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International Journal of Primatology
The Official Journal of the International Primatological Society

ISSN 0164-0291

Int J Primatol
DOI 10.1007/s10764-016-9941-x

ONLINE FIRST

Springer

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Impact of Snare Injuries on Parasite Prevalence in Wild Chimpanzees (*Pan troglodytes*)

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Received: 3 October 2016 / Accepted: 13 October 2016

Abstract Many primate populations are severely threatened by human activity. Illegal hunting with snares frequently causes fatal injuries and permanent mutilations in wild primates. Traumatic injuries and stressful experiences can reduce the efficacy of the immune system to fight parasitic infections. Snare-related changes in primate behavior may also influence the probability of exposure to parasites. We hypothesized that primates with permanent snare-related injuries would have a higher prevalence of intestinal parasites than control individuals. We tested the relationship between snare injuries and the prevalence of intestinal parasites in wild chimpanzees (*Pan troglodytes*) of Budongo forest, Uganda. We collected 487 fecal samples from known individuals (70 control and 20 snare-injured chimpanzees) and used flotation and sedimentation to isolate helminth eggs and an immunochromatographic assay to identify protozoan cysts. We found that the prevalence of Strongylida nematodes was significantly higher in snare-injured chimpanzees than in control individuals. In contrast, we found no association between snare injuries and three other parasite taxa: *Ascaris*, cestode, and *Cryptosporidium parvum*. Our study suggests that snare-injured primates may have higher exposure and/or be more susceptible to developing infections with helminth

Handling Editor: Joanna M. Setchell

Electronic supplementary material The online version of this article (doi:10.1007/s10764-016-9941-x) contains supplementary material, which is available to authorized users.

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Published online: 22 December 2016

parasites than control individuals. Future studies should investigate whether snare injuries influence parasite prevalence in other species of wild primates.

Keywords Conservation · Helminths · Intestinal parasites · *Pan troglodytes* · Protozoa · Snare injury

Introduction

Illegal snare setting is common in many parts of subtropical Africa, especially in areas where the local population relies on wild game for its livelihood (National Environment Management Authority 2010; Tumusiime *et al*. 2010). In tropical forests in West and Central Africa, >70 mammal species are hunted (Fa *et al*. 2005). Poachers usually target animal species indiscriminately, and terrestrial primates are frequent victims, often with fatal consequences. The use of snares is the preferred technique for many rural population because it is easy to set them in a short period of time (Tumusiime *et al*. 2010).

When caught in a snare, an animal usually reacts by trying to pull the snare from its substrate, which causes the wire to tighten and to cut deeper into the flesh (Noss 1998). Although larger primates can separate the snare from the substrate, the wire often remains tightly wrapped around the affected body part, causing obstruction in blood circulation, infections, necrosis, loss of function, and mutilation. Although not directly targeted, chimpanzees (*Pan troglodytes*) are sometimes accidentally caught in snares, which can cause severe and permanent mutilations (Waller 1995). These injuries are a substantial problem in many chimpanzee communities. For example, in Budongo Forest, Uganda, an estimated third of the entire chimpanzee population suffers from some form of snare injury (Reynolds 2005).

Snare injuries can affect chimpanzee behavior in various ways. One study found that severely disabled females spent more time in small parties than control females, probably to avoid food competition and because they have more difficulty in following larger traveling parties (Hermans 2011). Another study found that female chimpanzees with snare injuries carried their offspring less often than uninjured females, especially once the infants grew older and heavier (Munn 2006). In the same study, the severity of a snare injury also negatively correlated with the daily travel distance, suggesting that disabled mothers may be disadvantaged in their foraging capacities. In addition, snare-injured mothers spent more time in trees than uninjured mothers, suggesting that snare injuries influence climbing abilities. Snare injuries may also reduce the ability of male chimpanzees to rise in social rank, which will negatively affect their mating opportunities and their ability to compete for food (Smith 1995). Finally, chimpanzees rely heavily on their hands when processing food (Byrne and Stokes 2002), suggesting that hand injuries will reduce their ability to access food and require them to use suboptimal techniques, such as using their mouth or feet to manipulate food items.

Despite the obvious physical harm of a snare injury, the long-term fitness consequences for injured chimpanzees remain poorly understood. In Budongo Forest, Uganda, there have been two reports of death due to snares between 1990 and 2005, although the true mortality rate is estimated to be much higher, around two or three fatalities per year (Reynolds 2005). Snare injuries do not seem to have an obvious negative impact on the physical condition of chimpanzees that survive (Smith 1995). However, one adult male of the Sonso community in Budongo Forest suffered from almost total paralysis of both hands due to snare injuries and developed chronic skin problems, presumably due to a lack of autogrooming (Hobaiter and Byrne 2010).

Chimpanzees harbor numerous intestinal parasites that can affect their immune systems (Strait *et al*. 2012). Chimpanzees can acquire these parasites when they come into contact with contaminated fecal matter. There is some circumstantial evidence to suggest that animals with snare injuries might have higher exposure rates to intestinal parasites than healthy animals. For example, snare-injured chimpanzees reuse old nests more often than control individuals (Plumptre and Reynolds 1997) and are therefore more likely to encounter parasite-contaminated fecal matter. The ability of chimpanzees to fight intestinal parasites also depends on the quality of their immune systems (Coe 2012). The efficacy of the immune system, in turn, depends on nutrition, stress, and other factors. Snare-injured individuals may have lower quality nutrition and higher stress levels, which will reduce their immunocompetence to fight parasitic infections.

We aimed to compare the prevalence of intestinal parasites between snare-injured and control chimpanzees in two communities of Budongo Forest, Uganda. We predicted that increased exposure and/or reduced immunocompetence would result in chimpanzees with snare injuries having a higher prevalence of intestinal parasites than control chimpanzees.

Materials and Methods

Study Area and Subjects

We conducted this study at the Budongo Conservation Field Station (BCFS), a Ugandan nongovernmental organization, in the Budongo Forest Reserve (latitude 1°37′N–2° 03′N, longitude 31°22′E–31°46′E), Masindi District, northwestern Uganda (Mwavu and Witkowski 2008). Budongo Forest is the largest natural forest in Uganda, with an area of *ca*. 825 km^2 (Reynolds 2005) and a mean altitude of 1100 m. This semideciduous tropical rainforest experiences a mean annual rainfall of 1600 mm. Peak precipitation occurs between March and May and between September and November, with a dry season from December to February. Temperatures vary between 19 and 32 °C (Reynolds 2005).

We obtained fecal samples from two chimpanzee communities, the Waibira group (partially habituated; observations since 2011) and the Sonso group (fully habituated; observations since 1990) over a period of 4 years. We collected samples from the Sonso community between 2011 and 2014 and from the Waibira community from 2013 to 2014. We classified the chimpanzees that had a morphological change due to a snare injury as “snare-injured.” These morphological changes included clenched toes, hooked hands, missing hands, or missing legs. We classified the chimpanzees that were never injured by a snare or that had suffered a snare injury earlier in life that did not result in a morphological disability as “controls.” For both communities, we collected fecal samples opportunistically from known individual chimpanzees using noninvasive sampling methods. Some chimpanzees were not well habituated (particularly those in the Waibira community), so it was difficult to collect many samples from these individuals. For the Sonso community, we were unable to obtain samples when chimpanzees foraged on crops in human settlements adjacent to the forest reserve because of the ethical guidelines of BCFS. As a result, we did not obtain a balanced dataset for the different focal animals. To obtain an estimate of population-wide patterns, we included fecal samples from all identified individuals, even if sample sizes were not balanced. We placed all fecal samples in sterile containers and labeled them with the individual's name, sex, age, and date of defecation.

Laboratory Analysis

We analyzed all fecal samples at the BCFS field laboratory for a range of intestinal parasites that are known to infect wild chimpanzees in the area (Barrows 1996; Mugisha 2004; Zommers 2010). We identified the following parasites: intestinal helminth worms, such as strongylid nematodes (Taylor *et al*. 2007), *Ascaris* nematodes, *Trichuris* nematodes, and cestodes. We lumped all cestodes, although this class includes many genera. We also identified intestinal protozoan parasites, such as *Cryptosporidium parvum*, *Giardia lamblia*, and *Entamoeba histolytica*.

We used the RIDA®QUICK Cryptosporidium/ Giardia/ Entamoeba Combi Test (R-biopharm AG, Germany), which is an antigen kit designed to detect protozoan parasites (*Cryptosporidium parvum*, *Giardia lamblia*, *Entamoeba histolytica*). For each fecal sample, we transferred *ca*. 50 mg of material into a tube without formalin and mixed with extraction buffer, before inserting the test strip into the resulting solution. The analysis is based on an immunochromatographic assay, with parasite-specific antibodies on the strip indicating parasite presence by specific colors. For all other parasites, we transferred samples into tubes with 10% buffered formalin for later analysis. We used two techniques to isolate helminth eggs: fecal flotation for light eggs using Sheather's solution (128 g of sugar in 100 ml of hot water) and fecal sedimentation for heavy eggs (Gillespie 2006). We visualized helminth eggs using a light microscope (40× and 10× objective) and identified them using a taxonomic key (Matsubayashi *et al*. 1965; Skrjabin *et al*. 1952). Parasite prevalence is typically defined by looking for eggs in 1 g of fecal matter. In this study, we used 3 g of fecal matter because the number of eggs was very low for some parasites.

Statistical Analysis

We considered four helminth taxa for our study: strongylid nematodes, *Ascaris* nematodes, *Trichuris* nematodes, and cestodes. We also considered three protozoan taxa: *Cryptosporidium parvum*, *Giardia lamblia*, and *Entamoeba histolytica*. We analyzed eight different parasite response variables: helminth richness (based on the four helminth taxa) and seven parasite prevalence variables (one variable per taxon).

We defined the helminth richness as the number of helminth genera found in one fecal sample. We defined the prevalence of a particular parasite taxon as the proportion of fecal samples infected by that parasite taxon (binomial data: 0 = parasite absent, 1 = parasite present). The analyses of the helminth richness and the four helminth prevalence variables were based on the entire dataset (487 fecal samples from 90 individual chimpanzees) whereas the prevalence of the three protozoa prevalence variables were based on a subset of fecal samples that had been processed with respect to these variables (98 fecal samples from 69 individual chimpanzees).

We used generalized linear mixed-effects (GLME) models to analyze these parasite response variables as a function of the fixed and random factors of interest. We modeled helminth richness and parasite prevalence using Poisson and binomial errors, respectively. The fixed factors included snare status (control, snare-injured), community membership (Sonso, Waibira), sex (female, male), age class (adult, juvenile, subadult), season (dry, wet), and the presence of road maintenance workers (no worker, worker). We included this last variable because road workers visited the study area from November 2013 to February 2014 as part of a project to reopen an old logging road for ecotourism. For snare status, we initially included the degree of injury in our analysis, but the sample sizes of the different categories were too low to carry out a meaningful analysis. We modeled chimpanzee identity as a random factor to control for pseudoreplication because some individuals were sampled more than once. We conducted the statistical analyses using R (R Core Team 2014) (see the Electronic Supplementary Material [ESM] document, "Script for R code used in statistical analyses"). We used the glmer () function to run the GLME models. For each parasite variable, we compared the full model (containing all the fixed factors of interest) to the null model (containing none of the fixed factors of interest) to determine the overall significance of the full model. To determine the statistical significance of each fixed factor, we used log-likelihood ratio tests to compare the residual deviance between the full model, which contained all fixed factors, and the reduced model, which was missing the fixed factor of interest. We considered the results significant at an α level of 0.05. For three parasite taxa (*Trichuris*, *Giardia lamblia*, and *Entamoeba histolytica*), the number of infected fecal samples was so low (6, 7, and 0, respectively) that the R software was unable to calculate the parameter estimates for the models (see ESM Table SII). We therefore do not present these parasite variables in the "Results" section.

Results

We collected a total of 487 fecal samples from chimpanzees in the Waibira and the Sonso communities. There were 366 and 121 fecal samples from 70 control and 20 snare-injured chimpanzees, respectively. Of the 90 individuals in this study, 36 belonged to the Waibira community (9 with snare injuries) and 54 to the Sonso community (11 with snare injuries).

For each of the five parasite variables for which there were enough infected fecal samples to run the analyses, the full model was statistically significant when compared to the null model (Table I). There was a significant association between snare status and the prevalence of Strongylida (Tables II and III; Fig. 1). If we consider an adult female chimpanzee in the Sonso community in the dry season in the absence of road workers as the reference point, the probability that a fecal sample was infected with Strongylida was 81.7% for a control individual and 91.8% for a snare-injured individual. There were no significant differences between snare-injured and control chimpanzees for the other parasite variables: helminth richness, prevalence of *Ascaris*, prevalence of cestodes, and the prevalence of *Cryptosporidium parvum* (Tables II and III).

Table I Statistical significance of the full model for five parasite variables based on fecal samples from control and snare-injured chimpanzees (*Pan troglodytes*) in Budongo Forest, Uganda, 2011–2014

	Helminth richness	Strongylida	*Ascaris*	Cestodes	*Cryptosporidium parvum*
Residual deviance of the full model	1256.3	290.6	410.27	583.86	109.23
Residual degrees of freedom of the full model	478	478	478	478	89
Residual deviance of the null model	1275.3	311.44	475.04	599.38	123.81
Residual degrees of freedom of the null model	485	485	485	485	96
Change in residual deviance between the null and full model (Δ Dev)	18.975	20.845	64.764	15.516	14.585
P-value associated with the Δ Dev and the Δ df	0.008	0.004	<0.001	0.029	0.041

The helminth richness and parasite prevalence were modeled as a GLME model with Poisson and binomial errors, respectively. The full model contains six fixed factors: community, sex, age class, snare status, season, and the presence of road maintenance workers. The null model did not contain any of the six fixed factors. The random factor was the identity of the chimpanzee. The change in residual degrees of freedom between the null and full model (Δ df) is 7 for all models

Other ecological factors that had effects on the parasitic prevalence variables were the chimpanzee community, the season, and the presence of road workers (Tables II and III). The chimpanzees in the fully habituated Sonso community had a higher prevalence for *Ascaris* and cestodes than the Waibira community. Parasite prevalence was higher in the dry season than the wet season for *Cryptosporidium parvum*. The presence of road workers decreased the following four parasite variables: helminth richness, the prevalence of *Ascaris*, the prevalence of *C. parvum*, and the prevalence of Strongylida. There was no effect of sex and the class of age on the parasite variables (Tables II and III).

Discussion

We found that snare-injured chimpanzees had significantly higher prevalence of Strongylida nematodes than control individuals. Snare injuries had no impact on the helminth richness and the prevalence of *Ascaris*, cestodes, and *Cryptosporidium parvum*. The most interesting result of this study was that snare-injured chimpanzees had a higher prevalence of Strongylida than control individuals. There are at least two possible explanations for this result. First, snare-injured individuals have higher exposure to Strongylida parasites than control individuals. Second, snare injuries facilitate the proliferation of these parasites because of a weakened immune system.

The first hypothesis suggests that snare-injured chimpanzees have higher exposure to helminth parasites than control individuals. Many helminth parasites, e.g., hookworms, have infective stages that penetrate the feet and hands of their chimpanzee hosts. Exposure rates should therefore be correlated with time spent on the ground (Zommers *et al.* 2013). However, a previous study found that snare-injured individuals spent less time on the ground than control individuals (Munn 2006). In addition, snare-injured individuals spent more time in small groups (Hermans 2011), where exposure

Table II Results of GLME testing the influence of ecological factors on parasite prevalence in control and snare-injured chimpanzees (*Pan troglodytes*) in Budongo Forest, Uganda, 2011–2014

	Helminth richness	Strongylida	*Ascaris*	Cestode	*Cryptosporium parvum*
Community	$\chi^2 = 2.91$, df = 1, $P = 0.088$	$\chi^2 = 3.26$, df = 1, $P = 0.071$	$\chi^2 = 4.84$, df = 1, $\boldsymbol{P = 0.028}$*	$\chi^2 = 7.48$, df = 1, $\boldsymbol{P = 0.006}$*	$\chi^2 = 0.18$, df = 1, $P = 0.670$
Sex	$\chi^2 = 2.79$, df = 1, $P = 0.094$	$\chi^2 = 1.29$, df = 1, $P = 0.256$	$\chi^2 = 2.59$, df = 1, $P = 0.106$	$\chi^2 = 2.18$, df = 1, $P = 0.139$	$\chi^2 = 0.00$, df = 1, $P = 1.000$
Age	$\chi^2 = 1.86$, df = 2, $P = 0.394$	$\chi^2 = 2.22$, df = 2, $P = 0.329$	$\chi^2 = 0.11$, df = 2, $P = 0.946$	$\chi^2 = 5.90$, df = 2, $P = 0.052$	$\chi^2 = 0.18$, df = 2, $P = 0.910$
Snare	$\chi^2 = 2.43$, df = 1, $P = 0.119$	$\chi^2 = 4.35$, df = 1, $\boldsymbol{P = 0.037}$*	$\chi^2 = 0.65$, df = 1, $P = 0.425$	$\chi^2 = 3.50$, df = 1, $P = 0.061$	$\chi^2 = 0.26$, df = 1, $P = 0.613$
Season	$\chi^2 = 0.07$, df = 1, $P = 0.778$	$\chi^2 = 3.27$, df = 1, $P = 0.071$	$\chi^2 = 1.18$, df = 1, $P = 0.275$	$\chi^2 = 0.21$, df = 1, $P = 0.644$	$\chi^2 = 9.92$, df = 1, $\boldsymbol{P = 0.002}$*
Workers	$\chi^2 = 7.80$, df = 1, $\boldsymbol{P = 0.005}$*	$\chi^2 = 4.38$, df = 1, $\boldsymbol{P = 0.037}$*	$\chi^2 = 52.11$, df = 1, $\boldsymbol{P < 0.001}$*	$\chi^2 = 0.15$, df = 1, $P = 0.691$	$\chi^2 = 8.90$, df = 1, $\boldsymbol{P = 0.003}$*

We modeled the helminth richness and parasite prevalence as a GLME model with Poisson and binomial errors, respectively. The six fixed factors were community (Sonso, Waibira), sex (female, male), age class (adult, juvenile, subadult), snare status (control, snared), season (dry, wet), and the presence of road maintenance workers (no worker, worker). The random factor was the identity of the chimpanzee. The significance of each fixed factor was determined using a log-likelihood ratio test that compared the full model to the model missing the factor of interest

*Indicates that the fixed factor had a *P*-value <0.05

Table III Parameter estimates (contrast ± standard error) for ecological factors that predict five parasite variables in control and snare-injured chimpanzees (*Pan troglodytes*) in Budongo Forest, Uganda

Fixed factor	Helminth richness	Strongylida	*Ascaris*	Cestode	*Cryptosporidium parvum*
Intercept	0.31 ± 0.096	1.49 ± 0.376	−1.02 ± 0.343	−1.13 ± 0.280	2.44 ± 1.144
Community	−0.18 ± 0.112	0.97 ± 0.578	**−1.01 ± 0.500***	**−0.90 ± 0.343***	−0.32 ± 0.701
Sex	0.13 ± 0.078	0.40 ± 0.354	0.46 ± 0.297	0.37 ± 0.246	0.03 ± 0.745
Age1	0.03 ± 0.141	0.65 ± 0.677	−0.15 ± 0.506	−0.08 ± 0.428	0.60 ± 1.478
Age2	0.12 ± 0.089	0.52 ± 0.414	0.01 ± 0.335	0.64 ± 0.274	0.09 ± 0.805
Snare	0.14 ± 0.090	**0.92 ± 0.476***	0.27 ± 0.344	0.56 ± 0.286	−0.50 ± 0.891
Season	0.02 ± 0.087	0.62 ± 0.344	−0.31 ± 0.286	−0.10 ± 0.234	**−2.68 ± 1.058***
Workers	**−0.26 ± 0.095***	**−0.76 ± 0.355***	**−3.34 ± 0.734***	−0.09 ± 0.248	**−2.10 ± 0.852***

We collected fecal samples from 2011 to 2014. Helminth richness and parasite prevalence were modeled as GLME models with Poisson and binomial errors respectively. The parameter estimates are contrasts (on the logit scale) between the levels of each fixed factor. The six contrasts are defined as follows: community (Waibira – Sonso), sex (male – female), age1 (juvenile – adult) age2 (subadult – adult), season (wet – dry), snare status (snared – control), and the presence of road maintenance workers (no worker, worker). The random factor was the identity of the chimpanzee

*Indicates that the fixed factor had a *P*-value <0.05

to ground-dwelling helminth parasites is presumably lower than in large groups. These observations suggest that snare-injured individuals do not have higher exposure rates to ground-dwelling helminth parasites than not snared-injured individuals. However, snare-injured chimpanzees reuse old nests more often than control individuals (Plumptre

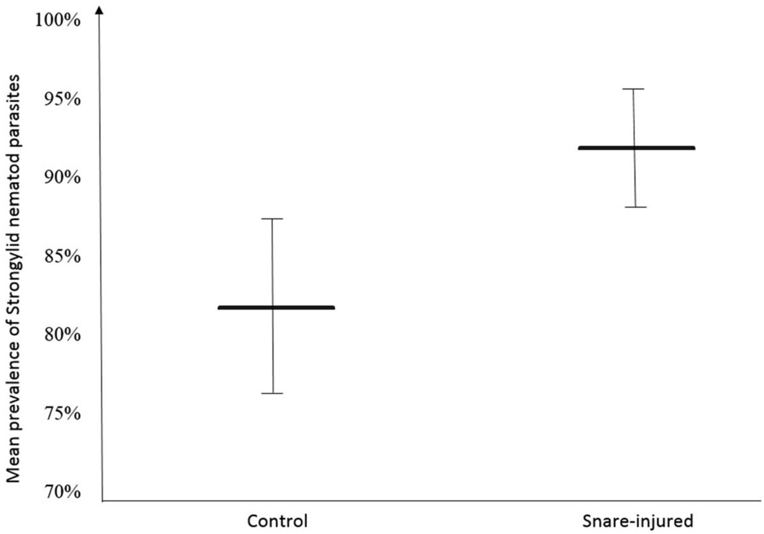

Fig. 1 Prevalence of Strongylida in control and snare-injured chimpanzees (*Pan troglodytes*) in Budongo Forest, Uganda, 2011–2014. The parameter estimates were taken from the generalized linear model analysis (see Table III) and were back-calculated to the original scale. The effect of snaring is shown for a reference fecal sample, taken from a female adult in the Sonso community during the dry season and in the absence of road workers. The bars show the standard errors.

and Reynolds 1997), and this behavior may enhance their probability to encounter parasite-contaminated fecal matter. Thus, it is currently not clear whether snare-injured chimpanzees are more or less likely to encounter helminth parasites than control individuals.

The second hypothesis suggests that snare injuries directly facilitate intestinal parasite infections. The skin is an important defense against pathogens (Janeway *et al*. 2001) and snare-induced skin injuries trigger inflammatory responses to heal the wound and to kill invading microbial pathogens (Davis 2008). Severe snare injuries may thus compromise the immune system and, as a consequence, facilitate intestinal infections because of trade-offs between the different components of the immune response (Sadd and Schmid-Hempel 2009). The efficacy of the immune system also depends on nutrition, stress, and other factors. Snare-injured individuals may have lower quality nutrition and higher stress levels, which would reduce their immunocompetence to fight parasitic infections. In summary, snare-injured individuals may have a higher prevalence of intestinal parasites because their immune systems are less competent.

Chimpanzees are known to carry multiple cestode species (Strait *et al.* 2012). We did not identify the cestode parasites to subgroups. As a result, the cestode variable contained many genera. The statistical analysis found no effect of snare injuries on the prevalence of cestode parasites. However, this test is limited in value because we lumped all the cestode taxa into a single group.

An intriguing question for the future is whether snare-injured chimpanzees, given their higher prevalence of Strongylida infections, are more likely to use medicinal plants than control individuals. Some plants eaten by chimpanzees are used by humans in traditional medicine as treatment for intestinal parasite infections (Ghai *et al*. 2015; Krief *et al*. 2005). However, severely injured chimpanzees generally suffered from impaired feeding efficiency (Stokes and Byrne 2001), which may prevent them from harvesting medicinal plants and control their parasite infections. Foraging data would be necessary to address this point.

Acknowledgments We are grateful for the support of the field assistants, staff, and researchers of the Budongo Conservation Field Station (BCFS). We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology for permission to conduct this project. We thank the Royal Zoological Society of Scotland for providing core funding to the BCFS. We thank the ARCUS Foundation for funding the Chimpanzee Monitoring Programme. Funding for fieldwork was provided by the Institute of Biology and the Fonds des Donations of the University of Neuchâtel, as well as the M. Wüthrich and A. Mathey-Dupraz Foundation and an ERC grant (PRILANG 283871) to K. Zuberbühler. We thank the reviewers and the editor for their helpful comments.

Compliance with Ethical Standards

Conflict of Interest The authors have no conflict of interest or any competing financial interest.

Ethical note This research complied with ethical requierements for research involving animals as established by "Uganda Wildlife Authority" and "the Ugandan National Council for Science and Technology".

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