

McLester, E, Stewart, FA and Piel, AK

Observation of an Encounter between African Wild Dogs (*Lycaon pictus*) and a Chimpanzee (*Pan troglodytes schweinfurthii*) in the Issa Valley, Tanzania

<http://researchonline.ljmu.ac.uk/id/eprint/4029/>

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

McLester, E, Stewart, FA and Piel, AK (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). pp. 27-36. ISSN 1093-8966

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

Observation of an Encounter between African Wild Dogs (*Lycaon pictus*) and a Chimpanzee (*Pan troglodytes schweinfurthii*) in the Issa Valley, Tanzania

Edward McLester^{1,2}, Fiona A. Stewart^{1,3} and Alexander K. Piel^{1,2}

¹Ugalla Primate Project, Uvinza, Tanzania; ²School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK; ³Department of Archaeology, University of Cambridge, Cambridge, UK

Abstract: There has been considerable discussion of chimpanzees (*Pan troglodytes*) as predators, most commonly of red colobus monkeys (*Procolobus* spp.). Far more infrequent are published descriptions of chimpanzees as prey. The paucity of direct observations of chimpanzee-predator encounters is an obstacle in situating chimpanzees in both predator and prey roles. For the first time, we describe an observation of an encounter between African wild dogs (*Lycaon pictus*) and a chimpanzee in the Issa Valley, Tanzania, one of the driest and most open chimpanzee habitats. Whilst the initiation of the encounter was missed, here we nonetheless interpret the data that we did record. Our observations of behavior in both parties suggest the possibility of an investigatory rather than predatory encounter on the part of the wild dogs.

Key words: wild dog, chimpanzee, *Pan troglodytes*, predation, carnivore, prey

INTRODUCTION

The role of predation as a selection pressure on great ape evolution remains unclear; however, this can in part be attributed to an absence of records describing primate-predator interactions (Cheney & Wrangham 1987). Historically, researchers have identified four potential mammalian predators of wild chimpanzees (*Pan troglodytes*): lions (*Panthera leo*), leopards (*P. pardus*), spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) (Tutin *et al.* 1981; Boesch 1991; Stewart & Pruett 2013). Outside of Zuberbühler & Jenny's (2002) study of leopard predation in the Taï Forest, Côte d'Ivoire, none of these carnivore species have been studied in detail in areas of sympatry with chimpanzees. Consequently, substantiation of chimpanzee predators, and in turn our understanding of chimpanzee antipredator strategies, is derived

from anecdotal observations and playback studies (Crockford *et al.* 2012).

Reports of direct observation of carnivore predation on chimpanzees are rare in the literature (Table 1). First, most chimpanzees live in dense, tropical forests, which lack many of the large carnivore species that live in savanna mosaics (eg., lion, cheetah – Mills & Funston 2011). Second, the only fully habituated savanna-dwelling chimpanzee community, Fongoli, in Senegal, lives in an area where almost all of the natural predators no longer range due to human population expansion (Stewart & Pruett 2013). Finally, given the selective pressure on anti-predatory behaviors, actual predation events are themselves rare, even in the most pristine landscapes. Apes generally rely more on predator avoidance and vigilance than defensive counter-

Table 1 Summary of evidence describing carnivore interactions on *Pan troglodytes* (modified from Klailova *et al.* 2012).

Predator	Country	Population	Direct Evidence	Indirect Evidence	Notes	Source
Leopard (<i>Panthera pardus</i>)	Senegal	Mt. Assirik, Niokolo Koba National Park	X		Chimpanzees chased out of tree	Gandini & Baldwin 1978
				X	Multiple instances of chimpanzees vocalizing, hiding or fleeing in response to detection by leopard	Tutin <i>et al.</i> 1981
	Tanzania	Mahale Mountains National Park		X	Chimpanzees raided leopard den, killed cub	Hiraiwa-Hasegawa <i>et al.</i> 1986
				X	Leopard feces and prints near chimpanzee corpse	Nakazawa <i>et al.</i> 2013
				X	Chimpanzees threw branches at leopard	Nishida 1968
				X	Chimpanzees gave alarm vocalizations in response to leopard vocalizations	Kutsukake 2006
		Gombe National Park		X	Chimpanzee infant in tree vocalized at leopard below	van Lawick-Goodall 1968
				X	No reaction in response to leopard vocalizing in vicinity	“
				X	Chimpanzees threw branch at leopard	“
				X	Chimpanzees vocalized and mobbed leopard	Pierce 2009
		Kasakati Basin		X	Chimpanzees shook branches and vocalized in direction of leopard in vicinity	Izawa & Itani 1966
	Ivory Coast	Tai National Park	X		Multiple interactions, including chimpanzees mobbing and chasing leopards; 39% of chimpanzee mortalities attributed to leopard predation	Boesch 1991
			X		Dead chimpanzee juveniles scavenged by leopard; in some cases, leopards fled in response to chimpanzee drumming and vocalizations	Zuberbühler & Jenny 2002
	Gabon	Lopé National Park		X	Leopard feces contained chimpanzee remains	Henschel <i>et al.</i> 2005
		Petit Loango National Park		X	Leopard prints and feces containing chimpanzee remain found near a chimpanzee corpse	Furuichi 2000
	DRC	Idambo	X		Female chimpanzees attacked and infant killed	Rahm 1967
		Ituri Forest		X	Leopard feces contained chimpanzee remains	Hart <i>et al.</i> 1996
	Republic of Congo	Mbeli Bai, Nouabalé-Ndoki National Park		X	Leopard feces contained chimpanzee remains	Ososky 1998

Table 1 Summary of evidence describing carnivore interactions on *Pan troglodytes* (modified from Klailova *et al.* 2012) (continued).

Predator	Country	Population	Direct Evidence	Indirect Evidence	Notes	Source
Lion (<i>Panthera leo</i>)	Senegal	Mt. Assirik, Niokolo Koba National Park		X	Multiple instances of chimpanzees vocalizing, hiding or showing no reaction in response to detection by lion	Tutin <i>et al.</i> 1981
	Tanzania	Kigoma		X	Chimpanzee threw branches until lion forced to flee	M. Mbrisho (pers. obs.) in Goodall 1986
		Mahale Mountains National Park		X	Chimpanzees mobbed an adult lioness and killed cub	Hiraiwa-Hasegawa <i>et al.</i> 1986
				X	Lion feces contained chimpanzee remains (bones, hair, teeth)	Tsukahara 1993
				X	Lion feces contained chimpanzee remains	Inagaki & Tsukahara 1993
Hyena (<i>Crocuta crocuta</i>)		Ugalla		X	Chimpanzees fled up trees and vocalized in response to hiding lion	Kano 1972; Itani 1979
	Senegal	Mt. Assirik, Niokolo Koba National Park		X	No reaction	Tutin <i>et al.</i> 1981
	Senegal	Mt. Assirik, Niokolo Koba National Park		X	Chimpanzees vocalized in response to wild dog vocalizations and presence	Tutin <i>et al.</i> 1981
	Tanzania	Mahale Mountains National Park		X	Chimpanzees first vocalized and retreated in response to discovering python, then tracked and waited for python after it left area	Zamma 2011
		Gombe National Park		X	Chimpanzees vocalized and shook branches in response to dying python	van Lawick-Goodall 1968
Night Adder (<i>Causus rhombeatus</i>)	Tanzania	Gombe National Park		X	Chimpanzees hit night adder until it escaped, after which chimpanzees did not follow	van Lawick-Goodall 1968
Nile Monitor (<i>Varanus niloticus</i>)	Tanzania	Gombe National Park		X	Multiple instances of chimpanzees chasing, once throwing rocks at, and once showing no reaction in response to nearby monitor lizards	van Lawick-Goodall 1968

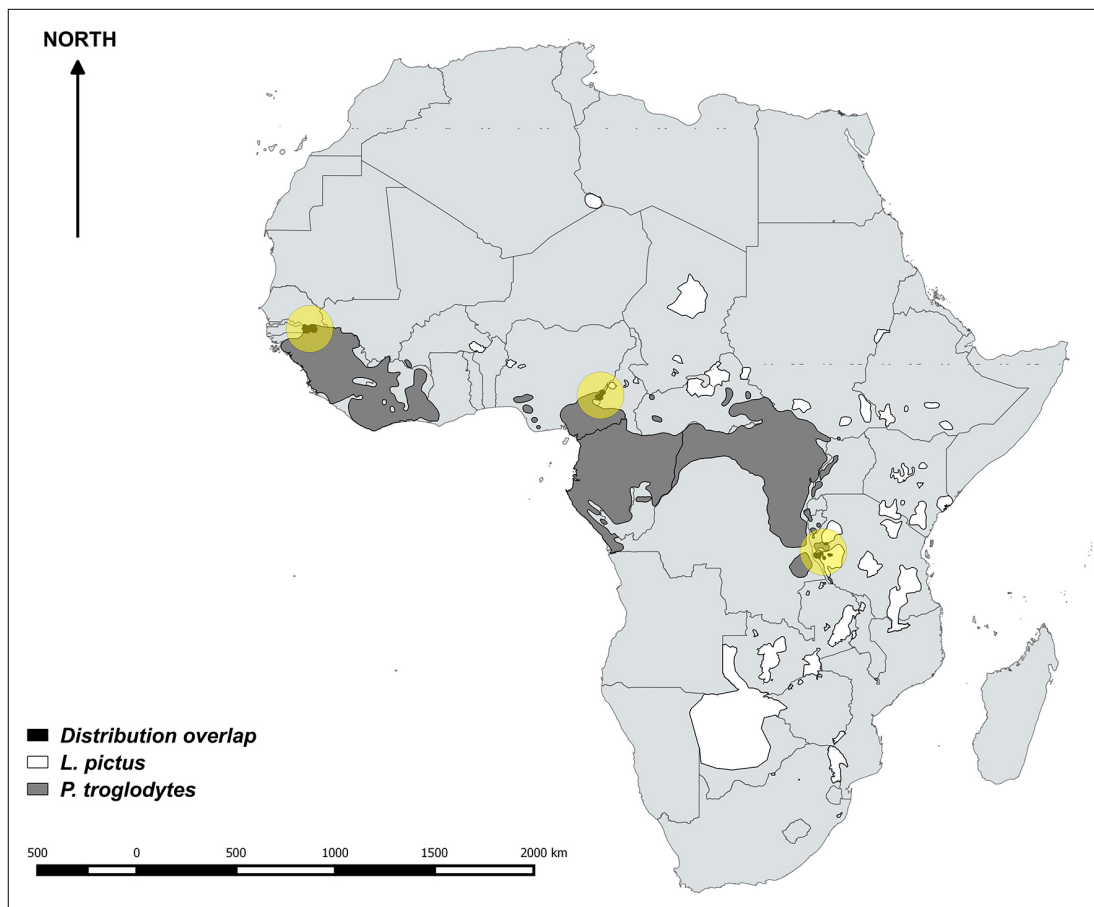


Figure 1. *L. pictus* and *P. troglodytes* ranges across sub-Saharan Africa (Oates *et al.* 2008; Woodroffe & Sillero-Zubiri 2015). Areas of range overlap are indicated by circles.

attacking (Treves & Palmqvist 2007). For example, chimpanzees produce alarm calls (“waa barks” - Schel *et al.* 2013) in response to terrestrial predators and adjust their sleeping behavior to predator presence, nesting higher in the canopy and on more peripheral branches when they co-exist with large carnivores (Pruetz *et al.* 2008; Stewart & Pruetz 2013).

Indirect evidence of carnivore predation on apes and especially chimpanzees is more common than direct evidence, yet still infrequent (Table 1). Of the four mammalian species identified as chimpanzee predators, only six cases have been inferred for lion predation, none of which involved direct observation. Numerous reports have described leopards as a primary threat to wild chimpanzees, but only four direct encounters have been described. Tutin *et al.* (1981) observed the sole chimpanzee-hyena encounter, in which chimpanzees in Mt. Assirik (Senegal) did not exhibit any anti-predatory or unusual behavior in response to wild spotted hyenas. Tutin *et al.* (1981) also briefly recorded

an encounter between wild dogs and a group of chimpanzees at the same site; however, only limited details were provided with no reference to the behavior of either party except for the vocalizations issued by the chimpanzees.

Aside from the single interaction reported in brief by Tutin *et al.* (1981), to date there have been no prior observations of chimpanzees encountering African wild dogs. Wild dogs have both extremely large home ranges (mean = 537km², range: 357-930km² - Mills & Gorman 1997) and live at very low densities (16.7 individuals per 1000km² - Maddock & Mills 1994), a similar pattern to savanna chimpanzees (reviewed in Moyer *et al.* 2006). At the Issa Valley in Tanzania, reports on chimpanzee and sympatric wildlife date to the 1950s (Kano 1971, 1972), and yet we describe here only the fourth researcher-encounter with wild dogs. Despite both species being widely distributed across Africa, current chimpanzee and wild dog ranges overlap in only three areas (Figure 1). Such a small degree of overlap also existed in historic distributions, largely

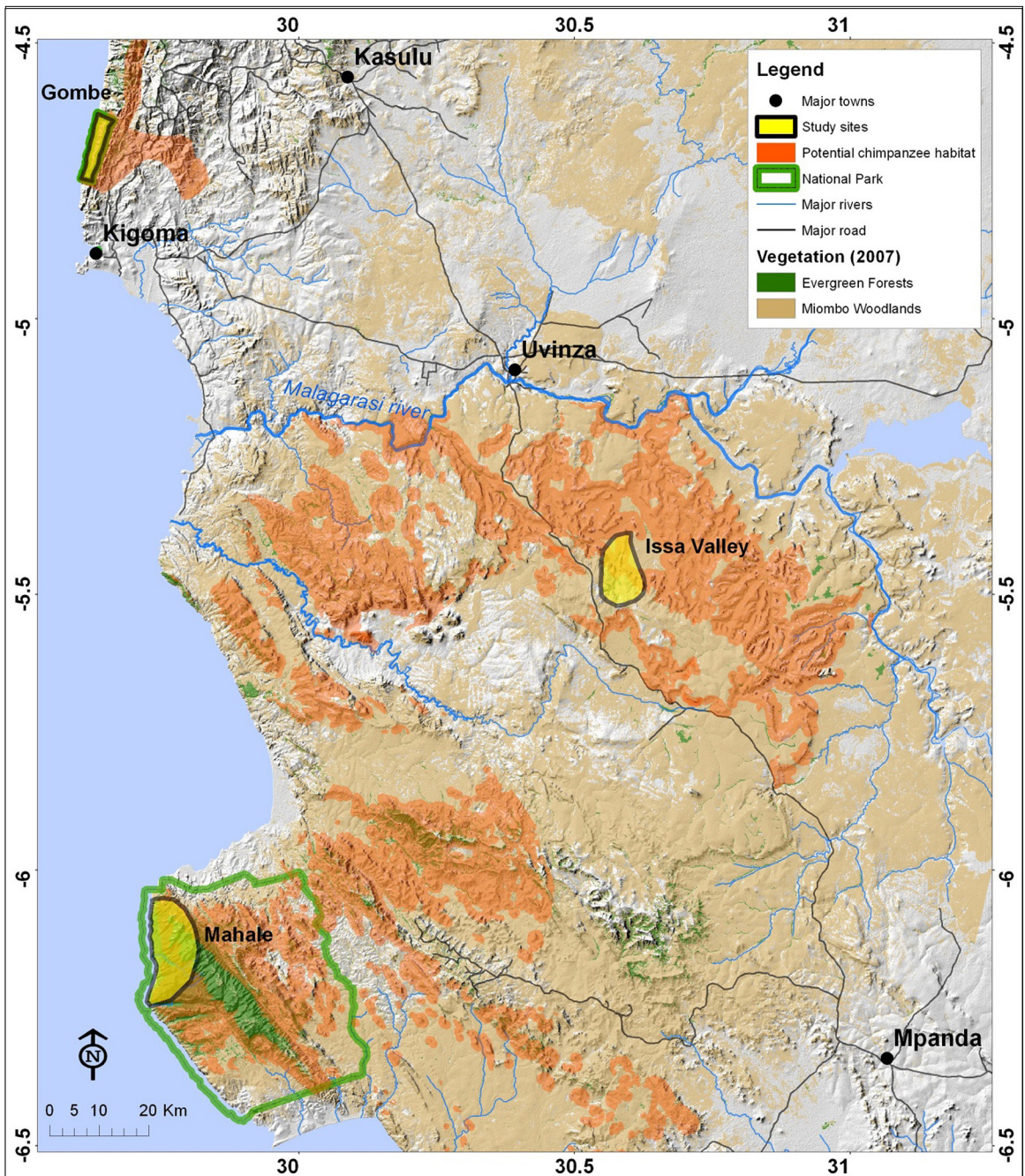


Figure 2. Map of western Tanzania, indicating location of Issa Valley study site in relation to Gombe and Mahale Mountains National Parks. Vegetation index shows woodland and forest cover; predicted chimpanzee distribution shows suitable nesting habitat (Pintea 2007).

due to the restriction of wild dog populations to dry, savanna landscapes (Creel & Creel 1998; Oates *et al.* 2008). Furthermore, given their population densities, it is extremely unlikely that these two species encounter each other frequently. Here, we report on only the second observation of such an encounter.

METHODS

The Issa Valley research station in western Tanzania is an “open area” with no formal protection status, situated in the north of the Greater Mahale Ecosystem (Figure 2). The entire region is characterized as a savanna-mosaic, with deep valleys



Figure 3. Adult male chimpanzee feeding on *Brachystegia spiciformis* in miombo woodland in the Issa Valley. Photograph by E. McLester.

containing evergreen, riverine forest and separated by steep slopes and expansive, flat plateaus of miombo (*Brachystegia* and *Julbernardia*) woodland, rocky outcrops and grassland swamps (Piel *et al.* 2015). From 2009–2014, annual rainfall averaged 1240mm and temperatures ranged from 11–35°C (Piel *et al.* 2015).

Ugalla chimpanzees were first studied by Kano over a half-century ago (Kano 1971, 1972), with brief surveys conducted subsequently (Nishida 1989), and a project ongoing in Nguye, south of Uvinza (Ogawa *et al.* 2007; Iida *et al.* 2012; Yoshikawa & Ogawa 2015). Issa Valley chimpanzees (Figure 3) were first studied in 2001 by Hernandez-Aguilar (2009) for two years, and since 2008 have been under continuous study, with habituation efforts beginning in 2012. As of December 2015, fourteen chimpanzees were individually recognizable to researchers, and genetic analyses suggested a single community of at least 67 individuals (Rudicell *et al.* 2011), which may range over 150km² based on population density (0.25 individuals/km² - Piel *et al.* 2015). In addition to chimpanzees, the region has a rich faunal community, including eight species of primate and four species of large carnivores

(hyena, leopard, lion, and wild dog). Although there are no permanent settlements in the study area, illegal logging, poaching, and herding do account for human traffic throughout the region (Piel *et al.* 2015).

At least one two-person research team tracked chimpanzee parties daily by listening for loud calls and monitoring important feeding trees, as well as conducting reconnaissance walks around the study area. In collaboration with the Pan Africa Programme of the Max Plank Institute for Evolutionary Primatology, Leipzig (Germany), we also deployed twenty-six motion-triggered cameras (Bushnell HD) on known wildlife paths, with the aim of monitoring biodiversity, especially chimpanzees and cryptic species.

RESULTS

At 14:04 on 7 July 2015 EM and a field assistant heard two simultaneous vocalizations – the first chimpanzee “waa barks” (Schel *et al.* 2013), the other dog barks – approximately 25 meters away from a clearing in a patch of evergreen forest, bordered

by a river on one side and a woodland slope on the other side. On approaching the sounds, we observed an adult chimpanzee (sex unknown) approximately 20 meters away and 15 meters high in a tree (*Vitex doniana*) and a pack of nine wild dogs moving around the base of the tree, looking up and barking at the chimpanzee. We never observed more than nine dogs at a single time during the encounter.

For over a minute, both the chimpanzee and dogs barked continuously. Whilst issuing these vocalizations, the chimpanzee jumped up and down, and paced back and forth about ten meters along a single branch, raising and lowering its arms in a rapid motion. It was not observed whether the hair of the chimpanzee was erect. Eventually, the chimpanzee's vocalizations became more regular, being produced approximately every two minutes. The dogs in our view fixed their attention on the chimpanzee, tracking it from the ground as the chimpanzee continued to pace on the branch. As bark and growl vocalizations continued to be heard, the dense undergrowth and rapid movement of the dogs prevented us from identifying whether all dogs in the party were vocalizing.

After approximately six minutes, four dogs looked at and began to approach us, stopping about 20 meters from us. These dogs, moving toward us in stagger, eventually reached about 15 meters from us. The dogs looked directly at us, but remained silent. They appeared to be investigating us, and did not adopt a stalking posture (see Estes & Goddard 1967). For example, the ears of each individual remained clearly upright versus flattened down against the head. This shift in attention lasted almost three minutes.

After approximately eight minutes without vocalizing, the chimpanzee descended in the tree to about ten meters from the ground, and out of our sight. We were unable to see its position. At this point, the activity of all of the dogs' activity changed, resulting in more dog vocalizations and movement of the entire pack toward the last location of the chimpanzee (and, consequently, out of our sight). As we attempted to gain a better view, we continued to hear dog vocalizations approximately 30 meters away for a further minute, but we could see neither pack members nor the chimpanzee. When we attempted to follow both parties at approximately 14:13, we saw a single wild dog moving out of the forest and into the woodland approximately 20-30 meters away from the encounter site. We did not see or hear the dogs again.

On 21 June, two weeks after the encounter, two sequential videos on the same camera trap



Figure 4. Image of a wild dog captured on a motion triggered camera in the Issaa Valley on 21 August, 2015. Photograph courtesy UPP/MPI-EVA.

captured wild dogs (Figure 4; see supplementary video¹), including one of dogs chasing a blue duiker (*Philantomba monticola*). This is the first camera encounter with wild dogs in five years of monitoring wildlife with 20-25 motion-triggered cameras (>20,000 photos and videos). The camera was located approximately 1.61km from the wild dog encounter described above. The spatiotemporal information of each encounter, combined with what we know of wild dog ranging behavior (see below), means it is extremely likely these observations represent the same pack.

DISCUSSION

Whereas numerous characteristics ultimately determine prey preference, a comparison of weight preference, for example, in fourteen wild dog populations by Hayward *et al.* (2006) found that wild dogs prefer animals between 16-32kg and 120-140kg (Hayward *et al.* 2006). The mean weight of small adult and juvenile chimpanzees (males: 28-56kg; females: 20-46kg - Foley *et al.* 2014) suggests that chimpanzees would fit wild dog prey preferences; however, prey of this smaller size would probably only be targeted opportunistically or during times of food scarcity (Schaller 1972). Numerous other species found in the study area, including common (*Sylvicapra grimmia*) and blue (*P. monticola*) duikers, klipspringers (*Oreotragus oreotragus*), and roan antelope (*Hippotragus equinus*), provide wild dogs with targets that are more vulnerable

¹ Supplementary video may be viewed at: <https://www.youtube.com/watch?v=IP1gDqnjw50>.

to exhaustion after a sustained chase (Taylor *et al.* 1971), versus those that can escape into the canopy like chimpanzees and other primates. Arboreal prey provide a different stimulus to prey fleeing along the ground and are less likely to elicit a chase reflex in wild dogs, which is critical to prey selection (Estes & Goddard 1967).

Our observation suggests the possibility of investigatory behavior by the dogs. The wild dogs produced alarm barks, indicating alertness (Estes & Goddard 1967), rather than the “twittering” typically issued during a hunt. The chimpanzee also issued alarm calls and only attempted to move away from the wild dogs at least eight minutes into the encounter, despite access to the tree canopy throughout. This is consistent with the use of alarm calls as a deterrent in primates (Zuberbühler *et al.* 1999). On the part of the chimpanzee, the agitation seen suggests aversion or threatening behavior toward the wild dogs rather than curiosity. Curiosity typically involves soft “huu” vocalizations and persistent observation without agitation (Schel *et al.* 2013).

The behavior exhibited by the dogs toward the research team (curiosity) can also not be compared directly with their behavior toward the chimpanzee (excitement). This may be because the density of chimpanzees in the area and the large range of the wild dogs has resulted in the dogs being more familiar with chimpanzees than with humans. Given the presence of poachers and herders in the area who are known to react antagonistically to predators (AKP personal observation), we suspect that any previous wild dog encounters with humans would likely have been persecution and, therefore, our quiet and motionless presence was probably novel for them. This behavior from the dogs is consistent with what has been described previously for wild dog investigation of sympatric, non-prey species (Darnell *et al.* 2014).

Previous observations of wild dogs in the Issa Valley study area are limited. Aside from the sole camera encounter following this interaction, Hernandez-Aguilar (2006) observed indirect evidence of wild dogs approximately every three months, with two direct observations in 21 months. Likewise, Stewart & Pruetz (2013) observed wild dogs only once in twelve months. The consistently low number of wild dog observations over a ten-year period at Issa suggests that wild dog presence, and in turn wild dog-chimpanzee encounters, do not occur frequently enough for wild dogs to have played a significant role on chimpanzee anti-predatory behavioral evolution. Relationships

established between other predators (e.g., leopards – Zuberbühler & Jenny 2002) and chimpanzees indicate that predation from African wild dogs is similarly unlikely to have acted as a significant selection pressure. Even when these species do encounter each other, the circumstances suiting opportunistic predation – such as in times of food scarcity or when encountering an ill, old, or weak chimpanzee – are limited and depend on both an appropriate trigger that will provoke a chase reflex, and the prospect of the prey being caught through pursuit; however, we are confident that in encounters with such suitable conditions wild dogs would be capable of predating chimpanzees.

Savanna chimpanzees are known to exhibit behaviors not observed in forest-dwelling populations (e.g., using tools to hunt bushbabies – Pruetz & Bertolani 2007), suggesting that behavior in predator-ape interactions is also likely different given such contrasting environments. Although we cannot conclude from our observation that African wild dogs actively hunt chimpanzees, our description provides the first direct evidence of the behavior of both predator and potential prey in a wild dog-ape encounter.

ACKNOWLEDGMENTS

We thank the Tanzanian Wildlife Research Institute (TAWIRI) and the Commission for Science and Technology (COSTECH) for permission to conduct research in the Issa Valley, and to the UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA) for support to the Ugalla Primate Project. The Max Plank Institute for Evolutionary Anthropology, Leipzig, provided the camera used in this study and also partial financial support. We thank Mlela Juma for helping to record and recount events and Adrian Treves and three anonymous reviewers for providing extremely helpful feedback on an earlier version of this manuscript.

LITERATURE CITED

- Boesch, C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117: 220–242.
- Cheney, D.L. & R.W. Wrangham. 1987. Predation. In *Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, T.T. Struhsaker, eds. University of Chicago Press, Chicago. Pp. 227–239.

- Creel, S. & N. Creel. 1998. Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Animal Conservation* 1: 1–9.
- Crockford, C., R. M. Wittig, R. Mundry & K. Zuberbühler. 2012. Wild chimpanzees inform ignorant group members of danger. *Current Biology* 22: 142–146.
- Darnell, A.M., J.A. Graf, M.J. Somers, R. Slotow & M. Szykman Gunther. 2014. Space use of African wild dogs in relation to other large carnivores. *PLoS One* 9:e98846.
- Estes, R.D. & J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. *Journal of Wildlife Management* 31: 52–70.
- Foley, C., L. Foley, A. Lobora, D. De Luca, M. Msuha, T. Davenport, S. Durant. 2014. *A field guide to the larger mammals of Tanzania*. Princeton University Press, Princeton.
- Furuichi, T. 2000. Possible case of predation on a chimpanzee by a leopard in the Petit Loango Reserve, Gabon. *Pan Africa News* 7: 21–23.
- Gandini, G. & P.J. Baldwin. 1978. An encounter between chimpanzees and a leopard in Senegal. *Carnivore* 1: 107–109.
- Goodall, J. 1986. *The chimpanzees of Gombe: Patterns of behaviour*. Harvard University Press, Cambridge, MA.
- Hart, J.A., M. Katembo & K. Punga. 1996. Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology* 34: 364–379.
- Hayward, M.W., J. O'Brien, M. Hofmeyr, G.I.H. Kerley. 2006. Prey preferences of the African wild dog *Lycaon Pictus* (Canidae: Carnivora): Ecological requirements for conservation. *Journal of Mammalogy* 87: 1122–1131.
- Henschel, P., K.A. Abernethy, L.J.T. White. 2005. Leopard food habits in the Lope National Park, Gabon, Central Africa. *African Journal of Ecology* 43: 21–28.
- Hernandez-Aguilar, R.A. 2006. Ecological and nesting patterns of chimpanzees (*Pan troglodytes*) in Issa, Ugalla, Western Tanzania. PhD thesis, University of Southern California, USA.
- Hernandez-Aguilar, R.A. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution* 57: 350–64.
- Hiraiwa-Hasegawa, M., R.W. Byrne, H. Takasaki & J.M. Byrne. 1986. Aggression toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. *Folia Primatologica* 47: 8–13.
- Iida, E.G., G. Idani & H. Ogawa. 2012. Mammalian fauna of the miombo forest in the Ugalla area, western Tanzania. *African Study Monographs* 33: 253–270.
- Inagaki, H. & T. Tsukahara. 1993. A method of identifying chimpanzee hairs in lion feces. *Primates* 34: 109–112.
- Itani, J. 1979. Distribution and adaptation of chimpanzees in an arid area. In *The Great Apes*. D.A. Hamburg & E.R. McCown eds. Benjamin/Cummings, Menlo Park (CA), USA. Pp 55–71
- Izawa, K. & J. Itani. 1966. Chimpanzees in Kasakata Basin, Tanganyika. Ecological study in the rainy season 1963–1964. *Kyoto University African Studies* 1: 73–156.
- Kano, T. 1971. The chimpanzee of Filabanga, western Tanzania. *Primates* 12: 229–246.
- Kano, T. 1972. Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto University African Studies* 7: 37–129.
- Klailova, M., C. Casanova, P. Henschel, P. Lee, F. Rovero & A. Todd. 2012. Non-human predator interactions with wild great apes in Africa and the use of camera traps to study their dynamics. *Folia Primatologica* 83: 312–328.
- Kutsukake, N. 2006. The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology* 112: 581–591.
- Maddock, A.H. & M.G.L. Mills. 1994. Population characteristics of African wild dogs *Lycaon pictus* in the Eastern transvaal lowveld, South Africa, as revealed through photographic records. *Biological Conservation* 67: 57–62.
- Mills, M.G.L. & P.J. Funston. 2011. Large carnivores and savanna heterogeneity. In *The Kruger Experience: Ecology And Management Of Savanna Heterogeneity*. J.T. du Toit, K.H. Rogers, H.C. Biggs, eds. Island Press, Washington, D.C., USA. Pp. 370–386.
- Mills, M.G.L. & M.L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology* 11: 1397–1406.
- Moyer, D., A.J. Plumptre, L. Pintea, A. Hernandez-Aguilar, J. Moore, F.A. Stewart, T.R.B. Davenport, A.K. Piel, S. Kamenya, H. Mugabe, N. Mpunga & M. Mwangoka. 2006. Surveys of chimpanzees and other biodiversity in western Tanzania. Unpublished report submitted to USF&W, Great Apes Fund, USA.
- Nakazawa, N., S. Hanamura, E. Inoue, M. Nakatsukasa & M. Nakamura. 2013. A leopard ate a chimpanzee: First evidence from East Africa. *Journal of Human Evolution* doi:

- 10.1016/j.jhevol.2013.04.003
- Nishida, T. 1968. The social groups of wild chimpanzees in the Mahale Mountains. *Primates* 9: 167–224.
- Nishida, T. 1989. A note on the chimpanzee ecology of the Ugalla area, Tanzania. *Primates* 30: 129–138.
- Oates, J.F., C.E.G. Tutin, T. Humle, M.L. Wilson, J.E.M. Baillie, Z. Balmforth, A. Blom, C. Boesch, D. Cox, T. Davenport, A. Dunn, J. Dupain, C. Duvall, C.M. Ellis, K.H. Farmer, S. Gatti, E. Greengrass, J. Hart, I. Herbinger, C. Hicks, K.D. Hunt, S. Kamenya, F. Maisels, J.C. Mitani, J. Moore, B.J. Morgan, D.B. Morgan, M. Nakamura, S. Nixon, A.J. Plumptre, V. Reynolds, E.J. Stokes & P.D. Walsh. 2008. *Pan troglodytes*. The IUCN Red List of Threatened Species 2008: eT15933A5322627 doi: 10.2305/IUCN.UK.2008.RLTS.T15933A5322627.en
- Ogawa, H., G. Idani, J. Moore, L. Pintea, A. Hernandez-Aguilar. 2007. Sleeping parties and nest distribution of chimpanzees in the savanna woodland. *International Journal of Primatology* 28: 1397–1412.
- Ososky, J.J. 1998. *Diet of leopards and golden cats in Ndoki Park, Republic of Congo*. MSc dissertation, University of Chicago, DeKalb, USA.
- Piel, A.K., A. Lenoel, C. Johnson, F.A. Stewart. 2015. Detering poaching in western Tanzania: The presence of wildlife researchers. *Global Ecology & Conservation* 3: 188–199.
- Pierce, A. (2009) An encounter between a leopard and a group of chimpanzees at Gombe National Park. *Pan Africa News* 16: 22–24
- Pintea, L. 2007. *Applying satellite imagery and GIS for chimpanzee habitat change detection and conservation*. PhD thesis, University of Minnesota, St. Paul, USA.
- Pruetz, J.D., P. Bertolani. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17: 412–417.
- Pruetz, J.D., S.J. Fulton, L.F. Marchant, W.C. McGrew, M. Schiel & M. Waller. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *American Journal of Primatology* 70: 393–401.
- Rahm, U. 1967. Observations during chimpanzee captures in the Congo. In *Neue Ergebnisse der Primatologie*. D. Starck, R. Schneider, H.J. Kuhn eds. Gustav Fischer, Stuttgart, Germany. Pp. 195–207.
- Rudicell, R.S., A.K. Piel, F. Stewart, D.L. Moore, G.H. Learn, Y. Li, J. Takehisa, L. Pintea, G.M. Shaw, J. Moore, P.M. Sharp, B.H. Hahn. 2011. High prevalence of simian immunodeficiency virus infection in a community of savanna chimpanzees. *Journal of Virology* 85: 9918–9928.
- Schaller, G. 1972. *The Serengeti Lion*. University of Chicago Press, Chicago, USA.
- Schel, A.M., S.W. Townsend, Z. Machanda, K. Zuberbühler & K.E. Slocumbe. 2013. Chimpanzee alarm call production meets key criteria for intentionality. *PLoS ONE* 8:e76674. doi: 10.1371/journal.pone.0076674
- Stewart, F. & J.D. Pruetz. 2013. Do chimpanzee nests serve an anti-predatory function? *American Journal of Primatology* 75: 593–604.
- Taylor, C.R., K. Schmidt-Nielsen, R. Dmiel & M. Fedak. 1971. Effect of hyperthermia on heat balance during running in the African hunting dog. *American Journal of Physiology* 220: 823–827.
- Treves, A. & P. Palmqvist. 2007. Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 Ma). In *Primate Anti-Predator Strategies*. S. Gursky, K.A.I. Nekaris, eds. Springer, USA. Pp. 355–381.
- Tsukahara, T. 1993. Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 11: 1–11.
- Tutin, C.E.G., W.C. McGrew & P.J. Baldwin. 1981. Responses of wild chimpanzees to potential predators. In *Primate Behaviour and Sociobiology*. A.B. Chiarelli, ed. Springer Berlin, Heidelberg, Germany. Pp. 136–141.
- van Lawick-Goodall, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1: 161–311.
- Woodroffe, R. & C. Sillero-Zubiri. 2015. *Lycaon pictus*. The IUCN Red List of Threatened Species. Version 2015.2. doi: 10.2305/IUCN.UK.2012.RLTS.T12436A16711116.en
- Yoshikawa, M. & H. Ogawa. 2015. Diet of savanna chimpanzees in the Ugalla area, Tanzania. *African Study Monographs* 36: 189–209.
- Zamma, K. 2011. Responses of chimpanzees to a python. *Pan Africa News* 18: 13–15.
- Zuberbühler, K., D. Jenny & R. Bshary. 1999. The predator deterrence function of primate alarm calls. *Ethology* 105: 366–379.
- Zuberbühler, K. & D. Jenny. 2002. Leopard predation and primate evolution. *Journal of Human Evolution* 43: 873–886.

Received: 16 March 2016

Accepted: 1 June 2016