



## Short communication

## Hard ticks (Acari: Ixodidae) parasitizing bushbabies (Mammalia: Galagidae) in a biodiversity hotspot of northern South Africa

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## ABSTRACT

South Africa has six species of primates, three of which are bushbabies (family Galagidae). Very little information is available on their parasites due to the lack of longitudinal studies, although *Rhipicephalus appendiculatus*, *Amblyomma hebraeum* and *Haemaphysalis elliptica* were previously reported from the brown greater galago (*Otolemur crassicaudatus*) in South Africa. During 2014–2019, 83 *O. crassicaudatus* (70 live-trapped and 13 deceased animals) were checked for the presence of hard ticks, all from Limpopo Province, South Africa. Seventy-three of 83 (88 %) galagos were found to be tick-infested. Among ixodid genera, *Haemaphysalis* had the highest prevalence (46 % of the bushbabies), followed by *Rhipicephalus* (25 %) and *Ixodes* (18 %). In total, ten tick species were identified. Importantly, all infestations were monospecific. Ticks occurred on various body parts of bushbabies, thus no predilection site was noted. In conclusion, while previously only three ixodid species were known to infest bushbabies in South Africa, the present study showed that these animals can be parasitized by a much broader range of hard ticks.

## 1. Introduction

In South Africa, about 65,500 animal species are known to occur, but it is thought that this only represents less than half of the actual faunal richness (Victor et al., 2013). Among mammals of this region, six species of primates are indigenous, including the chacma baboon (*Papio ursinus*), the vervet monkey (*Chlorocebus pygerythrus*), the samango monkey (*Cercopithecus albogularis*) and three species of galagos (bushbabies), the Mohol bushbaby (*Galago moholi*), the brown greater galago or greater bushbaby (*Otolemur crassicaudatus*) and Grant's bushbaby (*Galagoideus granti*) (Génin et al., 2016). The brown greater galago (*O. crassicaudatus*) is the largest species of the family Galagidae. Its geographical range

includes countries south and east of the Congo Basin, extending in the east through Tanzania (Bearder and Svoboda, 2013) and south to KwaZulu-Natal Province in South Africa, where it inhabits forest, mesic savanna woodlands and riparian forests (Masters and Génin, 2016).

Although the vast majority of animal species (more than 40,000) in South Africa belong to insects (Victor et al., 2013), non-insect arthropods like hard ticks (Acari: Ixodidae) also contribute to this biodiversity. We know so far that the tick fauna of Southern Africa is represented by at least 83 ixodid species of which 22 are restricted to this region (Horak et al., 2018). Regarding the tick-infestation of primates, until recently relevant data were reported only from one galago species, *O. crassicaudatus*, indicating the occurrence of *Rhipicephalus*

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*appendiculatus* (larvae) (Hoogstraal and Theiler 1959), *Amblyomma hebraeum* (larvae) and *Haemaphysalis elliptica* (female) on this host species (Horak et al., 2018). These three ixodid tick species were also reported from another arboreal primate, the vervet monkey in South Africa (Horak et al., 2018). Nevertheless, information on Ixodidae associated with primates in South Africa is scarce (Ledwaba et al., 2022).

In north-eastern South Africa, the Soutpansberg mountain range (Limpopo Province) is a region with high biodiversity (Foord et al., 2002; Hahn, 2017). However, in this area, only a limited number of taxa have been investigated as hosts for ixodid ticks, primarily carnivores (Baauw et al., 2019). Therefore, as part of an ongoing surveillance of tick species of wildlife in Limpopo Province, and in light of the scarcity of knowledge on primates as tick-hosts in the whole of South Africa as outlined above, this study aimed at investigating the diversity of ixodid ticks infesting bushbabies in this area.

## 2. Materials and methods

As part of ongoing research on the diversity and ecology of ticks in the Limpopo Province at the Parasitology Laboratory, University of Limpopo, this work was carried out in collaboration with a longitudinal study of *O. crassicaudatus* health, ecology and genetics at the Lajuma Research Centre, a temperate forest located in the western Soutpansberg Mountain Range, Limpopo Province, South Africa (29°26'E, 23°01'S, altitude ca. 1300 m) (Phukuntsi et al., 2020). This site is part of the Vhembe Biosphere Reserve in the Soutpansberg Mountains of South Africa, a globally-recognized biodiversity hotspot for plants and animals.

From 2014 to 2019 annual captures of wild *O. crassicaudatus* were carried out using Havahart® live traps (Woodstream Corp., Lititz, PA, USA). During routine health evaluations of the study population, 70 individuals were examined for the presence of ixodid ticks (Phukuntsi et al., 2020). All captured animals were measured, weighed and checked for various health parameters under the supervision of a veterinarian. In addition, parasite examinations were also carried out on 13 *O. crassicaudatus* that had died accidentally, including eight animals that had been killed on regional highways of Limpopo Province (referred to as road-kills), one that was killed by a black mamba (*Dendroaspis polylepsis*) bite (Medike, Makhado, Louis Trichardt), three that had been killed by a dog and one that had been electrocuted on a power line (in Haenertsburg). Only fresh carcasses were examined, within a few hours of death. The sex was recorded for 77 bushbabies (41 males, 36 females).

All the animals were thoroughly checked for ectoparasites. Ticks were preserved in 70 % ethanol and were morphologically identified using an EZ4 stereomicroscope (Leica Microsystems, CMS GmbH, Wetzlar, Germany) and standard keys (Horak et al., 2018; Walker et al., 2003; Arthur, 1965).

Fisher's exact test (<https://www.langsrud.com/fisher.htm>) and Student's *t*-test (in Excel®) were used to compare the prevalence rates and intensities of tick-infestation, respectively, between male and female bushbabies. Differences were regarded significant if  $P < 0.05$ .

## 3. Results and discussion

Ten species from three genera of ixodid ticks were found on various body parts of greater bushbabies. From each bushbaby, only one tick species was identified. The overall prevalence of tick-infestation was 88 % from the 83 animals. The prevalence was not significantly different between the sexes, i.e., 61 % among male ( $n = 25$ ) and 67 % among female ( $n = 24$ ) bushbabies. The mean intensity of tick-infestation was higher among males than among females (3.7 vs 2.8 tick/animal, respectively), but this was also not significantly different between the sexes. These data reflect that although galagids have territorial behavior (Pozzi et al., 2014), implying that males have larger home ranges than females, this did not significantly influence the rate and severity of their tick-infestation.

Considering the genus-level distribution of ticks, *Haemaphysalis* spp. were collected from 46 % ( $n = 38$ ), *Rhipicephalus* spp. from 25 % ( $n = 21$ ) and *Ixodes* spp. from 18 % ( $n = 15$ ) of examined animals (Table 1). Out of eight road-killed bushbabies, ixodid ticks were found on two. The single electrocuted animal, as well as two out of the three dog-killed bushbabies had ticks still attached to their body. Taken together, larvae of at least seven ixodid species occurred on bushbabies, whereas females of only four tick species were found. This may be related to the observation that adult ticks are more host-specific than larvae, as reported based on a large South African dataset (Espinaze et al., 2016).

*Ixodes* larvae occurred on the ears, legs and tails of 13 animals (15.7 %), whereas nymphs from this genus were found on the ears and digits of only three animals. These ticks were not identified to the species level, because for several species only females have been described (Arthur, 1965; Horak et al., 2018). In addition to immature stages, one female *Ixodes rhabdomysae* was found on the neck of one *O. crassicaudatus* (Table 1). This specimen has also been included in molecular-phylogenetic analyses (Hornok et al., 2023). Until recently, *I. rhabdomysae* was reported only from the four-striped grass rat (*Rhabdomys pumilio*) in South Africa (Horak et al., 2018). In a broader geographical context, the host range of *I. rhabdomysae* has been regarded as limited to rodents and insectivorous small mammals (Soricidae, Macroscelididae) (Guglielmone et al., 2014), which (based on the present results) should be extended to include primates (Galagidae).

*Haemaphysalis* larvae were recovered from the ears, legs, hands, tails, back and groins of 25 animals (30.1 %), while only three animals had nymphs on the tail and groin. Females and males were found on the ears and tails of five and only on the ears of six animals (Table 1). To our knowledge, the *Haemaphysalis* (*Rhipistoma*) group has not been reported in South Africa, but *H. elliptica* is considered to be widespread in the country (Horak et al., 2018). The taxonomy of *Haemaphysalis spinulosa* is currently uncertain, therefore it is referred to as *H. spinulosa*-like (Horak et al., 2018). The immatures of both *H. elliptica* and *H. spinulosa*-like were only identified as *Haemaphysalis* (*Rhipistoma*) group, based on the shape of their mouthparts. Considering specimens of this genus identified to the species level, *O. crassicaudatus* is a new host record for *H. elliptica*, *H. aciculifer* and *H. zumpti* in South Africa, and primates in general for the latter two species (Guglielmone et al., 2014; Hoogstraal and El Kammah, 1972). Considering that (1) *H. elliptica* may transmit *Rickettsia conorii*, the causative agent of tick-bite (or spotted) fever in humans (Horak et al., 2018), and (2) *R. conorii* has been detected in rodents (Essbauer et al., 2018) and (3) its antibodies in primates in South Africa (Kaschula et al., 1978), the above results justify investigations into the susceptibility of galagids to spotted fever rickettsiosis in the region.

*Rhipicephalus* larvae were found on the ears, tail, head and limbs of 20 animals (24 %), whereas a nymph was collected from the tail of one animal (Table 1). Among the three *Rhipicephalus* species identified here, *Rh. appendiculatus* and *Rh. simus* have host ranges including several orders of mammals. On the other hand, *Rh. warburtoni* is reported here for the first time from the family Galagidae, adding to already known hosts in Bovidae, Leporidae and Macroscelididae (Guglielmone et al., 2014). For the latter two *Rhipicephalus* spp., *O. crassicaudatus* is a new host record in South Africa. Importantly, similar to *H. elliptica*, *Rh. sanguineus* sensu lato and *Rh. simus* are vectors of *R. conorii* (Horak et al., 2018). In addition, recently a new *Rickettsia* strain was reported in *Rh. simus* of donkeys (Halajian et al., 2018).

Data on the seasonality of tick genera and species (Table 1) reflect that *Haemaphysalis* spp. infested bushbabies in the autumn and winter periods, except for *H. zumpti* that also occurred in the summer similarly to *Ixodes* spp. By contrast, *Rhipicephalus* spp. predominated in the winter time (Table 1). Most of these observations are in line with previous studies, e.g., in the case of *H. elliptica* (adults reported between February and June), *Rh. simus* (larvae found from March to September) and *Rh. warburtoni* (larvae active from December to July) (Horak et al., 2018). However, *Rh. appendiculatus* and *Rh. sanguineus* s.l. are known as

**Table 1**

Hard ticks collected from 83 examined *Otolemur crassicaudatus*. Among the seasons, summer is symbolized with full circle (●), autumn with triangle (▲), and winter with open circle (○).

Tick species	Year(s) of collection	Number of infested animals	Life stage and sex of ixodid ticks (month and season of collection)			
			Larvae	Nymphs	Males	Females
<i>Haemaphysalis</i> sp.*	2018	2	2 (March ▲)	–	–	–
<i>H. aciculifer</i>	2018, 2019	22	77 (March ▲, May ▲, June ○)	–	–	–
<i>H. elliptica</i>	2016, 2018	2	–	–	–	2 (March ▲, June ○)
<i>Haemaphysalis</i> ( <i>Rhipistoma</i> ) group*	2014, 2017, 2019	5	4 (June ○)	1 (June ○)	–	–
<i>H. spinulosa</i> -like	2019	1	–	–	1 (June ○)	1 (June ○)
<i>H. zumpti</i>	2014, 2018, 2019	6	–	2 (January ●, June ○)	6 (January ●, February ●, March ▲, June ○)	2 (January ●, March ▲)
<i>Ixodes</i> sp.*	2014, 2016, 2017, 2018, 2019	14	21 (February ●, March ▲, June ○)	3 (February ●, March ▲, June ○)	–	–
<i>I. rhabdomysae</i>	2018	1	–	–	–	1 (March ▲)
<i>Rhipicephalus appendiculatus</i>	2019	1	–	1 (June ○)	–	–
<i>Rh. sanguineus</i> group	2016, 2018	2	6 (June ○)	–	–	–
<i>Rh. simus</i>	2014, 2019	4	4 (June ○)	–	–	–
<i>Rh. warburtoni</i>	2014, 2016, 2017, 2018	14	30 (February ●, March ▲, June ○)	–	–	–

\* Not identified to species.

summer-associated ticks (Horak et al., 2018), but showed winter activity based on infestations of bushbabies in this study.

It is also necessary to consider those traits of the target host species in this study, which can influence its tick infestation. *Otolemur crassicaudatus* is known for its arboreal life, but it is also capable of walking, running and hopping on the ground in excess of 100 m (Bearder and Svoboda, 2013), thus allowing ticks (which are usually present on the lower vegetation) to infest them. However, conditions of acquiring tick-infestation may also be present in arboreal nests. Some of the ticks identified from bushbabies in this study are nidicolous (nest-dwelling), as exemplified by larvae and nymphs of *Ixodes* spp. and *Rh. simus* (Horak et al., 2018). Immatures of *H. moreli* (belonging to the *Rhipistoma* group also identified in this study) were found not only on rodents but also in bushbaby nest (Camicas et al., 1972). On the other hand, social grooming among greater brown galagos (Ehrlich, 1977) may reduce their tick-infestation, probably to a lesser extent among males (Roberts, 1971; Ehrlich, 1977).

Based on the above, the highest prevalence of tick infestation was observed in the genus *Haemaphysalis*, members of which were found on nearly half of examined animals. This genus, together with *Ixodes*, contains three-host tick species, in the case of which (as indicated by the present results) bushbabies are suitable hosts for all three life cycle stages. It is noteworthy that, as shown here, adult ixodid ticks infested galagos only from these two genera. In the ecological categorization of ticks according to open country vs forest habitats (Uspensky, 2002) both *Haemaphysalis* and *Ixodes* species represent the so-called forest ticks. This is well illustrated by observations that arboreal primates (lemurs) have host specific *Ixodes* and *Haemaphysalis* ticks, *Ixodes lemuris* and *Haemaphysalis lemuris* in Madagascar (Blanco et al., 2013; Hokan et al., 2017).

In conclusion, it was shown here for the first time that the brown greater galago, *O. crassicaudatus* can significantly contribute to tick life cycles. From this primate host, only *A. hebraeum*, *H. elliptica* and *Rh. appendiculatus* were previously reported in South Africa (Hoogstraal and Theiler, 1959; Horak et al., 2018), *Ixodes schillingsi* in Mozambique and Zanzibar (Arthur, 1965), as well as *Rh. sanguineus* (s.l.) and *Rh. simus* on *O. crassicaudatus agisymbanus* in Zanzibar (Hoogstraal and Theiler, 1959). Therefore, as outlined above, for the majority of tick-species identified in the present study, *O. crassicaudatus* or Galagidae in

general are new host records.

As reported in Zambia (north of South Africa), zoonotic tick-borne pathogens can reach high (up to 40 %) prevalence among primates (Nakayima et al., 2014), supporting the veterinary-medical significance of relevant studies. At the same time, virtually nothing is known about the reservoir role of this galagid species in the local maintenance of tick-borne pathogens with veterinary-medical importance. In addition, tick-borne pathogens may also affect bushbabies, with potential impact for wildlife conservation issues. However, to the best of our knowledge, only one species of tick-borne pathogens, the piroplasm *Babesia galagolata* (Apicomplexa: Piroplasmida) has been reported from *O. crassicaudatus* (Dennig, 1973). Last but not least, tick infestation might have consequences beyond the transmission of tick-borne pathogens: for instance, it may entail behavioral and physiological adaptations to reduce tick exposure and thus probably plays a role in primate evolution (Brown, 2021). These reasons increase the merits of this pilot study, which will hopefully serve as a driver of future research on the diversity of tick species and tick-borne pathogens associated with bushbabies in Africa.

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#### CRediT authorship contribution statement

**Ali Halajian:** Conceptualization, Writing – original draft, Writing – review & editing. **Frank P. Cuzzo:** Investigation, Writing – review & editing. **Heloise Heyne:** Methodology, Writing – review & editing. **Michelle L. Sauter:** Investigation, Writing – review & editing. **Birthe Linden:** Investigation, Writing – review & editing. **Jabu Linden:** Investigation, Writing – review & editing. **Adrian SW. Tordiffe:** Investigation, Writing – review & editing. **Kgethedi Michael Rampedi:** Investigation, Writing – review & editing. **Sándor Hornok:**

Conceptualization, Writing – original draft, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no conflict of interest.

## Data availability

Data will be made available on request.

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## References

- Arthur, D.R., 1965. Ticks of the Genus *Ixodes* in Africa. The Athlone Press, London, United Kingdom, p. 356.
- Baauw, A.H., Heyne, H., Williams, K.S., Hill, R.A., Heitkönig, I.M.A., Williams, S.T., 2019. First records of *Hyalomma rufipes* and *Ixodes neitzi* (Acari: Ixodidae) found on large carnivores in South Africa. *Ticks. Tick. Borne Dis.* 10, 128–131. <https://doi.org/10.1016/j.ttbdis.2018.08.011>.
- Bearder, S.K., Svoboda, N.S., 2013. *Otolemur crassicaudatus* – Large-eared greater galago. In: Butynski, T.M., Kingdon, J., Kalina, J. (Eds.), *Mammals of Africa—Volume II primates*. Bloomsbury Publishing, London, pp. 409–413.
- Blanco, M.B., Elfawal, M.A., Durden, L.A., Beati, L., Xu, G., Godfrey, L.R., Rich, S.M., 2013. Genetic diversity of ixodid ticks parasitizing eastern mouse and dwarf lemurs in Madagascar, with descriptions of the larva, nymph, and male of *Ixodes lemuris* (Acari: Ixodidae). *J. Parasitol.* 99, 11–18. <https://doi.org/10.1645/GE-3183.1>.
- Brown, J.G., 2021. Ticks, Hair Loss, and Non-Clinging Babies: A Novel Tick-Based Hypothesis for the Evolutionary Divergence of Humans and Chimpanzees. *Life (Basel)* 11, 435. <https://doi.org/10.3390/life11050435>.
- Camicas, J.L., Hoogstraal, H., el-Kammah, K.M., 1972. Notes on African *Haemaphysalis* ticks. 8. *H. (Rhipistoma) moreli* sp. n., a carnivore parasite of the *H. (R.) leachi* group (Ixodoidea: Ixodidae). *J. Parasitol.* 58, 1185–1196.
- Dennig, H.K., 1973. *Babesia galagolata* n. sp., a *Babesia* of the galago (*Galago crassicaudatus*). *Z. Parasitenkd.* 41, 281–290 [in German].
- Ehrlich, A., 1977. Social and individual behaviors in captive greater galagos. *Behaviour* 63, 192–214.
- Espinaze, M.P., Hellard, E., Horak, I.G., Cumming, G.S., 2016. Analysis of large new South African dataset using two host-specificity indices shows generalism in both adult and larval ticks of mammals. *Parasitology* 143, 366–373. <https://doi.org/10.1017/S0031182015001730>.
- Essbauer, S., Hofmann, M., Kleinemeier, C., Wölfel, S., Mathee, S., 2018. *Rickettsia* diversity in southern Africa: a small mammal perspective. *Ticks. Tick. Borne Dis.* 9, 288–301. <https://doi.org/10.1016/j.ttbdis.2017.11.002>.
- Foord, S., Dippenaar-Schoeman, A.S., Van der Merwe, M., 2002. A check list of the spider fauna of the Western Soutpansberg, South Africa (Arachnida: Araneae). *Koedoe* 45, 35–43.
- Génin, F., Yokwana, A., Kom, N., Couette, S., Dieuleveut, T., Nash, S.D., Masters, J.C., 2016. A new galago species for South Africa (Primates: Strepsirhini: Galagidae). *Afr. Zool.* 51, 135–143. <https://doi.org/10.1080/15627020.2016.1232602>.
- Guglielmine, A.A., Robbins, R.G., Apanaskevich, D.A., Petney, T.N., Estrada-Peña, A., Horak, I.G., 2014. *The Hard Ticks of the World*. Springer, Dordrecht, p. 738.
- Hahn, N., 2017. Endemic flora of the Soutpansberg, Blouberg and Makgabeng. *S. Afr. J. Bot.* 113, 324–336. <https://doi.org/10.1016/j.sajb.2017.09.006>.
- Halajian, A., Palomar, A.M., Portillo, A., Heyne, H., Romero, L., Oteo, J.A., 2018. Detection of zoonotic agents and a new *Rickettsia* strain in ticks from donkeys from South Africa: implications for travel medicine. *Travel. Med. Infect. Dis.* 26, 43–50. <https://doi.org/10.1016/j.tmaid.2018.10.007>.
- Hokan, M., Strube, C., Radespiel, U., Zimmermann, E., 2017. Sleeping site ecology, but not sex, affect ecto- and hemoparasite risk, in sympatric, arboreal primates (*Avahi occidentalis* and *Lepilemur edwardsi*). *Front. Zool.* 14, 44. <https://doi.org/10.1186/s12983-017-0228-7>.
- Hoogstraal, H., Theiler, G., 1959. Ticks (Ixodoidea, Ixodidae) parasitizing lower primates in Africa, Zanzibar, and Madagascar. *J. Parasitol.* 45, 217–222.
- Hoogstraal, H., El Kammah, K.M., 1972. Notes on African *Haemaphysalis* ticks. X. *H. (Kaiseriana) aciculifer* Warburton and *H. (K.) rugosa* Santos Dias, the African representatives of the spinigera subgroup (Ixodoidea: Ixodidae). *J. Parasitol.* 58, 960–978.
- Horak, I.G., Heyne, H., Williams, R., Gallivan, G.J., Spickett, A.M., Bezuidenhout, J.D., Estrada-Peña, A., 2018. *The Ixodid ticks (Acari: Ixodidae) of Southern Africa*. Springer International Publishing AG, Basel, Switzerland, p. 676.
- Hornok, S., Kontschán, J., Takács, N., Heyne, H., Kovács, Á.B., Plantard, O., Keve, G., Fedorov, D., Gyuranez, M., Halajian, A., 2023. Molecular-phylogenetic analyses of *Ixodes* species from South Africa suggest an African origin of bird-associated exophilic ticks (subgenus *Trichotoixodes*). *Parasit. Vectors* 16, 392. <https://doi.org/10.1186/s13071-023-05998-5>.
- Kaschula, V.R., Van Dellen, A.F., de Vos, V., 1978. Some infectious diseases of wild vervet monkeys (*Cercopithecus aethiops pygerythrus*) in South Africa. *J. S. Afr. Vet. Assoc.* 49, 223–227.
- Ledwaba, M.B., Nzopho, K., Tembe, D., Onyiche, T.E., Chaisi, M.E., 2022. Distribution and prevalence of ticks and tick-borne pathogens of wild animals in South Africa: A systematic review. *Curr. Res. Parasitol. Vector Borne Dis.* 2, 100088 <https://doi.org/10.1016/j.crvbd.2022.100088>.
- Masters, J., Génin, F., 2016. A conservation assessment of *Otolemur crassicaudatus*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T. (Eds.), *The Red List of Mammals of South Africa. Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Nakayima, J., Hayashida, K., Nakao, R., Ishii, A., Ogawa, H., Nakamura, I., Moonga, L., Hang'ombe, B.M., Mweene, A.S., Thomas, Y., Orba, Y., Sawa, H., Sugimoto, C., 2014. Detection and characterization of zoonotic pathogens of free-ranging non-human primates from Zambia. *Parasit. Vectors* 7, 490. <https://doi.org/10.1186/s13071-014-0490-x>.
- Phukuntsi, M.A., Du Plessis, M., Dalton, D.L., Jansen, R., Cuozzo, F.P., Sauter, M.L., Kotze, A., 2020. Population genetic structure of the thick-tailed bushbaby (*Otolemur crassicaudatus*) from the Soutpansberg Mountain range, Northern South Africa, based on four mitochondrial DNA regions. *Mitochondrial DNA A DNA Mapp. Seq. Anal.* 31, 1–10. <https://doi.org/10.1080/24701394.2019.1694015>.
- Pozzi, L., Disotell, T.R., Masters, J.C., 2014. A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC Evol. Biol.* 14, 72. <https://doi.org/10.1186/1471-2148-14-72>.
- Roberts, P., 1971. Social interactions of *Galago crassicaudatus*. *Folia Primatol. (Basel)* 14, 171–181. <https://doi.org/10.1159/000155348>.
- Uspensky, I., 2002. Preliminary observations on specific adaptations of exophilic ixodid ticks to forests or open country habitats. *Exp. Appl. Acarol.* 28, 147–154. <https://doi.org/10.1023/a:1025303811856>.
- Victor, J.E., Hamer, M., Smith, G.F., 2013. *A Biosystematics Research Strategy For the algae, animals, Bacteria and archaea, Fungi and Plants of South Africa 2013-2018*. South African National Biodiversity Institute.
- Walker, A., Bouattour, A., Camicas, J.L., Estrada-Peña, A., Horak, I., Latif, A., Pegram, R., Preston, P., 2003. Ticks of domestic animals in Africa: a guide to identification of species. *Bioscience Repots, Edinburgh* 221.