TITLE: Chimpanzees and their mammalian sympatriates in the Issa valley, Tanzania

RUNNING TITLE: Chimpanzee sympatriates in Tanzania

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Abstract

Chimpanzees have been studied for nearly 300 combined years across Africa, but aside from their roles as predators or prey, remarkably little is known about the diverse species with whom they share habitats. We calculated likely chimpanzee encounter rates with sympatric mammals in the Issa Valley, Tanzania through modelling actual researcher encounter rates with all medium and large mammals. Compared to other long-term chimpanzee study sites, Issa had a relatively high diversity in medium and large mammal species present, with 36 species documented. We encountered common duiker (*Sylvicapra grimmia*) most frequently, followed by yellow baboons (*Papio cynocephalus*) and bushbuck. Chimpanzees ranked fifth overall. Chimpanzees, on the other hand, were predicted to most frequently encounter bushbuck, klipspringer, and hartebeest – all woodland species. We compare these results to published literature and contextualise them in light of reconstructing diverse mammalian communities in which hominins lived during the Plio-Pleistocene and the use of chimpanzees as flagship species for conservation policy.

Key words: Chimpanzee; Sympatry; Savanna-mosaic; Mammals; East Africa

MAIN TEXT

Introduction

There are numerous reasons why it is important to examine the diversity of mammalian fauna that live sympatrically with wild chimpanzees. First, whilst there has been investigation into interactions between chimpanzees and sympatric primates at various sites, studies almost always concern predatory patterns, with chimpanzees as predators (Basabose & Yamagiwa, 1997; Stanford, Wallis, Matama, & Goodall, 1994; Uehara, 1997; Wrangham & van Zinnicq Bergmann Riss, 1990) or prey (Boesch, 1991), rather than understanding how species coexist by using different niches, i.e. niche partitioning (but see Russak, 2013). To know more about how chimpanzees and other species share landscapes and mutually exploit resources, more study is needed into broader, community-ecological relationships. In one of the few studies directly examining inter-specific interactions, Russak (2013) reported remarkably low spatial (<20%) and dietary (<40%) overlap between chimpanzees and those of other mammals from the Issa valley, Tanzania. Chimpanzees and carnivores (incl. Herpestidae) had especially minimal spatial overlap. By contrast, members of families Rodentia and Artiodactyla showed the highest rates of spatial overlap. She concluded that overall habitat use overlap between chimpanzees and all other species, including frugivorous birds, to be 46%.

A second reason to consider chimpanzees as part of a broader faunal community is to better understand the role that they play in helping model how early hominins might have responded to similar conditions, especially in open, arid habitats with environmental heterogeneity (Copeland, 2009; Moore, 1992, 1996; Pruetz & LaDuke, 2010). Understanding extant chimpanzee-sympatriate dynamics informs how we contextualise hominins within diverse mammalian communities (Bobe, Behrensmeyer, & Chapman, 2002) and also how we develop hypotheses on adaptations regarding inter-specific competition (Egeland, 2014). Moreover, ecological data from contemporary (especially diverse) mammal communities reveal distributions across mosaic habitats that can provide models for understanding bone assemblages in the fossil record (Su & Harrison, 2008). Habitat reconstructions of *Ardipithecus ramidus*, for example, were informed in large part by isotopic signatures and fossil assemblages of diverse fauna found in the Aramis biotope (White et al., 2009). Whilst there has been discussion into hypothesized hominin-sympatriate dynamics, especially with carnivores (Treves & Palmqvist, 2007), comparatively little has been examined for extant chimpanzees, one of the most common analogues for hominins.

Finally, monitoring encounter rates over time allows researchers to make crude assessments on population trends of species that especially live at low densities. Whilst systematic line transects are more reliable for numerous reasons, namely in their controlling of survey effort, transect data often under-estimate actual population sizes due to low sample sizes (Fragoso et al., 2016). Data from reconnaissance walks provide some metric for at least relative changes in abundance and thus have implications for conservationists interested in trends over time in population size.

Russak and McGrew (2008) produced the first compilation of sympatric mammals from the six (medium or long-term) chimpanzee study sites where data were available at the time. They reported high variability in mammalian biodiversity across the six chimpanzee communities: Bossou, Guinea; Mt. Assirik, Senegal; Gombe and Mahale, Tanzania; Kibale and Budongo, Uganda (Figure 1). They concluded that it was likely that the lists were not exhaustive and thus interpretations were tentative. Nonetheless, the authors showed that with 33 genera of medium-large mammals, Mt. Assirik ranked second only to Kibale Forest in mammalian diversity. This is surprising given that Mt. Assirik is described as one of the hottest, driest, and most open chimpanzee study sites (McGrew, Baldwin, & Tutin, 1981) and more broadly, that savanna mosaics are considered “marginal” landscapes (Kortlandt, 1983). Such may be the case for apes compared to tropical forest populations, but clearly not for other mammalian species.

Figure 1 ABOUT HERE

Whilst there is substantial evidence for inter-community social variation in chimpanzees (van Leeuwen, Cronin, Haun, Mundry, & Bodamer, 2012; Luncz, Mundry, & Boesch, 2012; Whiten et al., 1999), there is far less comparative data on physical environment variation, especially for savanna chimpanzees (but see van Leeuwen, Hill, Newotn, & Korstjens, 2017). One example comes from McGrew et al.’s (2014) work at Mt. Assirik, Senegal. Located in the northern portion of the Park National Niokola Koba (PNNK), Senegal, Mt. Assirik is a mosaic habitat, comprised of five different vegetation types: woodland (37%), laterite plateau (28%), grassland (27%), bamboo (5%), and closed gallery forest (3%) (McGrew et al., 2014). Over four years (1976-1979), they built a dataset of all researcher encounters with medium-large mammals. The authors acknowledged that their data were inherently biased towards larger, diurnal and vocally conspicuous species, as those were more likely to be detected than smaller, nocturnal, and cryptic species. From those species that met the sample size minimum, they calculated that marsh mongoose (*Atilax paludinosus*), leopards (*Panthera padus*), and bushbuck (*Tragelaphus scriptus*) were the most likely species to encounter chimpanzees, versus jackals (*Canis adustus*), which were the least likely. Their results provide an important springboard off which others can follow to contextualize chimpanzees in a diverse ecosystem of sympatric wildlife species.

We sought to provide comparative analyses by extracting a similar data set from another open habitat[3] site, the Issa valley, Tanzania, in East Africa. Comparisons to the Mt. Assirik data allow us to assess whether the interspecific patterns that they described are regionally-specific, versus being part of a broader pattern for open-habitat chimpanzees, with implications for chimpanzee adaptation to drier landscapes. Our hypotheses were that (1) Issa and Mt. Assirik, which share broadly similar vegetation and climate, would have comparably diverse wildlife communities and thus accordingly (2) researchers (and chimpanzees) at both sites would encounter mammals at similar rates.

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[3] Chimpanzees can crudely be distinguished into those communities that inhabit areas characterised by tropical, closed-canopy forest, and those that live in drier, savanna-woodland mosaic habitats, hereafter classified as “open-habitat” for simplicity. For a discussion, see Moore (1992) and Dominguez-Rodrigo (2014).

Materials and Methods

Study area

The Issa valley in western Tanzania lies ~100km east of Lake Tanganyika and about 70km southeast of the town of Uvinza, in the Greater Mahale Ecosystem (GME). The area has no formal protective status, and is characterized by a mosaic landscape, dominated by miombo woodland of predominantly *Brachystegia*, *Julbernardia* and *Isoberlinia*. Separating large stretches of woodland are seasonally-inundated swamps, rocky outcrops, and thin strips of evergreen, riverine forest with continuous canopies and open understories (Russak, 2014). Such riverine forest comprises less than 7% of the study area. Mean daily temperatures of the region ranges from 11–36°C and rainfall averages 1245mm/year (range: 1000-1650 from 2009-2015). Issa is characterized by an extreme seasonality with typically over six dry months (<100mm of rainfall) lasting from May to October, during which human-started grass fires burn >70% of the landscape (pers. observation). The elevation ranges from ~1050m to 1750m, all within an 85km^2 study area.

Since 2008, there has been a continuous research presence at Issa, focused on chimpanzees (Piel et al., 2017; Piel, Lenoel, Johnson, & Stewart, 2015), red-tailed monkeys, and yellow baboons (Johnson, Piel, Forman, Stewart, & King, 2015). Chimpanzee habituation efforts only began in 2012, with initial work focused on using indirect methods of assessing behavior, namely passive acoustics (Kalan et al., 2016) and nest building (Stewart, Piel, & McGrew, 2011). Genetic analyses suggest a minimum chimpanzee community size of at least 67 individuals (Rudicell et al., 2011) that live at an extremely low population density (0.25 individuals/km^2 - Piel et al., 2015). Whilst the area is remote, there is evidence of illegal human activity, namely small scale logging, poaching, and agriculture (Piel et al., 2015).

Fauna

Russak (2014) has produced the most thorough mammal list to date of the area (Table 1). She recorded 40 mammal species from seven different orders. Whilst historically, megafauna like elephants (*Loxodonta africanus)*, giraffe (*Giraffa camelopardalis***)**, zebra (*Equus burchelli)* and topi (*Damaliscus lunatus)* have been reported for the area (Kano, 1971; Suzuki, 1969), she reported no observations of these larger species. Iida et al. (2012) also provided an exhaustive list of 50 mammal species, but their study area was situated ~30km north of the current one.

Data collection

Research teams followed chimpanzees, red-tailed monkeys and baboons, as well as patrolled the study area boundary for human activity daily for 84 months, from January 2009-December 2015. For all work, teams recorded all fresh or recent evidence of medium-large mammal activity (direct observations, prints, feces, nests), as well as the age and quantity of each, and the vegetation type, topography, and GPS coordinate for each observed encounter.

TABLE 1 ABOUT HERE

Analyses

We followed McGrew et al. (2014) and calculated the probability of encountering each of the medium and large mammal species[4] at Issa in each of open (woodland and grassland) and closed (riverine forest) vegetation. Accordingly, the likelihood of any two species encountering each other is the combined likelihood of these encounters across each vegetation type:

$$P_{XY} = (P\,_{X}{}^{o}\ x\ P\,_{Y}{}^{o}) + (P\,_{X}{}^{c}\ x\ P\,_{Y}{}^{c})$$

where X = *species 1, Y = species 2, O = open vegetation* and C = *closed vegetation,* and

$$P\,^{c}{}_{Z} = \int^{O} / (\int^{o} + \int^{c}),\ etc.$$

where X = species 1, $\int$ = frequency of encounters in a given vegetation type (open or closed) and $\int^{o} + \int^{c}$ = total encounters in both vegetation types.

To compare Mt. Assirik results with those at Issa, we controlled for search effort in three ways. First, we divided total encounters by McGrew et al. by the number of months over which data were recorded (n=48), and total encounters at Issa by n=84 months. Second, because the numbers of researchers at Issa have slowly grown over the study period (versus at Mt. Assirik, which was consistently one team), we further incorporated the mean number of researcher teams in the forest each day, calculated independently for each study year. Finally, encounter rates will be influenced by not just *how many* research teams are deployed, but *where* those teams spend time.

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[4] Despite species differences, we collapsed green monkeys from Assirik (*Chlorocebus sabaeus*) and Issa (*Chlorocebus pygerythrus*) into a single group

Accordingly, for Issa data, we further included measures of proportion of time spent in each vegetation type. To calculate this, we randomly selected all-day GPS track logs from two research assistants for each month during two successive years (a total of 46 day GPS track logs) and projected them over a vegetation classification of the study area in ArcMap (version 10.2.2). We then extracted the proportion of collected waypoints (auto-recorded at five-minute intervals by Garmin GPS/2-way radios) within 50x50m grid cells, each of which was classified as one of the previous described vegetation types (see Johnson, 2014). We were unable to do this for Mt. Assirik data, which were not available.

All research was observational and complied with Tanzanian Wildlife Research Institute ethical regulations and conformed to UK legislation under the Animals (Scientific Procedures) Act 1986 Amendment Regulations (SI 2012/3039).

Results

We found Issa to have a relatively high diversity in medium and large mammal species present, with 36 species documented, of which 30 were directly encountered. We found common duiker (*Sylvicapra grimmia*) was the most commonly encountered mammal at Issa, followed closely by yellow baboons (*Papio cynocephalus*) and bushbuck (Table 2). Chimpanzees were one of the most frequently encountered species, ranking fifth overall. Chimpanzees and bushpigs were found nearly as often in open vegetation as they were closed, whereas most other species showed clear habitat preference (Figure 2).

Figure 2, Table 2 ABOUT HERE

When we looked at encounter rates across years, some species were consistently, frequently encountered, namely common duikers, baboons, red-tailed monkeys, bushbuck, and klipspringers, and all species showed increased trends over the seven years (Figure 3). All three non-primate species are characterized as woodland species (Hinde et al., 2001) and the frequent encounter rate is consistent both with a miombo-dominated landscape, but also search effort. Researchers spent disproportionately more time in woodland (84.1%) than in forests (14%). Of the large carnivores, we observed leopard the most often (n=10), but the others extremely rarely: wild dog (n=5), lion (n=1), and we never encountered hyena.

Figure 3 ABOUT HERE

Our final analysis integrated researcher encounter rates with chimpanzees and that with their sympatriates to make predictions on which species chimpanzees would encounter most. Here we found that chimpanzees were most likely to encounter bushbuck far more than any other species, followed by three woodland specialists: klipspringer, hartebeest, and common duiker (Table 2).

Discussion

We report here on encounter rates with 36 of the medium-large sized mammalian species that researchers encountered at the Issa valley, Tanzania. Researchers encountered common duikers and yellow baboons most frequently and broadly the carnivores the least frequently. We used encounter rates across vegetation types and found that chimpanzees were most likely to encounter other habitat generalists (e.g. bushbuck) more than forest-specialists (e.g. red-tailed monkeys). In a previous study from Issa that investigated habitat co-use between chimpanzees and sympatric mammals using patch-focals, Russak (2014) reported frugivorous birds and rodents most frequently with chimpanzees (Table IV, Russak, 2014). As we didn't monitor either of those here, we cannot say if our data are consistent or diverge from Russak's findings.

A single other study from another long-term chimpanzee study site provides similar data to which we can compare our findings. McGrew et al. (2014) documented 35 different mammalian species to occur in the chimpanzee home range at Mt. Assirik. While these two savanna-dwelling chimpanzee populations live amongst a diversity of hetero-specifics, both are less diverse than Kibale National Park (Uganda), the most diverse site described in Russak and McGrew's (2008) compilation. When we included cumulative datasets from camera trap and patch-focal data (Russak, 2014) at Issa, the mammalian diversity level reaches 47 species, the most of any medium-long term chimpanzee study. Remote sensing methods like camera trapping have not been used at all sites, but even at Issa only three additional species are known from camera traps only (Table 1), suggesting the mammalian diversity to be a real, rather than methodological phenomenon.

Based on the method used here, McGrew et al. predicted that Mt. Assirik chimpanzees would encounter leopards, mongoose, and bushbuck most often. We hypothesized that Issa and Mt. Assirik would have comparably diverse wildlife communities and thus would encounter sympatric mammals at similar rates. However, when we compared our data to those from Mt. Assirik, despite 21 species that exist at both sites, encounter rates between researchers and wildlife and predicted encounter rates between chimpanzees and sympatriates varied dramatically between sites (Table 2). At Issa, chimpanzees were instead likely to encounter bushbuck, klipspringer, and then baboons most often, as well as other woodland specialists like roan antelope and hartebeest.

That bushbuck and klipspringer are primarily browsers (Codron, Codron, Lee-Thorp, Sponheimer, & de Ruiter, 2005) suggests a non-competitive relationship with chimpanzees. Baboons, however, are a well-described food competitor with chimpanzees (Matsumoto-Oda & Kasagula, 2000) and compete for woodland species such as *Brachsytegia, Parinari,* and *Strychnos,* especially in the dry season (unpublished data). Whereas chimpanzees prefer ripe fruit and baboons are selective generalists, during scramble competition baboons may have the upper hand, being better able to digest unripe fruit far better than the apes (Okecha & Newton-Fisher 2006). Nevertheless, as both species have been documented to prey on small-medium vertebrates (Hausfater, 1976; Ramirez-Amaya, McLester, Stewart, & Piel, 2015), chimpanzees may have an advantage during contest competition, seizing prey from baboons (Hausfater, 1976; Morris & Goodall, 1977). What seems clear is the high expected encounter rates between these two species, especially in woodlands. What remains unclear is what influence they have on each other’s feeding ecology and movement patterns.

Other striking differences between the sites emerged in researcher encounters, and thus predicted chimpanzee encounters with other primates. Issa chimpanzees were predicted to encounter both forest (e.g. red-tailed monkeys) and savanna-dwelling (vervet monkeys) species more frequently than at Mt. Assirik. And whilst McGrew et al. (2014) did not calculate encounter rates with guinea baboons because they were seen multiple times daily near the research camp, at Issa baboons were the second most frequently encountered species after common duikers, and so we can assume that chimpanzee-baboon encounters may be similarly high at each site.

Finally, chimpanzees at Issa were far less likely to encounter large carnivores than at Mt. Assirik, where grasslands likely support larger herds of ungulates (Shorrocks & Bates, 2015). Researcher encounters at Mt. Assirik were higher for all three large carnivores: lion, leopard, and spotted hyena (*Crocuta crotuta*). Leopards were observed only ten times at Issa, compared to 53 at Mt. Assirik. In general, large carnivores - wild dogs (n=5), lions (n=1) and hyenas (0) - were infrequently encountered by Issa researchers and thus highly unlikely to be encountered by chimpanzees.

Issa vs. Mt. Assirik: What explains variation?

It is surprising that few studies go further than either listing sympatric mammalian fauna in chimpanzee-inhabited areas (e.g. Iida et al., 2012) or discussing chimpanzee-carnivore encounters (Boesch, 1991; McLester, Stewart, & Piel, 2016; Newton-Fisher, Notman, & Reynolds, 2002; Stanford et al., 1994; Teelen, 2008). In two open-habitat environments where chimpanzees are studied – Mt. Assirik and Issa valley - we now have comparative efforts and analyses to predict chimpanzee encounters with hetero-specifics. The most likely explanations of inter-site variation in researcher-wildlife encounter rates are the proportions of different vegetation at each site (which determines species abundance) and poaching activity.

Both areas are categorised as mosaic landscapes with minimal gallery forest, but whereas Issa is dominated by miombo woodland, Mt. Assirik has a larger proportion (>25%) of grassland than at Issa (<1%). Grassland species rely on group vigilance to detect stalking predators, and thus typically travel in large herds (Scheel, 1993; Thaker, Vanak, Owen, Ogden, & Slotow, 2010), which are more conspicuous to researchers. Abundance data, which would be useful to compare absolute numbers at each site, are only available from Issa. Piel et al. (2015) used four years of line transect results to show that common duikers were the most abundant mammal, followed by bushbucks and then baboons. No data on actual mammal abundance are available from Mt. Assirik.

Poaching also shapes species composition. Western Tanzania was once home to herds of giraffe, zebra, and eland, amongst other large mammalian species (Kano, 1971). Conversion of habitat to farmland and poaching (Wilfred & MacColl, 2014) have contributed to the extermination of giraffe and reduced zebra, eland, and even buffalo to small herds that travel mostly at night (unpublished data). Removal of these species may open up niches for smaller, medium sized mammals (Keesing & Young, 2014). Most recently, Piel et al. (2015) described poaching to mainly be confined to areas peripheral to the core study area at Issa. Mt. Assirik has also experienced poaching over the years (Pruetz, 2013), but it is unclear what impact poaching had during the late 1970s when these mammal data were collected.

Open-habitat chimpanzees, sympatric fauna, and the fossil record

Isotopic data now firmly put some of the earliest, and most critical hominin species in mosaic habitats (Cerling et al., 2011; White et al., 2009), similar to the vegetation that comprise both Issa and Mt. Assirik. Contemporary data like those from Issa and Mt. Assirik (McGrew et al., 2014) and Issa (Russak, 2014; Current study) provide us an analogue system for hominoid-mammal interaction that could be useful in reconstructing hominin lifeways. For example, by integrating taphonomic and ecological data we can identify biases in bone assemblages, demonstrate that habitat distributions of the major herbivore species are reflected in the bone assemblage, and establish that community structure of a given assemblage reflects that of the source community. In short, there are diverse utilities of high-resolution modern ecological data, especially of areas where great apes live, for paleoecological studies (Behrensmeyer & Miller, 2012; Su & Harrison, 2008).

Moreover, fossils of mammalian species are used to date hominin fossils (DeMenocal, 2004; White, Moore, & Suwa, 1984), inform paleo-habitat characterization (White et al., 2009) and, more indirectly, reconstruct with what species hominins were sharing and/or competing for resources (Andrews, 1996; Hatley & Kappelman, 1980; Kappelman, 1984). Mammalian fossils are also useful in examining hominin evolutionary processes. For example, in Omo (Ethiopia) climate variability during the late Pliocene influenced environmental changes (namely a shift from closed forest to open woodlands) and in turn, the tempo of faunal variability, e.g. changes in ecological dominance of suids, cercipithcids, and bovids (Bobe et al., 2002). These shifts in fauna were paralleled by shifts in hominins: the appearance of *Homo* and disappearance of the gracile australopithecines at ~ 2.5mya (Bobe et al., 2002; Foley, 1993).

References

Andrews, P. (1996). Palaeoecology and hominoid palaeoenvironments. *Biological Reviews*, *71*, 257–300.

Basabose, K., & Yamagiwa, J. (1997). Predation on mammals by chimpanzees in the montane forest of Kahuzi, Zaire. *Primates*, *38*(1), 45–55. http://doi.org/10.1007/BF02385921

Behrensmeyer, A. K., & Miller, J. H. (2012). Building links between ecology and paleontology using taphonomic studies of recent vertebrate communities. In J. Louys (Ed.), *Paleontology in Ecology and Conservation* (pp. 69–91). Berlin, Heidelberg: Springer Verlag. http://doi.org/10.1007/978-3-642-25038-5

Bobe, R., Behrensmeyer, A. K., & Chapman, R. E. (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution*, *42*(4), 475–497. http://doi.org/10.1006/jhev.2001.0535

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, *117*, 220–242.

Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., … Remien, C. H. (2011). Woody cover and hominin environments in the past 6 million years. *Nature*, *476*(7358), 51–6. http://doi.org/10.1038/nature10306

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., & de Ruiter, D. (2005). Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research*, *35*(1), 43–52. http://doi.org/10.5167/uzh-25362

Copeland, S. R. (2009). Potential hominin plant foods in northern Tanzania: semi-arid savannas versus savanna chimpanzee sites. *Journal of Human Evolution*, *57*(4), 365–78. http://doi.org/10.1016/j.jhevol.2009.06.007

DeMenocal, P. B. (2004). African climate change and faunal evolution during the Pliocene Pleistocene. *Earth and Planetary Science Letters*, *220*, 3–24. http://doi.org/10.1016/S0012-821X(04)00003-2

Domínguez-Rodrigo, M. (2014). Is the “Savanna Hypothesis” a dead concept for explaining the emergence of the earliest hominins? *Current Anthropology*, *55*(1), 59–81. http://doi.org/10.1086/674530

Egeland, C. P. (2014). Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Olduvai Basin. *Quaternary International*, *322–323*, 95–106. http://doi.org/10.1016/j.quaint.2013.11.021

Foley, R. (1993). Seasonality of environment and diet. In S. J. Ulijaszek & S. S. Strickland (Eds.), *Seasonality and Human Ecology: 35th Symposum Volume of the Society for the Study of Human Biology* (pp. 83–116). Cambridge, U.K.: Cambridge University Press.

Fragoso, J. M. V., Levi, T., Oliveira, L. F. B., Luzar, J. B., Overman, H., Read, J. M., & Silvius, K. M. (2016). Line transect surveys underdetect terrestrial mammals: Implications for the sustainability of subsistence hunting. *Plos One*, *11*(4), e0152659. http://doi.org/10.1371/journal.pone.0152659

Hatley, T., & Kappelman, J. (1980). Bears, pigs, and Plio- Pleistocene hominids: a case for the exploitation of below- ground food resources. *Human Ecology*, 371–387.

Hausfater, G. (1976). Predatory behaviour of yellow baboons. *Behaviour*, *56*(1), 44–67.

Hinde, R. J., Corti, G. R., Fanning, E., Jenkins, R. K. B., Programme, E., & Monitoring, W. C. (2001). Large mammals in miombo woodland, evergreen forest, and a young teak (Tectona grandis) plantation in the Kilombero Valley, Tanzania. *Journal of African Ecology*, *39*, 318–321.

Iida, E. G., Idani, G., & Ogawa, H. (2012). Mammalian fauna of the miombo forest in the Ugalla area, western Tanzania. *African Study Monographs*, *33*(December), 253–270.

Johnson, C. (2014). *The feeding and movement ecology of yellow baboons (Papio cynocephalus) in a primate rich habitat: the Issa valley of western Tanzania*. Doctoral dissertation. University of Swansea.

Johnson, C., Piel, A. K., Forman, D., Stewart, F. a, & King, A. J. (2015). The ecological determinants of baboon troop movements at local and continental scales. *Movement Ecology*, *3*(1), 14. http://doi.org/10.1186/s40462-015-0040-y

Kalan, A. K., Piel, A. K., Mundry, R., Wittig, R. M., Boesch, C., & Kühl, H. S. (2016). Passive acoustic monitoring reveals group ranging and territory use: a case study of wild chimpanzees (*Pan troglodytes*). *Frontiers in Zoology*, *13:34*, 1–11. http://doi.org/10.1186/s12983-016-0167-8

Kano, T. (1971). The chimpanzees of Filabanga, Western Tanzania. *Primates*, *12*(December), 229–246.

Kappelman, J. (1984). Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoclimatology*, *48*, 171–196.

Keesing, F., & Young, T. P. (2014). Cascading consequences of the loss of large mammals in an African Savanna. *BioScience*, *64*(6), 487–495. http://doi.org/10.1093/biosci/biu059

Kortlandt, A. (1983). Marginal habitats of chimpanzees. *Journal of Human Evolution*, *12*, 231–278.

Leeuwen, E. J. C. Van, Cronin, K. A., Haun, D. B. M., Mundry, R., & Bodamer, M. D. (2012). Neighbouring chimpanzee communities show different preferences in social grooming behaviour. *Proceedings of the Royal Society B*, (August), 4362–4367. http://doi.org/10.1098/rspb.2012.1543

Luncz, L. V, Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology*, *22*(10), 922–6. http://doi.org/10.1016/j.cub.2012.03.031

Matsumoto-Oda, A., & Kasagula, M. B. (2000). Preliminary study of feeding competition between baboons and chimpanzees in the Mahel Mountains National Park, Tanzania. *African Study Monographs*, *21*(December), 147–157.

McGrew, W. C., Baldwin, P. J., Marchant, L. F., Pruetz, J. D., & Tutin, C. E. G. (2014). Chimpanzees (*Pan troglodytes verus*) and their mammalian sympatriates: Mt. Assirik, Niokolo-Koba National Park, Senegal. *Primates*, *55*(4), 525–32. http://doi.org/10.1007/s10329-014-0434-2

McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1981). Chimpanzees in a hot, dry, and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution*, *10*, 227–244.

McLester, E., Stewart, F. A., & Piel, A. K. (2016). Observation of an encounter between African wild dogs (*Lycaon pictus*) and a chimpanzee (*Pan troglodytes* *schweinfurthii*) in the Issa Valley, Tanzania. *African Primates*, *11*(1), 27–36.

Moore, J. (1992). “Savanna” Chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in Primatology, Vol 1, Human Origins* (pp. 99–118). University of Tokyo Press.

Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 275–292). Cambridge: Cambridge University Press.

Morris, K., & Goodall, J. (1977). Competition for meat between chimpanzees and baboons of Gombe National Park. *Folia Primatologica*, *28*, 109–121.

Newton-Fisher, N. E., Notman, H., & Reynolds, V. (2002). Hunting of mammalian prey by Budongo forest chimpanzees. *Folia Primatologica*, *73*(5), 281–283. http://doi.org/10.1159/000067454

Okecha, A. A., & Newton-fisher, N. E. (2006). The diet of olive baboons (*Papio anubis*) in the Budongo Forest. In N. E. Newton-Fisher, H. Notman, V. Reynolds, & J. D. Paterson (Eds.), *Primates of Western Uganda* (pp. 61–73). Nwe York: Springer. http://doi.org/10.1007/978-0-387-33505-6_4

Piel, A. K., Lenoel, A., Johnson, C., & Stewart, F. A. (2015). Deterring poaching in western Tanzania: The presence of wildlife researchers. *Global Ecology and Conservation*, *3*, 188–199.

Piel, A. K., Strampelli, P., Greathead, E., Hernandez-aguilar, R. A., Moore, J., & Stewart, F. A. (2017). The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western Tanzania. *Journal of Human Evolution*, *112*, 57–69. http://doi.org/10.1016/j.jhevol.2017.08.016

Pruetz, J. D. (2013). Studying Apes in a Human Landscape. In K. Strier (Ed.), *Primate Ethnographies* (pp. 228–237). Pearson Publishers.

Pruetz, J. D., & LaDuke, T. C. (2010). Reaction to fire by savanna chimpanzees (pan troglodytes verus) at fongoli, senegal: Conceptualization of “fire behavior” and the case for a chimpanzee model. *American Journal of Physical Anthropology*, *141*(4), 646–650. http://doi.org/10.1002/ajpa.21245

Ramirez-Amaya, S., McLester, E., Stewart, F. A., & Piel, A. K. (2015). Savanna chimpanzees (*Pan troglodytes schweinfurthii*) consume and share blue duiker (Philantomba monticola) meat in the Issa Valley, Ugalla western Tanzania. *Pan Africa News*, *22*(2).

Rudicell, R. S., Piel, A. K., Stewart, F., Moore, D. L., Learn, G. H., Li, Y., … Hahn, B. H. (2011). High prevalence of simian immunodeficiency virus infection in a community of savanna chimpanzees. *Journal of Virology*, *85*(19), 9918–9928. http://doi.org/10.1128/JVI.05475-11

Russak, S. (2013). Ecological Role of Dry-Habitat Chimpanzees (*Pan troglodytes schweinfurthii*). Doctoral dissertation. Arizona State University.

Russak, S. M. (2014). Using patch focals to study unhabituated dry-habitat chimpanzees (*Pan troglodytes schweinfurthii)* and sympatric fauna at Issa, Ugalla, Tanzania. *International Journal of Primatology*, *35*(6), 1202–1221. http://doi.org/10.1007/s10764-014-9803-3

Russak, S. M., & McGrew, W. C. (2008). Chimpanzees as fauna: Comparisons of sympatric large mammals across long-term study sites. *American Journal of Primatology*, *70*(4), 402–409. http://doi.org/10.1002/ajp.20506

Scheel, D. (1993). Profitability, encounter rates, and prey choice of African lions. *Behavioral Ecology*, *4*, 90–97.

Shorrocks, B., & Bates, W. (2015). *The Biology of African Savannas* (Second). Oxford, UK: Oxford University Press.

Smits, C. M. M. (1986). Diet composition and habitat use of the West African bushbuck *Tragelaphus scriptus scriptus* (Pallas, 1776) during the first half of the dry season. *South African Journal of Zoology*, *21*(1), 89–94. http://doi.org/10.1080/02541858.1986.11447964

Stanford, C. B., Wallis, J., Matama, H., & Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. *American Journal of Physical Anthropology*, *94*(2), 213–28. http://doi.org/10.1002/ajpa.1330940206

Stewart, F. A., Piel, A. K., & McGrew, W. C. (2011). Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, *61*(4), 388–395. http://doi.org/10.1016/j.jhevol.2011.05.005

Su, D. F., & Harrison, T. (2008). Ecological implications of the relative rarity of fossil hominins at Laetoli. *Journal of Human Evolution*, *55*(4), 672–681. http://doi.org/10.1016/j.jhevol.2008.07.003

Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. *Primates*, *148*, 103–148.

Teelen, S. (2008). Influence of chimpanzee predation on the red colobus population at Ngogo, Kibale National Park, Uganda. *Primates*, *49*(1), 41–9. http://doi.org/10.1007/s10329-007-0062-1

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., & Slotow, R. (2010). Group dynamics of zebra and wildebeest in a woodland savanna: Effects of predation risk and habitat density. *PLoS ONE*, *5*(9), 1–6. http://doi.org/10.1371/journal.pone.0012758

Treves, A., & Palmqvist, P. (2007). Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 Ma). In S. Gursky & K. A. I. Nekaris (Eds.), *Primate Anti-Predator Strategies* (pp. 355–381). Springer, U.S. http://doi.org/10.1007/978-0-387-34810-0_17

Uehara, S. (1997). Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*, *38*(2), 193–214. http://doi.org/10.1007/BF02382009

van Leeuwen, K., Hill, R., Newotn, A., & Korstjens, A. (2017). *Chimpanzee landscape use in different envirionments: an Indiivdually based modelling approach.* Primate Society of Great Britain. London, UK.

White, T. D., Ambrose, S. H., Suwa, G., Su, D. F., Degusta, D., Bernot, R. L., … Vrba, E. (2009). Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science*, *326*, 87–93. http://doi.org/10.1126/science.1175822

White, T. D., Moore, R. V, & Suwa, G. (1984). Hadar biostratigraphy and hominid evolution. *Journal of Vertebrate Paleontology*, *4*, 575–583. http://doi.org/10.1080/02724634.1984.10012033

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*, 15–18.

Wilfred, P., & MacColl, A. (2014). The pattern of poaching signs in Ugalla Game Reserve, western Tanzania. *African Journal of Ecology*, *52*(4), 543–551.

http://doi.org/10.1111/aje.12161

Wrangham, R. W., & van Zinnicq Bergmann Riss, E. (1990). Rates of predation on mammals by gombe chimpanzees, 1972-1975. *Primates*, *31*(2), 157–170. http://doi.org/10.1007/BF02380938

Table 1 - Species list from Russak (2014) with comparative data on species presence at Mt. Assirik (Senegal) and in the current study

✓ = direct evidence only
☑ = indirect evidence only
✓ (d) = Issa hosts the same genus but a different species
C = known from camera trap only

Common	Latin	McGrew et al. 2014 (Assirik)	Russak (2013)	Current
Artiodactyla				
Lichtenstein hartebeest	*Alcelaphus lichtensteinii*	✓(d)	✓	✓
Roan antelope	*Hippotragus equinus*	✓	✓	✓
Common waterbuck	*Kobus ellipsiprymnus*	-	✓	✓
Klipspringer	*Oreotragus oreotragus*	-	✓	✓
Warthog	*Phacochoerus africanus*	✓ (d)	✓	✓
Blue duiker	*Philantomba larvatus*	✓ (d)	✓	✓
Bushpig	*Potamochoerus larvatus*	✓ (d)	✓	✓
Reedbuck	*Redunca redunca*	-	✓	✓
Common duiker	*Sylvicapra grimmia*	✓	✓	✓
African buffalo	*Syncerus caffer*	✓	☑	✓
Derby's eland	*Taurotragus oryx*	✓	☑	✓
Bushbuck	*Tragelphus scriptus*	✓	✓	✓
Carnivora				
African clawless otter	*Aonyx capensis*	-	☑	☑
Bushy-tailed mongoose	*Bdeogale crassicauda*	-	☑	☑[c]
Black backed Jackal	*Canis mesomeles*	✓ (d)	✓	✓

Africa civet	*Civettictis civetta*	✓	☑	✓
Spotted hyena	*Crocuta crocuta*	✓	☑	✓
Serval	*Felis serval*	-	☑	☑[c]
African wild cat	*Felis sylvestris*	✓	☑	✓
Common genet*	*Genetta genetta*	✓ (d)	☑	☑
Dwarf mongoose	*Helogale parvula*	✓ (d)	✓	☑[c]
Egyptian mongoose	*Herpestes ichneumon*	✓	✓	
Slender mongoose	*Herpestes sanguinea*	✓	☑	
East African honey badger	*Mellivoria capensis*	✓	☑	✓
Lion	*Panthera leo*	✓	☑	✓
Leopard	*Panthera pardus*	✓	✓	✓
Hyracoidea				
Tree hyrax	*Dendrohyrax arboreus*	-	✓	☑
Yellow spotted/bush hyrax	*Heterohyrax brucei*	-	☑	✓
Pholidota				
Ground pangolin	*Smutsia temminckii*	-	☑	✓
Primates				
Vervet monkey	*Chlorocebus*	✓ (d)	✓	✓
Red-tailed monkey	*Cercopithecus ascanius*	-	✓	✓
Blue monkey	*Cercopithecus mitis*	-	✓	✓
Senegal galago	*Galago senegalensis*	✓	✓	✓
Eastern chimpanzee	*Pan troglodytes schweinfurthii*	✓	✓	✓
Yellow baboon	*Papio cynocephalus*	✓ (d)	✓	✓

Red colobus			✓	✓
Rodentia				
Sun squirrel	*Heliosciurus sp.*		✓	✓
Porcupine	*Hystrix africaeaustralis*		✓	✓
Smith's bush squirrel	*Paraxerus cepapi*		✓	
Giant forest squirrel	*Protoxerus stangeri*		✓	
Tubulidentata				
Ant-bear (aardvark)	*Orycteropus afer*		☑	
TOTAL SPECIES PRESENT		24	41	36

* listed by Russak as common genet, but is likely large spotted genet (*Genetta tigrina*)

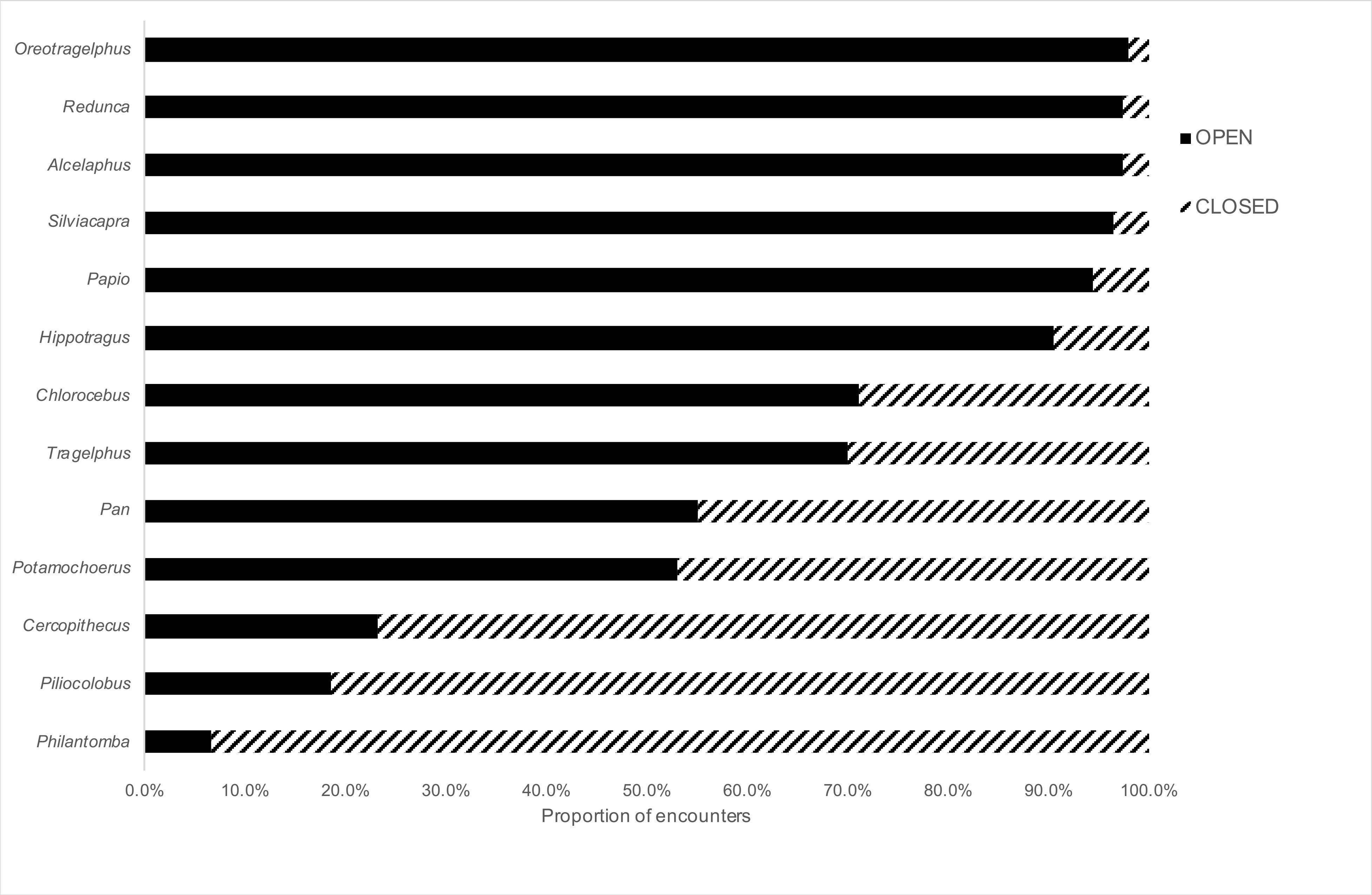
Oreotragelphus
Redunca
Alcelaphus
Silviacapra
Papio
Hippotragus
Chlorocebus
Tragelphus
Pan
Potamochoerus
Cercopithecus
Piliocolobus
Philantomba
■ OPEN
▨ CLOSED
0.0%
10.0%
20.0%
30.0%
40.0%
50.0%
60.0%
70.0%
80.0%
90.0%
100.0%
Proportion of encounters

Figure 2

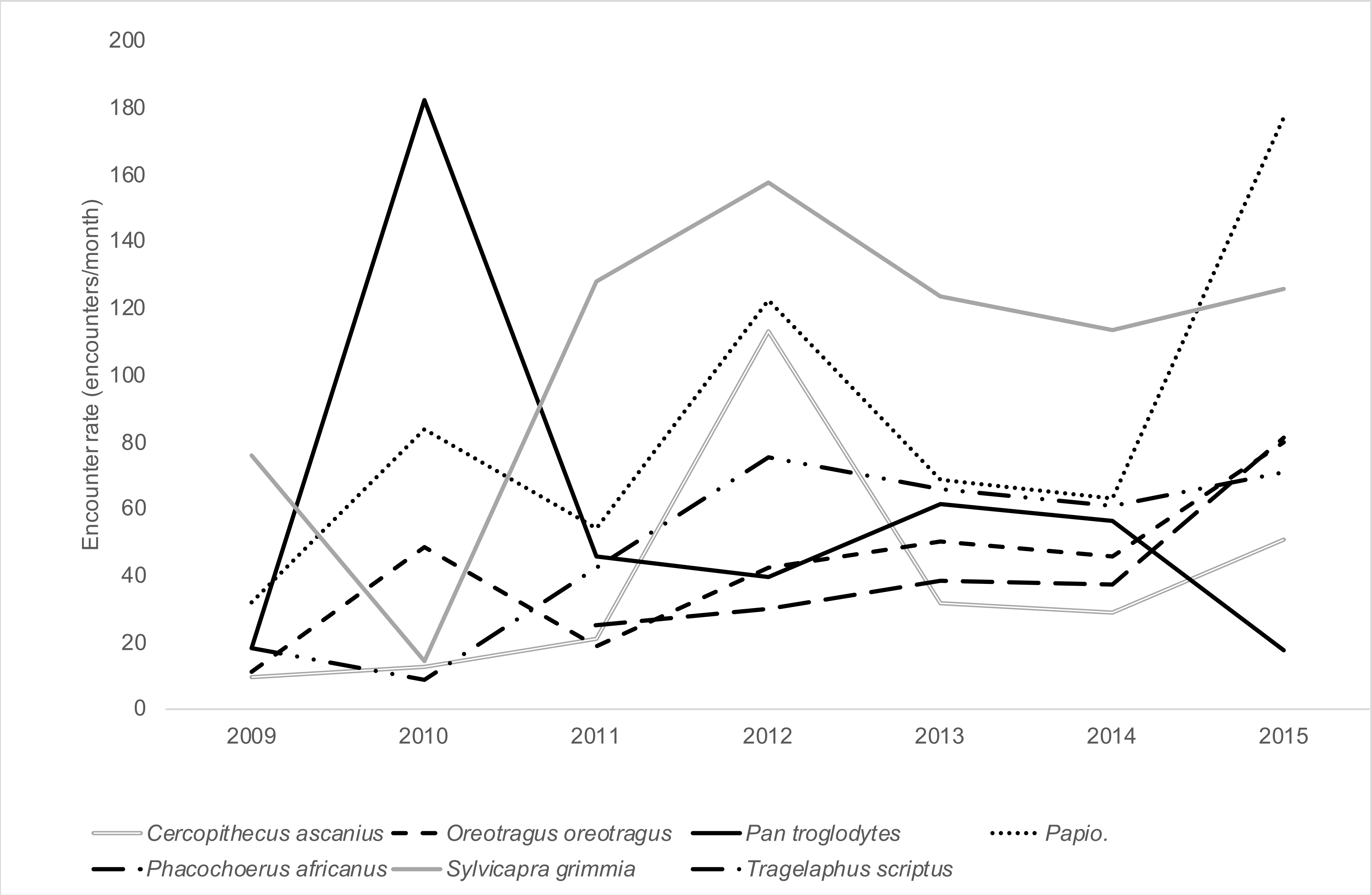
Encounter rate (encounters/month)
0
20
40
60
80
100
120
140
160
180
200
2009
2010
2011
2012
2013
2014
2015
Cercopithecus ascanius
Oreotragus oreotragus
Pan troglodytes
Papio.
Phacochoerus africanus
Sylvicapra grimmia
Tragelaphus scriptus

Figure 3