male chimpanzees who maintain proximity and frequently groom each other are not necessarily related through the maternal line as assayed by mtDNA haplotype sharing and genetic distances. Our own observations of males at Ngogo support this finding and extend it by revealing that mtDNA genetic relatedness is not significantly correlated with levels of cooperation as measured by participation in coalitions, meat-sharing, and patrols.[84]

These studies raise two important and related questions: Why don't male chimpanzees selectively bias their behavior toward kin? What factors account for the observed patterns of affiliation and cooperation among wild male chimpanzees? Although chimpanzee demography and life history have the potential to provide answers to both of these questions, they have received scant attention. Chimpanzees are an extremely long-lived and slowly reproducing species. With an equal sex ratio at birth and high mortality among infants and juveniles,[25,41,52] the probability is relatively low that a female will give birth successively to sons that reach adulthood together. Thus, males will only rarely live with maternal kin who can effectively join them in behaviors that have important fitness consequences. If kin are not generally available, then males might solicit and use others opportunistically.[74,85] Individuals belonging to the same age cohort may be particularly attractive social partners because they grow up together, are generally familiar with each other, and share similar social interests and power throughout their lives. Similar points raise the possibility that males close in dominance rank may also be inclined to form strong affiliative and cooperative relationships.[78]

We have recently examined the effects of age and rank on aspects of male social behavior using observations of male chimpanzees living in the extremely large community at Ngogo.[86] We have found that members of the same age cohort and individuals that are close in rank are more likely to affiliate and cooperate than are males belonging to different age and rank classes. Additional analyses replicate earlier findings and show that males who affiliated and cooperated were not close maternal relatives as assayed by mtDNA haplotype sharing. A role for kinship might still be implicated if reproductive skew is high and male chimpanzees selectively cooperate with age-mates who are paternal siblings.[87] Evaluating this possibility will require additional information regarding nuclear and Y chromosome genetic markers. Until these data are available, we can only conclude that demographic and social factors may constrain patterns of male chimpanzee social behavior to a greater extent than does maternal kinship.

HUNTING, MEAT-EATING, AND MEAT-SHARING

Hunting and meat-eating by wild chimpanzees captures widespread anthropological attention because of its obvious relevance to the study of human origins and evolution.[88–94] Research on chimpanzee hunting and meat-eating also contributes more broadly to our understanding of traditional ecological and ethological problems, such as predator-prey relationships and the evolution of cooperation in animals.[95–98]

Since Goodall's[4] seminal observations, field workers at sites scattered across Africa have documented the regular occurrence of hunting and meat-eating by chimpanzees.[99–104] As a result, we now possess extensive data on chimpanzee prey choice, as well as hunting frequency, success, and participation.[33,98,104,105] With respect to prey choice, we know that chimpanzees selectively hunt red

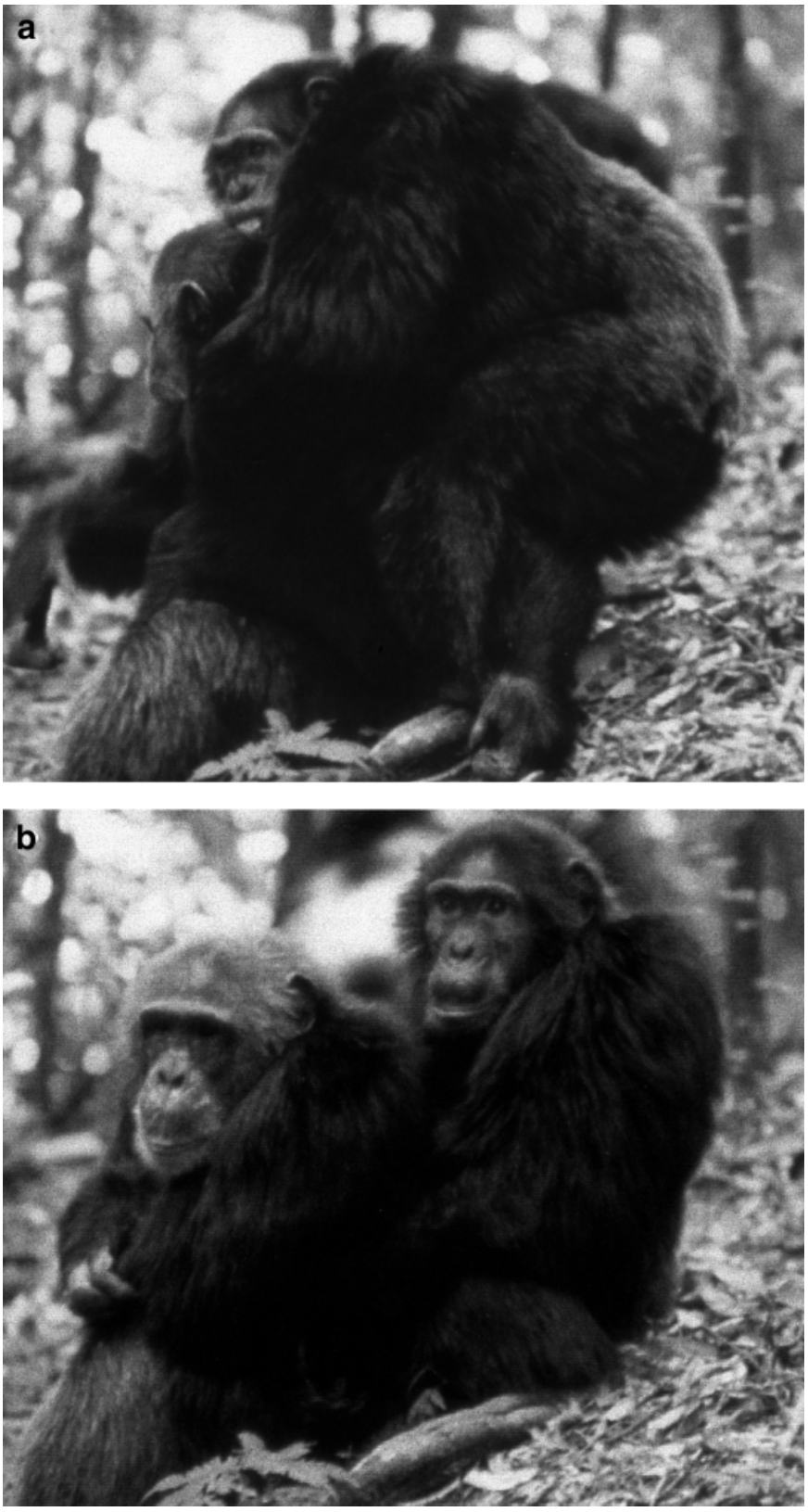

Figure 4. Male chimpanzees form strong social bonds with each other. Here one adult male chimpanzee hugs another (a) to seek reassurance (b).

colobus monkeys (*Procolobus badius*) everywhere they live sympatrically (Fig. 5). Hunts of red colobus occur frequently, on an average of 4 to 10 times per month. Chimpanzees are extraordinarily successful in preying on red colobus; hunting success rates average over 50% across study sites. Independent field studies have consistently shown that adult male chimpanzees are responsible for the vast majority of all kills.

Despite this wealth of information about chimpanzee predatory behavior, two fundamental questions have remained unanswered. First, what factors affect decisions to hunt? This question arises because chimpanzees sometimes quickly pursue red colobus on encounter, yet forego hunting attempts at other times.[106,107] Second, why do chimpanzees share meat with conspecifics? Hunts are costly in terms of time and energy, and during predation attempts chimpanzees take considerable risks, given that red colobus males mob them.[108,109] Why, then, do chimpanzees relinquish meat, a scarce and valuable resource, to others?

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Five nonmutually exclusive hypotheses have been advanced to provide answers to these two questions. Geza Teleki[110] first made the simplest and most direct proposal. Teleki, who conducted the first systematic investigation of chimpanzee hunting behavior at Gombe, hypothesized that chim-

Figure 5. Chimpanzees prey selectively on red colobus monkeys. Here an adult male chimpanzee feeds on a portion of an adult female red colobus.

panzees hunt because they are hungry. Chimpanzees are frugivores that rely on sugar-rich fruits that are seasonally available.[111] Teleki proposed that chimpanzees hunt to compensate for the nutritional shortfalls they experience, primarily during the seasonal troughs of fruit availability. Despite the elegant simplicity and intuitive appeal of this hypothesis, it has remained untested for more than 25 years. Our recent studies at Ngogo have provided the first direct test.[107,112] Our results show that instead of hunting during fruit-poor times, chimpanzees actually increase the frequency of their hunting attempts when fruit is abundant.

A second hypothesis advanced to explain why chimpanzees hunt and share meat was also developed by Teleki.[110] This hypothesis has recently been revived by Stanford,[92,98,106] who also studied the Gombe chimpanzees. Stanford's work there showed that the single best predictor of a male chimpanzee's decision to hunt was the presence of estrous females. Stanford has used this finding, along with the additional observation that male chimpanzees occasionally exchange meat for matings, to argue for a provocative "meat-for-sex" hypothesis. According to this hypothesis, male chimpanzees hunt in order to obtain meat that they can swap for matings.

The meat-for-sex hypothesis has generated intriguing claims and has received considerable publicity,[113,114] but neither the claims nor the hypothesis appear to stand up well under close scrutiny. Unlike the situation at Gombe, the presence of estrous females does not predict the tendency of the Ngogo males to hunt.[107] Moreover, the predicted behaviors occur infrequently at Ngogo and elsewhere. At Ngogo, estrous females do not reliably obtain meat from their begging efforts nor do matings typically ensue following meat exchanges.[107] Most tellingly, however, our observations indicate that males at Ngogo do not gain any mating advantage by sharing meat with estrous females.[107]

One of the more surprising suggestions stemming from the meat-for-sex hypothesis is that female chimpanzees have a keen interest in acquiring meat because eating meat improves their reproductive performance.[106] Data compiled by McGrew[115] based on observations made from Gombe[25] revealed a positive relationship between the amount of meat a female obtains and her reproduction (Fig. 6). Care needs to be taken when interpreting this result, however, for an important confounding factor related to both of the variables of interest could lead to the posited association. Using long-term observations from Gombe, Pusey and colleagues[116] have shown that female chimpanzee dominance rank is related to lifetime reproductive success. Given that high-ranking females are likely to obtain more meat than low-ranking females do, dominance rank is a probable confounding variable that produces a spurious correlation between female reproduction and meat eating.

If neither hunger nor sex provides the prime motivation to hunt, what does? We suggest that a male chimpanzee's decision to hunt is affected by his assessment of the likelihood of success.[107] Field studies consistently have shown that party size and the number of male hunters are good predictors of hunting success.[101,104,106,117] Male chimpanzees appear to swamp red colobus prey defenses with strength in numbers, so that hunting success increases when chimpanzees form large parties with

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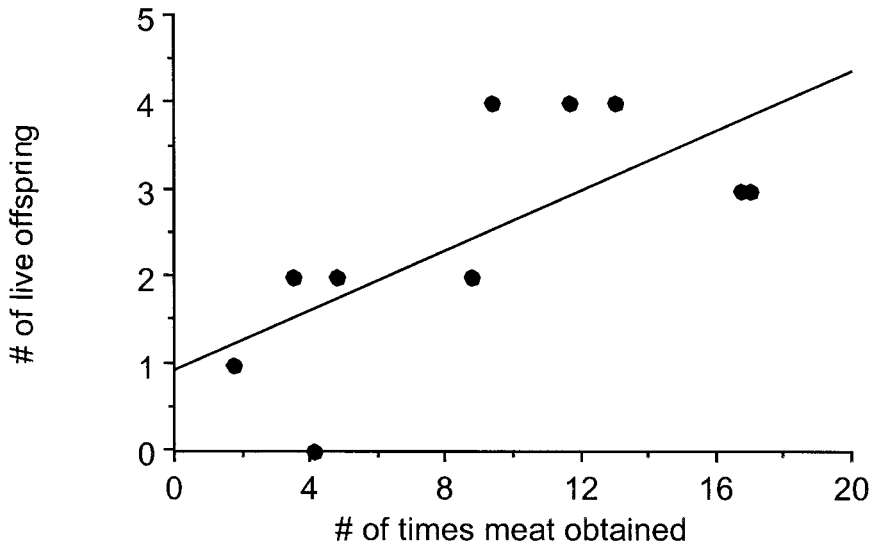

Figure 6. Female chimpanzee reproduction and meat acquisition. Data adapted from Goodall[25] (Table 11.15, p. 310).

many male hunters. Ecological constraints limit the formation of large parties, however. During periods of low food availability, when the ecological costs of feeding competition are high, chimpanzees form relatively small parties.[27,35,118] It is only during periods of relative food abundance that chimpanzees regularly gather in large parties. The positive relationship between party size and fruit abundance provides a transparent explanation for our finding that hunting frequency at Ngogo increases during periods of food abundance. We conclude from these considerations that at Ngogo male chimpanzees hunt when they are likely to be successful, which is when they are in large parties with several male hunters. Males forego most hunting attempts when they are in smaller parties because the odds of success are greatly reduced.

Another finding from Ngogo is also consistent with the hypothesis that hunting decisions depend on the likelihood of success and provides quantitative support for the longstanding proposal that chimpanzees preferentially hunt red colobus in situations where the monkeys have few or no escape routes.[119] Hunts that occur in areas where the tree canopy is broken are generally more successful than those where the canopy is continuous and closed.[112] Consequently, chimpanzees are much more likely to hunt red colobus groups that they encounter in forest with a generally low and broken canopy than those they meet in mature forest where the canopy is tall and continuous.[112]

Still open is the question of why male chimpanzees share meat readily with conspecifics. One hypothesis invokes an important role for cooperation. Chimpanzees at Taï appear to hunt cooperatively on a regular basis, both in the sense that individuals coordinate their behavior with each other and that per capita energy gain from hunting increases with the number of active hunters.[97,101] These observations led Boesch[97] to propose that male chimpanzees selectively share meat with others who have cooperated with them to make kills. According to this hypothesis, selective meat sharing ensures that "bystanders," individuals who are present but fail to participate in hunts, do not obtain meat and thus cannot exploit the hunting efforts of cooperators.

We recognize that distinguishing cooperative hunters from bystanders is theoretically important. We also acknowledge that the cooperative hunting hypothesis may explain meat sharing among the Taï chimpanzees. Evaluating the generality of this hypothesis, however, will be difficult due to conceptual and methodological reasons. As Stanford[98] has noted, the notion of behavioral cooperation in chimpanzee hunting has been hard to operationalize. We lack an objective way to distinguish whether males who pursue prey actually coordinate their efforts to capture the prey or simply pursue their own selfish strategies while taking into account each other's movements and the response of the prey to these movements. Observers at Gombe,[98] Mahale,[117] and Ngogo[112] report that individuals often switch between standing by and pursuing prey during the course of the same hunt. This makes it difficult to differentiate cooperators and cheaters reliably because to do so requires complete information on the activities of all individuals present. Prevailing observation conditions often preclude obtaining complete records; during hunts, multiple chimpanzees frequently pursue red colobus prey high in the tree canopy over areas that sometimes cover several hundred meters.

Still open is the question of why male chimpanzees share meat readily with conspecifics. One hypothesis invokes an important role for cooperation. Chimpanzees at Taï appear to hunt cooperatively on a regular basis, both in the sense that individuals coordinate their behavior with each other and that per capita energy gain from hunting increases with the number of active hunters.

The use of outcome-based criteria to investigate whether hunting is cooperative in an ecological sense—that is, whether success increases as a function of the number of hunters—also presents problems. Researchers have used various measures, including some that apply to hunting parties as a whole, such as the probability of at least one kill, the total number of kills, and the total amount of meat obtained. Alternatively, others have applied measures that are based on the behavior of individuals, such as the amount of meat obtained per individual or the net energy gained per individual. The results of some studies satisfy some of these criteria,[92,97,112,120] but others do not.[92,96,97,112] As Boesch[33,97] has noted, net energy gain per individual constitutes a theoretically sound measure, and, employing this criterion, cooperation appears to occur at Taï but not Gombe.[97] However, constraints on visibility during hunts and the common occurrence of multiple kills[101,104,112,117,121] make it difficult to monitor the activities and prey intake of all chimpanzee hunters. As a result, field observers have been unable to estimate per capita net energy gain consistently across study sites. Until these data become available, questions about the extent of cooperation will remain open.

A final hypothesis proposed to explain meat sharing implicates the use of meat as a political tool. Using observations of the alpha male of M group at Mahale, Nishida and colleagues[122] suggested that male chimpanzees share meat strategically with others in order to curry their favor and support. These researchers' observations indicated that a particularly shrewd male shared meat nonrandomly and selectively with other males he depended on for support in long-term alliances. Our recent observations at Ngogo are largely consistent with this male social bonding hypothesis.[107] There as elsewhere,[101,122] the vast majority of all sharing events take place between males. Males share nonrandomly and selectively with only certain others and sharing is reciprocated at a group level. In addition, male chimpanzees at Ngogo exchange meat for coalitionary support.

Part of the interest generated by the meat-for-sex hypothesis lies in its claim that male chimpanzees use meat to achieve matings. The male social bonding hypothesis, however, provides a more compelling rationale for how males might use meat in a mating strategy. The great deal of male sexual coercion among chimpanzees[25,51] probably renders female mate choice relatively unimportant in this species. In contrast, levels of male-male competition are high.[25,123,124] Other male chimpanzees are the main obstacle facing individuals who attempt to increase their mating success. Forging long-term alliances with other males via meat-sharing provides an indirect yet effective way to improve mating opportunities. In chimpanzees, alliances are important in the establishment and maintenance of rank,[74,85] and high rank appears to confer mating and reproductive advantages.[48–50,66,73,77]

Behavior during patrols is striking and unusual. Males are silent, tense, and wary. They move in a tight file, often pause to look and listen, sometimes sniff the ground, and show great interest in chimpanzee nests, dung, and feeding remains.

INTERGROUP AGGRESSION

Chimpanzees are well known for their territorial behavior. They are among the few animals that engage in lethal between-group coalitionary aggression.[80] Encounters between communities are typically hostile and sometimes result in the death of both infants and adults, particularly males.[76,80,99,123–128] Extreme intergroup aggression has led to the extermination of one community at the hands of another at Gombe[76]; a similar process is inferred at Mahale.[72] The functional significance of territoriality and lethal aggression is unclear, but several fitness benefits fall under the imbalance-of-power hypothesis, which holds that attacks on members of neighboring communities result from a motivation to dominate others.[80] This could lead to improved safety, improved access to food, and incorporation of more females into a community.[19,25,80,129]

Assessing the imbalance-of-power hypothesis requires analysis of male patrolling behavior, which is an integral part of chimpanzee territoriality. Male chimpanzees occasionally form parties that move to and along the periphery of their territory, where they search for signs of chimpanzees from other communities. Patrols sometimes make deep incursions into neighboring territories. Behavior during patrols is striking and unusual. Males are silent, tense, and wary. They move in a tight file, often pause to look and listen, sometimes sniff the ground, and show great interest in chimpanzee nests, dung, and feeding remains. Goodall and colleagues[76] were the first to describe patrolling, but this behavior has received little subsequent attention and is still poorly understood. New studies have started to rectify this situation.

Boesch and Boesch-Achermann[33] have described patrolling by chimpanzees in the Taï National Park. Patrols occurred an average of about once a month during 45 months of study, but rates of patrolling varied over time. Much of this variation was a result of changes in the composition of the study community. As the number of adult males declined, the remaining males became more cautious. When male numbers were reduced to four or fewer, they switched from searching for neighbors to avoiding encounters. Although patrols at Taï consisted mostly of males (Fig. 7), females joined to an unusual extent; female participation at other sites is generally rare.[25,73] Patrolling chimpanzees typically made deep incursions, sometimes well over 1 km, into the territories of other groups, but contacted neighbors on

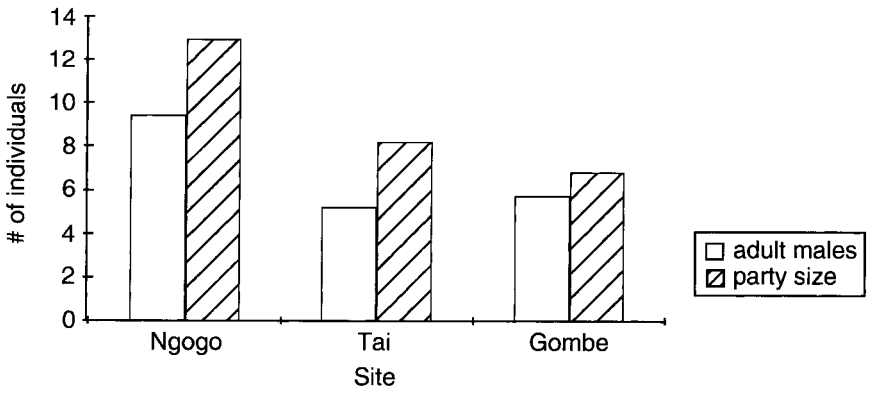

Figure 7. Intercommunity variation in patrol size and composition. The mean number of adult male patrollers and average patrol size are shown for three different communities.

only about a quarter of all patrols. Especially intriguing are the complex tactics Taï patrollers used to attack neighbors. These included direct frontal attacks, selective "lateral" attacks on the smallest of several parties nearby, and more complicated assaults supported from the rear by fellow patrollers. Use of these tactics varied with the size and composition of patrols, with large patrols containing many males being those most likely to make direct frontal attacks.[33]

We have also described patrolling by males at Ngogo in the Kibale National Park.[73] At Ngogo, as elsewhere, males are the primary participants in patrols (Fig. 7). Patrols at Ngogo are larger and contain more males than do those at Taï or Gombe. This is a simple consequence of the fact that the Ngogo community is much larger than the communities at Taï and Gombe and has many more males. The large number of males probably helps to explain the relatively high rate of patrolling at Ngogo, about three times per month.

Patrol participants minimally lose time, expend energy, and face opportunity costs. At worst, patrollers risk injury or even death. These costs could be offset by several benefits, including improved safety, increased access to food, female recruitment, and improved foraging efficiency for resident females.[19,73,129] All patrollers and other members of their communities would benefit from improved safety and increased access to food. If these are the only benefits and males share them equitably, then a collective action problem is likely to ensue.[73] If male mating skew is high, however, males would not share evenly any increases in mating opportunities gained by recruiting females. Males would also obtain unequal shares of increases conferred on the reproductive success of resident females by improved foraging efficiency. Given the potential for unequal benefits, males might be inclined to adjust their participation in patrols to reflect their expected current and future reproductive gains.[73]

Until recently, assessing how individual male chimpanzees weigh these costs and benefits and make decisions to patrol has been difficult. The high frequency of patrols at Ngogo has allowed us to document patrolling effort by individual males to an extent not previously possible.[73] We found significant interindividual variation in patrolling effort. Some males patrol quite frequently, while others do so less often. Some males are especially likely to join patrols whenever the opportunity occurs, whereas others are less inclined to participate. Our observations support the hypothesis that this variation arises partly because males do not derive equal benefits from patrolling. Patrol participation is correlated with mating success. Males who mate frequently and may have the most offspring in the group to protect now and in the future appear to be motivated to patrol often. In addition, males seem to minimize the costs of patrolling by doing so with partners with whom they have strong social bonds and on whom they can rely to take risks. Our observations from Ngogo indicate that joint participation in patrols is positively related to joint participation in grooming bouts and coalitions. Patrolling effort is also positively correlated with frequency of participation in red colobus hunts and with success at capturing prey. Willingness to pursue prey, which involves risk, and hunting skill should give others some indication of a male's willingness and ability to take risks in intergroup aggression.[73]

The ostensible goal of patrols is to seek information or contact with members of other communities. At Ngogo, males encounter members of other communities, either aurally or visually, on 30% to 40% of all patrols.[73] They approach or attack members of the other group in roughly half of all encounters, and either avoid them or flee in the other half. Part of the variation in the tendency to attack or flee can be attributed to the patrollers' assessment of their relative strength. The likelihood of attack increases when patrols are large, whereas small patrol parties are more likely to flee. These data are consistent with the hypothesis that intergroup aggression among chimpanzees occurs whenever the potential costs are low.[130] These observations provide only a weak test of this hypothesis, however, given our lack of data on the respective size of groups with which the Ngogo chimpanzees have interacted.

Stronger support for the low-cost hypothesis comes from experimental play-back studies conducted with the Kanyawara community in Kibale.[131] Here a male's decision to participate in simulated territorial encounters depended primarily on whether a favorable numerical asymmetry existed. When the call of a single extra-group male was played back, parties containing three or more males consistently chorused and approached the speaker. Parties with fewer adult males usually remained silent and approached the speaker less often. In these simulated encounters, the position that males occupied in parties that approached the speaker varied significantly among individuals. This position was independent of current dominance rank, although two former alpha males had the highest mean approach rates. Willingness to respond

Figure 8. A group of male chimpanzees on patrol.

to intrusions did not differ among individuals, and all males approached when they overwhelmingly outnumbered the caller.[131]

These results suggest that male chimpanzees obtain mutual benefits from cooperating in intergroup aggression,[131] but further observations of actual territorial encounters are needed to exclude the alternative hypothesis that males participate and benefit unequally because their prospective reproductive gains differ. The play-back experiments did not resolve this issue because most were performed well within the community's territory and all simulated the presence of only one extra-group male. Field observations indicate that intergroup encounters are more likely in border areas, and frequently involve multiple males on both sides.[25,33,73] Under such conditions the potential costs of involvement to individual males may be greater, and individual differences in participation thus more likely to emerge. At Taï, Gombe, and Ngogo, communities neighboring the main study groups have been or are being habituated, which will facilitate recording the details of both sides of actual intergroup encounters.

Fatalities during intergroup aggression are a well-documented aspect of chimpanzee behavior. In some cases, attacks on females and their infants result in infanticide.[25,73,99,126–128] Infanticide has also been documented within communities.[132] Chimpanzees also kill adult members from other groups.[25,76,80,124] Intraspecific killing by chimpanzees is unusual among primates in that the perpetrators also cannibalize their victims.[25,99,123,125–128] Our understanding of the causes of lethal attacks and cannibalism is incomplete. Infanticide among chimpanzees does not obviously satisfy the conditions of the sexual-selection hypothesis[133] because female secondary transfer appears to be rare[19] and males often kill infants in their own communities.[132] Instead of increasing male reproductive opportunities, between-group infanticide may be a male tactic to push females from neighboring communities away from boundary areas, thereby allowing females in their own communities safer and better access to food in these areas.[129] Success in between-group aggression could have this effect in general. In support of this argument, long-term data from the Kasakela community at Gombe show that female reproductive performance was higher when the community's territory was relatively large than it was when pressure from neighbors reduced the size of the territory (A. Pusey, personal communication). Irrespective of the many questions that

Infanticide among chimpanzees does not obviously satisfy the conditions of the sexual-selection hypothesis because female secondary transfer appears to be rare and males often kill infants in their own communities.

surround between-group infanticide, within-group infanticides continue to remain a major puzzle in the study of chimpanzee behavior.[132,134]

BEHAVIORAL ENDOCRINOLOGY

Recent developments in sampling and assaying steroid hormones have provided new insights into the physiological mechanisms of primate behavior.[135] Urinary and fecal assays have proven particularly attractive to field workers. Urine and fecal sampling are generally easy and inexpensive to conduct, allow for frequent resampling of individuals, and integrate the short-term fluctuations in hormone production that can confound serum measurements. More importantly, such sampling is noninvasive and does not adversely affect the welfare or behavior of study subjects. There is, consequently, a burgeoning literature on the hormonal correlates of behavior in wild primates,[136–139] to which studies of chimpanzees are contributing.[140]

We have recently completed a set of studies on the behavioral endocrinology of chimpanzees in the Kanyawara community, Kibale National Park. This research has focused on the steroid hormones testosterone and cortisol. Testosterone influences numerous aspects of male reproductive physiology. Cortisol has been widely employed as a marker of both physiological and psychological stress.[141] The stress response is of special interest. Although this response clearly is adaptive in many situations, its chronic activation can lead to increased susceptibility to pathology, including gastric ulcers, atherosclerosis, and suppressed immune function.[141] Thus, there are circumstances in which cortisol measurements can help to assess the costs of particular behavioral strategies.

Sapolsky's[142,143] research on stress physiology in baboons provides the most complete picture available of the interaction between hormones and behavior in a wild primate, and furnishes a context for our findings from the Kanyawara chimpanzees. Sapolsky measured basal cortisol levels in high- and low-ranking baboon males and found that the patterns observed were influenced by the stability of the dominance hierarchy. During a period in which the dominance hierarchy was stable, high-ranking males were less aggressive than low-ranking males and exhibited lower circulating levels of cortisol and testosterone. During a period of extreme dominance instability, however, high-ranking males were more aggressive and had higher levels of cortisol and testosterone than did low-ranking males.

In our studies at Kanyawara, we have observed that across the adult males rates of aggression are positively and significantly correlated with rank, even when the dominance hierarchy appears to be stable; that is, when there are no rank reversals and the rate of reversals in decided agonistic bouts is low.[124] Similar correlations between aggression and rank during periods of relative dominance stability have been reported from Gombe,[144] Mahale,[77] and Taï.[33] At Kanyawara we have also found that dominance rank consistently correlates positively with measures of urinary cortisol.[145] Taken together, these findings suggest that the trials and tribulations of life at the top of the hierarchy are persistently more stressful for male chimpanzees than for male baboons.

Similar correlations between aggression and rank during periods of relative dominance stability have been reported from Gombe, Mahale, and Taï. At Kanyawara we have also found that dominance rank consistently correlates positively with measures of urinary cortisol.

What can account for this apparent difference? One possibility is that the fission-fusion nature of chimpanzee social organization introduces an element of unpredictability to male social relationships that is not present in baboon society. Because baboons travel and forage in relatively cohesive groups, it presumably is easy for a male baboon to make accurate assessments of his position in the dominance hierarchy. Furthermore, a high-ranking male can continually monitor developing social relationships between other individuals that might affect the hierarchy in the future. Chimpanzee males, on the other hand, frequently break into small groups that may not come together again for hours, days, or even weeks. Thus, it is more difficult for a high-ranking chimpanzee to monitor the political maneuverings among potential challengers. A dominant male is constantly at risk from opportunistic coalitions formed by lower-ranking individuals and must continually assert his dominance through agonistic display. This idea is supported by the high frequency of aggression that takes place in the context of reunions.[123,124] In sum, even a stable chimpanzee hierarchy may be unstable in comparison to a baboon hierarchy, despite having a low rate of actual reversals.

Of course, as with baboons,[146] dominance rank probably is not the entire story when it comes to chimpanzee stress physiology. The personalities of different individuals may partially mediate the relationship between rank and stress. Ongoing studies at Kanyawara and Gombe will soon allow us to address this issue. In the meantime, it appears that increased stress imposes a general cost on social dominance for male chimpanzees, which must be set against the reproductive benefits described earlier.

An additional cost of social dominance suggests itself in the form of chronically elevated testosterone levels. At Kanyawara, urinary androgen levels also correlate with dominance rank. Although the correlation is not as robust as that with cortisol, there is a clear alpha-male effect,[147] with the highest-ranking male persistently exhibiting the highest levels of testosterone. Additional physiological costs

associated with high testosterone include direct energetic costs resulting from increased metabolic rate and immunosuppression.[148]

Testosterone influences multiple aspects of male reproductive physiology, from the development of the male reproductive anatomy to the maintenance of both reproductive function and motivation. It has also classically been associated with aggression. A large body of research, mostly on birds, suggests that variation in circulating testosterone levels is associated primarily with male aggression in reproductive contexts, rather than changes in reproductive physiology.[149] The extent to which this idea, formally known as the challenge hypothesis,[149] applies to mammals is not yet clear.[138,150] Data from Kanyawara permit a preliminary test of this hypothesis in chimpanzees.

In birds, testosterone induces male reproductive aggression at the expense of paternal care.[149] Therefore, cross-species correlations are predicted between basal levels of breeding-season testosterone and mating system. Monogamous birds are expected to maintain high testosterone levels during territory formation and breeding, but to decrease testosterone production when providing paternal care. They should also react strongly to challenges from conspecifics with increased testosterone production. Polygynous birds, on the other hand, engage in less paternal care, so they should exhibit high levels of testosterone throughout the breeding season. They are not expected to show a heightened endocrine response to challenges because their testosterone levels are already close to the physiological maximum. These predictions are supported by data from a large number of avian species.[149]

Chimpanzees are not seasonal breeders and do not engage in direct paternal care, so they represent a special case for the challenge hypothesis. Because the availability of cycling females varies temporally and the presence of maximally swollen females is attended by high rates of male aggression, the challenge hypothesis suggests that male testosterone levels should increase during periods of reproductive competition. Our data from Kanyawara support this prediction. Adult males at Kanyawara exhibited significant increases in rates of aggression, particularly escalated aggression such as chases and attacks, on days when maximally swollen parous females were present.[124] Males also exhibited significant increases in mean testosterone levels during these periods of intense competition.[145] Mean cortisol levels also increased significantly, which is consistent with the known role of this hormone in mobilizing energy during periods of crisis.

Estrous females are frequent targets of male aggression, particularly when high-ranking males are attempting to maintain exclusive mating access to them.[25,151] Being mate-guarded is likely to be extremely stressful for females, a proposition that is supported by our preliminary data. We were able to collect multiple samples from one parous female who was intensively mate-guarded during her periovulatory period. During this time the aggression she received from males more than doubled, and she showed dramatic increases in urinary cortisol levels. We also examined multiple samples from a nulliparous female during both swelling and nonswelling periods. Because nulliparous females are not as attractive to males as mothers are, males do not mate-guard them, and they do not appear to receive as much aggression during the late follicular phase.[152] Such was the case with this female, and she did not exhibit the increases in urinary cortisol during maximal swelling that were observed in the parous female. Future work in this area at both Kanyawara and Gombe will help us to document the physiological costs imposed on females by male sexual aggression.

DIRECTIONS FOR FUTURE RESEARCH

This is an especially exciting time for those of us who study chimpanzees in the wild. Years of dedicated field work by numerous researchers at sites scattered throughout Africa have produced a rich body of information regarding the behavior of our closest living relatives. We are now in a unique position to build on previous findings and stand on the threshold of filling several critical gaps in understanding. We conclude by reviewing some topics that warrant more research.

First, what explains intraspecific variations in gregariousness, association patterns, and range use? Ecological factors such as the spatial and temporal distribution of food are frequently invoked as explanatory variables.[153–156] Comparative studies that provide systematic data on food availability and feeding competition promise to provide answers in the case of chimpanzees. Demographic and social factors that affect the description, measurement, and analysis of associations should also be examined to seek clues to intraspecific variations in gregariousness and range use.

Second, we require additional study of the factors that account for differences in dispersal patterns across study sites. Why do female chimpanzees at Gombe frequently remain in their natal group while those at other sites almost always disperse? Feeding competition that ultimately limits female reproduction has been invoked as a causal factor[19,116,129] and here too direct measures of food availability will be necessary to unlock the key to this puzzle. The flip side of female dispersal, male philopatry, constitutes an associated problem seldom addressed in discussions of chimpanzee behavior. We need a new body of theory and empirical research to address the evolutionary causes and proximate determinants of male philopatry, not only in chimpanzees but other animals as well.[157]

Females have taken a back seat to males in the study of chimpanzee behavioral ecology and we require more and better observations of them and their behavior. These data will not only furnish insights into the nature of female competition, reproduction, and social behavior,[158] but also will help to clarify aspects of male-female social relationships and the significance of male coercion in this species.[51] As we have noted, chimpanzee hunting and meat eating take on special significance for anthropologists who seek an understanding of human behavioral evolution. The extent to which male chimpanzees cooperate

during hunts remains an empirically challenging area in need of future study. While current evidence suggests that male chimpanzees share meat selectively with others in order to curry their favor and support, alternate hypotheses proposed to explain meat sharing in humans, such as sharing to enhance status and tolerated theft are still to be invoked and tested.[159,160] Technical advances that involve the measurement of genetic relatedness and steroid hormones between and within individuals promise to yield deeper understanding of both the ultimate and proximate factors affecting chimpanzee behavior. Finally, no easy answers regarding the evolutionary factors that contribute to infanticide and cannibalism have emerged, despite decades of study. Understanding here will require more observations of the contexts of these infrequent events.

We would be remiss if we failed to note the critically endangered status of chimpanzees in the wild. It has become depressingly common for field workers to comment on how time is running out to save these animals. This is a regrettable fact. We are fortunate to have been given an opportunity to share in the lives of these animals in the wild. Anyone who has been similarly blessed instantly realizes the extraordinary nature of chimpanzees and recognizes the void that will exist if we do not meet the challenge by doing everything in our power to conserve these remarkable creatures and their habitat in the wild.

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