RESEARCH ARTICLE

Genetic Analyses Suggest no Immigration of Adult Females and Their Offspring Into the Sonso Community of Chimpanzees in the Budongo Forest Reserve, Uganda

KEVIN E. LANGERGRABER[1,2]*, CAROLYN ROWNEY[2], CATHERINE CROCKFORD[2], ROMAN WITTIG[2], KLAUS ZUBERBÜHLER[3,4], AND LINDA VIGILANT[2]

[1]*Department of Anthropology, Boston University, Boston, Massachusetts*
[2]*Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[3]*Cognitive Science Center, University of Neuchâtel, Neuchâtel, Switzerland*
[4]*School of Psychology & Neuroscience, University of St. Andrews, St. Andrews, Fife, United Kingdom*

Chimpanzees are frequently used to illustrate the relationship between sex differences in dispersal and sex differences in cooperation in primates and other group-living mammals. Male chimpanzees are highly philopatric, typically remaining in their natal communities for their entire lives to cooperate with related males in competition against less related males from other groups, whereas females typically disperse once at adolescence and cooperate with each other less frequently. However, there have been a few reports of dependent male offspring joining groups when their mothers transferred between communities as adults. Although such events are difficult to document, determining how often they actually occur is important for elucidating the links between philopatry, kinship, and cooperation in both chimpanzees and group-living animals more generally. Here we use genetic analyses to investigate a previous report of a large-scale transfer of many females and their offspring into the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda. Using autosomal microsatellite genotypes, we assigned a Sonso father to ten of the fourteen putative immigrants, and found that the four putative immigrants for whom we could not assign a Sonso father (perhaps due to incomplete sampling of all Sonso candidate fathers) nevertheless had Y-chromosome microsatellite haplotypes that were common in Sonso males but absent in males from four other chimpanzee communities at Budongo. These results suggest that these putative immigrant females and their offspring were probably actually long-term residents of Sonso whose identifications were delayed by their peripheral or unhabituated status. These results are consistent with other genetic and behavioral evidence showing that male between-community gene flow is exceedingly rare in east African chimpanzees. Am. J. Primatol. 76:640–648, 2014. © 2014 Wiley Periodicals, Inc.

INTRODUCTION

Sex-biased dispersal, the tendency of one sex to travel further from or more frequently leave the natal area before reproduction, is common in birds and mammals [Lawson Handley & Perrin, 2007]. Among animals that live in relatively cohesive and long-lasting social groups, such as many primates, considerable attention has been paid to the link between sex-biased dispersal and sex differences in social behavior and cooperation [Langergraber, 2012; Silk, 2009; van Hooff, 2000]. For example, in several old world monkey species, females nearly always remain in the group in which they were born for their entire lives, where they increase their direct and indirect fitness by forming strong social bonds with their close same-sex maternal kin [Silk, 2007a,b]. Except for rare cases of kin-biased immigration,

males in such societies are not closely related, and relationships among males are accordingly indifferent or antagonistic [van Hooff, 2000]. Enduring

*Correspondence to: Kevin E. Langergraber, Department of Anthropology, Boston University, 232 Bay State Road, Boston MA 02215, USA. E-mail: langergr@bu.edu

affiliative and cooperative relationships among males are largely limited to those few species where males are strongly philopatric, living alongside same-sexed kin in their natal group for a large proportion of—or even for their entire—lives [van Hooff, 2000]. Perhaps no species illustrates this link between male philopatry and sociality better than chimpanzees (*Pan troglodytes*), a strongly male philopatric species where males practice kin-biased cooperation at two distinct levels: (1) at the within-community level, where males preferentially cooperate with their maternal brothers, if available, in competition against other males of their own community for dominance rank and access to fertilizable females [Langergraber et al., 2007a; Mitani, 2009a,b], and (2) at the between-community level, where males cooperate with their fathers, sons, brothers, uncles, cousins, and other types of relatives to compete with more distantly related males from other communities for territories and the food and females they contain [Langergraber et al., 2011; Mitani et al., 2010].

As long-term field studies of a wider variety of primate species have accumulated, it has become apparent that particular populations or groups do not always follow the species-typical dispersal pattern. Several primate species that are typically characterized as strongly male philopatric have reported occasional cases of adult or adolescent males migrating between groups [Aureli et al., 2013]. In support of the hypothesis that male philopatry is linked to cooperation among males, particularly in the context of the indirect fitness benefits [Hamilton, 1964a,b] males gain when they cooperate against groups of males who are less closely related to themselves than are males of their own group, there is some evidence to suggest that both between-group competition and male philopatry are lower in the western (*P.t. verus*) than the eastern (*P.t. schweinfurthii*) subspecies of chimpanzee. Despite ample opportunities for observation due to the long-term study of multiple chimpanzee communities, only two between-group killing have been observed in west African chimpanzees, compared to dozens in the east African subspecies [Boesch et al., 2006; Wrangham, 2010]. Genetic studies of paternity show that the percentage of offspring born in a community that are fathered by males from other communities is 5–25% in west African and 0% in east African chimpanzees [West Africa: Taï, 4.2%, $N = 48$, Boesch et al., 2006; Bossou, 25%, $N = 4$, Sugiyama et al., 1993. East Africa: Mahale, $N = 10$, Inoue et al., 2008; Ngogo, $N = 62$, Langergraber et al., 2013; Sonso, $N = 21$, Newton-Fisher et al., 2010; Gombe, $N = 34$, Wroblewski et al., 2009]. There has even been one reported case of a male immigrating into a community as an adult in west African chimpanzees [Sugiyama, 1989, 1999], although because this event occurred early on in the study it is difficult to completely rule out the possibility that this male was a long-term resident who had not yet been identified because he was poorly habituated [Kawanaka, 1984]. Better documented are several cases of weaned western chimpanzee juvenile males accompanying their mothers as they transferred between communities as adults [Boesch et al., 2008; Wittig, unpublished data]. Eastern chimpanzee females have also been observed to transfer between communities with weaned male offspring. Two parous adult females have immigrated into the Kasekela community, one with a 4-year old daughter [Rudicell et al., 2010] and the other with a 5-year old son [Williams et al., 2002]. The fact that the male was weaned and that his mother may have been born in the Kasekela community may have contributed to his survival. At Mahale, two weaned males accompanied their mothers as they transferred from the K-group to the M-group following the death of most of the adult males in K-group and the dissolution of that community [Nishida et al., 1985]. One of these juvenile males disappeared within a few years, while the other survived to adulthood but probably would have been killed by M-group males if not for protective interventions by human researchers [Nishida & Hiraiwa-Hasegawa, 1985; Nishida et al., 1985]. This apparent subspecies difference in the extent of between-community male gene flow is reflected in patterns of Y-chromosome variation, with the west African subspecies showing more sharing of Y-chromosome haplotypes between communities and the occasional presence of Y haplotypes that are very divergent from the others present in the community and were likely introduced by gene flow from extra-community males [Langergraber et al., 2007b; Schubert et al., 2011].

These results suggesting extremely low levels of male gene flow between communities of east African chimpanzees are contradicted by a recent report of a purported case of large-scale transfer of adult females and their dependent offspring into the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda [Emery Thompson et al., 2006; hereafter ET 2006]. The inference of transfer of adult females with offspring was largely based on new identifications of several individuals during a relatively narrow period of time, several years after the onset of long-term study and well after the last adult female had previously been identified. However, the authors also acknowledged that because many eastern chimpanzee females are relatively nongregarious and elusive, it is also possible that these newly identified adult females were actually peripheral long-term residents of the Sonso community who had only just become sufficiently habituated for researchers to identify.

Whether or not this large-scale transfer of adult females and their offspring actually occurred has important implications for our understanding of the relationship between the extent of male philopatry

and between-group competition in chimpanzees. This is not only because between-community transfer by females and their offspring is a rare event in chimpanzees in general, but also because the purported case at Sonso is unique compared to all previously described cases in that it involved four offspring under 2 years of age and three males at or near reproductive age (9 years). No chimpanzees this young, and no male chimpanzees this old, have ever been observed to transfer between chimpanzee communities; the former presumably because their deaths would accelerate the return to reproductive conditions of their mothers, and the latter presumably because they represent immediate and direct competitors for matings with females. Here we use genetic analyses to determine if these adult parous females at Sonso did indeed transfer into Sonso from other communities, based on the assumption that if they did then their offspring will not have Sonso fathers and their male offspring will not have Sonso-typical Y-chromosome haplotypes.

METHODS
Study Site and Subjects

The Sonso community of chimpanzees, located in the Budongo Forest Reserve, Uganda, has been continuously studied since 1990 [Reynolds, 2005]. ET [2006] reported that from 2000 to 2003, Budongo Forest Project field researchers observed 11 new parous, adult females with dependent offspring in association with the Sonso community. ET [2006] reported that five of these parous females (FL, ML, PL, SB, WL) were recognized by all observers and sighted frequently enough to confirm them as members of the Sonso community, but were unsure whether the remaining six parous adult females (E, G, H, I, J, L) were new permanent residents or were merely temporary visitors to the Sonso community's home range. Subsequent to the publication of ET [2006], three of these latter six parous adult females have been confirmed as permanent Sonso residents rather than temporary visitors, and formally named (G = GL, H = BC, I = SE). Adult E was almost certainly subsequently named as permanent Sonso resident TJ, although we cannot be completely certain of this because ET [2006] reported that Adult E had a juvenile male when she was first sighted at Sonso in December of 2003, and TJ would have had a juvenile female at this time. As it is quite possible that this offspring sex mismatch was simply an error in observation or reporting (her habituation status is listed as "very nervous" in ET [2006], which may have limited observation opportunities), we considered TJ to be Adult E in ET [2006]. The remaining two females that were never subsequently confirmed as Sonso community members (J and L) may actually represent cases of the same individual

being given two identifications. Judging from the descriptions of their appearance and the estimated ages and sexes of their dependent offspring in Table 1 of ET [2006], L may have been the same individual as H/BC, while J is the least well-described of all of the individuals. Thus, in this paper we examined the offspring of the nine adult females who may have immigrated into the Sonso community as adults and subsequently remained as long-term residents.

This research complied with protocols approved by the Department of Primatology at the Max Planck Institute for Evolutionary Anthropology and the Uganda Wildlife Authority, adhered to the legal requirements of Uganda (fieldwork) and Germany (labwork), and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Paternity Analyses

The nine parous adult females had a total of 13 offspring (five females, seven males, and one of unknown sex) at the time of their putative immigrations into the Sonso community. If these parous adult females did indeed immigrate into Sonso from other communities, then their offspring should not have Sonso fathers. We collected fecal samples from and successfully genotyped nine of these 13 offspring at up to 19 autosomal microsatellite loci. Unfortunately, we did not successfully genotype four of the candidate fathers who were present in the Sonso community at the estimated time of conception of the offspring of the putative immigrant parous adult females, as these males died before they could be successfully sampled. The failure to assign a Sonso father to the offspring of a putative immigrant parous adult female is therefore not a strong indicator that s/he was fathered by a male from a non-Sonso community.

We also examined the paternity of two additional offspring (GR, SK) who were conceived in 2004–2005, after their mothers (GL, SE) were first observed in association with the Sonso community but before they were confirmed as permanent residents instead of just temporary visitors. Although these two mothers were later confirmed as permanent Sonso residents, during this time period they may have been simultaneously associating and reproducing with males of more than one chimpanzee community. We were able to successfully genotype all candidate fathers among the Sonso males for these two offspring. Thus, if we fail to assign a Sonso father to these two offspring, this would indicate that that they were indeed sired by non-Sonso males.

ET [2006] also identified five new adolescent, nulliparous females during this 2000 - 2003 period, one of whom (JL) was observed frequently enough to be considered a new permanent member of the Sonso community rather than a temporary visitor. This (JL)

and one other adolescent female (Subadult F, subsequently formally named as AN) were subsequently confirmed as permanent Sonso residents, while the identities of the three other putative immigrant adolescent females were never subsequently confirmed. We examined the paternity of these two putative immigrant adolescent females to determine whether they actually were natal individuals whose mothers were not well known. Although immigrant adolescent females are of course not unexpected in chimpanzees, if we were to find that these two nulliparous females have Sonso fathers and are thus natal, this would indirectly support the suggestion that the putative immigrant adult parous females were also long-term Sonso residents that escaped identification until the 2000–2003 period.

We also examined the paternity of two individuals not included in ET [2006] who Budongo researchers also thought were new immigrants when they first were identified. An adolescent male (HW) was reported [Reynolds, 2005] to have been born in another community and immigrated into Sonso with his mother (HT) in 1996, long before the purported large-scale immigration of 2000–2003 reported by ET [2006]. A juvenile female (VR) was thought to have immigrated into Sonso after the purported large-scale immigration, in 2006 (Crockford and Wittig, unpublished data).

Y-Chromosome Analyses

To overcome the limitations of the paternity analyses (i.e., the failure to assign a Sonso father to a putative immigrant could be either because the Sonso father was not sampled and genotyped or because the individual was indeed fathered in another community), we examined Y-chromosome variation among the male offspring of the putative immigrant females. In previous research we genotyped the Y-chromosomes of many of the long-term resident Sonso males ($N = 18$), along with males from three additional communities in the Budongo Forest Reserve (Busingiro, $N = 16$; Kanyiyo-Pabidi, $N = 16$; Waibira, $N = 18$) and one community in a remnant forest patch located about 10 km to the south of the Budongo Forest Reserve (Kasokwa, $N = 4$) (Langergraber et al., in press). We found that, as would be expected based on their high levels of male patrilocality and between-community aggression, haplotype sharing between communities was exceedingly rare: of the 20 different Y-chromosome haplotypes, only one was shared between chimpanzee communities (Kasokwa and Waibira), and the actual number of males that had the same haplotype as a male in a different community was low (several Waibira males but only one Kasokwa male had the multi-community haplotype). Importantly for the current study, all haplotypes of the long-term

resident Sonso males were unique to Sonso. Thus, if the putative immigrant parous adult females indeed transferred into Sonso after reproducing in another chimpanzee community, then the Y-chromosomes of their sons should be different from those of the other Sonso males. We successfully genotyped six of the seven putative immigrant male offspring at 13 Y-chromosome microsatellite loci.

This previous research (Langergraber et al., in press) also showed, however, that more extensive Y-chromosome haplotype sharing between east African chimpanzee communities can occur, particularly if they are direct neighbors: in Kibale National Park, also in Uganda, the neighboring Ngogo and Kanyantale communities shared a haplotype that was the most frequent haplotype in both communities, probably because they fissioned from one another within the last 500 or so years. One limitation of our results, addressed in more depth in the discussion, is that we sampled only one (Waibira) of the perhaps three or four communities that directly neighbor Sonso.

Genetics Methods

We genotyped autosomal and Y-chromosome microsatellites following procedures described in previous publications [Langergraber et al., 2007b, 2009; Schubert et al., 2011]. Briefly, we noninvasively collected chimpanzee feces using the two-step ethanol–silica method, and extracted DNA using the QIAamp DNA stool kit with slight modifications of the manufacturer's (QIAGEN, Germantown, MD, USA) protocol [Nsubuga et al., 2004]. We used a two-step amplification method, where we initially combined all primer pairs with template DNA in a multiplex PCR, then used dilutions of the resultant PCR products for subsequent amplification of each individual locus using fluorescently labeled forward primers and nested reverse primers in singleplex PCR reactions [Arandjelovic et al., 2009]. We assigned paternity through likelihood-based methods implemented in the program CERVUS [Marshall et al., 1998], conducted using the following parameters: 10,000 simulated offspring, 0.01 mistyping error rate, genotypes 0.95 complete. We set the number of candidate fathers as 100, and set the proportion of these sampled according to the number of genotyped Sonso candidate fathers that were present at the estimated birthdate of the offspring. Based on previous paternity studies on the minimum ages of fathers and potential errors in age estimates in chimpanzees [Langergraber et al., 2012], all Sonso males estimated to be ≥ 8 years at the time of conception were considered to be candidate fathers. All paternity assignments reported here, even those where we lacked a genotype form the offspring's mother, achieved the 95% level of confidence based on LOD scores.

RESULTS

Paternity Analyses

Of the nine genotyped putative immigrant offspring, we assigned four (GN, PS, SM, TP) fathers among the long-term resident Sonso males (Table I). A fifth offspring (BG), an infant female who was only about 2 months old when her mother was first seen at Sonso, was sired by one of the other, older putative immigrant males (FD). This result may seem to suggest that BG was conceived in another chimpanzee community, after which time her mother (BC), father (FD), and paternal aunt (FD's mother, FL) emigrated to Sonso. However, two additional pieces of evidence suggest that this scenario is unlikely. First, this infant was estimated to have been conceived in July 2003, which is several months after the time at which the father (FD) and his mother (FL) first began to be regularly observed in the Sonso territory (May 2003). Second, this offspring's (BG's) older maternal brother (SQ), who was accompanying the offspring (BG) and mother (BC) at the time of their first sighting at Sonso, although not assigned a Sonso father, has a Sonso-typical Y-chromosome haplotype.

We also assigned Sonso fathers to the two genotyped offspring (GR, SK) whose mothers (GL, SE) may have been temporary visitors to Sonso that simultaneously associated with males of other communities. Although these results cannot exclude the possibility of multiple-community associations, they do indicate that such associations did not lead to reproduction.

We assigned a father to one (AN) of the two (AN, JL) adolescent females that ET [2006] identified as part of the purported large-scale emigration event of 2000–2003.

Finally, we assigned a Sonso father to the adolescent male offspring (HW) of the adult female (HT) who was suggested to have immigrated into Sonso in 1996, before the purported large-scale immigration. We also assigned a Sonso father to the juvenile female (VR) reported to have immigrated into Sonso in 2006, after the purported large-scale immigration.

In sum, we assigned a Sonso father to 10 of the 14 putative immigrants whose paternity was examined using autosomal genotypes.

Y-Chromosome Analyses

As noted above, four of the nine putative immigrant offspring were not assigned a Sonso father (FD, FK, SQ, MR), but this could have occurred either because we did not sample four of the candidate fathers from Sonso who were alive at the time of conception, or because these four offspring were indeed conceived by non-Sonso males and immigrated into the Sonso community along with their mothers. Fortunately, all four of the offspring

TABLE I. Paternity Assignments and Y-Chromosome Haplotypes of Putative Immigrants Into the Sonso Community

Individual	Sex	Estimated birthdate	Mother's ID in ET [2006]	Mother's current ID	Mother's first sighting date	Offspring born prior to first sighting at Sonso?	Father	Offspring Y haplotype
TM	F	2004 ± 2 years	Adult E	TJ	12/01/2003	Yes	UK, ONG	N/A
Unnamed	UK	05/2004 ± 1 month	Adult I	SE	05/2004	Yes	UK, ONG	UK
SA	F	1996 ± 1 year	Adult SB	SB	11/2000	Yes	UK, ONG	N/A
WS	M	1996 ± 2 years	Adult WL	WL	10/16/2001	Yes	UK, ONG	UK
BG	F	04/2004 ± 4 months	Adult H	BC	21/05/2004	Yes	FD	N/A
GN	F	1996 ± 2 years	Adult G	GL	04/2004	Yes	VN	N/A
PS	M	1998 ± 1 year	Adult PL	PL	01/2003	Yes	CH	Q
SM	M	1993 ± 1 year	Adult I	SE	05/2004	Yes	NJ	Q
TP	F	1999 ± 2 years	Adult E	TJ	12/01/2003	Yes	BO	N/A
FD	M	1994 ± 1 year	Adult FL	FL	01/2003	Yes	UK, FNG	S
FK	M	1999 ± 1 year	Adult FL	FL	01/2003	Yes	UK, FNG	S
SQ	M	1991 ± 1 year	Adult H	BC	5/21/2004	Yes	UK, FNG	S
MR	M	1997 ± 1 year	Adult ML	ML	10/05/2001	Yes	UK, FNG	Q
GR	F	2006 ± 1 year	Adult G	GL	04/2004	No	MS	N/A
SK	M	10/06/2006 ± 2 weeks	Adult I	SE	05/2004	No	NK	S
Subadult F/AN	F	1990 ± 1year	N/A	N/A	N/A	N/A	CH	N/A
Subadult JL	F	1990 ± 1year	N/A	N/A	N/A	N/A	UK, FNG	N/A
HW	M	1993 ± 1 year	N/A	HT	1996	Yes	JM	T
VR	F	1997 ± 1 year	N/A	N/A	2006	N/A	VN	N/A

UK, ONG, unknown, offspring not genotyped; UK; FNG, unknown, all candidate Sonso fathers not genotyped; N/A, not applicable; UK, unknown. Letters for Y haplotypes represent arbitrary identification codes, as used in previous research [Crockford et al., 2013]. Individuals are listed according to the order they are discussed in the text.

with no assigned Sonso father happened to be male, permitting us to use their Y-chromosomes to help indicate their father's community. We found that the four male offspring with no assigned Sonso fathers had Y-chromosome haplotypes that are common in Sonso but absent in the four other chimpanzee communities we have genotyped in the Budongo area (Table I). These four male offspring with no assigned Sonso father showed two (Q and S) of the four Y-chromosome haplotypes that exist among the long-term resident Sonso males (Q, R, S, T). Including the adolescent male (HW) suggested to have immigrated into Sonso in 1996, before the purported large-scale immigration, the seven male putative immigrant offspring showed three (Q, S, T) of the four Sonso-typical Y-chromosome haplotypes.

DISCUSSION

Autosomal paternity analyses showed that four of the nine offspring purported to have immigrated into Sonso from other communities alongside their mothers were actually fathered by Sonso males, and a fifth was sired by one of the putative immigrant males. The four genotyped offspring to whom we could not assign a Sonso father nevertheless had Y-chromosome haplotypes that were common in Sonso but absent in other genotyped Budongo communities. We cannot definitively conclude that these four male offspring were sired by Sonso males, as we did not assay Y-chromosome variation in every potential source community at Budongo, including some that directly neighbor Sonso. And even if we could sample all extant Budongo communities, we could not rule out the possibility that the males of the source community of the putative immigrants had all died around the time of the purported transfer, and that these males shared Y-chromosome haplotypes with the Sonso males. However, previous research at Budongo and at Kibale National Park showed that the sharing of Y-chromosome haplotypes between east African chimpanzee communities is extremely rare [Langergraber et al., 2007b, in press]. Moreover, this research also showed that even directly neighboring chimpanzee communities share a maximum of one Y-chromosome haplotype, with a maximum of only one other community. The four males with no assigned Sonso father that were purported to be part of the putative large-scale emigration described in ET [2006] had two of the same Y-chromosome haplotypes of the long-term resident Sonso males, while another male who was thought to have emigrated earlier showed the third Sonso-typical haplotype. Thus, if these male offspring really were fathered by non-Sonso males, this would involve a previously unknown pattern of between-community haplotype sharing. Thus, it is highly likely that all genotyped putative immigrant offspring were actually sired by Sonso males. There

are two possible explanations for the finding that offspring who purportedly accompanied their mothers when they transferred into Sonso were fathered by Sonso males.

The first is that these adult females were actually members of other communities, and their offspring were conceived by Sonso males, either during temporary visits by Sonso males to these communities or during temporary visits by these females to Sonso. These females then emigrated permanently to Sonso accompanied by Sonso-fathered offspring, among which the males had Sonso-specific Y-chromosome haplotypes. Given the lack of evidence for extra-group paternities in other east African chimpanzee communities, this scenario would likely have to involve a very unusual demographic situation, such as an extreme decline in the number of community males, as has been associated with between-community transfer of females with offspring observed elsewhere [Boesch et al., 2008; Nishida et al., 1985; Rudicell et al., 2010].

The second possible explanation for the finding that the offspring of the newly identified adult females were sired by Sonso males is that these females were actually long-term Sonso residents who had escaped previous identification by researchers due to their peripheral or unhabituated status. This interpretation is supported by our finding that one of the newly identified adolescent females was also sired by a Sonso male, as was a juvenile female who was also thought to be a new immigrant. These females were likely natal, as no paternity study has ever found that a female was fathered by a male of the community into which she immigrated. That this juvenile female escaped a firm identification even as late as 2006, 16 years after long-term study at Sonso began in 1990, shows that identifying all of the individuals in a chimpanzee community can be a difficult and lengthy process. The timing of female identification at Sonso actually shows a reasonably close match with that at the Ngogo community in Kibale National Park, Uganda, which has been studied intermittently since 1979 and continuously since 1995, but where all adult females were not firmly identified until 2004 [Langergraber et al., 2009; Wakefield, 2008]. At Ngogo this sudden burst in the identifications during a relatively narrow time frame coincided with increased research effort focused on females; a similar phenomenon may have occurred at Sonso. That we examined the paternity of 14 individuals thought to have immigrated into Sonso, and the only one for whom we failed to find strong evidence for a Sonso father was an adolescent female, indicates that incomplete identification of all individuals in the community is the most likely explanation for the surge of new identifications reported in ET [2006].

That we did not find evidence at Sonso for the between-community transfer of adult females and

their offspring of course does not indicate that reports of this phenomenon in other communities are incorrect. There are two important differences between the purported cases at Sonso and those in other chimpanzee communities. The first is that in all other reports of females transferring with dependent offspring, there was also additional evidence for serious demographic collapse of the likely or known source community of the immigrants, caused by disease epidemics, hunting by humans, and/or high levels of lethal territorial aggression by the community to which the females eventually emigrated [Boesch et al., 2008; Köndgen et al., 2008; Nishida et al., 1985; Rudicell et al., 2010; Williams et al., 2002]. The second is that in all other cases of females transferring between communities with dependent offspring, all offspring were juveniles who were beyond the age of weaning and thus not especially vulnerable to infanticide, or if male, were not old enough to be immediate, direct competitors for reproduction.

Our finding that no large-scale transfer of females and dependent offspring occurred at Sonso is in line with previous research on other east African chimpanzee communities showing that male between-community gene flow is exceedingly rare, and supports previous empirical and theoretical research linking strict male philopatry to high levels of cooperation in the context of between-group competition. Research at the Kasekela community at Gombe National Park, Tanzania, suggests that larger territories result in increased food availability and shorter inter-birth intervals [Pusey et al., 2005; Williams et al., 2004]. The transfers of parous females following severe reductions in community size, known (Gombe [Goodall, 1986]) or suspected (Mahale [Nishida et al., 1985]) to have occurred as a result of lethal between-community aggression, show that male chimpanzee communities that successfully cooperate to expand their territory can also increase their reproductive success by attracting more adult females to their community. Finally, research from Ngogo shows that the males that cooperate to patrol the boundaries of their territory most frequently are the males with the highest mating success [Watts & Mitani, 2001], and thus will benefit most from an increased number of better fed and more quickly reproducing females.

All of the preceding lines of evidence suggest that males increase their direct fitness when they successfully cooperate to expand the size of their territory at the expense of males in neighboring communities. The extent to which these direct fitness benefits are supplemented by indirect fitness benefits will be determined by the extent to which those direct fitness gains are shared with related males of the same community and come at the expense of less related males in other communities [Hamilton, 1964a,b; West et al., 2002, 2007]. Despite the positive effect of dominance rank on reproductive success in male chimpanzees, most males that reach adulthood manage to reproduce [Langergraber et al., 2013]. Sufficiently low levels of reproductive skew, combined with sufficiently high levels of between-group genetic differentiation—to which strict male philopatry would contribute—have been suggested to have played a key role in the evolution of cooperation via between-group competition in both humans and chimpanzees [Bowles, 2006, 2009; Choi & Bowles, 2007; Langergraber et al., 2011].

Our finding that no large-scale transfer of females and dependent offspring occurred at Sonso also has implications for the understanding of cooperation and competition among female chimpanzees at Sonso and elsewhere. From 2004 to 2006, during the time period immediately after the purported large-scale transfer of parous and nulliparous females, Sonso researchers observed one and inferred two infanticides committed by adult females that were long-term residents of Sonso [Townsend et al., 2007]. Two of the victims were the offspring of females who were unknown to the researchers and may have been immigrants. The researchers interpreted these infanticides as the response to increased competition among females over food, brought about by the recent influx of females that was not accompanied by a corresponding increase in the territory size. Our finding that no such large-scale immigration event occurred at Sonso, along with previous cases from other communities of female-led infanticides in the absence of increases in adult female density from immigration, suggest that other proximal factors are involved in this rare and puzzling behavior [Goodall, 1977].

Finally, our results show the value of noninvasive genetic studies in helping document the existence of demographic events that are rare but have potentially important fitness consequences. Genetic approaches are particularly valuable in species like chimpanzees, which have a fission–fusion social system and a tremendous amount of variation between and even within individuals over time in levels of gregariousness, and are thus difficult to consistently monitor.

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