NOTICE: This is the accepted version of the following article:
Nishie H, Nakamura M (2018) A newborn infant chimpanzee snatched and cannibalized immediately after birth: Implications for "maternity leave" in wild chimpanzee. *American Journal of Physical Anthropology* 165(1): 194–199. DOI: 10.1002/ajpa.23327
The final version has been published at [http://onlinelibrary.wiley.com/doi/10.1002/ajpa.23327/full]. This article may be used for non-commercial purposes in accordance with the Wiley Self-Archiving Policy [https://authorservices.wiley.com/author-resources/Journal-Authors/licensing-open-access/open-access/self-archiving.html].

A newborn infant chimpanzee snatched and cannibalized immediately after birth: Implications for "maternity leave" in wild chimpanzee

Nishie H, Nakamura M

Laboratory of Human Evolution Studies, Graduate School of Science, Kyoto University

Abstract:
Objectives: This study reports on the first observed case of a wild chimpanzee infant being snatched immediately after delivery and consequently cannibalized by an adult male in the Mahale Mountains, Tanzania. We demonstrate "maternity leave" from long-term data from the Mahale M group and suggest that it functions as a possible counterstrategy of mother chimpanzees against the risk of infanticide soon after delivery.
Materials and methods: The subjects of this study were the M group chimpanzees at Mahale Mountains, Tanzania. The case of cannibalism was observed on December 2, 2014. We used the long-term daily attendance record of the M group chimpanzees between 1990 and 2010 to calculate the lengths of "maternity leave," a perinatal period during which a mother chimpanzee tends to hide herself and gives birth alone.
Results: We observed a very rare case of delivery in a wild chimpanzee group. A female chimpanzee gave birth in front of other members, and an adult male snatched and cannibalized the newborn infant immediately after birth. Using the long-term data, we demonstrate that the length of "maternity leave" is longer than that of nonmaternity leave among adult and adolescent female chimpanzees.
Discussion: We argue that this cannibalism event immediately after birth occurred due to the complete lack of "maternity leave" of the mother chimpanzee of the victim, who might lack enough experience of delivery. We suggest that "maternity leave" taken by expecting mothers may function as a possible counterstrategy against infanticide soon after delivery.

Keywords: cannibalism, delivery, Mahale, *Pan troglodytes*

Contact address:
Laboratory of Human Evolution Studies, Graduate School of Science, Kyoto University
Kitashirakawa-Oiwake-cho, Sakyo-ku, Kyoto, 606-8502, Japan
E-mail: nishie.hitonaru@gmail.com

1. INTRODUCTION

Infanticide by males has been observed in many primate species (Palombit, 2012) and has been explained mainly in terms of male reproductive strategy known as the sexual selection hypothesis (Hrdy,1974): males kill unrelated infants; infanticide makes the mother resume cycling quickly; and infanticidal males increase their probability of siring subsequent infants after the infanticide. Among wild chimpanzees, researchers have reported intragroup infanticide 45 times in nine different groups within six populations (Wilson et al., 2014); however, infanticide immediately after delivery has never been observed because of the rarity of observed delivery in the wild (Fujisawa, Hockings, Soumah, & Matsuzawa, 2016; Goodall & Athumani, 1980; Kiwede, 2000; Zamma, Sakamaki, & Kitopeni, 2012). This rarity of observed delivery among wild chimpanzees has been believed to derive from "maternity leave" (Nishida, Takasaki, & Takahata, 1990), a perinatal period during which a mother chimpanzee tends to hide herself and gives birth alone. "Maternity leave" was first described at Mahale (Nishida et al., 1990), but has only been analyzed quantitatively at Gombe (Pusey et al., 2008). Pusey et al. (2008) suggested that maternity leave functions as a female counterstrategy to reduce the risk of infanticide around the time of parturition.

While incidents of infanticide in most primate species are largely consistent with the sexual selection hypothesis, the circumstances of infanticide in wild chimpanzees are diverse and not entirely consistent with it (Palombit, 2012; Watts & Mitani, 2000). Alternative hypotheses have also been discussed as adaptive explanation of infanticide committed by male chimpanzees. The nutritional benefit hypothesis assumes that infanticide benefits the attacker(s) with important nutrients through cannibalism, which has occurred in most instances after infanticide among wild chimpanzees (Hiraiwa-Hasegawa, 1992). The resource competition hypothesis assumes that the attacker(s) reduce resource (mating) competition by eliminating unrelated male infants as possible future competitors (Nishida & Kawanaka, 1985; Takahata, 1985). The sexual coercion hypothesis predicts that the attacker male(s) can coerce the mother female to mate more restrictively with them by killing her offspring (Arcadi & Wrangham, 1999; Hamai, Nishida, Takasaki, & Turner, 1992). Here, we show the first observed case of a wild chimpanzee infant being snatched immediately after delivery and consequently cannibalized by an adult male in the Mahale Mountains, Tanzania. We hypothesize that the complete lack of "maternity leave" can be a reason for this rare incident. This study also demonstrates "maternity leave" from long-term data from the Mahale M group and suggests that it functions as a possible counterstrategy of mother chimpanzees against the risk of infanticide soon after delivery.

2. MATERIALS AND METHODS

2.1. Study site and subjects

The Mahale Mountains National Park (6°15′S, 29°55′E) is situated on the eastern shore of Lake Tanganyika in Tanzania at an altitude of approximately 780–2,400 m. The study site (Kasoje area, the home range of the M group chimpanzees) is located in the northwestern part of the park at an altitude of approximately 780–1,300 m and has an annual rainfall of approximately 1,700 mm. The area is dominated by semi-deciduous forest with small patches of woodland and secondary forest distributed in a mosaic pattern.

The M group chimpanzees at Mahale have been studied continuously since 1968. It had 84 members in 1990; the total decreased to 45 in the mid-1990s, but subsequently increased. At the time of obser- vations reported here (2014), it had 60 members, including 10 adult males (16 years ≤) and 20 adult females (13 years ≤).

Devota, the mother of the victim infant, had immigrated into the M group in 2012 and was estimated to be 14 years of age at the time of the reported case in 2014. This case was presumably her first delivery, as she had not been observed to give birth since she had immigrated. Darwin, the male who snatched and ate the infant, was born in the M group in 1988 and was 25 years of age in 2014. He was the second- or third-ranking male at the time.

2.2. Analysis of "maternity leave"

To determine whether expecting mother chimpanzees isolated themselves from other members during the perinatal period, we counted the inter-sighting intervals for new mothers ("maternity interval") and for all other adult or adolescent females ("nonmaternity interval"). From the daily attendance record of the M group chimpanzees from 1990 to 2010 (21-year period), we extracted 94 births to 36 females (one each to 12 females and 2–7 to 24 females). "Maternity interval" was counted as the number of each mother's absent days before the first appearance with her newborn infant. "Nonmaternity interval" was similarly counted as the number of absent days of all other adult or adolescent (9–12 years) females who were observed on the same day of the mother's first appearance with the newborn infant. The definition of "nonmaternity interval" in this study is different from that of Pusey et al. (2008), because the inter-sighting interval may well

be affected with the seasonal fluctuation of party size at Mahale (Itoh & Nishida, 2007). To evaluate the effect of delivery on the length of inter-sighting intervals, we used a GLMM (generalized linear mixed-effects model) with gamma distribution and log link function, using the glmmADMB package (Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016) implemented for the statistical software R ver. 3.3.0 (R Core Team, 2016). At Mahale, the overall gregariousness of chimpanzees largely changes with the availability of main fruit food, especially *Saba* (Itoh & Nishida, 2007), which enables researchers to divide a year into two seasons: the gathering season, roughly from August to January, and the dispersing season, from February to July. In the former, most of the group members gather together, making the length of inter-sighting interval shorter, while in the latter, they split into many small parties, making the inter-sighting interval longer (Nakamura, 2015). Therefore, we set the length of inter-sighting interval (days) as the response variable, the status of each inter-sighting interval (2 levels: maternity or nonmaternity interval) and the season in which each birth event occurred (2 levels: gathering season: August–January, dispersing season: February–July) as fixed effects, and each female ID (n = 71) and each birth event ID (n = 94) as random effects. We used the Akaike's Information Criterion (AIC) for model selection. We calculated AIC values for all the possible models with or without the explanatory variables, and the model that yielded the smallest AIC value was selected as the best model to predict the length of inter-sighting interval. We conducted Wilcoxon rank sum test to compare the length of maternity interval of primiparous females with that of multiparous females. Primiparous females here were defined as those who had not previously been observed, by the researchers, to have infants.

3. RESULTS

3.1. The case of cannibalism

On December 2, 2014 at 11:01, HN and an assistant located a party of 21 chimpanzees, including 4 adult males (Primus, the alpha male; Carter; Bonobo; Caesar) and 10 adult females. Devota, who would give birth soon after that, was included in the party; however, at this stage, we did not notice any obvious signs that she would give birth, such as pushing her hand into vagina or discharging amniotic fluid prior to delivery described in previous studies (Goodall & Athumani, 1980; Kiwede, 2000; Zamma et al., 2012). At 11:28, the assistant who was sitting approximately 20 m from HN witnessed Devota crouching down and suddenly giving birth on the ground. Immediately after the delivery, Darwin, a dominant adult male who was sitting behind Devota, picked up the newborn infant and rushed into the bush. Therefore, Devota did not even have the opportunity to touch the infant. The entire incident occurred very rapidly; therefore, we could not confirm whether a live-birth or stillbirth had occurred or even the sex of the infant. Approximately 30 s later, when HN arrived at the position where Devota had given birth, a placenta with umbilical cord remained on the ground, following which Effie, an adult female, picked up the placenta and climbed a nearby tree.

Effie held the placenta for a while, but never ate it, although she occasionally licked her hand holding the placenta. At 12:08, Darwin reappeared holding the infant under the tree where Effie sat on a branch (Figure 1). Slight bleeding was observed on the infant's nostril and its entire body was inactive; however, we could not confirm whether it was dead or still alive. The body of the infant at that time remained intact. Although HN managed to take some photographs, the heavy rain and darkness at that time prevented a better view of the infant, and we could not confirm the sex of the infant.

Approximately 30 s later, Darwin holding the infant once again rushed into the dense bush, after which we soon lost sight of him. When we located Darwin again sitting on a tree at a height of approximately 15 m at 12:57, he had already started eating the infant from the lower half of its body. Darwin ate the infant alone on a branch, whereas some adult females and adolescent males were observing Darwin on the same tree, several to 10 m away.

Between 13:32 and 13:38, Xantip, an adult female, and Azam, an adolescent male, picked up and ate some pieces of meat or bones falling from the branch where Darwin was positioned. An adolescent female, Genie, approached Darwin and tore a small piece of meat from the body of the infant held by Darwin; however, he showed no reaction. At 13:43, Bonobo, an adult male, approached Darwin and peered at the body held by Darwin; however, Bonobo did not attempt to touch the body and soon moved away.

By 13:57, Darwin had finished eating the body of the infant. At 14:29, we witnessed Ichiro, an adolescent male, carrying the placenta which Effie had been carrying, but the placenta remained uneaten. After a while, when we once again observed Ichiro, he no longer had the placenta, and we could not locate it subsequently.

On December 3, the following day, we located Darwin at 11:30 and followed him throughout the day. As Darwin had severe diarrhea, we could not locate any bones or hairs of the infant in his feces.

FIGURE 1. Darwin holding Devota's newborn infant (approximately 40 min after delivery)

3.2. Length of "maternity leave"

The summary of the length of inter-sighting interval is presented in Table 1. We constructed GLMMs to verify whether expecting mother chimpanzees generally tend to hide themselves during the perinatal period. The AIC values and the parameter estimates (±SE) for all possible models are shown in Table 2. The full model, including both the type of interval and the season of birth, predicted the length of inter-sighting interval best (AIC = 5841.4). Maternity intervals were longer than nonmaternity intervals, and intervals were shorter during the gathering season than during the dispersing season ($\beta_0 = 0.917 \pm 0.131$, $\beta_{maternity} = 1.346 \pm 0.083$, $\beta_{dispersing} = 1.144 \pm 0.154$; Figure 2). This is consistent with the hypothesis that new mothers take "maternity leave." The length of perinatal absence did not differ significantly between primiparous and multiparous females (Wilcoxon rank sum test, $n_{primiparous} = 20$, $n_{multiparous} = 74$, $z = -0.005$, $p = .996$).

TABLE 1. Summary of the length of inter-sighting interval

	maternity interval (days)			nonmaternity interval (days)		
	median	**range**	***n***	**median**	**range**	***n***
gathering season (Aug.–Jan.)	7	1–64	37	2	1–46	629
dispersing season (Feb.–Jul.)	18	1–156	57	4	1–208	510

TABLE 2. Parameter estimates and AIC values in GLMMs for the length of inter-sighting interval

	Estimated coefficient ± SE		
AIC	**Intercept**	**Status (maternity)**	**Season (dispersing)**
5841.4	0.917 ± 0.131	1.346 ± 0.083	1.144 ± 0.154
5892.7	1.586 ± 0.105	1.374 ± 0.084	–
6153.2	1.122 ± 0.136	–	1.193 ± 0.156
6205.8	1.827 ± 0.115	–	–

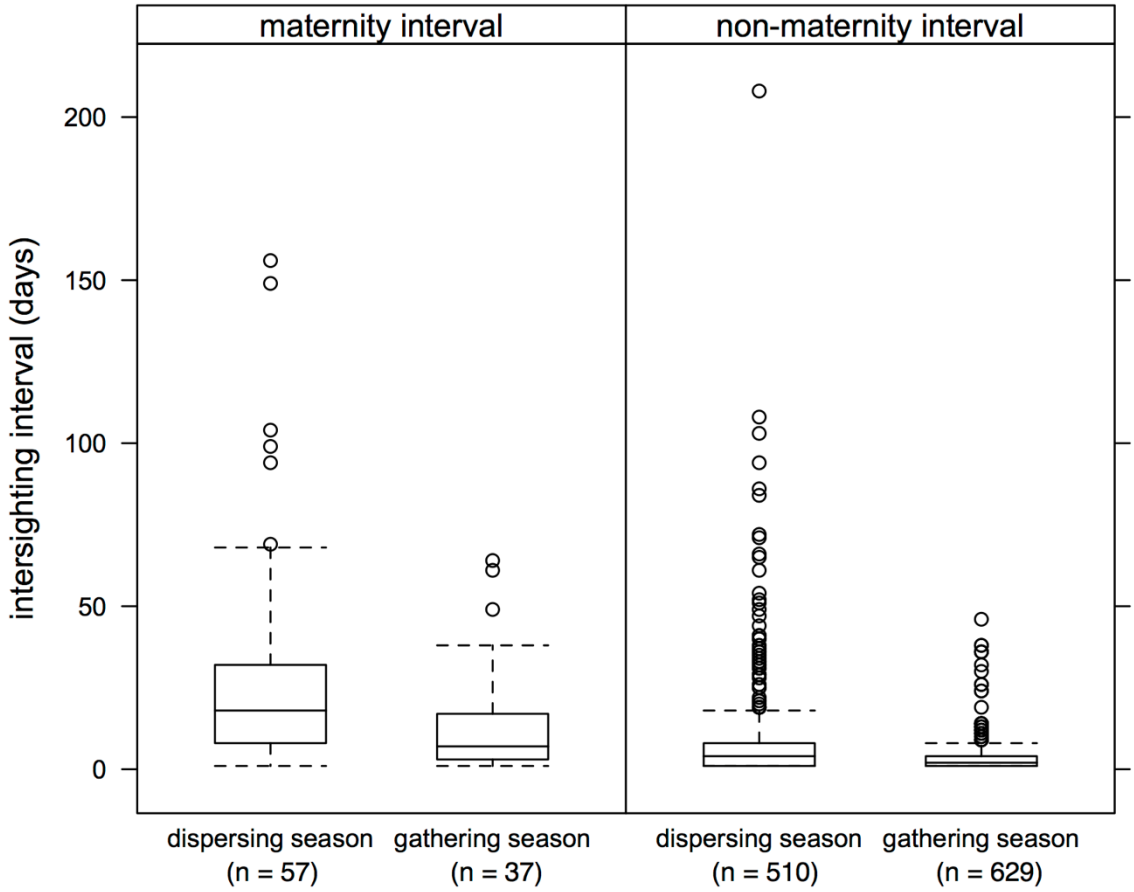

FIGURE 2. Maternity and non-maternity interval in dispersing (Feb.–Jul.) and gathering (Aug.–Jan.) season
The box plot contains the median and the range of inter-sighting intervals. The horizontal lines at the top and the bottom of the boxes indicate the first and the third quartiles. The horizontal lines in the boxes indicate the medians. The whiskers extend to the minimum and the maximum values which are no more than 1.5 times interquartile ranges from the first and the third quartiles, respectively. The points are outliers.

4. DISCUSSION

The "sexual selection hypothesis" seems consistent with this case, as it is unlikely that Darwin have fathered the Devota's infant. Devota might have conceived during April or May 2014 (estimated duration of gestation in wild chimpanzees: 208–235 d) (Wallis, 1997), though we did not observe any copulations of Devota during this period. Because Darwin had not been observed at all for an extraordinarily long duration between January 29 and June 5, 2014, including the Devota's estimated conception period, we assumed that he had been ill and could not range with other chimpanzees.

Nevertheless, the possibility of Darwin being the father cannot completely be ruled out as we did not observe Devota during all the possible days of conception and it is possible that she somehow met and copulated with Darwin during those days. In addition, because we could not collect any tissue samples from the infant, it was not possible to conduct a DNA analysis to confirm the paternity. Therefore, we cannot conclude whether the sexual selection hypothesis can simply be applicable to this case.

We also lack enough evidence for testing alternative hypotheses of infanticide. The nutritional benefit hypothesis seems partly applicable, since Darwin consumed the most part of the infant, although severe diarrhea might reduce the benefit. The resource competition hypothesis cannot be tested because we have no data on the sex of the victim and the relatedness between Darwin and the infant. The sexual coercion hypothesis may also be possible; however, we have few copulation data between Darwin and Devota before/after the infanticide and thus cannot test it.

We could not confirm whether the infant was alive

because Darwin snatched and ate the newborn immediately after birth. If this was a stillbirth, it was not Darwin who killed the infant; thus, there is a possibility that this case might not be a true case of infanticide.

We argue that the rarity of similar observations to this case is largely because of the rare chance to observe delivery among wild chimpanzees. Females tend to hide themselves during the perinatal period, termed "maternity leave," that is considered to be a possible female counterstrategy against male infanticide (Palombit, 2012). Devota's delivery in front of many other chimpanzees including adult males might have induced, or at least increased the risk of the subsequent suspected infanticide and cannibalism.

For "maternity leave" to work as a counterstrategy against infanticide, it is particularly important for a mother to be spatially situated away from males around the time of delivery. If a male is to maximize his benefit by killing an infant, infanticide immediately after birth may be the best tactic. Infants are most vulnerable, females may be least able to resist, and the interval between parturition and resumption of cycling would be shortest. In fact, some previous studies at Mahale also reported relevant cases. In one case, an adolescent male was observed carrying a dead infant presumed to have been born on that day. It was suspected to have been killed and cannibalized because it showed some antemortem wounds and its right foot was lost, as if bitten off (Hosaka, Matsumoto, Huffman, & Kawanaka, 2000). In another case, two high-ranking adult males severely attacked an adult female and her infant born on that day. In this case, the infant, protected by the mother and some other females, barely escaped being killed (Sakamaki, Itoh, & Nishida, 2001). Given how rarely births have been seen in the wild, the possibility exists that infanticide immediately or very soon after delivery occurs more often than these two cases indicate.

If "maternity leave" is an effective counterstrategy against infanticide soon after delivery, the reason for Devota not employing this strategy is a mystery. We suggest some possible reasons, not mutually exclusive. First, females might need to learn when and how to take "maternity leave" through experience, and Devota, presumed to be primiparous, had not yet had the experience. This "need to learn" hypothesis is possible; however, it is not consistent with the result that there was no significant difference in the length of perinatal absence between primiparous and multiparous females. Nevertheless, this result should be considered with caution: it is possible in the wild that infanticide soon after delivery is completely unnoticed by the researchers. If primiparous females face more such risks because of the lack of "maternity leave," we might have missed some of the *true* first deliveries, and some of those we included as "primiparous females" in the above analysis may not really be primiparous. Then the length of perinatal absence of "primiparous females" could be overestimated, as we might have omitted some short perinatal absences of true primiparous females consequently resulting in infanticide, and instead, we might have included some perinatal absences of females who actually are giving their second or third deliveries. Second, the infant was born prematurely and Devota was not prepared to give birth then. This "premature delivery" hypothesis is also possible; however, Toshifumi Udono, a veterinarian who has observed many chimpanzee deliveries in captivity and investigated the photographs taken by HN, suggested that this presumption may be ruled out because the infant was large enough to be viable (Toshifumi Udono, pers. comm.). Third, Devota might not have perceived any risk of infanticide at the delivery because there might have been possible father males who had copulated with Devota around the time of conception. This "father's protection" hypothesis is also possible; however, we cannot draw any conclusion because we have no copulation data of Devota during the conception period, nor have we any tissue sample of the victim infant for paternity confirmation.

ACKNOWLEDGMENTS

We thank all the members of the Mahale Mountains Chimpanzee Research Project for their cooperation, Tanzania Commission for Science and Technology (COSTECH), Tanzania Wildlife Research Institute (TAWIRI), Mahale Gombe Wildlife Research Centre, Tanzania National Parks (TANAPA), and Mahale Mountains National Park for permission work in Tanzania. We also thank Toshifumi Udono for his comments on the photographs of the infant, and Daisuke Muramatsu and Shun Hongo for helpful suggestions on the statistical analysis of maternity leave; and David Watts and two anonymous referees for constructive comments. This study was funded by JSPS KAKENHI #14J00963 and #17J40059 to HN.

REFERENCES

Arcadi, A. C., & Wrangham, R. W. (1999). Infanticide in chimpanzees: Review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates*, 40, 337–351.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J.,

Magnusson, A., Maunder, M. N., ... Sibert, J. (2012). AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27, 233–249. https://doi.org/10.1080/10556788.2011.597854

Fujisawa, M., Hockings, K. J., Soumah, A. G., & Matsuzawa, T. (2016). Placentophagy in wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *Primates*, 57, 175–180. https://doi.org/10.1007/s10329-016-0510-x

Goodall, J., & Athumani, J. (1980). An observed birth in a free-living chimpanzee (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. *Primates*, 21, 545–549.

Hamai, M., Nishida, T., Takasaki, H., & Turner, L. A. (1992). New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates*, 33, 151–162.

Hiraiwa-Hasegawa, M. (1992). Cannibalism among non-human primates. In M. A. Elger & B. J. Crespi (Eds.), *Cannibalism: Ecology and evolution among diverse taxa* (pp. 323–338). Oxford: Oxford University Press.

Hosaka, K., Matsumoto, A., Huffman, M. A., & Kawanaka, K. (2000). Reactions to dead bodies of conspecifics by wild chimpanzees in the Mahale Mountains, Tanzania. *Primate Research*, 16, 1–15.

Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22,19–58. https://doi.org/10.1159/000155616

Itoh, N., & Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates*, 48, 87–96. https://doi.org/10.1007/s10329-006-0031-0

Kiwede, Z. T. (2000). A live birth by a primiparous female chimpanzee at the Budongo Forest. *Pan Africa News*, 7, 23–25.

Nakamura, M. (2015). Home range. In M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), *Mahale chimpanzees: 50 years of research* (pp. 94–105). Cambridge: Cambridge University Press.

Nishida, T., & Kawanaka, K. (1985). Within-group cannibalism by adult male chimpanzees. *Primates*, 26, 274–284.

Nishida, T., Takasaki, H., & Takahata, Y. (1990). Demography and reproductive profiles. In T. Nishida (Ed.), *The chimpanzees of the mahale mountains: Sexual and life history strategies* (pp. 63–97). Tokyo: University of Tokyo Press.

Palombit, R. A. (2012). Infanticide: Male strategies and female counterstrategies. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. Silk (Eds.), *The evolution of primate societies* (pp. 432–468). Chicago: University of Chicago Press.

Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journalof Primatology*, 29, 949–973. https://doi.org/10.1007/s10764-008-9281-6

R Core Team. (2016). R: A language and environment for statistical computing (Version 3.3.0). Vienna, Austlia: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Sakamaki, T., Itoh, N., & Nishida, T. (2001). An attempted within-group infanticide in wild chimpanzees. *Primates*, 42, 359–366.

Skaug, H. J., Fournier, D. A., Bolker, B., Magnusson, A., & Nielsen, A. (2016). Generalized linear mixed models using AD Model Builder (Version R package version 0.8.3.3.).

Takahata, Y. (1985). Adult male chimpanzees kill and eat a male newborn infant: Newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. *Folia Primatologica*, 44, 161–170.

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, 109, 297–307.

Watts, D. P., & Mitani, J. C. (2000). Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates*, 41, 357–365.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., ... Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, 513, 414–417. https://doi.org/10.1038/nature13727

Zamma, K., Sakamaki, T., & Kitopeni, R. S. (2012). A wild chimpanzee birth at Mahale. *Pan Africa News*, 19, 3–5.