WHERE ARE THE WILD THINGS? GUINEA WORM (*DRACUNCULUS MEDINENSIS*) AND THE ROLE OF WILDLIFE IN CHAD, AFRICA

by

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(Under the Direction of Michael Yabsley)

ABSTRACT

Guinea worm disease (dracunculiasis) is a painful infection caused by the filarial nematode *Dracunculus medinensis*. Natural wildlife infections have been found in several species, but the importance of wildlife hosts is not fully understood. This study aimed to increase understanding on species richness and carnivore interactions around villages with Guinea worm infections. Fifty-six game cameras were deployed around seven villages in Sarh, Chad with varying levels of Guinea worm endemicity. Occupancy models supported that tantalus monkeys (*Chlorocebus tantalus*), patas monkeys (*Erythrocebus patas*), and Egyptian mongoose (*Herpestes ichneumon*) were present in endemic and/or sporadic villages. Co-occurring carnivores were observed to exhibit temporal, spatial, or dietary niche partitioning. This study provides valuable knowledge on the wildlife species present around villages in Chad, a key step to understanding their role in transmission of Guinea worm. Additionally, this research provides insight into how carnivores may interact in human-altered landscapes.

INDEX WORDS: Guinea worm, camera trap, zoonoses, intraguild interaction, competition

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DEDICATION

I would like to dedicate this to my parents, Jim and Christy Korns, for your love, support, and financial help. Thank you for always believing in me and helping me move across the country in a pandemic. This would not have been possible without you.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Guinea Worm Disease (GWD), also known as dracunculiasis, is a painful and debilitating disease caused by the nematode *Dracunculus medinensis* (Muller, 1971). The Guinea Worm Eradication Program (GWEP) has been successful at reducing the number of cases from 3.5 million in 1986 across 21 countries to only 15 cases in 2021 across 4 countries (Watts, 1987; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022a). Traditionally, an individual became infected by the consumption of contaminated water (Muller, 1971). However, recent changes in the epidemiology of cases in Chad, including the dramatic increase of domestic dog (*Canis lupus familiaris*) and domestic cat (*Felis catus*) infections, has led to the belief that a paratenic or transport host may now also be involved in the lifecycle (Eberhard et al., 2014). In addition, there are increasing numbers of infections being diagnosed in wildlife (e.g., wild cats, baboons, etc.). The overall goal of this study is to increase the understanding on potential wildlife reservoir hosts for Guinea worm. Additionally, data collected will provide further knowledge on wildlife diversity in and around villages near Sarh, Chad, an understudied area of research.

The specific objectives of this study are:

1. Determine occupancy of wildlife species, particularly wild carnivores and primates, as it relates to villages with differing levels of GWD endemicity.

    a. Hypothesis: Chadian villages with higher numbers of *D. medinensis* infections in domestic dogs will also have increased detections of wild carnivores and/or primates surrounding the village, indicating possible wildlife reservoir hosts of *D. medinensis*

2. Examine the spatiotemporal relationships and intraguild dynamics of mesocarnivores in the area.
    a. Hypothesis: Mesocarnivores around villages in the Sarh region of Chad will segregate in time and/or space based on habitat preferences, level of anthropogenic disturbance, and avoidance of inter-species resource competition.
3. Document wildlife diversity in and around villages in the Sarh region of Chad.

LITERATURE REVIEW

1. What are Dracunculus *species?*

Members of the genus *Dracunculus* (family Dracunculidae) are parasitic nematodes of mammals and reptiles that are related to filarial nematodes (International Helminth Genomes Consortium, 2019; Wijová et al., 2005). In general, the genus *Dracunculus* is an understudied group of parasites, with only 14 described species with a near-global distribution and numerous undescribed species (Cleveland et al., 2018). The exception is *D. medinensis*, the most heavily researched species due to its significance in human medicine, historically infecting people in parts of Africa and Asia (Cairncross et al., 2002; Muller, 1971). The second most commonly researched species, *D. insignis*, occurs in North America and infect primarily wildlife species. Raccoons (*Procyon lotor*) are the primary definitive host (DH). However, a variety of other mammals can also be infected, including fisher (*Martes pennanti*), mink (*Neovison vison*), and

North American river otter (*Lontra canadensis*). Additionally, parasites presumed to be *D. insignis* have been found in skunks (*Mephitis* spp.), coyotes (*Canis latrans*), foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), Virginia opossums (*Didelphis virginiana*), badger (*Taxidea taxus*), marten (*Martes americana*), muskrat (*Ondatra zibethicus*), Short-tailed weasel (*Mustela erminea*), and North American beaver (*Castor canadensis*) (Cleveland et al., 2018). Similar to *D. medinensis*, this parasite rarely infects domestic dogs and cats in the United States and Canada (Williams et al., 2018). Another relatively common parasite, *D. lutrae,* is another species reported from North American river otters. Unlike *D. insignis* and *D. medinensis*, *D. lutrae* appears to be host-specific. Finally, there are numerous other *Dracunculus* species that infect reptiles in many countries (Cleveland et al., 2018).

All *Dracunculus* spp. are large yellow-white nematodes with distinct sexual dimorphism, as the female is much larger than the male. Female *D. medinensis* are distinctive, reaching lengths up to 1 meter long when they emerge (Cairncross et al., 2002). Females recovered from animals tend to be smaller, with a length of 280-600 mm by 1.0-1.2 mm wide (Moorthy and Sweet, 1938; Muller, 1971). The gut is compressed and non-functional, and the uterus fills the entire body cavity (Cairncross et al., 2002; Muller, 1971). Male worms are very small (15-40 mm in length by 0.4 mm wide) and do not emerge; therefore, they are only recovered during necropsy (Cairncross et al., 2002). Historically, species identification relied only on host information and morphological features. However, many key morphological structures (length of the spicules and gubernaculum) are only present on males. Morphology can typically only identify females to the genus level. Thus, molecular analysis of the 18S rRNA gene and DNA barcoding on the cytochrome *c* oxidase I (COI) gene have been useful tools for distinguishing between *D. medinensis*, *D. oesophageus, D. insignis*, and *D. lutrae* (Bimi et al., 2005; Elsasser et al., 2009; Wijová et al., 2006, 2005)

Human dracunculiasis has afflicted people in parts of Africa and the Middle East for much of recorded history (Adamson, 1988; Grove, 1990; Muller, 1991, 1971). Some believe that perhaps the oldest reference to Guinea worm comes from Numbers 21:6: "Then the Lord sent fiery serpents among the people, and they bit the people, so that many people of Israel died… And the Lord said to Moses, 'Make a fiery serpent, and set it on a pole; and every one who is bitten, when he sees it, shall live'" (Revised Standard Version). There is little physical evidence to support this claim. However, the findings of calcified Guinea worms in Egyptian mummies, along with multiple texts that seem to describe GWD, support that Guinea worm was established in Egypt around 1,500 BC, if not earlier (Adamson, 1988; Cole, 1979; David, 1984, p. 40; Muller, 1985). The life cycle of *D. medinensis*, first described in the late 1800s, is complex and includes an obligate invertebrate intermediate host and several vertebrate definite hosts (Fedchenko, 1870; Muller, 1971). Transmission occurs when a DH ingests the water containing infected cyclopoid copepods (Fedchenko, 1870; Leiper, 1907). The entirety of the lifecycle occurs in 10-14 months (Chippaux and Massougbodji, 1991; Gore, 1932; Manson, 1903; Powell, 1904). While dracunculiasis rarely results in mortality, afflicted persons may be disabled for weeks or months due to pain or secondary infections of the emerging worm, which often occurs at the time of year when labor is needed in the fields (Muller, 1971). In 1986, there was an estimated 3.5 million cases of GWD across 21 countries in northern, western, central, and eastern Africa, as well as India and Pakistan (Watts, 1987). The Guinea Worm Eradication Program (GWEP) has been successful at reducing the number of cases to 15 in 2021 in only four countries (Chad, Ethiopia, Mali, and South Sudan) (WHO Collaborating Center for Research, Training and

Eradication of Dracunculiasis, CDC, 2022a). Due to the large body of literature on this parasite, this review will focus on only some of the historical data. Instead, emphasis will be placed on the current epidemiology of *D. medinensis*, particularly on the role of wildlife as reservoirs and the current situation in Chad.

2. Traditional life cycle and transmission

2.1 Release of larvae into the environment

Typically, the first sign of infection in a DH is the formation of a painful, burning blister on the lower extremity, resulting in the desire to submerge the blister into water for relief (Fedchenko, 1870; Manson and Aberd, 1895). The blister is caused by the host immune response when the female worm releases small amounts of larvae under the skin (Cairncross et al., 2002). Upon contact with water, the uterus will rupture, and first-stage larvae (L1) will be released directly into the water. One study of five patients in Nigeria showed an average of 557,600 L1s were released on first immersion. The female will continue to release larvae for 3-4 weeks upon contact with water; however, the number of embryos released will gradually decrease each subsequent immersion (Moorthy, 1932; Muller, 1971). The larvae have been found to survive in pond water for seven days with decreasing activity after the fourth day (Moorthy, 1932; Southwell and Kirshner, 1938).

2.2 Role of cyclopoid copepods

Cyclopoid copepods, the obligate intermediate host, use their legs to catch and swallow the L1 (Leiper, 1907; Moorthy, 1938, 1932; Southwell and Kirshner, 1938). No other aquatic organisms are known to be susceptible to infection by L1 (Fedchenko, 1870; Leiper, 1907;

Moorthy, 1932). After ingestion, the L1 migrates through the stomach wall and into the hemocoel within 1-6 hours (Moorthy, 1938; Muller, 1972; Southwell and Kirshner, 1938). However, the ability of the larvae to infect copepods drops significantly after three days in the water, with a complete decrease after six days, likely due to a lack of energy to penetrate the gut wall (Muller, 1972). Inside the copepod, larvae undergo two molts, differentiation of internal structures, and increase in size to become infectious to a DH (Fedchenko, 1870; Moorthy, 1932).

The rate of larval development to the infectious L3 stage depends on temperature and copepod species. Development is faster in warmer temperatures and will pause below 19°C (Leiper, 1907; Manson and Aberd, 1895; Muller, 1971). Inside the copepods, the L1 undergo their first molt to second-stage larva (L2) in 5-12 days and their second molt to third-stage larva (L3) in 8-16 days (Moorthy, 1938, 1932; Muller, 1972, 1971; Onabamiro, 1954). Following their second molt, larvae may continue to develop marginally and increase in size for an additional 1-3 weeks (Leiper, 1907; Moorthy, 1938). However, dogs have been successfully experimentally infected with cyclops 4-8 days following the second molt (Moorthy and Sweet, 1936a).

All cyclopoid copepods were previously categorized within the genus *Cyclops*; however, many species are now included in multiple genera (Muller, 1971). One of the main copepods previously implicated in transmission, *Mesocyclops leuckarti* (previously *Cyclops leuckarti*), has been revised and does not occur in Africa anymore (Van de Velde, 1984). This has caused some difficulty in identifying the intermediate hosts in older publications. Presently, there are three genera implicated in the transmission of *D. medinensis*: *Mesocyclops* (*M. aequatorialis* and *M. kieferi*), *Thermocyclops* (*T. oblongatus*, *T. crassus*, *T. inopinus*, and *T. incisus*), and *Metacyclops* (*M. margaretae*) (Muller, 1991; Steib and Mayer, 1988). Some species of cyclops are more suitable intermediate hosts and carry heavier L1 burdens (Moorthy, 1938). In nature, cyclops are typically only infected with one larva (Lyons, 1972; Steib and Mayer, 1988). However, they have been infected with up to 20 larvae in laboratory conditions. These high infections typically lead to low motility or death of the cyclops, depending on host competency, though those with <5 larvae finished developing at the same time (Leiper, 1907; Moorthy, 1938, 1932; Muller, 1971; Onabamiro, 1954; Southwell and Kirshner, 1938). However, across species, immature cyclops (nauplii) are more easily infected than adults. In some cases, cyclops infected as nauplii experience stunted development (Moorthy, 1938).

In laboratory studies, the majority of infected copepods died 20-42 days after infection (maximum 107 days), while uninfected cyclops remained alive for 108 days (Moorthy, 1938, 1932). The larvae inside the cyclops will remain alive as long as the cyclops is alive, but movement inside the cyclops will decrease over time. Larvae can be awakened into activity again by adding HCl (0.2-0.4%) (Moorthy, 1932). Infected cyclops show reduced vertical activity after the first molt, followed by another reduction after the second molt (Moorthy, 1938; Muller, 1972; Onabamiro, 1954).

Cycloid copepods thrive in stagnant or low-flow water sources with tree shade and decaying organic material, the primary transmission source to the DH (Muller, 1971; Watts, 1984). Villages relying on ponds as their water source during the dry season are especially at risk for dracunculiasis outbreaks (Belcher et al., 1975; Lyons, 1972). Step wells, hafirs, or other similar water sources that allow the user to enter the water may also facilitate transmission (Cairncross and Tayeh, 1988; Muller, 1971). Deep or draw wells are an unlikely transmission source, as individuals do not usually enter into these water sources to contaminate them and conditions (lack of light and zooplankton for the cyclops to eat) are not ideal for cyclops (Cairncross et al., 2002; Cairncross and Tayeh, 1988; Muller, 1972). This contributes to the seasonality of GWD, which varies based on the climate. In areas of low rainfall (e.g., northern Nigeria, desert areas of Pakistan and India, etc.), ponds dry very quickly, and thus transmission occurs during the rainy season when surface water is available to be consumed. In areas of greater rainfall (e.g., western Nigeria, Guinea, Ghana, etc.), transmission occurs during the dry season when tributaries dry and there is an increased reliance on pond or stagnant water. However, variations can occur based on local weather events, such as flooding or drought (Cairncross et al., 2002; Muller, 1971; USA National Research Council, 1983).

2.3 Life in the definitive host: development, signs, and symptoms

The development of *D. medinensis* within the DH begins with ingesting water containing copepods infected with L3 (Fedchenko, 1870). While the exact migration route of L3 inside humans is not fully understood, experimental infections in non-human primates, domestic dogs, and domestic cats have provided insight. Upon reaching the stomach, the hydrochloric acid activates the L3 to break through the copepod exoskeleton (Leiper, 1906; Moorthy, 1932). The L3 migrate through the DH small intestine wall by 13 hours post-infection (Muller, 1968a). The L3 have traveled to the abdominal mesenteries by approximately day 10 and the chest and abdominal wall muscles by day 15 (Muller, 1968a). At this stage, the L3 have not undergone any significant development, as they have only reached an average length of 0.59 mm (Muller, 1968a). By 22 days, the L3 have reached the subcutaneous tissues, primarily in the axillary and inguinal regions, but also the thoracic and abdominal wall. They have begun to increase in size (Muller, 1968a). The third ecdysis has not been observed and is assumed to occur while migrating through the tissues. The fourth ecdysis has been observed occurring around day 43 (Onabamiro, 1956). Fertilization occurs between 3-4 months, as evidenced by the presence of the mucous plug on the female. Males are approximately 3 cm long. Females have reached 12.5 cm, and some may have begun to migrate down the hind limbs (Moorthy and Sweet, 1936a, 1938; Onabamiro, 1956). Males will die around six months and be resorbed by the body, occasionally calcifying instead (Moorthy and Sweet, 1938). By eight months, the female's uterus is full of developing eggs which develop into fully formed embryos by month 10 (Muller, 1971). By 11 months, most females are located in the limbs and are nearing emergence (Moorthy and Sweet, 1938; Onabamiro, 1956). The biological mechanism that allows the females to reach the preferred anatomical location is unclear. While the majority of females travel to the lower extremities, they can also migrate to aberrant locations, such as the trunk, scrotum, perineum, upper extremities, head, tongue, and eyelids (Chippaux et al., 1991; Edungbola, 1983; Lyons, 1972; Moorthy, 1932; Muller, 1971; Nwosu et al., 1982; Onabamiro, 1952). Additionally, females may fail to reach the surface and become encysted in the body. While extremely rare, there are a few documented cases of *D. medinensis* migrating to the extradural space, encysting, and causing paraplegia (Dinakar et al., 1977; Donaldson and Angelo, 1961; Khwaja et al., 1975; Legmann et al., 1980; Lodha et al., 1972; Mitra and Haddock, 1970; Monteiro and Hountondji, 1982; Odaibo et al., 1986; Reddy and Valli, 1967).

There are typically no symptoms for 9-10 months post-infection while mating and development occur (Moorthy, 1932). Palpation of the worm under the skin may be possible, but blister formation accompanied by local itching and burning pain are the first infection signs most patients experience (Cairncross et al., 2002; Muller, 1971; USA National Research Council, 1983). Upon the emergence of the female, an ulcer is formed (Cairncross et al., 2002; USA National Research Council, 1983). Other clinical signs and symptoms that may accompany infection include fever, urticaria, cyanosis, dyspnea, vomiting, giddiness, fainting, or diarrhea

(Chitale, 1912; Gore, 1932; Moorthy, 1932; Muller, 1971; Nwosu et al., 1982; USA National Research Council, 1983). The female worm is extracted by wrapping around a rod, stick, or other object and gently pulling a few centimeters daily. This practice has been done since antiquity and still is used today, with the addition of bandages, antibiotics, and/or anti-inflammatories, if possible (Cairncross et al., 2002; Fairley, 1924). If no complications arise during emergence and extraction, disability may last a few weeks (Belcher et al., 1975; Cairncross et al., 2002; Muller, 1971; Nwosu et al., 1982; Rao, 1942). However, secondary bacterial infections or complications occur in about half of cases and can cause cellulitis, abscesses, fistulae, ankylosis, synovitis, tetanus, or septicemia (Belcher et al., 1975; Cairncross et al., 2002; Chitale, 1912; Fairley and Liston, 1924a; Gore, 1932; Moorthy, 1932; USA National Research Council, 1983). Serious permanent disabilities are rare (reported in less than 1% in endemic villages from a study in Ghana). However, secondary infections cause longer-term disabilities, with 34% of Ghana villagers having difficulty performing daily activities 12-18 months after emergence (Hours and Cairncross, 1994). An Indian study reported a large proportion of individuals in endemic areas were incapacitated for 5-6 months (Moorthy, 1932). Surveys in Nigeria and Benin showed symptoms lasted anywhere from 3-29 weeks (Chippaux et al., 1991; Edungbola, 1983; Smith et al., 1989; Watts, 1984).

While dracunculiasis rarely causes death, it does cause social and economic problems for those already in poverty-stricken areas. GWD has been referred to as “the disease of the empty granary” by the Dogon people of Mali (*Yoro, the empty granary. Film (35 mm) and videotape. Coproduction by WHO/ORSTOM/ENMP*, 1998). The seasonality of transmission causes many to be disabled at the time of year when labor is needed in the fields to tend to crops (Belcher et al., 1975; Nwosu et al., 1982; Rao, 1942; Smith et al., 1989; USA National Research Council, 1983;

Watts, 1984). From studies in Nigeria, severe disability resulting in individuals unable to leave the house occurred in just over half the cases studied. Most individuals incapacitated were adults in the providing sector (~70%), causing additional labor losses during the agricultural season (Edungbola, 1983). A previous report estimated that eradicating dracunculiasis from Nigeria would result in a 20 million dollar profit from increased rice sales (de Rooy, 1987). When GWD was endemic in India, it was estimated that there was a loss of approximately 70 days of wages for each infection among the economically active population, resulting in a loss of about 11.7 million workdays annually (Rao, 1985). Children are also impacted, as a survey from Sudan found children under 6 years were more likely to be malnourished if over half of the adults in their household suffered from infection the previous year (16.9% compared to 6%) (Tayeh and Cairncross, 1996). Additionally, school-aged children (5-14 years) in Nigeria accounted for up to 40% of cases and experienced severe disability for an average of 24.3 days. During GW season, school absences rose to approximately 60% due to incapacitation or caring for another incapacitated child (Edungbola, 1983; Nwosu et al., 1982; Smith et al., 1989).

4. Risk factors

Multiple factors may increase an individual's risk for Guinea worm infection. Studies from Ghana showed that only 6.6% of infections reported in 1970 were new infections, while 39.7% of individuals previously infected developed reinfections (Lyons, 1972). Ghanaians infected in 1990 were ~5x more likely to become infected in 1991 than those who did not have infections (Tayeh et al., 1993). Villages in Benin reported that 20% of people had a significantly higher frequency of recurrent infections (Chippaux et al., 1991). A study in the Osmanabad district of India found approximately 67% of cases were from individuals with a history of GWD

(Rao, 1942). From 40 villages sampled in the Chitaldrug district of India, nearly 84% of cases were from patients with a history of dracunculiasis (Moorthy, 1932). The reason for more infected individuals with prior infections is unknown. However, it could be due to individual behaviors (drinking unfiltered water, eating raw aquatic hosts, etc.) or individual susceptibility.

Age, sex, and occupation may also be risk factors but are likely more due to behavior and activity rather than a biological mechanism. Children < 5 years consistently report the lowest risk, with one Ghana study reporting a prevalence of 5.7% (Belcher et al., 1975; Cairncross and Tayeh, 1988; Chippaux et al., 1991; Lyons, 1972; Tayeh et al., 1993). Individuals aged 5-30 are most at risk. In India, over 50% of cases were seen between 11-30 years (Rao, 1942). In a 1970 study from northwestern Ghana, those aged 15-19 had the highest infection prevalence at 40.2%, while all individuals from 5-39 had a prevalence of over 30% (Lyons, 1972). In southern Ghana, males aged 25-44 had an 80% infection prevalence rate (Belcher et al., 1975). A later study from northern Ghana confirmed that individuals aged 10-24 had the highest risk of infection (Tayeh et al., 1993). A study from Benin reported a significant difference in incidence between active males (aged 18-45; 66.2%) and non-active males (39.8%) (Chippaux et al., 1991). From cases in Chad from 2010-2018, 65.8% of cases occurred in people 30 years or younger, and the average age of an infected person was 26 years (Guagliardo et al., 2021a). These younger adults likely participate in more work activities (i.e., farming for extended periods or frequent water fetching). The more time spent being active away from their village, the more risk that they will consume water from a nearby unsafe source, such as a pond. Some studies report higher incidence in males than females or vice versa, but this is also likely due to other individual risk factors (such as occupation and traveling) rather than a biological mechanism. Multivariate analysis showed that sex was not a significant risk factor for individuals in northern Ghana, concluding differences in infection between sexes were due to behavioral factors (Tayeh et al., 1993). Individuals whose occupation is farming are at higher risk of infection. In southern Ghana, adult male farmers were most at risk, with some villages reporting 75% infected (Belcher et al., 1975). Villages in northern Ghana reported a higher prevalence of infection among adult farmers (10%) than adult non-farmers (6%) (Tayeh et al., 1993). In recent cases in Chad, 39.5% had an occupation related to farming and/or fishing (Guagliardo et al., 2021a).

Ultimately, the prevalence in different areas is likely a complex interaction of behavior and knowledge of transmission pathways. In southern Ghana, farmers were observed to drink from ponds while traveling to and from fields, a behavior that would put them more at risk (Belcher et al., 1975). Additionally, there was a slightly increased risk of infection among those who fetched water versus those who did not in northern Ghana (Tayeh et al., 1993). After traveling to obtain water, individuals may drink by stirring up the water, bringing potentially infected copepods residing on the bottom closer to the water surface and placing them more at risk. Furthermore, individuals who travel frequently are also more at risk. In northern Ghana, those who traveled during the 1990 dry season had a higher prevalence of infection (11.4%) than those who did not (6.2%) (Tayeh et al., 1993). Those who frequently travel from endemic areas also risk transporting Guinea worm to non-infected areas (Cairncross and Tayeh, 1988; Guagliardo et al., 2021a; Watts, 1984). These groups (farmers, water fetchers, frequent travelers) represent the most mobile groups in a population. They are typically young adults, which may explain why certain age groups are more at risk than others.

5. Control and eradication efforts

After smallpox was eradicated in 1979, the CDC began focusing on GWD as the next pathogen to eradicate in association with the International Drinking Water Supply and Sanitation Decade (Hopkins and Ruiz-Tiben, 1992). Dracunculiasis was considered an appropriate contender for eradication due to several factors: humans are not able to act as a carrier after worm emergence, seasonal transmission patterns, easy diagnosis by observation of emerging worm, having no known animal reservoir, relatively easy and effective methods of interrupting transmission, and moderate estimated cost of the effort (Hopkins and Ruiz-Tiben, 1991). India became the first country to launch a national eradication program in 1982, which aided in spurring other countries to join the effort (Cairncross et al., 2002). The World Health Assembly released a formal declaration endorsing the efforts to eliminate GWD in 1986 (World Health Organization, 1986). Following this, The Carter Center began its involvement and leadership in the eradication effort, supported by UNICEF and WHO (Hopkins and Ruiz-Tiben, 1992, 1991). In 1991, the World Health Assembly declared an eradication goal by 1995, a target date set earlier by the African Ministers of Health (Hopkins and Ruiz-Tiben, 1992; World Health Organization, 1991). Pakistan was the first previously endemic country to eliminate dracunculiasis in 1993 (Hopkins et al., 1995). The target eradication date would ultimately not be met, but all endemic countries had assembled national programs by then (Cairncross et al., 2002).

The eradication initiative consists of three main phases: forming a national program office and conducting baseline surveys, employing transmission intervention strategies, and containing cases. Intervention strategies are facilitated by cooperation between international organizations, national government leaders, and village-based workers and focus on interrupting the transmission cycle by providing safe water and preventing water contamination. These village-based workers are critical to the success of monitoring and reporting suspected GWD cases and providing health education to villagers. International organizations and government leaders provide a system of support for providing necessary supplies and aiding access to or construction of a safe source of drinking water. Villagers can receive cloth filters that filter out copepods from the water (Hopkins and Ruiz-Tiben, 1992, 1991). Additionally, Abate® (temephos), an insecticide effective at killing cyclops with low toxicity to mammals, is regularly used to contain cases if a water source has been infected (Grunert et al., 2022; Hopkins and Ruiz-Tiben, 1991; Muller, 1970; Sastry et al., 1978). There is currently no drug or vaccine effective against dracunculiasis (Biswas et al., 2013). Despite this, the GWEP, led by The Carter Center, has successfully reduced the number of human cases from 3.5 million across 21 countries in 1986 to only 15 cases in 4 countries (Chad, Ethiopia, Mali, and South Sudan) in 2021 (Watts, 1987; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022a; World Health Organization, 1996).

After a country reports no indigenous cases for a year, that country enters a pre-certification stage for dracunculiasis elimination. The WHO will certify a country if it meets the following conditions: absence of indigenous cases for three years, evidence of adequate surveillance in a sizeable geographic unit (country), and limited risk of reintroduction (World Health Organization, 1990). Therefore, even if a country has reported no cases of GWD for multiple consecutive years, it cannot qualify for elimination unless its neighboring countries also have a low transmission that does not pose a significant risk of reintroduction. The WHO defines eradication of dracunculiasis as the “confirmed absence of clinical manifestations (the interruption of transmission of *Dracunculus medinensis* in man) for three years or longer from a continent" (World Health Organization, 1990).

6. History of Dracunculiasis in Chad

The GWEP reported 1,231 cases in 1993 after beginning the first national search for GWD in Chad in March (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 1994, 1993). GWD was present in Chad for years before that (an estimated 2,200 cases in 1986). However, political unrest made it impossible to conduct surveys or provide aid (Watts, 1987). In 1999, one year following the last reported indigenous case, Chad entered the pre-certification stage for dracunculiasis elimination (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 1999). However, in 2000, Chad could not acquire the needed support to continue its surveillance (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2000). Chad had an assessment by the WHO certification team in 2001, which unearthed three indigenous GWD reports from August-September of 2000 (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2001). Though these cases were found and occurred in 2000, regular public reports by the WHO Collaborating Center for Research, Training, and Eradication of Dracunculiasis (Guinea Worm-Wrap-ups) continued to list 1998 as the last year of indigenous cases in Chad (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2009, 2008, 2007a, 2007b, 2006, 2005, 2004, 2002). Evaluations in 2006 and 2008 both concluded that, while they did not discover any GWD cases, Chad could not be certified due to a lack of sufficient surveillance and documentation (Hopkins et al., 2011, 2018a;

WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2009, 2010, 2011).

7. Reemergence and Response

In 2010, Chad reported its first human GWD cases after a ten-year absence (Djidina et al., 2011). However, it is likely transmission was still occurring undetected at low levels due to insufficient surveillance, which was later supported by a retrospective phylogenetic analysis of worms (Durrant et al., 2020; Hopkins et al., 2011). As more cases were reported in the following years, a "peculiar epidemiology" was observed (Eberhard et al., 2014). Cases were not associated with breakouts surrounding an infected water source as typically seen with a water-borne disease. Furthermore, investigators could not determine common water sources for infections (Eberhard et al., 2014). From 2010-2012, there were 30 human cases reported, with the majority from different villages and not reoccurring in the same village the year after (Eberhard et al., 2014; Hopkins et al., 2013, 2011; Ruiz-Tiben et al., 2012). Additionally, there was a lower number of emerging worms per person (average of 1.27 from 2010-2012) than in other endemic countries (e.g., Ethiopia: 1.96; Mali: 1.7) (Eberhard et al., 2014).

However, one of the most distinct differences in the current transmission in Chad was the rise of cases in domestic dogs. There are numerous historical reports of natural *Dracunculus* infections and experimental infections in domestic dogs, so this occurrence was not a novel host jump (Gaiger, 1910; Lalitha and Anandan, 1980; Leiper, 1910; Manson and Aberd, 1895). Notably, some of these historical cases were identified morphologically and with similar clinical presentation as *Dracunculus medinensis* but were not genetically confirmed. However, infections in dogs were sporadic and believed to be spill-over infections from humans, as they generally disappeared when, or soon after, infections in humans were eliminated (Cairncross et al., 2002). The first report of a dog infection in Chad occurred in 2012. Surveys of dog owners inside the endemic area in 2012 stated they were aware of Guinea worm infections in dogs; however, these infections were new within the past few years (Eberhard et al., 2014). Since then, Chad dog infections have outnumbered human cases in Chad and continued to grow until outnumbering the global human cases in 2015 (Eberhard et al., 2014; Hopkins et al., 2015). However, it is critical to note that improved surveillance likely plays a role in increased reports. The first report of an infection in a domestic cat occurred in 2013 and has continued to rise. Since 2010, global human cases have continued to decrease while cases in Chad have remained relatively stable, except for 2019 when a water-borne outbreak occurred in the Salamat region of Chad for the first time since 2010 (Guagliardo et al., 2022; Hopkins et al., 2020). Table 1.1 provides a summary of GW infections in each host since 2010 along with the number of active surveillance villages in Chad.

Phylogenetic studies were conducted because of the belief that independent cycles could occur in humans and dogs. Those data showed that all *D. medinensis* from humans and wild and domestic mammals were the same parasite species (Thiele et al., 2018; Durrant et al., 2020). Additionally, genetic variation within *D. medinensis* follows a spatial pattern, with worms, regardless of host, clustering into an East African group (Ethiopia and South Sudan), West African group (Mali, Ghana, and Côte d'Ivoire), and a Chad group. Chad and East African samples were more closely related and showed a higher genetic diversity, but also showed a decline in population size likely due to eradication efforts. This higher level of genetic diversity in Chad, combined with the lack of a population bottleneck, supports that transmission was occurring undetected in Chad from 2000-2010 (Durrant et al., 2020; Thiele et al., 2018).

TABLE 1.1. Reported global human infections, Chad infections across hosts, and Chad villages under active surveillance, 2010-2022

Year	Global human cases	Human	Dogs	Cats	Chadian villages under Active Surveillance	Reference
2010	1,797	10	0	0	0	Hopkins et al., 2011; Ruiz-Tiben et al., 2012
2011	1,058	10	0	0	42	Hopkins et al., 2013; Ruiz-Tiben et al., 2012
2012	542	10	27	0	693	Hopkins et al., 2013; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2015a
2013	148	14	54	1*	703	Hopkins et al., 2014; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2015a
2014	126	13	113	1*	756	Hopkins et al., 2015
2015	22	9	503	5	1,015	Hopkins et al., 2016
2016	25	16	1,011	11	1,799	Hopkins et al., 2017
2017	30	15	817	13	1,860	Hopkins et al., 2018b
2018	28	17	1,040	25	1,895	Hopkins et al., 2019
2019	54	49**	1,935	47	2,211	Hopkins et al., 2020
2020	27	13**	1,508	63	2,332	Hopkins et al., 2021
2021	15	8	767	64	2,309	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022a Fultz, personal communication
2022	9***	6***	453***	58***	Unknown	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022b, 2022c

* Exact cat infection numbers are not known for 2013 and 2014. It is known that there were 32 infected domestic cats from 2013-2017 (Hopkins et al., 2018a).

** One case was reported from Cameroon in both 2019 and 2020 in villages near the Chad-Cameroon border. These infections are believed to have been acquired in Chad and have been added into the Chad total.

*** Provisional as of 11/21/2022

By the end of 2010, the Chadian Ministry of Public Health (MSP) and WHO had requested aid from the CDC to begin active surveillance, evaluate and increase public knowledge on dracunculiasis, and identify at-risk areas (Djidina et al., 2011). Villages were categorized as levels 1, 2, or 3 based on transmission and risk factors. Level 1 villages have consistently reported transmission since 2010 and include the areas around the Chari River and its tributaries. Village volunteers conduct household searches 3-4 times per week. Level 2 villages are those where transmission is not considered endemic, and there are ≤ 10 cases reported (considered to be caused by importation from endemic areas). Level 2 villages are typically adjacent to level 1 villages and share roads and water sources. Villagers may frequently move between them. Level 3 villages are considered at risk for importation of GW but have never reported a case. They rely on passive reporting through the MSP. Villages under levels 1 and 2 are considered to be active surveillance villages (See Table 1.1 for the number of active surveillance villages since 2010). Regardless of level, all villages receive health education on dracunculiasis, though the intensity and distribution of the information do differ. Additionally, all individuals can receive a cash reward for reporting a suspected case, which is investigated within 24 hours at all levels. Cash rewards vary from 10,000-50,000 CFA, equal to approximately 15-80 USD, depending on the type of case (animal vs. human), time of reporting (before vs. after worm emergence), and who reports it (self vs. informant). Periodic evaluations of cash reward awareness and dracunculiasis education are done at all levels. Differences in levels can be seen in the intensity of surveillance. Villages in level 1 and 2 have household screenings and training of Chad GWEP staff. Villages in level 1 have an additional supervision unit (Guagliardo et al., 2020).

Information is collected for every suspected case, including: name, age, sex, ethnicity, village, GPS coordinates, occupation, travel history, date of worm detection, date of worm emergence, date of worm extraction, date admitted and discharged from the health center, location of emergence, number of worms emerged, late detection of the lesion, late or irregular bandaging, whether worm was initially confirmed by supervisor, case and worm containment (yes/no), contamination of water (yes/no), case importation from another region (yes/no), availability of potable water in the village (Guagliardo et al., 2021a). All suspected worms are extracted manually and sent for confirmatory testing. Worms are visually inspected in Chad and preserved before being sent to the CDC. All worms that emerged from humans are further tested at the CDC by morphological investigation followed by PCR analysis if necessary. Worms from animals are selectively tested due to the large volume. Due to this, the Chad GWEP does not require canine cases to have been laboratory-confirmed, but they must be verified as *D. medinensis* by a supervisor in Chad (Guagliardo et al., 2020).

A human case is classified as 'contained' if it meets the following criteria (Hopkins et al., 2017):

- Investigation of human infection occurs within 24 hours of worm emergence
- The individual has not entered any water source since worm emergence
- The individual has been properly cared for by a village volunteer or health care provider
- The lesion has been satisfactorily cleaned and bandaged until all worms have been removed
- Health education has been provided to encourage the individual to not enter any water source
- The entirety of the containment process is validated by a GWEP supervisor within 7 days of worm emergence

- Temephos is applied to any potentially contaminated water source

The exact criteria to classify a dog infection as contained has changed over the years. However, currently, the infection must meet the following criteria (Guagliardo et al., 2020):

- Investigation of dog infection occurs within 24 hours
- The dog was tethered and not allowed to enter any water source until infection symptoms have dissipated and wound has healed
- Supervisor confirms the worm as GW and inspects the containment process within 7 days of worm emergence

8. Transmission in domestic animals

The traditional infection route (drinking contaminated water) cannot explain the high number of dog infections. The drinking behavior of dogs (lapping) does not allow for adequate ingestion of copepods, especially when considering infected copepods remain at the bottom of the water column (Garrett et al., 2020). This, along with the unusual pattern of infections, led to the proposal that a paratenic or transport host (likely with an aquatic lifestyle, e.g., fish, frog, etc.) was potentially involved in the life cycle (Eberhard et al., 2014). Paratenic hosts are known to be involved with other *Dracunculus* species, so this seemed a reasonable hypothesis for the unusual epidemiology in Chad. Additionally, it has been suggested that the main route of *D. insignis* infection of raccoons is through an amphibian paratenic host or fish transport host (Crichton and Beverley-Burton, 1977).

Generally, in regards to parasites, the terms transport host and paratenic host refer to a host that carries a parasite in between hosts but is not involved in the lifecycle (i.e., no parasite development occurs). A transport host refers to a host who does not acquire an infection, while a paratenic host does acquire an infection. They may benefit the parasite by providing a place to survive unfavorable environmental conditions or increase the probability of reaching the DH. However, paratenic host and transport host are often used synonymously. In the context of *Dracunculus*, the definition of transport host is more strict. It refers to hosts who have consumed infective larvae within copepods, but the larvae do not leave the gastrointestinal tract. Infection can be possible if the definitive host consumes the transport host while infective larvae pass through the gastrointestinal tract. Paratenic host refers to hosts who have consumed infective larvae, whose larvae leave the gastrointestinal tract and travel to the musculature, and whose infective larvae in the musculature can then be consumed by a definitive host.

8.1. Transport hosts and D. medinensis

Fish are well known predators of copepods (Piasecki et al., 2004). Historical records show Moorthy (1932) was able to recover live, active larvae from *Barbus puckelli* [now *Puntius bimaculatus*] intestines 12 hours after introducing infected copepods to a tank. There are several occurrences of dracunculiasis in people with no travel history in non-endemic areas, and this was believed to have occurred because of the consumption of infected loaches (Hashikura, 1927; Kobayashi et al., 1986; Wang et al., 1995). However, this was considered a rare transmission pathway and not of concern in endemic African countries. In fact, it was postulated that introducing fish into water sources could reduce infections, as fish would consume the infected larvae instead of people (Moorthy and Sweet, 1936b). Using *D. insignis* as an experimental model, exposures of fish (Nile tilapia [*Oreochromis niloticus*] and fathead minnow [*Pimephales promelas*]) to infected copepods and then feeding them to domestic ferrets (*Mustela putorius* *furo*) proved this theoretical route of transmission. Similarly, experimental exposure of fish (mosquitofish [*Gambusia affinis*]) has shown they can also serve as transport hosts for *D. medinensis* transmission to domestic ferrets (Cleveland et al., 2017). Experimental research has shown fish consume more copepods than frogs on average and thus may be more at risk for becoming infected (Box et al., 2021a; Eberhard et al., 2016b). No field-based research has sampled the GI tract of fish for L3. No field-based research has found L3 in the GI tract of amphibians, though 88 frogs have been studied in Chad (Eberhard et al., 2016a).

8.2. Paratenic hosts and D. medinensis

Experimental infections of anurans (*Rana [Lithobates]* spp. and *Xenopus laevis* [African clawed frog]) with *D. insignis* proved their competency as paratenic hosts for transmission to raccoons and domestic ferrets, *D. ophidensis* to common garter snakes (*Thamnophis sirtalis*) and northern water snakes (*Nerodia sipedon*), and *D. medinensis* to domestic ferrets (Brackett, 1938; Crichton and Beverley-Burton, 1977; Eberhard et al., 2016b; Eberhard and Brandt, 1995). The length of time a paratenic host remains infected is unknown, but multiple experimental studies have shown that *D. insignis* L3 can persist in anurans through metamorphosis (Box et al., 2021b; Eberhard and Brandt, 1995). A single *D. medinensis* L3 was recovered from an African clawed frog two months post-infection and *D. insignis* L3 were recovered from African clawed frogs for up to 8 months post-infection (Box et al., 2021b). It is unknown if a paratenic host can become infected from consuming another infected paratenic host. One experimental trial failed to recover infective larvae from African clawed frogs after administering infective larvae recovered from other experimentally infected paratenic hosts (*Hyla chrysoscelis* and *Synodontis eupterus*), though this experiment had a small sample size (n=2) (Box et al., 2021b). The recovery of L3 from the musculature of wild fish has proven to be difficult, despite sampling 234 fish in Chad (21 species) and 68 fish (1 species) in Georgia, USA (Cleveland et al., 2019, 2020a). Field studies have recovered *D. medinensis* L3 from crowned bullfrogs (*Hoplobatrachus occipitalis*) and puddle frogs (*Phrynobatrachus francisci*) in Chad (Cleveland et al., 2019; Eberhard et al., 2016a). Additionally, *D. insignis* L3 have been recovered from wild-caught American bullfrogs (*Rana [Lithobates] catesbeiana*) and Southern leopard frogs in Georgia, USA (Cleveland et al., 2020a).

Experimental infections have recovered *Dracunculus* larvae from either the intestines or musculature from several other species, although transmission to definitive hosts have not been proven. Experimental infections have recovered *D. medinensis* and *D. insignis* L3 from green frogs (*Rana [Lithobates] clamitans*). *Dracunculus medinensis* L3 have been recovered from Cope's gray treefrog (*Hyla chrysoscelis*), American toad (*Bufo americanus*), African clawed frog, and featherfin catfish (*Synodontis eupterus*). *Dracunculus insignis* L3 have been recovered from African clawed frog, Northern leopard frog (*Rana [Lithobates] pipiens*), Southern leopard frog (*Rana [Lithobates] sphenocephalus*), Nile monitor (*Varanus niloticus*), green anole (*Anolis carolinensis*), white sucker (*Catostomus commersonii*), and rainbow trout (*Oncorhynchus mykiss*) (Box et al., 2021b; Crichton and Beverley-Burton, 1977; Eberhard et al., 2016b).

9. Current Epidemiology in Chad

The current epidemiology seen in Chad is not only different from other endemic countries but also different from what was seen in Chad historically. No cases were reported from the Chari Baguirmi Region after 1993 until the re-emergence of cases in 2010 (Eberhard et al., 2014). This is in contrast to human cases from 2010-2018, where 35.9% were from the Chari

Baguirmi Region, followed by Moyen Chari at 31.1% (See Figure 1.1 for a map of the distribution and frequency of current human cases) (Guagliardo et al., 2021a). The two highest regions for dog infections from 2015-2018 are reversed, with 41.9% from Moyen Chari and 38.1% from Chari Baguirmi (Guagliardo et al., 2020). This order is also the same when analyzing the number of emerging worms (dog infections presenting with multiple worms), with 41% from Moyen Chari and 34% from Chari Baguirmi (Guagliardo et al., 2021b). While cases and dog infections occur in the same geographic area (along the Chari River), they do not generally occur in the same villages (Eberhard et al., 2014; Guagliardo et al., 2021a, 2020; Hopkins et al., 2013). Note that transmission is not likely to occur from water directly in the Chari River but in the lagoons that form at the end of the dry season and small ponds in villages (Eberhard et al., 2014).

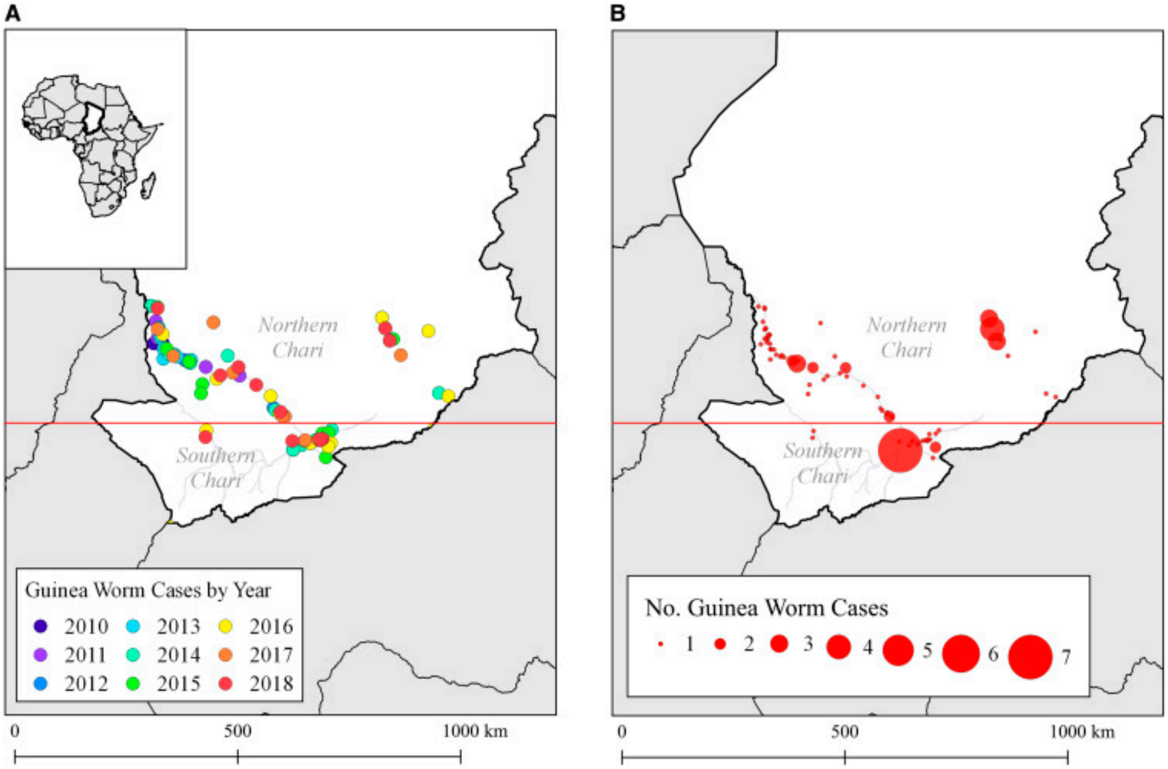

FIGURE 1.1. Distribution and number of human Guinea worm cases 2010-2018. The dark red line distinguishes the northern Chari area and the southern Chari area. From Guagliardo et al., 2021a.

Additionally, there is a lower number of infected people per village than previously reported. From 1995-1997, there were 3.0 infected people per village in Chad compared to 1.15 people per village from 2010-June 2013 (Eberhard et al., 2014). Furthermore, there has been a change in the seasonality of transmission. In the 1990s, the peak transmission season in western Chad/Northern Chari River area was January-March (Eberhard et al., 2014). In contrast, peak human cases in the same area from 2010-2018 occurred in April and August, with a higher peak in August (See figure 1.2) (Guagliardo et al., 2021a). No strong seasonal pattern of human cases in eastern Chad/Southern Chari River area was observed from 2010-2018 (Guagliardo et al., 2021a). Most dog infections from 2015-2018 occurred in March-August and peaked in June

(Guagliardo et al., 2021b, 2020). This seasonality was not observed for the Mandoul region of southern Chad, which peaked in October (Guagliardo et al., 2020).

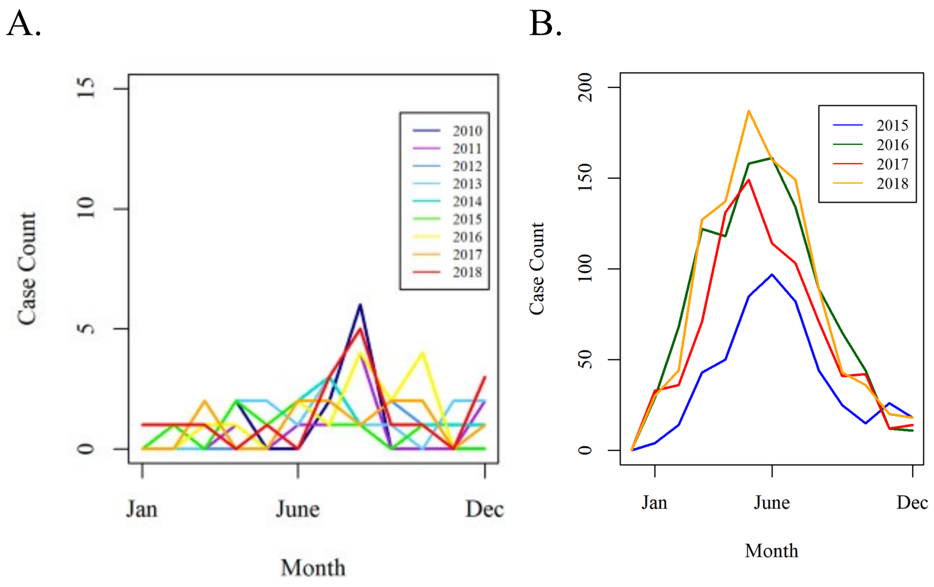

FIGURE 1.2. Guinea worm cases in humans (A) and canines (B) by month and year. (A) From Guagliardo et al., 2021a (B) From Guagliardo et al., 2020.

From human cases from 2010-2018, 65.8% of cases occurred in people 30 years or younger, and the average age of an infected person was 26 years. There was a relatively even distribution between male and female infected people (50.9% female; 49.1% male). When comparing the occupations of infected humans (data from 2010-2018) and humans who owned an infected dog (data from 2015-2018), it is clear that most cases are associated with farming-related occupations. Of the human cases, 34.2% of patients had a farming-related occupation. Of the dog infections, 73.5% were owned by people in a farming-related occupation. Of the human cases, 13.2% of patients had a fishing-related occupation. Of the dog infections, 17% were owned by people in a fishing-related occupation. However, 74% of dogs lived in fishing villages. Infected dogs were used for guarding homes (92%), hunting (40%), or both (~33%) (Guagliardo et al., 2021a, 2020). It is important to note here that while farming and fishing may appear risky for GW infection, most people in this area are involved in these occupations. The exact numbers are unknown, as uninfected individuals are not surveyed for GW. However, from a survey evaluating the effectiveness of the GW surveillance system, 468 villagers were surveyed across 45 active surveillance villagers, and 73.7% identified themselves as farmers (Rubenstein et al., 2021). Therefore, identifying occupations that may put an individual at risk for GWD is difficult without complete information on those not infected. However, while there was only one infection of a nomadic pastoralist, this occupation and other traveling occupations may pose a significant risk of transmitting GW. There are an estimated 400,000- 2 million nomadic pastoralists in Chad. While only 7% of GW patients reported traveling during their infection, 37.5% had uncontained infections (compared to containing 63.4% of cases in active surveillance villages). Thus, frequent travelers not only pose a risk of contaminating water sources and transporting GW to non-endemic areas, but they also may be less likely to be diagnosed or have infections documented due to their lifestyle (Guagliardo et al., 2021a).

In Chad, the mean number of dogs owned per owner was 2.3, and owners reported a previous infection the year before in only 12.6% of dogs (Guagliardo et al., 2020). However, dogs with previous GW infections were more likely to present with a higher number of emerging worms (Guagliardo et al., 2021b). Humans and dogs report similar mean numbers of emerging worms per case; however, dogs have a much higher variance. Humans reported a mean of 1.5 worms per case from 2010-2018, with 27.2% of cases presenting with multiple worms ranging from 1-9 (Guagliardo et al., 2021a). Dogs had an average of 1.9 worms per infection from 2015-

2018, with 38.5% of infections presenting with multiple worms ranging from 1-79 (Guagliardo et al., 2021b, 2020). Increased worm burden was associated with a decreasing number of dogs owned, potentially due to contaminated food shared by more dogs or an issue in surveillance methods (as those who own many dogs may not notice if one is infected). While 74% of infected dogs lived in fishing villages, increased worm burden was negatively associated with living in a fishing village. Univariate models showed that increased worm burden was negatively associated with farming and hunting occupations. Therefore, dog worm burden is associated with both household and owner traits (Guagliardo et al., 2021b). Interestingly, dogs located in the same village seem to be encountering multiple uncontained infections, as those with multiple emerging worms also frequently exhibited multiple maternal parasite lineages (Thiele et al., 2018).

Although various paratenic and transport hosts have been identified experimentally and in the field, it is difficult to determine how a particular dog became infected (i.e., ingestion of water or a possible paratenic/transport host). Furthermore, the primary transmission routes to Chad dogs may differ in other countries (i.e., paratenic or transport hosts may occur more in Chad for some ecological reason). Chad has consistently reported the majority of global dog infections. For example, Chad reported 1,508 dog infections in 2020, which was 98.9% of the global dog infections (Hopkins et al., 2021). Additionally, infections in Chad are clustered around the major river systems, while infections in Ethiopia cluster around villages. Similarly designed studies tracking dog movement and diet in Chad and Ethiopia have provided insight into the potential importance of different transmission pathways in each country. In Chad, dogs with poor body conditions spent more of their time near ponds, while the opposite was observed in Ethiopia. Dogs in both Chad and Ethiopia spent their time at a minority of the total ponds detected, with most pond visits being close to their household. Dogs in both Chad and Ethiopia spent less time near ponds if their owners provided water for them. Also, Chad dogs were less likely to have had an infection if water was provided for them. The opposite was observed in Ethiopia, where dogs that received water frequently (> 4 times a day) were more likely to have had a previous infection. This was believed to be due to education after a dog's infection that providing water would reduce the likelihood of future infections. Water provided to dogs in Ethiopia comes from a safe source and thus cannot be contaminated at the time of collection. Isotope analysis was performed on dog whiskers to analyze diet. In Chad and Ethiopia, most of the dog's diet was comprised of C4 plant food (e.g., maize, sorghum) followed by human feces. Other foods found were C3 plant food (e.g., potatoes, rice), fish, livestock, and other wild food (samples taken from amphibians, reptiles, birds, and mammals) (McDonald et al., 2020; Wilson-Aggarwal et al., 2020). This confirms a previous survey of Chad dog owners who reported it was most common for dogs and people to share "boule", a cooked grain-based paste (C4 plant food), followed by other food caught (fish, frogs, and reptiles). While people do not generally consume raw fish, frogs, or reptiles, dogs may consume/steal entrails left on the ground during food preparation. They also may steal fish left out to dry during the mass harvest at the end of the dry season (Eberhard et al., 2014). In Chad, dogs whose analysis showed higher fish diet proportions had a higher probability of infection, suggesting transmission via a paratenic or transport host may play a role in Chad dog infections. This correlation was not seen in Ethiopia, suggesting that the traditional transmission pathway should be of more concern in Ethiopia (McDonald et al., 2020; Wilson-Aggarwal et al., 2020).

The water-borne outbreak in Chad in 2019 had a much longer timeframe than other outbreaks in Ethiopia. This outbreak infected 20 people and two dogs and is the first record of a single worm resulting in infections of both humans and dogs. Emerging worms were traced back through the maternal lineage and emerged over 147 days. In comparison, outbreaks in Ethiopia in 2017 and 2020 lasted 103 days and 25 days, respectively. Although not proven, the involvement of a paratenic host in this outbreak could have extended the lifecycle and explained the longer timeframe (Guagliardo et al., 2022).

From 2013-2017, 19.1% of villages in Chad reported a dog infection. Villages across Chad did not report a consistent number of infections. However, infections generally increased over time, likely due to increased infections and more effective surveillance and education. The number of healthcare supervisor visits was an important covariate for predicting villages with dog infections using boosted regression tree models, supporting that improved surveillance has identified more infections. Other demographic and geographic variables were also identified, such as dog population size, whether the village was a fishing village, the standard deviation in elevation, and mean annual precipitation (Richards et al., 2020). Within Chad, two subpopulations of *D. medinensis* exist, located north and south of Manda National Park (located to the west of Sarh, Chad). These subpopulations are defined more by geographic origin rather than DH species (Thiele et al., 2018). Interestingly, the predictor variables change when accounting for subpopulations in the previously described model. In the northern subpopulation, identity as a fishing village and elevation standard deviation were most important. In the southern subpopulation, mean annual precipitation and mean temperature of the driest quarter were most important. The difference in the importance of the identity of a fishing village between regions may indicate a difference in the primary transmission route. The northern region may rely more heavily on dogs consuming fish entrails, while the southern region may rely more on the seasonal stagnant water sources relating to precipitation. Identification of predictor variables, both on a broad and regional scale, supports the GWEP in identifying potential at-risk villages to aid control efforts (Richards et al., 2020).

To better understand the potential importance of paratenic and transport hosts in transmission, Gonzalez Engelhard et al. (2021) modeled the population dynamics of *D. medinensis*, copepods, fish, dogs, and humans. Their model was the first to include a transport or paratenic host and supported the hypothesis that the GWD transmission cycle, to some degree, involves fish and frogs. The data suggested that increasing the proportion of people that bury the fish entrails from the current 81% to about 90% would significantly disrupt the dog cycle, causing a sharp decline of canine GWD and eventually leading to GWD elimination. Although, it is important to remember that transmission cannot occur without infected copepods. Along those lines, Ghosh et al. (2018) concluded that increasing copepods' mortality would significantly contribute to GWD elimination. Finally, as noted by Ghosh et al. (2018), the containment of infected dogs is also an effective way to further reduce GWD incidence because limiting dog access to water during worm emergence would decrease the number of infected copepods.

Therefore, all these data combined suggest that dogs are serving as a maintenance host for GW transmission in Chad, causing spill-over infections in humans and posing a challenge for the eradication initiative. The CGWEP has implemented several intervention strategies explicitly targeted at reducing dog infections. Around 2014, the CGWEP encouraged villagers to fully cook their fish, bury fish entrails, prevent dogs from consuming fish entrails, and tether their infected dogs until the worm has fully emerged (Hopkins et al., 2015). Additionally, CGWEP staff can aid in controlled immersions, where water is poured over the lesion or the lesion is submerged to allow for the safe disposal of contaminated water (Guagliardo et al., 2020). Encouraging owners to provide water for their dogs may help reduce dog infections (McDonald et al., 2020). Furthermore, metal containers are the optimal material to provide water (compared to plastic, glass, and gourd), as this material speeds copepod mortality (Cleveland et al., 2020b). These actions have helped increase containment of dog infections in Chad from 75% in 2017 to 81% in 2020 (Hopkins et al., 2021, 2018b).

Multiple anthelmintic drugs have been administered to dogs in Chad, but none have been successful at reducing infections (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2017, 2018a). Flubendazole has recently been investigated as a potential drug to interrupt transmission. Laboratory ferret trials showed promising results, but prevention was not observed during Chad dog trials (Cleveland et al., 2022). However, the ferrets received a higher dose during a shorter period, so more studies on dogs with higher doses or decreased treatment intervals are needed.

10. History in Wildlife

Historically, GW has been recorded from numerous wildlife hosts. However, these records are difficult to understand for many reasons, including lack of molecular confirmation (unavailable then), incomplete morphological details, and lack of details on the host or host taxonomy changes, among others. Assuming that identifications are reliable, natural GW infections have been reported in several mammalian hosts: horses (*Equus caballus*), cattle (*Bos taurus*), donkey (*Equus asinus*), chinkara (*Gazella bennettii*), jackal (no species provided), Egyptian wolf (likely referring to what is now the African wolf, *Canis lupaster*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), Asian small-clawed otter (*Aonyx cinereus*), green monkey (*Chlorocebus sabaeus*), rhesus monkey (*Macaca mulatta*), grivet monkey (*Chlorocebus aethiops*), and a hamadryas baboon (*Papio hamadryas*) in captivity (Leiper, 1910;

Muller, 1971; Turkhud, 1920). There is one recent report of an emerging worm from a donkey in Mali, but no detailed information could be obtained (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2016a). Most of these reports are observations of emerging worms and could represent other filarial parasites. For example, the CDC received 92 animal worms for diagnosis in 2020 and only 43 were confirmed as *D. medinensis*. Other parasitic nematodes received included *Dirofilaria* sp., *Filaria* sp., *Physaloptera* sp., *Protospirura* sp., *Skrjabinodera* sp., *Spirocerca* sp., spirurid nematodes, and *Toxocara cati* (Hopkins et al., 2021).

In addition to mammalian hosts, adult *Dracunculus medinensis* has been reported from several reptile hosts, including the Indian cobra (*Naja naja*) [reported as Yellow spectacled cobra *Naia tripudiens*] and several individuals of a *Varanus* species (Mirza and Basir, 1937; Turkhud, 1920). However, recent work suggests these likely were not GW. Large subcutaneous worms recently recovered from *Varanus niloticus* in Chad were not *Dracunculus medinensis*, but were most similar to *Ochoterenella* species (Cleveland et al., 2019). Additionally, there are numerous other *Dracunculus* species recognized now that could have been misidentified as *D. medinensis* that infect snakes (*D. coluberensis, D. alii, D. houdemeri, D. doi, D. dahomensis, D. oesophageus, D. mulbus, D. ophidensis,* and *D. brasiliensis*) and chelonians (*D. globocephalus*) (Cleveland et al., 2018). Interestingly, the case of the cobra involved experimental infection. A cobra was bought locally and brought to the Bombay Bacteriological Laboratory, where a worm was observed emerging from a swelling on the head after seven months. The worm was approximately 12cm long by 1mm wide, white, and excreted embryos that resembled Guinea worm but were smaller. These embryos were used to infect copepods fed to six other cobras. Three other cobras were fed copepods infected from human guinea worm, though no description was provided on how these worms were acquired. All of the cobras died, but a 3 cm x 1 mm worm was recovered after 2.5 months from a cobra fed cobra-infected copepods, and five worms (four 2 cm long; one 4 cm long) were recovered after 10 months from a cobra fed human-infected copepods (Turkhud, 1920).

Multiple experimental trials on non-human primates have had varying degrees of success. In the early 1900s, Leiper fed a monkey (no species provided; believed to be a species of vervet [*Chlorocebus* spp.] by Muller [1972]) a banana containing infected cyclops and recovered three immature females (not gravid; approximately 30cm in length) and two males (approximately 22mm) six months post-infection (Leiper, 1907). A silvery gibbon (*Hylobates moloch*) was infected through larvae obtained from a human infection, and an adult female GW was recovered (Brug, 1930). Marjitno and Essed (1938) were unable to infect a long-tailed macaque (*Macaca fascicularis*), though only nine larvae were used. Fairly and Liston (1924b) were unable to infect 22 toque macaques (reported as *Macacus sinicus;* now *Macaca sinica*), despite varying feeding delivery techniques and the number of copepods given. The most recent non-human primate experimental trials were performed by Muller (1972, 1968b) using larvae from a human infection to infect rhesus macaques (*Macaca mulatta*). Muller retrieved larvae from the macaque's emerging worms and used them to infect other non-human primates. Emerging worms were also recovered from 1 of 2 grivet monkeys (*Chlorocebus aethiops*). Worms were recovered upon necropsy of a single patas monkey (*Erythrocebus patas*) and a single olive baboon (*Papio anubis*) exposed and necropsied before allowing time for worm emergence. Of 33 attempted infections and reinfections of 15 monkeys (14 rhesus and 1 grivet), 19 were successful. Females emerged an average of 345 days post-infection. An average of 4.8 females emerged from those that developed infections. The number of larvae administered varied widely from 17-517, though the minimum number of larvae administered to an infected primate was 36. A rhesus monkey has also been shown to be susceptible to *D. insignis* (Crichton and Beverley-Burton, 1976).

10.1 Summary of recent D. medinensis cases in wildlife with more complete morphological data and/or molecular confirmation

Recent reports of GW from wildlife are primarily in wild felids in Chad and baboons in Ethiopia (Table 1.2). Information on wildlife infections comes mainly from the Carter Center's regularly published Guinea Worm Wrap-Up's. Additionally, other published manuscripts typically do not include information on wildlife infections. While Ethiopia typically provides all relevant information (location, date, and number) on baboon infections in the wrap-ups, fewer details on infections in Chad are generally available (i.e., a location and date are not usually provided).

In Ethiopia, the first recent natural wildlife case was reported in an olive baboon in 2013 (Table 1.2). Since this event, Ethiopia has regularly reported at least one case annually except for 2021. These infections have been reported from the same endemic region and are likely due to the same few troops re-infecting water sources. Around 2019, the Ethiopia Dracunculiasis Eradication Program began attaching telemetry collars to individuals to better understand troop movement, locate potentially contaminated water sources, and treat them with Abate (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2019a). Nine troops have been tracked since this research began (WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022b).

In Chad, all confirmed wildlife infections have been in wild felids, except a new host in 2022 that is still being identified (Table 1.2). The term "wild cat" is used non-specifically and could refer to an actual wildcat (*Felis lybica*), or another wild felid (e.g., serval, caracal, etc.); typically, specific host information is not provided. Occasionally, these “wild cat” infections are noted as provisional with no later confirmation found, so their status is unknown. Adam Fultz has been a help in sending line listings of all infections in Chad, which usually confirms the date and location of these wildlife infections. However, the lack of releasing complete reports on these infections leads to an inadequate and deficient understanding of the situation in Chad.

TABLE 1.2. Summary of recent *D. medinensis* wildlife infections

Species	**Location**		**Date**	**Number**	**Reference**
	Broad (Country; Region)	Specific (Wareda/District; Kebele/Ward; Village)			
Olive baboon (*Papio anubis*)	Ethiopia; Gambella	Gog; Atheti; Utuyo	August, 2013	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2015b
		Gog; Atheti; Ablem	August, 2014	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2015b
		Gog; Atheti; Ablem	June, 2015	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2015b
		Gog; Atheti; Abawiri	2016	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2017, 2016b
		Gog; Unknown; Unknown	2016	1	
		Gog; Atheti; Ablen	January, 2017	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2018b
		Gog; Atheti; Wichini	April, 2017	1	
		Gog; Atheti; Abawiri	June, 2017	1	
		Gog; Gog Dipach; Duli	June, 2017	1	
		Gog; Atheti; Ablen	August, 2018	1	WHO Collaborating Center for Research, Training and Eradication of

					Dracunculiasis, CDC, 2018c
		Gog; Unknown; Akweramero Farm	June, 2019	3	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2019b
		Gog; Unknown; Akweramero Village	June, 2019	1	
		Gog; Unknown; Lel Anyaro	June, 2019	1	
		Gog; Gog Dipach; Duli	June, 2019	1	
		Gog; Atheti; Ablen	March 2020	1	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2020
		Gog; Atheti; Ablen	July, 2020	1	
		Gog; Atheti; Wichini	August, 2020	1	
		Gog; Gog Dipach; Duli	May, 2020	1	
		Abobo; Unknown; Gutok	August, 2022	2	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022b
Leopard (*Panthera pardus*)	Ethiopia; Gambella	Gog; Unknown; Aregawi Farm	August, 2019	1*	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2019b

Species	**Location**		**Date**	**Number**	**Reference**
	Broad (Country; Province)	Specific (District; Zone; Village)			
Wildcat (*Felis lybica*)	Chad; Unknown	Exact location unknown. Believed to be along the Chari river south of Guelendeng	2014	2	Eberhard, personal communication Hopkins et al., 2018a
Serval (*Leptailurus serval*)	Chad; Salamat	Haraze; Ambissirigne; Ambissirigne	June, 2019	1	Fultz, personal communication
	Chad; Moyen Chari	Kyabe; Marabe; Marakouya 2	March, 2020	1	Fultz, personal communication
Undetermined wild felid	Chad; Moyen Chari	Sarh; Banda; Kemrimbe	June, 2021	1	Fultz, personal communication
	Chad; Salamat	Haraze; Ambissirigne; Ambissirigne	July, 2018	1	Fultz, personal communication
Small mammal-omnivore (Still being identified)	Chad; Salamat	Haraze; Ambissirigne; Goz Tougoula	June 19, 2022	1*	WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022b

* Found under skin, not emerged

Overall, the emergence of infections in dogs, cats, and wildlife has highlighted the need for a One Health approach to dracunculiasis eradication. Surveys of Chadian villagers determined the most noted prevention strategy was proper disposal of fish entrails and proper cooking of aquatic animals, suggesting that CWEP volunteers and supervisors may need to re-emphasize the more traditional prevention techniques (drinking safe water and filtering unsafe water). There was a disconnect between how often villagers reported being visit by volunteers and how often volunteers reported visiting villagers, with some villagers reporting they had never been visited by volunteers. However, villagers that owned dogs reported being visited by volunteers more frequently than those that did not, suggesting that volunteers may be biasing their searches towards dog owners in hopes of discovering worms rather than equally searching the entire village (Rubenstein et al., 2021). The continuing implementation and strengthening of health education to villagers on both human and animal infections, preventative measures, signs and symptoms, and treatment, combined with utilizing knowledge of geographic, topographic, and environmental predictors for infections is paramount.

11. Use of game cameras in wildlife management

Game camera technology has come a long way since its first uses to document wildlife in the late 1800s. George Shiras was the first to develop a system where wildlife would photograph themselves using a trip wire and flash system in the 1890s. Frank Chapman was the first to utilize remote cameras in a solely scientific context to document species presence, differentiate individuals, and note animal behavior in Panama in the 1920s (Kucera and Barrett, 2011). Since then, the number of studies has increased significantly, and technology has advanced considerably since the production of commercial camera traps in the 1990s. Cameras have been used to study many aspects of wildlife, such as activity patterns, the presence of rare and elusive species, nest ecology, species richness, occupancy, abundance, density, survivorship, and more. The main benefit of game cameras is that they allow for a noninvasive and less time-intensive method to study wildlife compared to trapping or direct observation. However, researchers must be aware of data loss that could occur because of failure to detect an animal due to vegetation, triggers when no animal is present, weather-induced mechanical problems, damage from people or animals, camera loss, or user error (Swann et al., 2011).

Specifically in Africa, the use of game cameras to study wildlife has increased in recent years. However, studies on non-protected land or desert and shrubland habitats focusing on human-wildlife conflict, poaching, and underrepresented taxonomic groups (small mammals, reptiles, and birds) remain understudied. In addition, there is a location bias for this research, as South Africa, Tanzania, and Namibia comprise over 50% of published camera trap studies. There has never been a published camera study in Chad. Additionally, most studies were on government-protected land (67%) or private reserves and sanctuaries (32%). Most studies focused on one species (45.3%) to characterize habitat use and species distribution (43%). Carnivores (86%) and herbivores (58%) were the most commonly studied species (Agha et al., 2018).

Estimating species abundance and density has long been used to monitor wildlife populations. However, monitoring abundance over large geographic and time scales requires a large amount of data, so long-term, financially expensive studies are needed. Thus, occupancy modeling was developed to evaluate the proportion of sites occupied. Due to study logistics, there are times when occupancy is a necessity and may be viewed as a proxy for abundance.

However, there are also studies where measuring occupancy is the ideal method, such as metapopulation dynamics, species distribution and range, invasive species monitoring, and disease dynamics (MacKenzie et al., 2018). It is important to remember that not detecting a species does not mean it is absent from the site. Occupancy modeling provides a framework for estimating the proportion of sites occupied by a species while managing non-detection bias by estimating a species' detection probability. The basic study design involves repeated visits to randomly selected sites within an area for a short time when detection/non-detection data is recorded. This detection data is used to estimate the probability of occupancy (ψ) and detection (p) using a maximum likelihood framework. Occupancy modeling relies on the following assumptions: the site is closed/there is no change in occupancy at the site during the study period (no emigration or immigration), species are not falsely detected when absent (false positives), and detection of a species at a site is independent of detecting that species at other sites (MacKenzie et al., 2002). The site closure assumption can be relaxed by expanding to a multi-season model that local extinction and colonization rates (MacKenzie et al., 2003). Occupancy and detection probability are assumed to be the same across all sites and occasions unless covariates are added to the model. Site covariates may vary among sites but not among occasions (e.g., elevation). Observation covariates may vary among sites and occasions (e.g., temperature). Since occupancy is assumed to not change over time, observation covariates cannot be used to account for changes in occupancy- only changes in detection (MacKenzie et al., 2002). The basic occupancy model with covariates is:

State model/Model for occupancy:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots$$

$$z_i \sim \text{Bernoulli}(\psi_i)$$

Observation model/Model for detection probability:

$$\text{logit}\left(p_{ij}\right) = \alpha_0 + \alpha_1 w_{ij1} + \alpha_2 w_{ij2} + \ldots$$

$$y_{ij} \sim \text{Bernoulli}(z_i * p_{ij})$$

Where:

ψ_i- the probability the species occurs at site *i*
x_i- value of site covariate at site *i*
z_i- binary presence/absence of the species at site *i*
p_{ij}- probability of detecting the species at site *i* on occasion *j*
w_{ij}- value of observation covariate at site *i* on occasion *j*
y_{ij}- species binary detection/non-detection data collected at site *i* on occasion *j*

12. Wildlife in Chad with respect to Guinea worm transmission

Table 1.3 below lists all species which may be relevant to Guinea worm transmission (carnivores and non-human primates) whose known range overlaps with the Sarh region of Chad. All individuals with a * are discussed more in detail in the following life history section.

Table 1.3. Wildlife species in Moyen-Chari, Chad that may be relevant to GW transmission

Family	**Species**	**Common name**	**Known host of Guinea worm?**
Canidae	*Lupulella adustus**	Side-striped jackal	No
	Lycaon pictus	African wild dog	No
	Canis lupaster	African wolf (previously called golden jackal and classified as *Canis aureus*)	No
	*Vulpes pallida**	Pale fox	No
Felidae	*Panthera leo*	Lion	No
	Panthera pardus	Leopard	Yes
	Acinonyx jubatus	Cheetah	No
	*Leptailurus serval**	Serval	Yes
	*Caracal caracal**	Caracal	No
	*Felis lybica**	Afro-Asiatic wildcat	Yes
Hyaenidae	*Crocuta crocuta**	Spotted hyaena	No
	*Hyaena hyaena**	Striped hyaena	No
Mustelidae	*Mellivora capensis**	Ratel/Honey badger	No
	Ictonyx striatus	Zorilla	No
	Aonyx capensis	African clawless otter	No
Viverridae	*Civettictis civetta**	African civet	No
	*Genetta genetta**	Common genet	No
	*Genetta maculata**	Rusty-spotted genet	No
Herpestidae	*Atilax paludinosus**	Marsh mongoose	No
	*Herpestes ichneumon**	Egyptian mongoose/ Ichneumon/ Large gray mongoose	No
	Herpestes sanguineus	Slender mongoose	No
	*Ichneumia albicauda**	White-tailed mongoose	No
	*Mungos mungo**	Banded mongoose	No
Primates	*Colobus guereza*	Guereza	No
	Papio anubis	Olive baboon	Yes
	*Erythrocebus patas**	Patas monkey	Experimentally
	*Chlorocebus tantalus**	Tantalus monkey	No, but other *Chlorocebus* sp. have been infected experimentally
	*Galago senegalensis**	Northern lesser galago	No

*12.1 Side-striped jackal (*Lupulella adustus*)*

The side-striped jackal is a medium-sized, grizzled, buff-brown-gray canid with a white side stripe (varies in distinctiveness) and a furry, black tail typically ending in a white tip. Categorized as Least Concern by the IUCN Red List, side-striped jackals have a broad geographic range covering most of sub-Saharan Africa except for the dry, arid areas of South Africa and most of the equatorial forest (Figure 1.3). Side-striped jackals favor well-watered woodlands and woodland mosaics but may also be found in cultivated areas, marshes, or peri-urban and urban areas. However, habitat use varies depending on the presence of other jackal species. The side-striped jackal utilizes grasslands when allopatric, and riverine and thicker vegetation areas when occurring sympatrically with other jackal species.

The side-striped jackal is omnivorous and opportunistic and feeds on small mammals (up to the size of a hare), birds, reptiles, insects, fruit (especially near farmland), carrion, and village offal. When near farmland, they have been observed to decrease time spent looking for preferred foods and instead use what is seasonally available by foraging through the crops. There is little data on side-striped jackals hunting domestic stock. Side-striped jackals are nocturnal, with activity peaks before dawn and after dusk. Side-striped jackals form monogamous, territorial mating pairs that may stay together for several years. Dens are modified from abandoned aardvark holes or termitaria, where 3-8 pups are born before or during the rainy season. Pups will disperse after they are independent (around one year), and the average life span in the wild is believed to be 3-4 years (Atkinson and Loveridge, 2004; Estes and Otte, 2012, pp. 408–410; Loveridge and Macdonald, 2013).

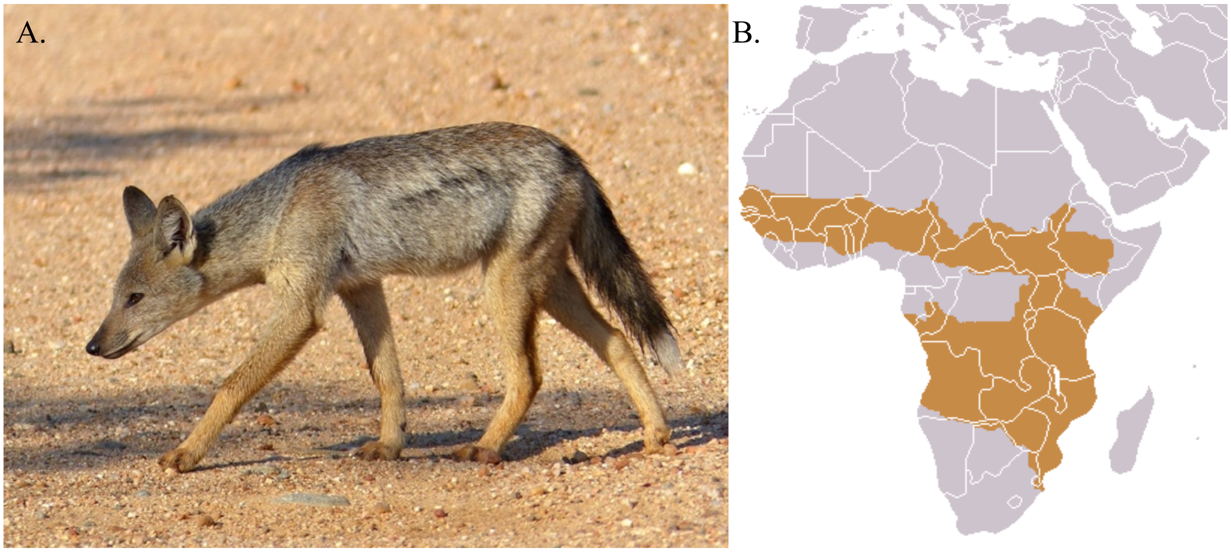

FIGURE 1.3. (A) Side-striped jackal (*Lupulella adusta*) from Kruger National Park (South Africa) (credit: Bernard Dupont, licensed by CC BY-SA 2.0). (B) Map showing distribution of side-striped jackal (credit: Chermundy, public domain).

*12.2 Pale fox (*Vulpes pallida*)*

The pale fox is one of the least studied canids in the world (Sillero-Zubiri, 2013, 2004), although they have recently been moved from Data Deficient to Least Concern by the IUCN Red List (Sillero-Zubiri and Wacher, 2012). The pale fox is a small canid with long legs and large ears. Their body is a sandy color transitioning to a white ventrum with a long (at least half the body length), bushy tail with a dark patch above the tail gland, and a black tip. The pale fox is one of the smallest canids in the world. However, recent body mass measurements from the Termit and Tin Toumma National Nature and Cultural Reserve (TTT) in eastern Niger were half of what was previously reported (1.0-1.5 kg compared to 2.0-3.6 kg), indicating body size may vary based on location and/or environmental factors (Sillero-Zubiri, 2004; Sillero-Zubiri et al., 2016).

Their distribution ranges across the semi-arid Sahel, with the southernmost of its range in Chad reaching Zakouma National Park. Some parts of their distribution reach the moister parts of Guinean savannahs (Figure 1.4). The pale fox may take advantage of the more abundant resources near cultivated areas (Sillero-Zubiri, 2013, 2004; Sillero-Zubiri and Wacher, 2012). Modeling the distribution of pale foxes in Niger showed that occurrence was most affected by precipitation (they were not detected in waterless areas but do tolerate heat well) and the presence of African wolves (*Canis lupaster*), whom they avoided (Burruss, 2014).

There is currently only one published study on their diet, which analyzed scat samples and showed pale foxes are primarily insectivorous (found in 91.8% of scat). Rodents (mostly *Gerbillus* spp.) were found in only 5.6% of scats but made up the second highest relative proportion of food items (43.7%), suggesting they are an important dietary component. Avian and squamate remnants were also rarely found but made up a large proportion (<38%). Plant material was rarely found (Burruss et al., 2017). Agama lizard and Chestnut-backed Sparrow-Lark (*Eremopterix leucotis*) remains were discovered outside a burrow in Chad (Sillero-Zubiri, 2013). They may face persecution for occasionally killing domestic birds (Sillero-Zubiri, 2013, 2004).

Details on social systems are not known, but they have been observed in pairs and small family units. They rest in groups during the day in extensive burrows that they dig, and they forage solitarily from dawn to dusk. Females give birth to 3-6 young before the rainy season (Sillero-Zubiri, 2013, 2004). Their home range has been investigated at the TTT using six radio-collared pale foxes. A low home range overlap and almost exclusive core area use were observed, suggesting pale foxes are generally territorial. Additionally, compared to other foxes in arid habitats, their relatively small home range size suggests that the TTT provides plentiful resources (arthropods) (Sillero-Zubiri et al., 2016).

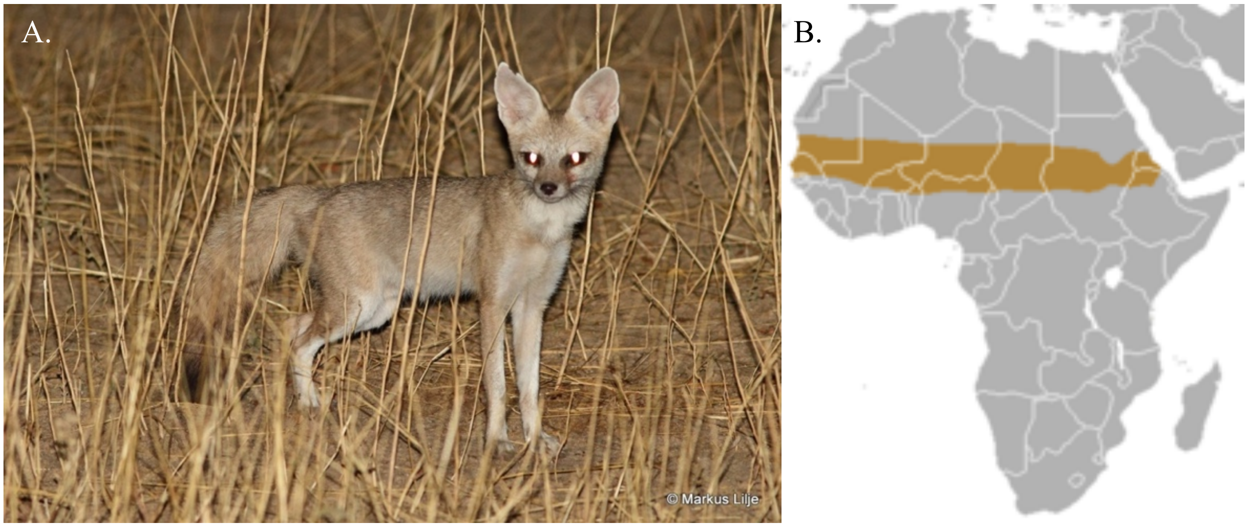

FIGURE 1.4. (A) Pale fox (*Vulpes pallida*) from Rohaya, Extreme-Nord, Cameroon (credit: Markus Lilje, https://www.inaturalist.org/photos/9140439, licensed by CC BY-NC-ND,). (B) Map showing distribution of pale fox (credit: Chermundy, public domain).

*12.3 Serval (*Leptailurus serval*)*

The serval is a medium-sized felid with long legs, prominent ears, a slender body shape, and a medium-length tail. Their pelage can vary from light to golden yellow with a lighter ventrum, black spots or blotches along the side, and stripes along the neck and shoulders. The back of the ears are black with a white horizontal band in the middle. The tail has around five rings and ends with a black tip. They are categorized as Least Concern by the IUCN Red List. Their geographic distribution follows the savanna habitat in a band from Senegal to Ethiopia and south Somalia and travels down to east and southern Africa. They are largely absent from coastal south Africa and north Africa, except for an isolated population in Morocco (Figure 1.5). In addition to savanna habitats, they are also associated with grasslands, gallery forests, wetlands, and permanent water sources. They may also be associated with agricultural areas as long as enough sufficient cover is available, but they are rarely associated with livestock deaths.

The servals' diet is comprised of primarily small mammals (mostly murids), supplemented by birds, frogs, reptiles, fish, and insects. There are some reports of servals catching larger prey, such as hares, young antelope, genets, and mongooses. Servals may become diurnal in protected areas but otherwise are crepuscular or nocturnal. They are both solitary and territorial. While home ranges may overlap, individuals avoid each other rather than displaying agonistic behavior. Servals behave fearfully of spotted hyaenas (*Crocuta crocuta*). Little is known about serval reproductive behavior, but litters of 2-3 kittens generally occur when rodent densities are the highest (usually in the rainy season) (Estes and Otte, 2012; Hunter and Bowland, 2013, pp. 361–363).

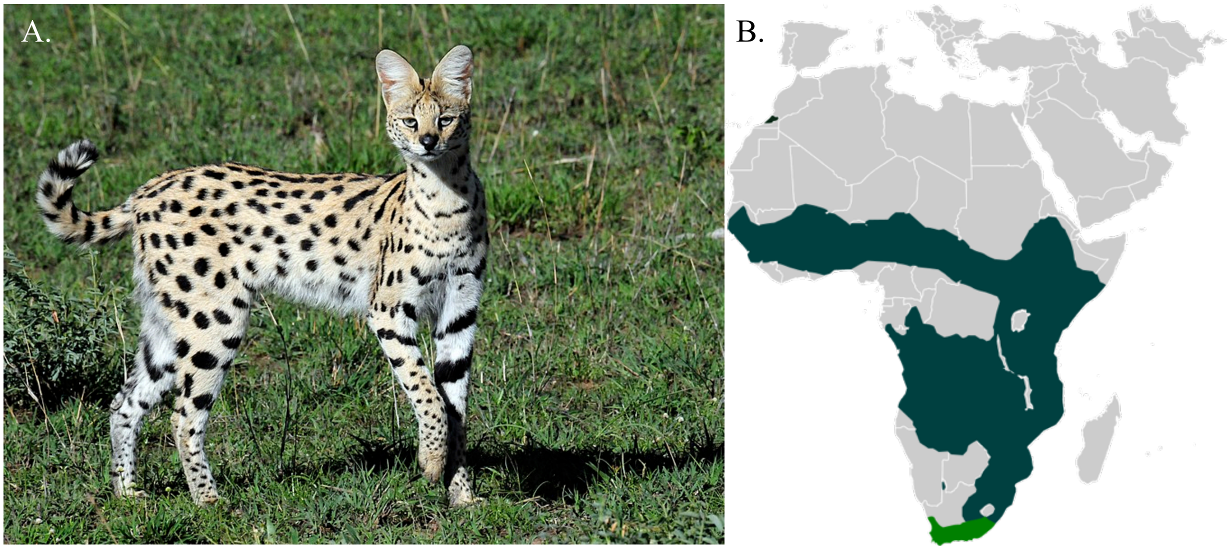

FIGURE 1.5. (A) Serval (*Leptailurus serval*) from Northern Serengeti, Tanzania (credit: Vince Smith, licensed by CC BY 2.0). (B) Map showing distribution of serval where dark green is extant range and light green is extinct range (credit: Lucas Hirschegger, licensed by CC BY-SA 3.0).

*12.4 Caracal (*Caracal caracal*)*

The caracal is a medium-sized felid with a uniform dorsal pelage that ranges from tawny to rufous. The ventral side is lighter and faint spotting may be seen. The ears have a dark back with a distinctive tuft. The tail is short (~1/3 body length). Caracals have a stockier build than servals. They are classified as Least Concern by the IUCN Red List. Caracals are distributed across Africa, central Asia, and southwest Asia. In Africa, they range everywhere but the equatorial forests and central Sahara (Figure 1.6). They have a high habitat variability, ranging from semi-deserts to open savannas to moist woodlands to montane forests. However, they prefer lower rainfall areas with some cover, like drier woodlands and savannas.

The primary diet includes small- to medium-sized mammals (from murids to ~50kg antelope), including domestic livestock (mainly sheep and goats. Their diet is supplemented by birds, reptiles, fish, invertebrates, and plant matter. Caracals are primarily solitary and nocturnal, but may become diurnal or crepuscular in protected areas. They are skilled tree-climbers. Caracals give birth to 1-4 kittens throughout the year, peaking when prey availability is the highest (Estes and Otte, 2012; Stuart and Stuart, 2013, pp. 363–365; Veals et al., 2020).

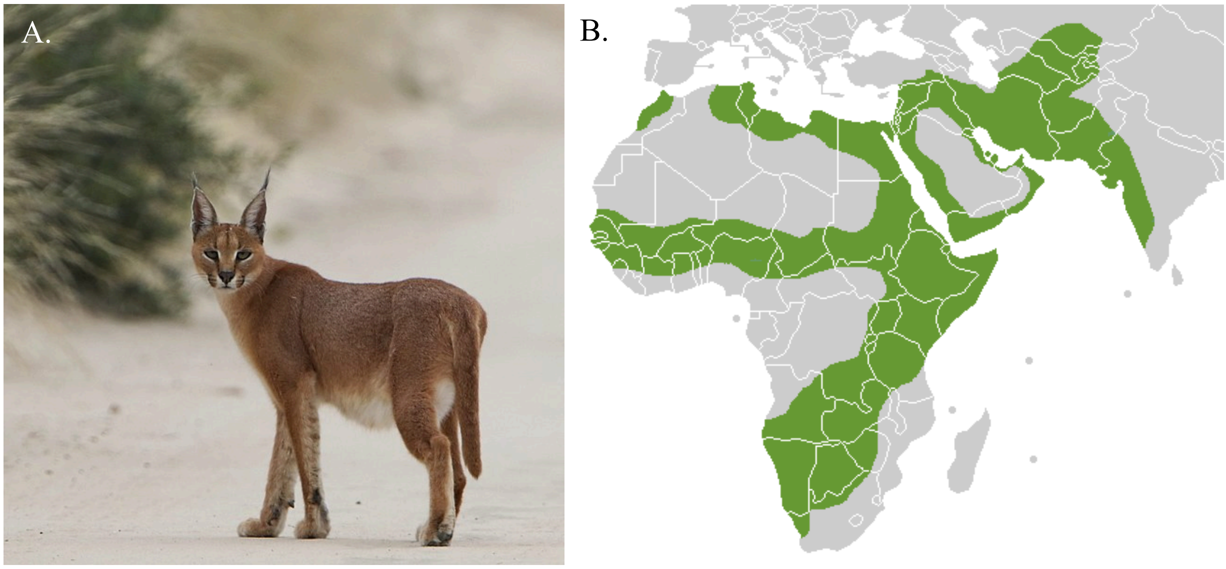

FIGURE 1.6. (A) Caracal (*Caracal caracal*) from Kgalagadi (credit: Derek Keats, licensed by CC BY 2.0). (B) Map showing distribution of caracal (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.5 Afro-Asiatic Wildcat (*Felis lybica*)*

Similar in appearance and size to the domestic cat, the wildcat can be differentiated from a tabby cat by having reddish, unmarked fur on the back of the ears and by its longer legs. Pelage coloration varies geographically from dark gray to sandy yellow. The forehead and cheeks generally possess distinct stripes, while the torso has fainter stripes, and the chest may have spots. There is typically dark ringing on the legs and tail, which ends in a black tip. The ventral side is paler, and the chin and throat are white. Wildcats are known to hybridize with domestic cats, which can alter their appearance across their distribution (Estes and Otte, 2012, pp. 357–359; Stuart et al., 2013). They are categorized as Least Concern by the IUCN Red List (Ghoddousi et al., 2022).

The wildcat group contains a few phylogenetically close species or subspecies that have been revised multiple times and whose taxonomic debate still occurs across its range. Currently, the African and Asian populations have been revised to be a single species, *Felis lybica*, while the European populations remain classified as *Felis silvestris.* Three distinct clades of *F. lybica* exist, which are believed to be subspecies: *F. l. lybica* (east, west, and north Africa, Arabian peninsula, Middle East, Corsica, Sardinia, and Crete)*, F. l. cafra* (southern Africa, the boundary with *F. l. lybica* believed to lie in Mozambique or Tanzania), and *F. l. ornata* (SW and central China, Afghanistan, Pakistan, India, Mongolia, and China) (Fgure 1.7) (Kitchener et al., 2017).

Wildcats occur in almost all habitats except tropical forests and open sand deserts. They strongly associate with woodlands, hill ranges, rocky outcroppings, and cultivated areas. Their diet comprises rodents (primarily murids), supplemented by lagomorphs, birds, reptiles, amphibians, and insects. Wildcats are solitary and territorial, but their home ranges frequently overlap. Wildcats can reproduce twice a year if conditions are optimal, giving birth to 1-5 kittens. Births typically peak over the warm summer months, and kittens will disperse after 2-4 months (Estes and Otte, 2012, pp. 357–359; Stuart et al., 2013).

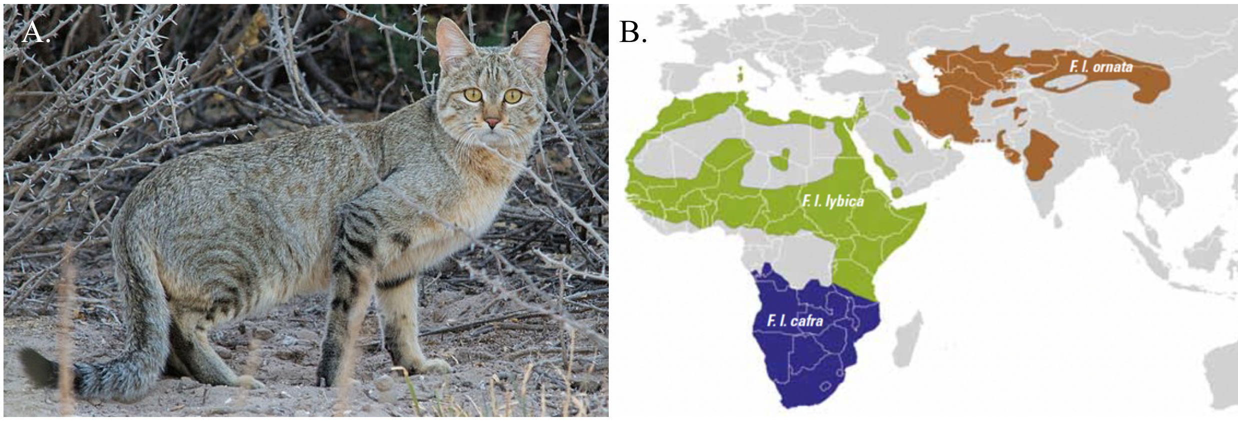

FIGURE 1.7. (A) Afro-Asiatic wildcat (*Felis lybica*) (credit: Leonemanuel, licensed by CC BY-SA 4.0). (B) Map of subspecies distribution; borders are speculative (Kitchener et al., 2017).

*12.6 Spotted hyaena (*Crocuta crocuta*)*

Crocuta is a monotypic genus including only the spotted hyaena, the largest and most common extant hyaena species with adaptations to hypercarnivory and scavenging. The spotted hyaena's pelage is a light brown to sandy coloration with black spots, and longer neck hair gives a maned appearance. Their body is muscular, with a large neck, shoulders, and a sloping back. Their ears are rounded. They have a short tail ending in black hairs. They are classified as Least Concern by the IUCN Red List. *Crocuta crocuta* has a widespread distribution across sub-Saharan Africa except for the dry, arid areas of South Africa and the equatorial forest (Figure 1.8). Spotted hyaenas can be found in almost every habitat except for extreme deserts and high altitudes in mountains and tropical rainforests. However, populations are patchy and usually concentrated in protected areas. They often occur in proximity to human habitation.

Spotted hyaenas are competent hunters, usually taking medium- to large-sized ungulates (African buffalo, wildebeest, gazelle, warthog, etc.). Additionally, they are scavengers and may kill livestock, domestic dogs and cats, and people. Spotted hyaenas can hunt independently (more common) or cooperatively in small groups (less common). They are known to travel incredibly long distances (30-80km) searching for food and may go on even longer “commuting trips” (80-140km) to areas with higher herbivores. *Crocuta crocuta* is a highly social species with a ‘fission-fusion’ society where clan females are at the top of the hierarchy. Adult females and immigrant males both have separate, subordinate linear dominance hierarchies. A clan may have several communal dens in their territory, usually modified warthog, aardvark, or bat-eared fox burrows. They are most active at night, dawn, and dusk. There is no reproductive season. Females give birth to 1-2 (rarely 3) cubs in a private birth den before returning to the communal den. There is no communal care of offspring. Males typically disperse from the natal clan when mature (around two years old), while females typically remain (East and Hofer, 2013; Estes and Otte, 2012, pp. 336–344).

FIGURE 1.8. (A) Spotted hyaena (*Crocuta crocuta*) in Etosha National Park, Namibia (credit: Charles J. Sharp, licensed by CC BY-SA 4.0). (B) Map of spotted hyaena distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.7 Striped hyaena (*Hyaena hyaena*)*

The striped hyaena is a large carnivore with black vertical stripes on the side, horizontal stripes on the legs, and a dark throat patch. Their back slopes down to a long, coarse tail. The ventral pelage is lighter. The black, grizzled dorsal mane may be erected to give a larger appearance. They are classified as near threatened by the IUCN Red List. They have a patchy distribution from northern and eastern Africa through the Arabian Peninsula and western and southern Asia (Figure 1.9). They generally prefer to live in scrub-woodlands, bushy, and mountainous/rocky regions throughout arid to semi-arid environments while avoiding open deserts and forests.

While parts of their range overlap with the better-studied spotted hyaena, they exhibit many behavioral differences. Striped hyaenas are more omnivorous scavengers when compared to spotted hyaenas. Due to their scavenging habits, they tend to remain around urban areas where they benefit from human refuse. They will readily consume fruits, vegetables, invertebrates, human waste, and carrion. They opportunistically hunt smaller mammals and birds. Striped hyaenas irregularly kill livestock, can destroy crop fields, and have been seen grave robbing.

The social organization of striped hyaenas is not well studied. It appears that they are solitary foragers in Africa, but groups have been observed at feeding sites in Israel. They are strictly nocturnal. They are thought to have small territories surrounding their breeding dens with larger home ranges, and there is little evidence that these territories are defended. Reproduction can occur during any season, and striped hyaenas give birth to 1-4 cubs. Cubs are reared in a den regularly visited by the mother. Around six months of age, juveniles will begin traveling with their mother on foraging outings. Sexual maturity is reached at 2-3 years (Abisaid and Dloniak, 2015; Estes and Otte, 2012, pp. 328–331; Rieger, 1981; Wagner, 2013).

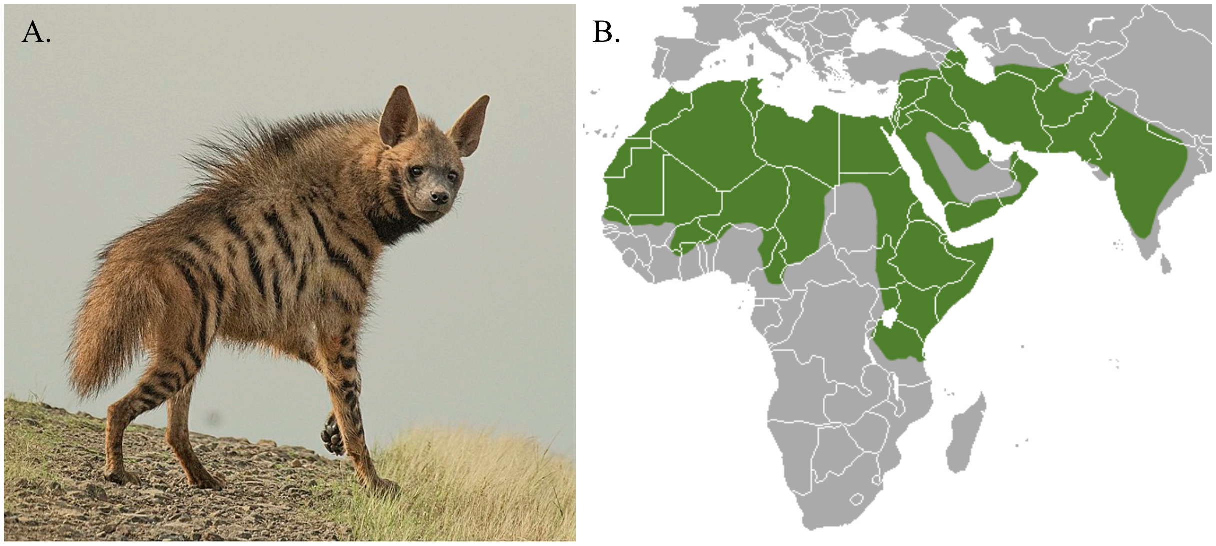

FIGURE 1.9. (A) Striped hyaena (*Hyaena hyaena*) (credit: Rushikesh Deshmukh DOP, licensed by CC BY-SA 4.0). (B) Map of striped hyaena distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0)

12.8 Ratel (Mellivora capensis)

The ratel, also known as honey badger, is a medium-sized carnivore with distinctive black and white coarse pelage. Their underside is black, the forehead is white, and the back is white-gray, which may extend onto the top part of the short tail, ending in black. The width/degree of white/gray can vary across individuals and regions. They have no noticeable external ears. The ratel's muzzle is short and sparsely furred. The broad forehead and thick, short neck give the ratel a stocky appearance. They are classified as Least Concern by the IUCN Red List. The ratel's distribution covers much of Africa, into Arabia, Iran, western Asia, Turkmenistan, and the Indian peninsula (Figure 1.10). The ratel can live in a wide variety of habitats and is only absent from the driest, sandiest parts of Africa (central Sahara and the Namib desert).

Ratels are opportunistic omnivores and may consume anything from insects to ungulate young. From a study analyzing the contents of seven stomachs in Zimbabwe and Botswana, scorpions were the most frequent prey, followed by spiders, murids, lizards, insects, myriapods, birds, snakes, and bee larvae and honey. It appears that there is some immunity to snake and scorpion venom. Ratels typically hunt their own prey but may steal or scavenge from other carnivores. In areas of commercial beehives, ratels are known to break in frequently. The ratel's muscular forelimbs make them excellent diggers, climbers, and excavators. There are several observations of different species (Pale Chanting-Goshawk [*Melierax canorus*], black-backed jackal [*Lupulella mesomelas*], etc.) following foraging ratels to prey on rodents that escape while the ratel is digging. Ratels are solitary and appear to shift between nocturnal and diurnal activity depending on the temperature. Ratels will change their denning site daily, except for females with cubs, and will either dig their own, use premade burrows (made by aardvark, springhare, or porcupines), or use hollow trees, caves, bushes, or termite mounds. Reproductively, ratels are categorized as polygynous or promiscuous, and their large home ranges overlap with other males and females. Females will usually give birth to one cub, who will stay with the mother for 12-18 months before dispersing. Ratels may be predated by large carnivores, such as lions and leopards (Begg et al., 2013; Estes and Otte, 2012, pp. 433–437).

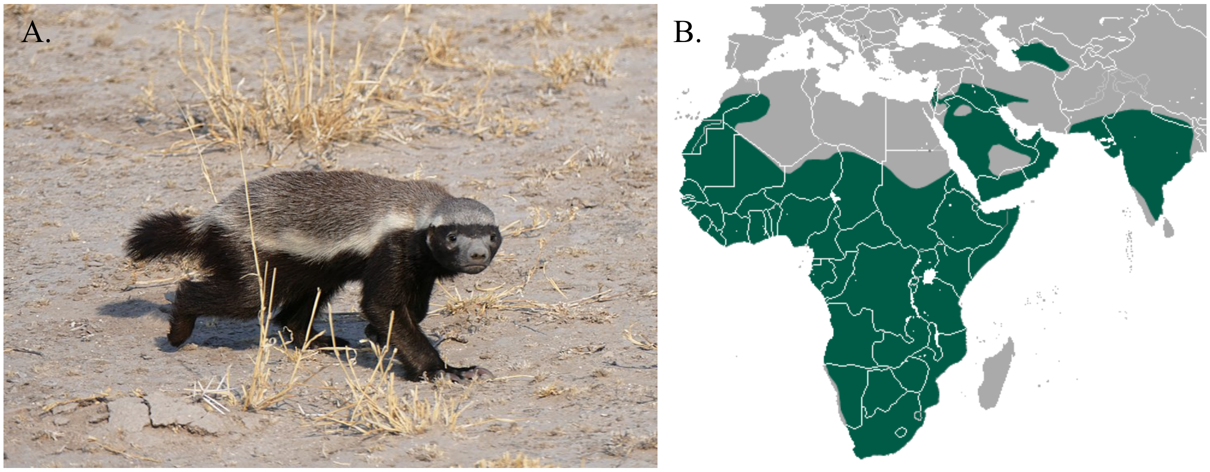

FIGURE 1.10. (A) Ratel (*Mellivora capensis*) (credit: Gerhard Mauracher, licensed by CC BY-SA 4.0). (B) Map of ratel distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

12.9 African civet (Civettictis civetta)

Civettictis is a monotypic genus that includes the African civet, a distinctive species and the largest species in the Viverridae family. The African civet is a dog-like carnivore with large hindquarters, buff pelage, a pattern of black blotches and lines, dark appendages, distinctive white stripes on the neck, small and round ears, a black raccoon-like mask, and a white snout. A black crest travels from the neck to the tip of the tail. The tail is approximately 1/3 of the body length, with around five black rings ending in a black tip. Black patterning varies by individual and across their range. They are classified as Least Concern by the IUCN Red List. Their distribution ranges across most of sub-Saharan Africa except for the drier regions in most South Africa, Botswana, Namibia, and Somalia (Figure 1.11). They can occur in various habitats but are most common in areas with suitable cover and water. They may be found in woodlands, bush, secondary forests, and riverine systems. They are absent from undisturbed, interior forest habitats and arid environments. They take advantage of deforestation in West and Central Africa, using logging roads to travel and live near villages.

African civets are omnivorous and tend to adapt their diet to whatever resource is available in their environment. They will consume fruits, vegetables, invertebrates, and vertebrates (generally up to the size of a hare). Vertebrate prey includes rodents, hares, shrews, birds, reptiles, and amphibians. They readily consume carrion. There are numerous reports of poultry houses and gardens being raided at night. There is evidence of some degree of resistance to chemicals, as African civets can consume poisonous fruits and insects, venomous snakes, and bufotoxin (as evidenced by finding African common toads [*Sclerophrys gutturalis*] in the stomach). African civets are nocturnal and appear to primarily use the same routes to forage at night. They require cover to sleep during the day using dense vegetation, thickets, roots, or already dug holes. African civets are solitary outside the breeding season. They are believed to be territorial due to feces containing anal gland secretions deposited in civetries (latrines) and regular marking along paths with perineal gland secretions. Some populations report a breeding season during the warmer months, but others have no specified season. Females give birth to 1-4 kittens and may reproduce 2-3 times a year. Predators are believed to be large carnivores (lions, leopards, and spotted hyaenas). African civet populations may be declining, as its meat is prized and is one of the more common bushmeat market species. Additionally, their perineal secretions have been used to produce civetone (a fixing agent in perfume) for centuries, which remains an important export for Ethiopia, despite synthetic alternatives (Estes and Otte, 2012, pp. 289–292; Ray, 2013, 1995).

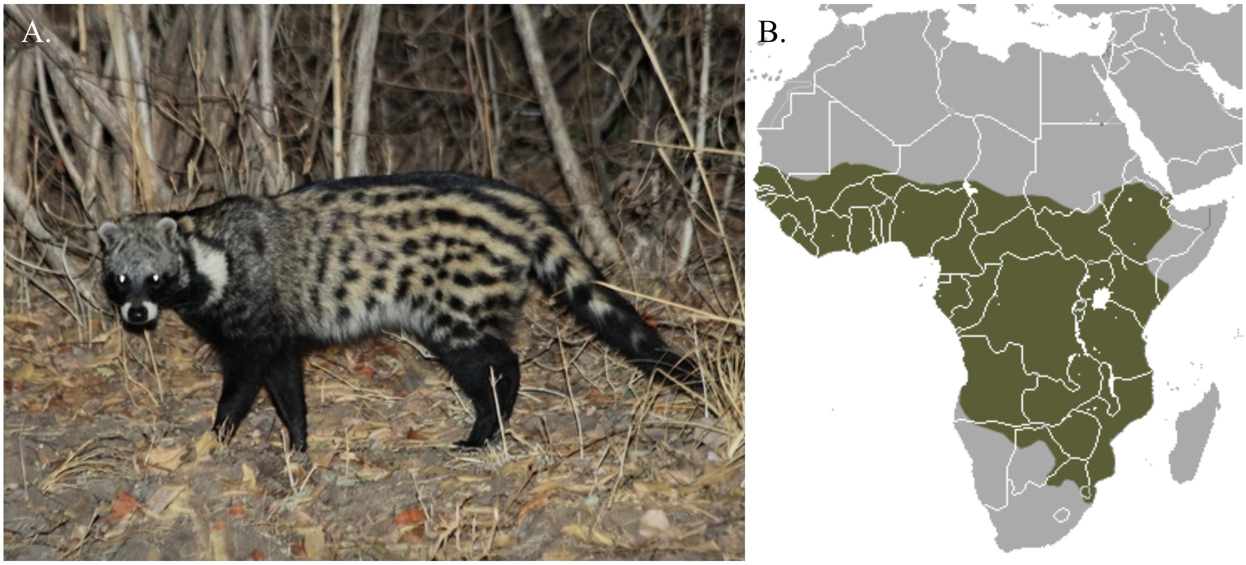

FIGURE 1.11. (A) African civet (*Civettictis civetta*) in South Luangwa, Zambia (credit: Michal Sloviak, https://www.inaturalist.org/photos/35635750, licensed by CC BY 4.0). (B) Map of African civet distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.10 Common genet (*Genetta genetta*) and rusty-spotted genet (*Genetta maculata*)*

Genetta includes 14 species distributed through almost all terrestrial habitats and niches in sub-Saharan Africa (exception for *G. genetta* which also ranges outside Africa) (Gaubert, 2013). Both *G. genetta* and *G. maculata* are small carnivores with yellow-rufous gray pelage, a dark mid-dorsal line, and distinct dark brown-black spots arranged in rows. Their tail is ringed and either almost equal or equal to body length. Their muzzle is elongated and pointed. Dark bands travel around the muzzle from the inner corner of the eyes and are emphasized by surrounding white marks. Their ears are rounded and prominent. *Genetta genetta* and *G. maculata* are similar in size and appearance but can be differentiated by a few characteristics. *Genetta genetta* has longer pelage and a mid-dorsal line with erectile hairs. In *G. genetta*, the dorsal spots are narrower and may fuse to form a line. In *G. maculata*, the dorsal spots are larger, square-ovoid shaped, and generally do not fuse (may see some fusion near the hind end). In *G. genetta*, the tail is slightly longer (95-97% of head-body length), ring edges may be blurred due to longer pelage, and the tip is white (though the degree of white varies and may be minimal). In *G. maculata*, the tail is slightly shorter (80-90% of head-body length), distinctly ringed, and ends with a dark tip. They are both classified as Least Concern by the IUCN Red List (Angelici and Gaubert, 2013; Delibes and Gaubert, 2013).

The common genet occurs in the coastal area of Northern Africa across Morocco, Algeria, and Tunisia. In sub-Saharan Africa, the common genet occurs in three areas: West Africa (from Senegal and southern Mauritania through southern Mali and Burkina Faso to southern Niger and northern Nigeria), East Africa (from Somalia and Ethiopia, through most of Sudan and South Sudan, to as far south as Tanzania), and South Africa (covering Namibia and Botswana and most of South Africa, Zimbabwe, and Angola). There is a distinct separation in range between the east and southern blocks, but the eastern and western blocks form a continuum meeting in southern Chad. Outside of Africa, the common genet occurs in Europe (Portugal, Spain, and parts of France), Mediterranean islands (Majorca, Ibiza, and Cabrera), and coastal Arabia, Yemen, and Oman (Figure 1.12). The common genet only seems to require cover and prey, but not permanent water. They are generally absent from rainforests and true deserts but can tolerate more arid environments than the rusty-spotted genet. They are also common in any environment that provides woody or rocky shelter or in human-altered areas (Delibes and Gaubert, 2013; Larivière and Calzada, 2001).

The rusty-spotted genet ranges through most of sub-Saharan Africa. Their northern limit travels from east of the Volta river through southern Chad and South Sudan through Ethiopia and southern Somalia. Its southern limit reaches northern Namibia, the northern tip of Botswana, Mozambique, then down along the coast venturing slightly into South Africa (Figure 1.13). The rusty-spotted genet can be found in various habitats, including rainforests, riverine habitats, swamp zones, woodlands, moist forests, savanna-forest mosaics, thickets, and grassy savanna. They are common to see in areas of farmland and cultivation (Angelici and Gaubert, 2013).

Both *G. genetta* and *G. maculata* are generalists. Their diet consists primarily small mammals supplemented by birds, bird eggs, reptiles, amphibians, fish, arthropods, fruits, fungi, and garbage. There are records of domestic poultry raids. Both species are nocturnal and primarily solitary outside of the breeding season. They likely exhibit some degree of territoriality, as latrines are regularly used. Common genets typically place their latrines on an area of high elevation (e.g., rocks and trees), while rusty-spotted genets may prefer their latrines on the ground (e.g., areas of thick brush). Several individuals may use them at the border of home ranges. Perineal gland secretions and urine are used for communication with others. Breeding season varies based on location. Females give birth in hollow trees or burrows. Litter size averages around two, but 1-5 may be born. Potential predators include large carnivores (serval, caracal, leopards, ratel, etc.) and large birds (eagles, owls). Genets are skilled climbers and may use trees to hide from predators (Angelici and Gaubert, 2013; Carpenter, 1970; Delibes and Gaubert, 2013; Larivière and Calzada, 2001; Palomares, 1993a; Palomares and Delibes, 2000).

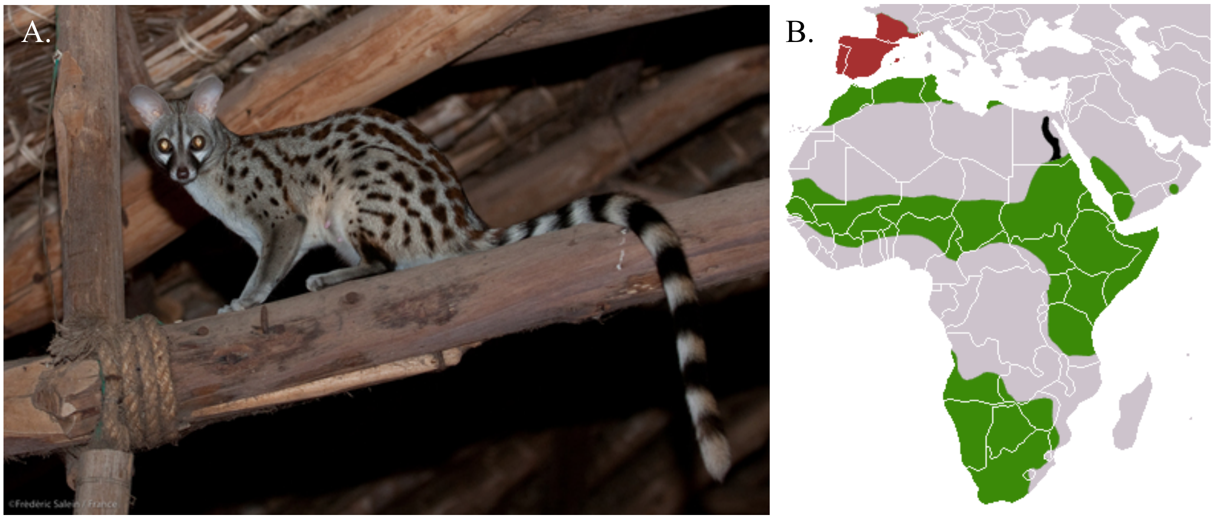

FIGURE 1.12. (A) Common genet (*Genetta genetta*) in Sateo camp, Kenya (credit: Frédéric SALEIN, https://www.flickr.com/photos/fredericsalein/4844873284/, licensed by CC BY-NC-SA 4.0). (B) Map of *G. genetta* distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

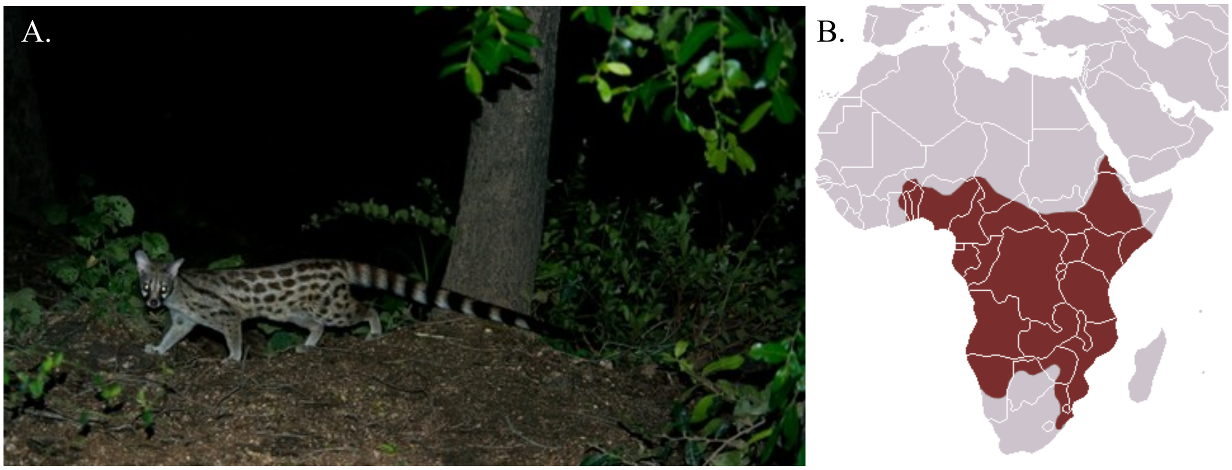

FIGURE 1.13. (A) Rusty-spotted genet (*Genetta maculata*) in Kruger National Park (credit: Clintonjonker, https://www.inaturalist.org/photos/593106, licensed by CC BY-NC-ND). (B) Map of *G. maculata* distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.11 Marsh mongoose (*Atilax paludinosus*)*

The marsh mongoose is a larger mongoose species of dark brown to black pelage with a grizzled, shaggy appearance. The hair around the mouth and chin may be lighter colored. Their tail is shorter than the body length and has longer hairs at the base. They are classified as Least Concern by the IUCN Red List. Marsh mongooses are widely distributed across sub-Saharan Africa wherever sufficient water and cover are available (Figure 1.14). They prefer riparian habitats but may also be found along estuaries or coasts.

Marsh mongooses are skilled swimmers and feed primarily on aquatic prey. Their diet comprises mainly crustaceans, with the addition of amphibians, fish, mollusks, terrestrial arthropods, and rodents. Birds, bird eggs, reptiles, and fruits are also eaten, but they are less preferred. There is some evidence of scavenging. They forage in the littoral zone, similar to a North American Northern raccoon (*Procyon lotor*), and spend much time along the shore.

Marsh mongooses are mainly nocturnal but may be seen during the day. They are solitary out of the breeding season and may possess some form of territoriality. It is believed that females hold territories, while males are more mobile. Breeding occurs variably (summer in southern Africa; no season in west Africa) when 2-3 individuals are born. Young marsh mongoose may be vulnerable to predation, but there are few reports for adult marsh mongooses. The marsh mongoose has been observed attacking and almost drowning a dog while its own leg was being bitten. (Baker, 1992; Baker and Ray, 2013; Estes and Otte, 2012, pp. 306–307; MacDonald and Nel, 1986).

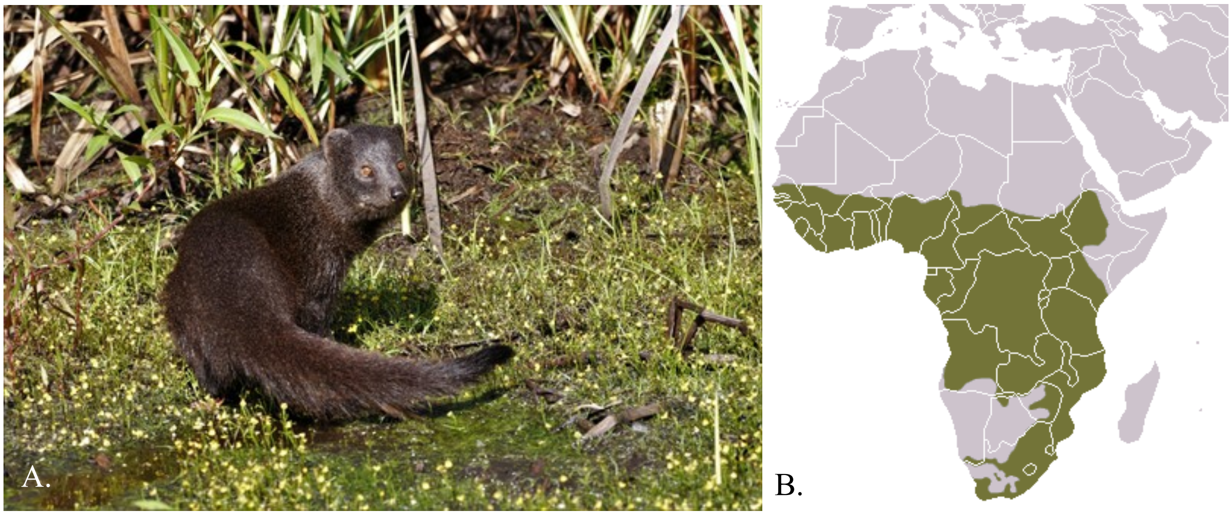

FIGURE 1.14. (A) Marsh mongoose (*Atilax paludinosus*) (credit: Colin Ralston, https://www.inaturalist.org/photos/59604524, licensed by CC BY-NC). (B) Map of marsh mongoose distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.12 Egyptian mongoose (*Herpestes ichneumon*)*

The Egyptian mongoose, also called the Ichneumon or large grey mongoose, is a larger mongoose species with a gray-brown grizzled appearance. Their appendages are shorter than some mongooses, giving the Egyptian mongoose a more squat appearance. Their guard hairs are long, giving a shaggy appearance, and the appendages are darker than the body coloration. Their tail is slightly shorter than their body, with long hairs at the base and ending in a black tassel. Their rhinarium is black. The Egyptian mongoose often occurs sympatrically with the white-tailed mongoose (*Ichneumia albicauda*), but they can be differentiated by the white-tailed mongooses' longer legs and white distal 2/3 of the tail (usually; see species description below). The Egyptian mongoose is often sympatric with the marsh mongoose (*Atilax paludinosus*), except for northern Africa. They can be differentiated by the marsh mongooses' darker, more uniform coloration and shorter tail length(see species account above) (Palomares, 2013). They are classified as Least Concern by the IUCN Red List. The Egyptian mongoose occurs in Africa, on the Sinai peninsula and into southern Turkey, and on the Iberian peninsula in southwestern Spain and southern and central Portugal. Within Africa, they range in a band from Senegal to Ethiopia, south through Tanzania, Zambia, Angola, and Mozambique, and along much of the coast of southern Africa. From Ethiopia, they range north through eastern Sudan and Egypt. In North Africa, they range in a strip from Morocco to Tunisia (Figure 1.15) (Do Linh San et al., 2016). Although, a recent ecological niche model gives slightly different limits to their distribution than the IUCN map (Ngatia et al., 2021). They appear to prefer habitats providing understory vegetation as cover, mainly in coastal, lacustrine, and riparian habitats. They can also be found in areas with tall grasses, cultivated areas, and areas with termitaries. They are largely absent from deserts and high-rainfall areas (Estes and Otte, 2012, pp. 298–302; Palomares, 2013; Palomares and Delibes, 1990).

The Egyptian mongoose is opportunistic and omnivorous, with its diet changing based on season and location. Vertebrates appear to comprise their primary prey source. Small mammals were the main prey in the Western Cape of South Africa and southeastern Nigeria (Angelici, 2000; Stuart, 1983). In Israel, the main prey was domestic poultry and rats (Ben-Yaacov and Yom-Tov, 1983). Among various locations in Spain, the primary prey source was rabbits, birds, and reptiles, though different sites may have had a different order of importance (Delibes et al., 1984; Palomares, 1993b). In Portugal, males consumed more mammals and amphibians, while females consumed more reptiles and invertebrates (Bandeira et al., 2018). Overall, they will consume small mammals, reptiles, amphibians, birds, eggs, fish, crabs, crayfish, insects, carrion, fungi, and fruit. They have adapted resistance to venomous snakes and are rarely affected

(Palomares, 2013). Egyptian mongooses have been recorded performing odd behaviors to attract prey. Individuals have been observed chasing their tails (Estes and Otte, 2012, p. 300). There is an older account of a mongoose performing a luring behavior by standing up and falling over repetitively until a flock of Guinea fowl came closer to investigate, in which the mongoose jumped up and killed four (Preston, 1950). In an event where twelve angulate tortoises (*Chersina angulate*) were found killed in a similar manner missing their head and neck, the Egyptian mongoose was believed to be the culprit from matching tracks around the remains, along with known predatory/hunting techniques (Ramsay, 2002).

Most studies on Egyptian mongoose come from Spain, so relatively little is known about the African populations. Believed to be a primarily solitary species in Africa, occasional family groups of 2-3 individuals have been observed. In Spain, the mean group size is 1.7, and the range is 1-5 individuals. Groups of two seen were mainly comprised of an adult female and young or a male and female. Males in Spain exhibited more territoriality than females, with little home range overlap and no core area overlap. Females may be territorial in their core areas (minimal overlap), but home ranges showed significant overlap. Temporary latrines may be used to communicate resting sites or home ranges. They are primarily a diurnal species. However, they have been recorded to be crepuscular in Israel. When they rest at night and during day siestas, Egyptian mongooses will use either underground dens (dug by rabbits or badgers [*Meles meles*]) or thickets. In Israel, they create permanent paths in their home range. When an individual strayed from the trail to chase prey, the Egyptian mongoose always returned to the trail via the shortest path possible, regardless of the distance to its end-goal location. The reproductive season varies across its distribution, but 1-4 cubs are born per litter. Predators in Spain are the Iberian lynx (*Lynx pardinus*) and large eagles. In Africa, predators are unknown, but they could be large carnivores and eagles (Ben-Yaacov and Yom-Tov, 1983; Estes and Otte, 2012, pp. 298–302; Maddock and Perrin, 1993; Palomares, 2013, 1991; Palomares and Delibes, 2000, 1993a, 1993b).

FIGURE 1.15. (A) Egyptian mongoose (*Herpestes ichneumon*) (credit: Artemy Voikhansky, licensed by CC BY-SA 4.0). (B) Map of Egyptian mongoose distribution (Do Linh San et al., 2016).

*12.13 White-tailed mongoose (*Ichneumia albicauda*)*

Ichneumia is a monotypic genus including only the white-tailed mongoose, one of the larger mongoose species in sub-Saharan Africa and the coastal area of the Arabian peninsula. The body is typically gray in coloration with black limbs and a gray bushy, tapered tail that transitions to white. However, black-tailed individuals have been recorded throughout the range. The white-tailed mongoose can be differentiated from the Egyptian mongoose by its bushier tail, less grizzly appearance, and longer legs. The white-tailed mongoose can be differentiated from the marsh mongoose by the white-tailed's longer tail and less uniform pelage coloration. They are classified as Least Concern by the IUCN Red List. White-tailed mongooses are an adaptable species occurring in woodland, grassland, savanna, and near towns and villages. Their distribution covers most of sub-Saharan Africa, with the exception of rainforests and true deserts (Figure 1.16). The highest densities have been recorded around urban areas and livestock, where human garbage and insects are readily available. They are absent from arid areas and equatorial forests.

White-tailed mongooses are principally insectivorous but may also consume amphibians, murids, reptiles, birds, bird eggs, or carrion. There are numerous reports of them preying on venomous snakes. *Ichneumia albicauda* are primarily nocturnal, though there are some reports of diurnal activity. They will use abandoned termitaria or holes dug by aardvarks or hares to den during the day. A primarily solitary species, white-tailed mongoose may be seen foraging together in areas where resources are concentrated. They are territorial, but territories usually overlap. Agonistic behaviors are not commonly observed; instead, individuals avoid each other based on scent markings and display behavior. The breeding season is not well studied and may vary across their range. There are usually 1-4 young born in dens. They are not believed to be preyed upon by larger carnivores often (Estes and Otte, 2012, pp. 302–305; Taylor, 2013, 1972).

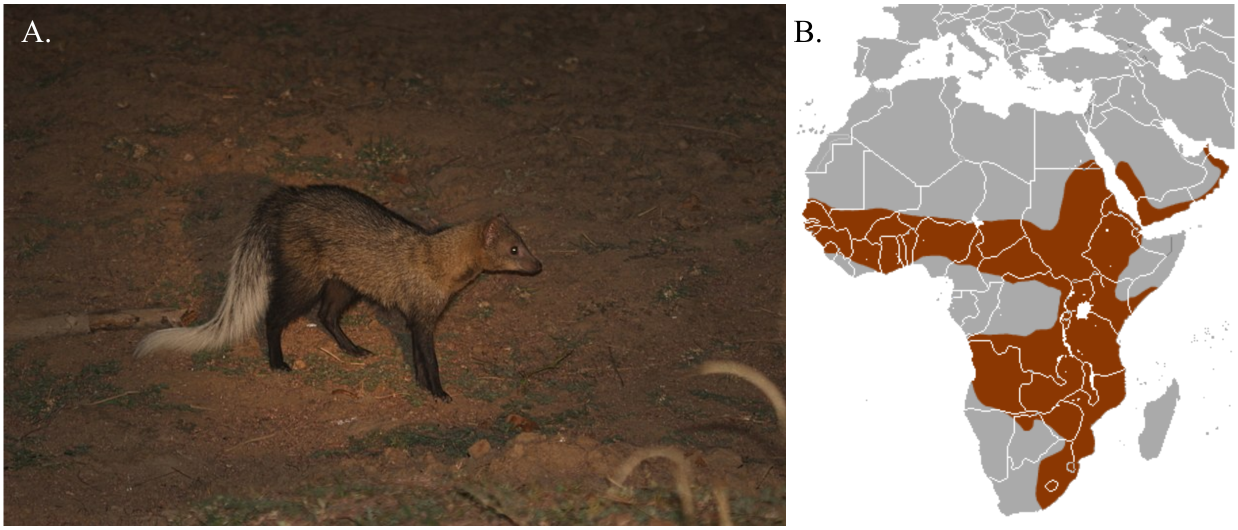

FIGURE 1.16. (A) White-tailed mongoose (*Ichneumia albicauda*) in Zambia (credit: MCSchaeffer, licensed by CC BY-SA 3.0). (B) Map of white-tailed mongoose distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.14 Banded mongoose (*Mungos mungo*)*

The banded mongoose is a medium-sized mongoose of gray-brown grizzled pelage recognized by its 10-15 transverse bands running across the dorsum. Their ventral pelage is sparse and of lighter coloration than the dorsal pelage, while the limbs are generally the same color as the dorsum. Their tail is slightly shorter than their body length and transitions to a darker tip. In areas of overlap, the banded mongoose can be differentiated from the Gambian mongoose (*Mungos gambianus*) by possession of transverse bands and lack of diagonal dark streaks on a light-colored neck. The banded mongoose is differentiated from the meerkat (*Suricata suricatta*) by larger size, longer tail, longer and less pointed muzzle, and more gray coloration (meerkat is more tan). The banded mongoose is classified as Least Concern by the IUCN Red List. They are distributed widely across sub-Saharan Africa in a band from Senegal to Somalia and south to about 31° in South Africa, where the meerkat replaces it (Figure 1.17). Their distribution in west Africa appears patchy, likely due to the presence of the Gambian mongoose, which occupies a similar habitat and has similar dietary preferences. Banded mongooses prefer woodland and savanna habitats, and they are typically found close to water and termitaria in areas with undergrowth.

Banded mongooses are highly gregarious and form integrated social groups/packs of 15-20 individuals (though a group of 70 has been recorded around a campsite). They are territorial, and physical conflict is often seen if neighboring packs are the same size and encounter each other. Individuals of the group travel together but forage independently. Their diet is primarily comprised of a variety of insects and arthropods, supplemented by occasional small reptiles, amphibians, murids, young birds, bird eggs, and human food waste. Banded mongooses are diurnal and are most active in the morning and evening when foraging and socializing, separated by a siesta during the hottest part of the day. Packs do not form an obvious social hierarchy except when females enter estrus. At this time, males will form hierarchies to compete for females. Banded mongooses are unusual when compared to other social carnivores, as most females in the pack will reproduce. The older females will enter estrus before the younger females and have larger litter sizes, indicating some form of age-based hierarchy. During this time, both males and females may enter neighboring groups to mate and avoid inbreeding depression, as males and females typically remain with the natal group. Due to this birth synchrony, the breeding season may vary between (not within) groups but generally occurs during the rains. Packs may produce up to four litters per year. Young remain in the den (usually termitaria) for 3-4 weeks and are cared for communally by individuals who remain behind while the group forages. Predators include lions (*Panthera leo*), leopards, and African rock pythons

(*Python sebae*). Smaller carnivores (servals, jackals, dogs) are generally intimidated by a pack's mobbing behavior. Young may be killed by marabou storks (*Leptoptilos crumeniferus*), Nile monitors (*Varanus niloticus*), and common warthogs (*Phacochoerus africanus*) (Cant and Gilchrist, 2013; Estes and Otte, 2012, pp. 314–318).

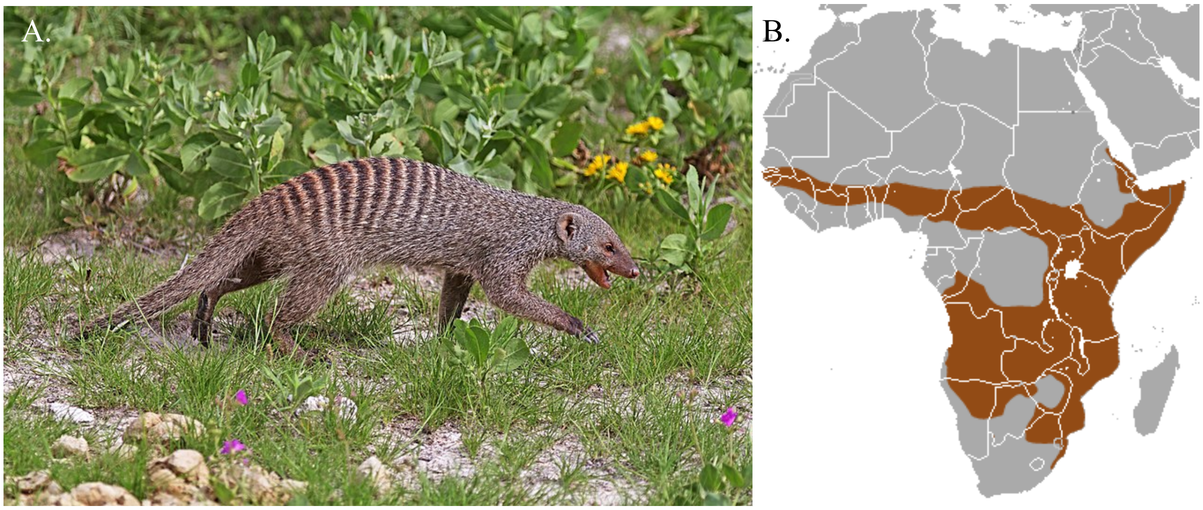

FIGURE 1.17. (A) Banded mongoose (*Mungos mungo*) (credit: Charles J. Sharp, licensed by CC BY-SA 4.0). (B) Map of banded mongoose distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

*12.15 Tantalus monkey (*Chlorocebus tantalus*) and Patas monkey (*Erythrocebus patas*)*

The subfamily Cercopithecinae is composed of two tribes: Papionini and Cercopithecini. Members of Cercopithecinae are known as the cheek-pouched monkeys, referring to the presence of elastic buccal sacs used for food storage, thought to have been evolved due to an increased risk from predators during their ancestral semi-terrestrial stage and intra-group competition in a rigid social structure (Kingdon and Groves, 2013a). Tantalus and patas monkeys are related species in the tribe Cercopithecini, which includes six genera known as the guenons. Cercopithecini are generally medium-sized, long-tailed monkeys known for their very well-coordinated and fast arboreal locomotion. However, *Chlorocebus, Erythrocebus*, and *Allochrocebus* monkeys are the less arboreal genera in this tribe, retaining their ancestral semi-terrestrial attributes. The guenons were previously under the same genus *Cercopithecus*, and the evolutionary history and taxonomic placement within the guenons remains debated. The patas monkey has such a distinctly different appearance from the other guenons that it would seem to be in a different taxonomic group. However, morphological and genetic studies support a close relationship between Patas, *Chlorocebus* (savanna monkeys), and *Allochrocebus* (mountain monkeys). The savanna monkey group now includes six species that, in various forms, were previously considered subspecies of *Cercopithecus aethiops.* Now under *Chlorocebus,* they are broadly referred to as vervets. Some researchers support placing vervets and patas into *Chlorocebus*, while some support placing vervets and patas into *Cercopithecus,* and others believe patas should remain a separate genus (Cronin and Sarich, 1976; de Jong et al., 2020; Groves and Kingdon, 2013a, 2013b; Kingdon and Groves, 2013b; Tosi, 2008; Tosi et al., 2005, 2004, 2003; van der Kuyl et al., 1995)

Savanna monkeys are semi-terrestrial monkeys that thrive in acacia woodlands and riverine galleries but can be found in most habitats of sub-Saharan Africa besides true forests and deserts (Groves and Kingdon, 2013a). Tantalus monkeys have black faces surrounded by a white fringe on the cheeks and a distinctive white-yellow browband. Their dorsum is a grizzled gray-yellow-green coloration, while their ventrum is white. Their legs and long tail are gray, but the tail transitions to white at the tip. They are classified as Least Concern by the IUCN Red List. The tantalus monkeys' distribution travels from eastern Burkina Faso and Ghana to the western edge of Kenya around Lake Victoria. Their northern range extends into the southern edge of Niger and into the southern half of Chad. Their southern range extends through most of Cameroon and the northern edge of the Democratic Republic of Congo (Figure 1.18). They have a habitat preference for riverine vegetation, so they can be close to water and trees to sleep in. However, they can also be found in other habitats, such as savanna woodland, gallery forest, swamp forest, and forest edge. In some areas, tantalus monkeys have been reported invading cultivated fields. Tantalus form multimale groups averaging around 29 individuals (range 11-76) with a lineal dominance hierarchy. Females give birth to one infant. Birth seasons vary but seem to coincide when energy and protein resources are most abundant. Both young and adult females exhibit allomothering behavior. There are few records on confirmed predators, but jackals (*Lupulella* spp.), African wild dogs (*Lycaon pictus*), spotted hyaenas, leopards, and servals are possibilities (Nakagawa, 2013).

The red/rusty colored dorsum and flanks and crown, white ventrum, and white mustache give the patas monkey a distinctive appearance. Face and nose color can change based on subspecies and reproductive status. They are also larger than tantalus monkeys with longer appendages and tarsal bones, shorter metatarsals, and are hindfoot digitigrade, which enable the patas monkey to travel efficiently and quickly. They are classified as Near Threatened by the IUCN Red List. Much of the patas monkey range overlaps with the tantalus monkey but travels farther north into Chad and Niger, and the western limit extends to the coast of Senegal, Guinea-Bissau, and Guinea (Figure 1.19). Additionally, they have been intentionally introduced into the islands of Puerto Rico, where they have since traveled to the mainland and are considered a nuisance species. They can be found in grasslands, savannas, and savanna-woodland habitats but appear to prefer woodland-grassland margins. Patas live in groups of one adult male and multiple females. The largest group recorded is 51 individuals, but size can fluctuate dramatically over time. Groups are intolerant of others, and encounters typically result in chasing but no physical altercations. Females give birth to one young about every year (ranging from 11.8-14.4 months) during the dry season. Patas females do not engage in normal allomothering behavior. Instead, infants may be taken unwillingly from their mothers- a situation termed ‘kidnapping’ by Isbell. Males will disperse from the natal group before becoming mature, while females will remain. Males will travel solitarily or in small groups and may temporarily join another group during the breeding season to mate. Domestic dogs and black-backed jackals are known predators of patas monkeys. Other smaller carnivores may be predators of young (servals, caracals, wild cats) (de Jong et al., 2020; Isbell, 2013).

Tantalus and patas monkeys are both generalist omnivores. The majority of their diet consists of gums, flowers, and arthropods. They will also consume fruits, seeds, leaves, stems, reptiles, bird eggs, and young birds. Diet can vary based on sex, energetic needs (pregnant, lactating, mating season, etc.), and other factors. They are both diurnal and forage in the morning and evening, resting for a few hours mid-day (Isbell, 2013; Nakagawa, 1989). Multiple studies have been conducted on populations of patas and tantalus monkeys living sympatrically near the Chari River in the Kala Maloue National Park in northern Cameroon. In these populations, patas monkeys tended to use animal matter and protein-rich seeds as a protein source, while tantalus monkeys consumed flowers and leaves. Fruits and lipid-rich seeds were consumed by both species for energy sources, while patas monkeys also consumed gums (Nakagawa, 2000). Tantalus monkeys will feed on a higher volume of less nutritious food (Nakagawa, 2003). From 1987-1989, the size of one group of tantalus monkeys ranged from 16-21 individuals (4-8 adult males, 4 adult females, and 8-9 subadults and juveniles), while one group of patas ranged from

8-14 individuals (1 adult male, 5-6 adult females, 2-8 subadults and juveniles) (Nakagawa, 1999). Although in 1974, the group of tantalus monkeys was recorded to be 76 (though over half were subadults and juveniles) (Kavanagh, 1981). Social systems among patas females may vary based on their surrounding environment. Previous studies in Laikipia, Kenya, showed that patas females had a poorly defined and unstable dominance hierarchy (Isbell and Pruetz, 1998). However, studies at Kala Maloue revealed that patas females there are despotic, creating linear dominance hierarchies. At Kala Maloue, patas monkeys have clumped resources in a low-density area, favoring agonistic behaviors. Those in Laikipia have dispersed resources in a high-density area, allowing females to equally share resources and favoring an egalitarian system (Nakagawa, 2008). Patas monkeys have a greater mean daily travel distance during the mid-dry and wet seasons and a greater mean daily travel distance than tantalus monkeys, regardless of the season. Due to their considerable travel distance, patas monkeys are not as restricted by water availability as tantalus monkeys, who must establish their home range near a permanent water source (Nakagawa, 1999). Patas monkeys preferred woodland habitats in the mid-dry season and grasslands during the wet season (Nakagawa, 1999). Tantalus monkeys preferred woodland and gallery forests regardless of the season (Kavanagh, 1981; Nakagawa, 1999).

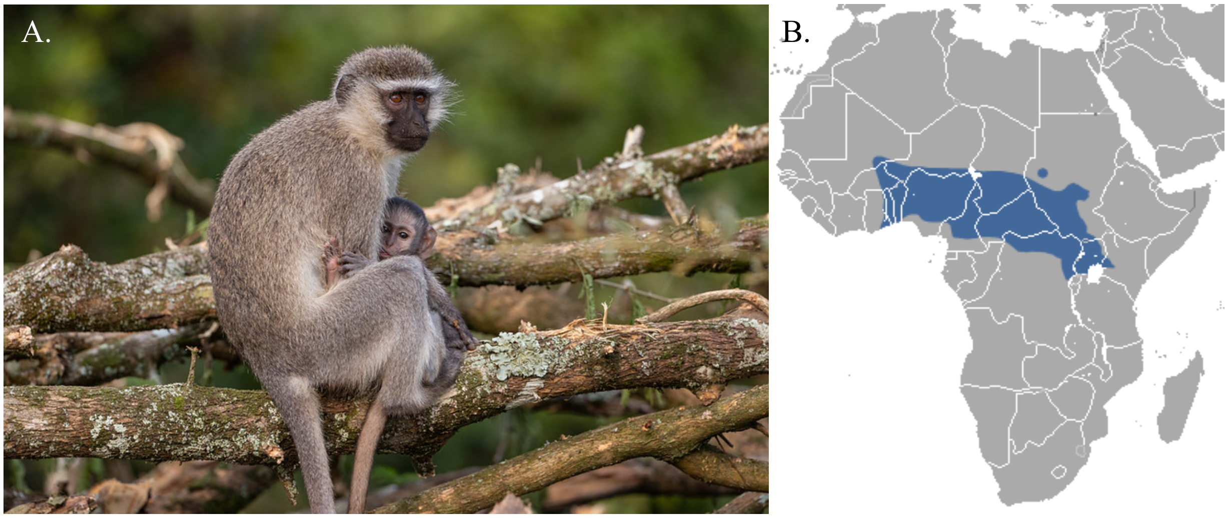

FIGURE 1.18. (A) Tantalus monkey (*Chlorocebus tantalus*) in Uganda (credit: Gregoire Dubois, https://www.flickr.com/photos/wildlifepictures/49430884968/, licensed by CC BY-NC-SA 4.0). (B) Map of tantalus monkey distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

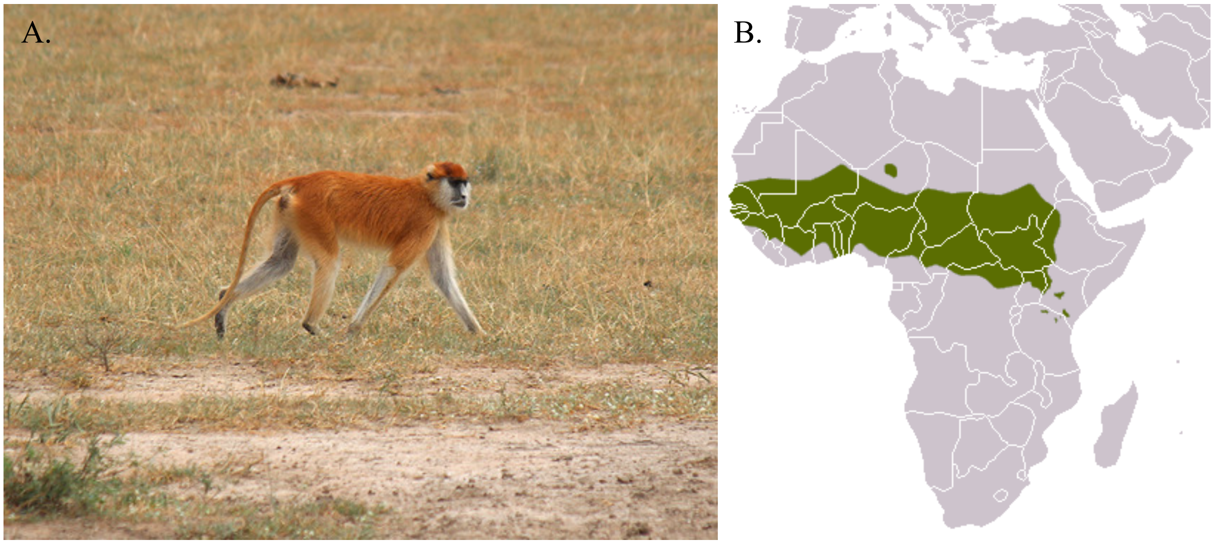

FIGURE 1.19. (A) Patas monkey (*Erythrocebus patas*) in Uganda (credit: cabrochu, https://www.inaturalist.org/photos/97255816, licensed by CC BY-NC 4.0). (B) Map of patas monkey distribution (credit: Chermundy, IUCN Red List of Threatened Species, species assessors and the authors of the spatial data, licensed by CC BY-SA 3.0).

12.16 Northern lesser galago (Galago senegalensis)

The Northern lesser galago, also known as the Senegal lesser bushbaby, is a medium-sized galago with gray-brown dorsal pelage and yellow-white ventral pelage. Their eyes are large with a dark eye ring and an inter-ocular white stripe. Their tail is gray-brown and long with short hair. The Northern lesser galago has a wide range that travels from Senegal to Ethiopia and Somalia and south through Kenya and Tanzania (Figure 1.20). The distribution limits are poorly understood. Throughout much of their range, the Northern lesser galago is the only small galago that utilizes the savanna, thorn scrub, and woodland habitats. They are closely associated with *Acacia* species, and they are not associated with grasslands.

The Northern lesser galago is an omnivorous species, consuming a diversity of insects, vegetable matter, and fruits. They are nocturnal and arboreal. They will rest in tree holes or make leaf nests if areas without large trees. Northern lesser galagos may be solitary or found in small groups, though they will forage separately. Vocalizations appear important for communication, as Northern lesser galagos can produce 18 calls of differing frequencies. Females usually give birth to one young twice a year. The reproductive season is induced by temperature and/or food availability changes. Northern lesser galagos may be preyed on by chimpanzees (*Pan troglodytes*), large raptors, large snakes, genets, and diurnal primate species (de Jong et al., 2019; Nash et al., 2013).

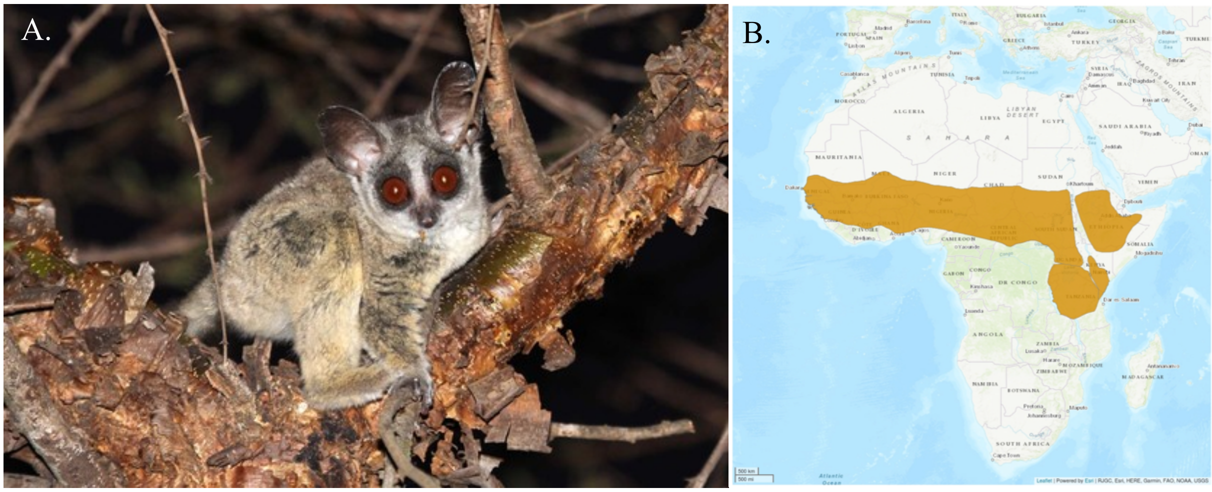

FIGURE 1.20. (A) Northern lesser galago (*Galago senegalensis*) in Tanzania (credit: Martin Grimm, https://www.inaturalist.org/photos/720222, licensed by CC BY-NC 4.0). (B) Map of *Galago senegalensis* distribution (de Jong et al., 2019).

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CHAPTER 2

WILDLIFE COMMUNITY COMPOSITION IN VILLAGES OF VARYING *DRACUNCULUS MEDINENSIS* (GUINEA WORM) PREVALENCE IN CHAD, AFRICA[1]

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[1] Korns, Avery L., Chandler, Richard B., Morin, Dana J., Yabsley, Michael J., Cleveland, Christopher A., To be submitted to *International Journal for Parasitology: Parasites and Wildlife*

ABSTRACT

Guinea worm disease (dracunculiasis) is a painful infection caused by the filarial nematode *Dracunculus medinensis*. The Guinea Worm Eradication Program (GWEP) has reduced human cases from 3.5 million across 21 countries in 1986 to only 15 human cases across 4 countries in 2021. Since 2012, Guinea worm (GW) infections have increased in domestic dogs and cats and have been confirmed in baboons and wild felids. Laboratory and field research support the belief that an aquatic paratenic and/or transport host is now an alternative transmission pathway. Little is known on the wildlife diversity surrounding villages in Chad, Africa, complicating our understanding of potential wildlife definitive hosts. To address this knowledge gap, we conducted a game camera study in Chad to document spatial variation in wildlife community composition. Seven villages were chosen for game camera deployment based on GWEP surveillance intensity, accessibility, spatial independence, and GW endemicity (3 endemic, 3 sporadic, and 1 negative village). Eight game cameras were deployed per village and recorded from February-November 2019. All wildlife detected were identified to the most specific taxonomic level possible. Species richness was greater in villages with GW. Specifically, we found more species of primates and mesopredators near endemic and sporadic villages than in the negative control. Single-season occupancy models were fit to data on tantalus monkeys (*Chlorocebus tantalus*), patas monkeys (*Erythrocebus patas*), Egyptian mongoose (*Herpestes ichneumon*), and pale fox (*Vulpes pallida*). Tantalus monkeys, patas monkeys, and Egyptian mongoose had higher occupancy estimates in endemic and/or sporadic villages. By providing valuable knowledge on the wildlife species present around villages in Chad, our results assist in the effort to understand the role of wildlife in transmission and sylvatic maintenance of GW. This study bridges the wildlife gap in a One Health approach to dracunculiasis eradication.

INTRODUCTION

Dracunculiasis, or Guinea worm disease (GWD), is a painful and debilitating disease caused by the parasitic nematode *Dracunculus medinensis* that has afflicted people in parts of Africa and the Middle East for much of recorded history (Adamson, 1988; Grove, 1990; Muller, 1991, 1971). Transmission to the definitive host occurs from ingestion of cyclopoid copepods containing infective third-stage larvae (L3) (Fedchenko, 1870). A gravid female forms a blister on a lower extremity, and upon contact with water, releases first-stage larvae (L1) to be consumed. The entirety of the lifecycle occurs in 10-14 months (Muller, 1971). The Guinea Worm Eradication Program (GWEP), led by the Carter Center, has been successful at reducing the number of human cases from 3.5 million across 21 countries in 1986 to only 15 cases in 4 countries (Chad, Ethiopia, Mali, and South Sudan) in 2021 (Watts, 1987; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022a; World Health Organization, 1996).

In 2010, Chad reported its first human GWD cases after a 10 year absence (Djidina et al., 2011). As more cases were reported in the following years, a “peculiar epidemiology” was observed , leading to the hypothesis that an aquatic paratenic or transport host was now involved in the lifecycle (Eberhard et al., 2014), which has been supported by experimental and field studies (Box et al., 2021; Cleveland et al., 2019, 2017; Eberhard et al., 2016b, 2016a). Additionally, infections began to emerge in domestic dogs (*Canis lupus familiaris*) and domestic cats (*Felis catus*) (Eberhard et al., 2014; Hopkins et al., 2018). Chad dog infections have consistently outnumbered Chad human cases since their first detection in 2012 and continued to grow until outnumbering the global human cases in 2015 (Eberhard et al., 2014; Hopkins et al., 2015). In 2020, there were 1,601 global animal infections reported, 98% of which originated from Chad (Hopkins et al., 2021). *Dracunculus medinensis* from humans and animals (both domestic and wild) have been molecularly confirmed as the same parasite species (Durrant et al., 2020; Thiele et al., 2018).

The rise in domestic dog infections led to the question of if wildlife species are also becoming infected. There are several successful *D. medinensis* experimental infections in numerous primate species (Brug, 1930; Leiper, 1907; Muller, 1972, 1968). Molecularly confirmed *D. medinensis* infections have been found in several wildlife species in Chad and Ethiopia (Hopkins et al., 2018; WHO Collaborating Center for Research, Training and Eradication of Dracunculiasis, CDC, 2022b, 2019). Information on wildlife infections comes mainly from the Carter Center's regularly published Guinea Worm Wrap-Up's. Ethiopia has regularly reported at least one olive baboon (*Papio anubis*) infection annually since 2013 except for 2021. Additionally, one leopard (*Panthera pardus*) was infected in 2019, although the worm had not emerged. In Chad, all confirmed wildlife infections have been in wild felids, except a new host in 2022 that is still being identified. The term "wild cat" is used non-specifically and could refer to an actual wildcat (*Felis lybica lybica*), or another wild felid (e.g., serval, caracal, etc.); typically, specific host information is not provided. To the author's knowledge, felid infections have been found in both wildcats (*Felis lybica lybica*) and servals (*Leptailurus serval*) (Fultz, personal communication). Occasionally, these "wild cat" infections are noted as provisional with no later confirmation found, so their status is unknown. The lack of releasing complete reports on these infections leads to an inadequate and deficient understanding of the situation in Chad.

The large volume of dog infections suggest that dogs are serving as a maintenance host for GW transmission in Chad, causing spill-over infections in humans and posing a challenge for the eradication initiative. The importance of wildlife in *D. medinensis* transmission is unknown, but wildlife infections may have the potential to infect water sources and act as a source of transmission to people or domestic animals. Furthermore, this issue is complicated by lack of documentation on both wildlife species present in the area and how they may interact with humans and domestic animals. This study aimed to determine possible wildlife reservoir hosts for *D. medinensis* through the deployment of game cameras in order to inform the eradication campaign. Occupancy models were created for several species detected on the cameras. To the authors knowledge, this is the first published game camera study in Chad (See Agha et al., [2018] for a recent review of camera studies in Africa).

METHODS AND STUDY AREA

Site Selection and Study Area

This study was conducted in seven villages in the Sarh region of southeastern Chad (Figure 2.1) (Eberhard et al., 2014; Guagliardo et al., 2020). Villages were chosen for game camera placement based on several factors: surveillance intensity, accessibility, spatial independence, and Guinea worm endemicity (Appendix A). Only villages with the highest level of surveillance activity (Level 1) were considered for game camera placement. Villages are classified as Level 1 if they meet the following conditions: have reported consistent transmission of GWD since 2010, have trained village volunteers that conduct household searches 3-4 times per week in search for signs of infection, offer cash rewards for reporting of suspected cases, rumors of suspected cases are investigated by a supervisor within 24 hours, health education is provided to villagers, and there is periodic evaluations of cash reward awareness and dracunculiasis education (Guagliardo et al., 2020). Village accessibility was also considered, as some villages are not easily accessible during the rainy season. Generally, these accessible villages were within 15km of an urban area. To ensure that selected villages had spatial independence, villages were at least 20 km away from each other. To classify guinea worm endemicity, data from 2014-2018 (provided by The Carter Center) were summarized, and villages were classified as having endemic transmission (categorized by reporting greater than 10 infections in any host during the four-year study), sporadic transmission (categorized by reporting 1-10 infections in any host during the four-year study), or no reported cases (no infections in any host during the four-year study) (Appendix B).

All of the villages included in this study are located along the Chari River or its tributaries and to the southeast of the Salamat floodplain. This area is in the Sudan-Savanna biotic zone, where abundant rainfall supports larger human populations and increased cultivation. Agriculture, alongside livestock grazing and browsing, have converted the area to broadleaf shrubby savanna (Keith and Plowes, 1997). Cattle and goats are the most commonly raised livestock. Peri-domestic dogs roam freely in every village. From WorldClim data collected from 1970-2000, average annual minimum and maximum temperature of the area ranges from 15°C to 39°C. Average annual precipitation is around 990mm, with the majority of rain falling from May-September (Fick and Hijmans, 2017). Average elevation for village centers was 368 meters (range 359.26-377 m) ("Airbus World DEM 24m," n.d.).

Game camera deployment

Eight Browning Dark Ops HD cameras (Forestry Suppliers, Inc., Jackson, MS) were deployed around each of the villages for a total of 56 cameras (Appendix C). The plan was to deploy four game cameras at the cardinal position (north, south, east, and west) 500 meters away from the village center and another four game cameras at the offset cardinal positions (northeast, southeast, southwest, and northwest) 1,000 meters away from the village center. However, in some cases, adjustments in placement were necessary because of land owner requests or geographic factors. Cameras were placed in a security box on a tree 24 in off the ground and secured with a nylon strap and locking cable. Cameras were triggered by motion with a 60 second delay and used an infrared flash. Cameras were deployed from 2/27- 3/5/2019 and picked up 11/4- 11/9/2019, with exact dates varying based on travel to villages. Cameras were checked at the end of May and August 2019 to replace batteries and SD cards.

Data analysis

All vertebrates seen on the cameras were identified to the most specific taxonomy possible and cataloged. Analysis was performed using single-season occupancy models to estimate site occupancy (ψ) and detection probability (p) and to account for the imperfect detection of individuals (MacKenzie et al., 2006). Analysis was done in R version 4.1.1 using package 'unmarked' and ArcGIS Pro version 2.9.0 (Fiske and Chandler, 2011; R Core Team, 2021).

The common genet (*Genetta genetta*) and rusty-spotted genet (*Genetta maculata*) are the two genet species whose range falls in southern Chad. They can be differentiated by length of pelage, shape/size of dorsal spots, and coloration of the tail tip (Angelici and Gaubert, 2013; Delibes and Gaubert, 2013). However, both species are nocturnal and were typically photographed too far from the camera to determine pelage characteristics and make a specific species identification. Both species were observed in the few close up pictures captured, but were included together for further analysis. They are hereafter referred to as genets.

Site covariates included endemicity level, Normalized Difference Vegetation Index (NDVI), percent landcover types, total trapping days, and the distance from the camera to the village center (m), the nearest water source (m), and the nearest path (m). Species-specific home range size estimates were used to calculate statistics for NDVI and percent landcover for each village using a dissolved buffer around each camera (Table 2.1). Landsat 8 images (Path 181 and 182, Row 54) processed using Level-1 Terrain Precision Correction (L1TP) were downloaded from the U.S. Geological Survey. Mean, maximum, minimum, and range NDVI were calculated for each village using as many cloud-free images as possible during the study period. Additional images with clouds were included after removing cloud cover, as long as clouds did not cover a significant portion of the buffered village area. Landcover data for 2019 were downloaded from Esri at the 10 m scale and projected into ArcGIS Pro version 2.9.0 (Karra et al., 2021). Landcover types in this area included water, trees, flooded vegetation, crops, built area, bare ground, and rangeland. Paths surrounding villages and cameras were digitized using the satellite base map of ArcGIS Pro version 2.9.0.

Observation covariates included average monthly temperature, maximum monthly temperature, minimum monthly temperature, monthly temperature range, and average monthly precipitation. Climate variables were calculated for all villages using WorldClim 1970-2000 data in ArcGIS Pro using a 30 km overlapping dissolved buffer, as differences in temperature and precipitation across villages at the same timepoint were minimal (Fick and Hijmans, 2017). However, changes in temperature and precipitation across the study may influence species' activity level, leading to biased detection probabilities (*p*). All covariates were standardized.

We predicted distance to village center and nearest path would influence a species' detectability (*p*), depending on sensitivity to anthropomorphic change (Easter et al., 2020). Distance to nearest water source may impact detectability, but may not be significant due to the inability to account for seasonal flooding creating temporary water sources. Maximum NDVI was included as a detection covariate to help account for taller grasses concealing smaller species. We predicted total trapping days for each camera would increase a species' detectability and help account for days lost due to camera failure or human disturbance.

We fit multiple models with a combination of occupancy and detection covariates and compared the models using Akaike's Information Criterion, relative Akaike model weights (w_i), and ΔAIC (Burnham and Anderson, 2002). Models were tested for goodness-of-fit using parametric bootstrapping of the sum of squared residuals with 1,000 simulations. The best fit models were used to calculate estimates for conditional occupancy and detection. Posterior distributions of latent occurrence were estimated using empirical Bayes methods. Estimates were calculated on the village level using the following formula: $\widehat{\psi_{Village}} = \left(1 - \left(\prod (1 - \widehat{\psi_{camera}}) \right)\right)$. Standard errors were calculated on the village level through summarizing predicted maximum posterior distribution estimates for each camera in the village over multiple simulations until estimates stabilized.

RESULTS

Four cameras were lost for the entire study due to damage and/or theft. Days were excluded from analysis if cameras were deemed inoperable due to the following reasons: cameras died before battery replacement, human interaction moved camera to point at ground, or dense vegetation obstructed camera view (generally occurred in August after high rainfall) (n=1,396). A full catalog of species identified is available in Appendix D. In total, cameras were fully operable for a total of 9,280 trapping days and a total of 1,070,891 pictures were acquired from which there were 5,578 detections of mammals (Table 2.2).

Detections

A total of 32 mammalian species were identified encompassing 17 families and 8 orders (Figure 2.2). The most frequently observed orders were Primates (n=1,547), Artiodactyla (n=1,436), and Carnivora (n=1,094). Of the wild species potentially relevant to GW transmission, there were 3 species in Primates and 15 species in Carnivora (Figure 2.3). The most wide-spread species detected in every village were the side-striped jackal (*Lupulella adustus*), white-tailed mongoose (*Ichneumia albicauda*), civet (*Civettictis civetta*), and genets. Additionally, 70 avian species and 3 reptile species were observed (Appendix D).

Tantalus monkeys (*Chlorocebus tantalus)* were detected at all villages except for Waltama, and the majority of detections (97.3%) came from endemic villages. Additionally, while there was over 200 detections of tantalus monkeys in every endemic village, Gentil comprised the majority of the tantalus detections (63%). Patas monkeys (*Erythrocebus patas*) were only detected at one sporadic village (Gongo). Northern lesser galagos (*Galago senegalensis*) had low detections (n=15), but were seen in Tarakoh, Ngangoli Tounia, Gongo, and Maicomb.

The enzootic, sporadic, and negative villages recorded a total of 12, 11, and 9 carnivore species, respectively. The highest number of carnivore species a single village detected was 10, which was found in both Ngangoli Tounia and Gentil. Both Tarakoh and Waltama detected 9 unique carnivore species. Gongo and Maicomb both recorded the least amount of unique carnivore detections (five and six, respectively) and the least amount of total carnivore detections (29 and 12, respectively).

The majority of Tarakoh's carnivore detections were from the side-striped jackal (62.3%). Additionally, the majority of side-striped jackals were detected in Tarakoh (66.7%). Ngangoli Tounia had a relatively even distribution of carnivore detections, with the most coming from the Egyptian mongoose (*Herpestes ichneumon*) (36.4%).

Gentil also had a relatively even distribution of carnivore detections, with the most coming from genets (39%). While Gongo had very little carnivore detections, over half (51.7%) were civets. Maicomb also had little carnivore detections, but 41.6% were genets.

In Dilbodo, the highest detections were from genets (38.7%) and pale fox (*Vulpes pallida*) (34.8%). While Waltama did detect the second highest carnivore species, it notably failed to detect many of the mongoose species, including the Egyptian mongoose, banded mongoose (*Mungos mungo*), and marsh mongoose (*Atilax paludinosus*) detected in other villages. Additionally, the majority of carnivore detections in Waltama comprised of the pale fox (49.0%) and spotted hyaena (*Crocuta crocuta*) (20.0%). Spotted hyaenas across villages were most frequently detected in Waltama (78.4%).

Occupancy models

The following species were detected in all villages during the study period, and thus no occupancy model was needed: side-striped jackal, white-tailed mongoose, genet, and civet. The following species had limited detections during the study period or their home ranges were too large to establish spatial independence, so no occupancy model could be created: serval (*Leptailurus serval*), caracal (*Caracal caracal*), African wildcat (*Felis lybica lybica*), ratel/honey badger (*Mellivora capensis*), marsh mongoose, banded mongoose, spotted hyaena, and striped hyaena (*Hyaena hyaena*).

Occupancy models were built for the following species: tantalus monkey, patas monkey, Egyptian mongoose, and pale fox (Table 2.3). Conditional occupancy and detection estimates for each species can be seen in Table 2.4. Tantalus monkeys were detected in every village except Waltama. With their best-fit model, it is very unlikely they were in Waltama during the study period ($\hat{\psi} = 6.9 \times 10^{-7} \pm 0.0$). Patas monkeys were only detected in Gongo, but the model predicted they may have been present but undetected in Maicomb and Dilbodo ($\hat{\psi} = 0.99 \pm 0.01$ for both). However, it is unlikely they were in any other village ($\hat{\psi}_{Ngangoli\ tounia} = 2.5 \times 10^{-3} \pm 0.05$; $\hat{\psi}_{Tarakoh} = 2.4 \times 10^{-3} \pm 0.05$; $\hat{\psi}_{Gentil} = 1.7 \times 10^{-3} \pm$

0.04; $\hat{\psi}_{Waltama} = 2.6 \times 10^{-5} \pm 0.005$). The Egyptian mongoose was detected in all endemic villages and Gongo, and it is unlikely that they occurred in other villages during the study period ($\hat{\psi}_{Maicomb} = 0.0 \pm 0.0$; $\hat{\psi}_{Dilbodo} = 0.0 \pm 0.0$; $\hat{\psi}_{Waltama} = 5.4 \times 10^{-8} \pm 0.0$). Pale foxes were detected in Waltama, Dilbodo, and Gentil, and their best-fit model agrees that it is unlikely they were in any other village during the study period ($\hat{\psi}_{Tarakoh} = 0.0 \pm 0.0$; $\hat{\psi}_{Ngangoli\ Tounia} = 3.8 \times 10^{-8} \pm 0.0$; $\hat{\psi}_{Gongo} = 0.0 \pm 0.0$; $\hat{\psi}_{Maicomb} = 1.7 \times 10^{-9} \pm 0.0$).

Detection estimates were calculated for each species on the camera-level, and several covariates were important for detection (Figure 2.4). Increasing distance to the village center had a negative effect on all species except the Egyptian mongoose. Higher maximum NDVI across villages was associated with decreasing detection probability for Egyptian mongoose and pale fox and increasing detection probability for both primates. Increasing maximum monthly temperature (tantalus and Egyptian mongoose) and average monthly temperature (patas ad pale fox) had a positive effect on detection. Tantalus monkey detection was negatively affected by increasing distance from the nearest path, while patas and Egyptian mongoose detection increased. Egyptian mongoose detection increased as distance from nearest water increased. Pale fox detection increased as average monthly precipitation increased. Accounting for differences in trapping lengths between cameras improved the models of both the tantalus monkey and the pale fox. However, contrary to the hypothesis, increasing trapping length decreased both species' detection probability.

DISCUSSION

Overall, there were fewer species of mesopredators, specifically mongoose species, and no primate detections in Waltama, the negative control. Interestingly, spotted hyaenas appear to be more active in Waltama, as 78.4% of detections were from Waltama. It is possible that the increased activity of spotted hyaenas there decreases the presence of smaller mesopredators and primates. Furthermore, decreased activity of spotted hyaenas in other villages may lead to mesopredator release and explain the increased biodiversity in other villages (Soulé et al., 1988). Striped hyaenas may be more active in endemic villages due to lack of spotted hyaena activity, as endemic villages recorded 10 of 11 striped hyaena detections. However, differences in presence, absence, or activity of species could be due to other environmental and anthropogenic factors. Percent landcover differences between villages were minor, but there was increased trees and decreased rangeland seen in Waltama. However, increased percentage of trees would have been likely to aid mesopredators as a way to avoid direct confrontations with spotted hyaenas (Ritchie and Johnson, 2009)

No primate species were detected in Waltama and our occupancy models did not predict that tantalus and patas monkeys were there undetected. Multiple experimental infections of primates (Brug, 1930; Crichton and Beverley-Burton, 1976; Leiper, 1907; Muller, 1972), along with natural infections in Ethiopian olive baboons, provide support that some primate species are susceptible to *Dracunculus* infections. A grivet monkey (*Chlorocebus aethiops*), a relative of the tantalus monkey, and a patas monkey have both been successfully experimentally infected (Muller, 1972), but whether natural infections are possible remains unknown. It is likely Ethiopian olive baboons are infected via the traditional route instead of through paratenic hosts, as the diet of olive baboons is primarily vegetation and insects (Palombit, 2013) and the importance of the paratenic transmission pathway in Ethiopia compared to Chad remains debated (McDonald et al., 2020; Wilson-Aggarwal et al., 2020). Similarly, tantalus and patas monkeys are both generalist omnivores consuming primarily gums, flowers, and arthropods, supplemented by fruits, seeds, leaves, stems, reptiles, bird eggs, and young birds (Isbell, 2013; Nakagawa, 2013). If natural infections of tantalus or patas monkeys do occur in Chad, it is likely also through the traditional route.

The Egyptian mongoose was also only detected in endemic and sporadic villages, and our occupancy model did not predict they were present in Waltama. The Egyptian mongoose is opportunistic and omnivorous, with its diet changing based on season and location. Overall, they will consume small mammals, reptiles, amphibians, birds, eggs, fish, crabs, crayfish, insects, carrion, fungi, and fruit. Vertebrates appear to comprise their primary prey source. Small mammals were the main prey in the Western Cape of South Africa and southeastern Nigeria, supplemented by reptiles, birds, amphibians, fish, and others (Angelici, 2000; Stuart, 1983). Among various locations in Spain, the primary prey source was rabbits, birds, and reptiles, though different sites had a different order of importance, indicating the adaptability of Egyptian mongoose to different resources (Delibes et al., 1984; Palomares, 1993; Palomares and Delibes, 1991a, 1991b). In Portugal, males consumed more mammals and amphibians, while females consumed more reptiles and invertebrates (Bandeira et al., 2018). The suitability of the Egyptian mongoose as a host for *D. medinensis* is unknown, but their carnivorous diet and presence in endemic villages suggests that they may be exposed to infection.

Pale foxes were detected most commonly in Waltama and Dilbodo with two detections in Gentil. The pale fox is one of the least studied canids in the world (Sillero-Zubiri, 2013; Sillero-Zubiri et al., 2004). The majority of pale fox research comes from populations in the Termit and

Tin Toumma National Nature and Cultural Reserve (TTT) in eastern Niger, an environment of hot summers, mild winters and low annual precipitation described as being dominated by sand dunes with patches of grasses, shrubs, and trees (Sillero-Zubiri et al., 2016). While the majority of the pale fox's distribution lies in the semi-arid Sahel, they are known to range into the moister parts of Guinean savannahs (Sillero-Zubiri, 2013; Sillero-Zubiri et al., 2004; Sillero-Zubiri and Wacher, 2012). The southernmost records in Chad come from Zakouma National Park, which is located approximately 240 km northeast of our study. This may be the southernmost detection of pale fox recorded. limited data on the pale fox, combined with the fact that previous research comes from their primary arid habitat, makes it difficult to determine the niche of the pale fox in our study area. In Niger, analyses of scats concluded pale foxes are primarily insectivorous. Rodents (mostly *Gerbillus* spp.), avians, and squamates were found in a low percentage of scats (<15%) but made up a high relative proportion of food items, suggesting they may be an important dietary component (Burruss et al., 2017). Agama lizard and Chestnut-backed Sparrow-Lark (*Eremopterix leucotis*) remains were discovered outside a burrow in Chad (Sillero-Zubiri, 2013). Many detections of pale foxes in Waltama came from a camera located near their burrows, which is also where a majority of striped ground squirrel (*Xerus erythropus*) detections came from. The squirrels were seen to run in and around the burrows. Similarly sized fox species, such as the kit fox (*Vulpes macrotis*) and swift fox (*Vulpes velox*) have been reported to consume larger vertebrate prey such as prairie dogs (*Cynomys* spp.), black-tailed jackrabbits (*Lepus californicus*), and ground squirrels (*Spermophilus* spp.) (Sillero-Zubiri et al., 2004). Pale foxes were seen to watch the squirrels run around but were not observed to actively hunt them, suggesting pale foxes may opt for smaller prey species in this area.

Detection probabilities were low for each species, but note that because of the study design, these estimates are on the camera-level scale instead of village-level. Including camera-level detection covariates can provide insight on relative space use and activity predictors. Distance to village center, maximum NDVI, and monthly temperature was an important detection covariate for all species. All species were more likely to be detected closer to the village center except for the Egyptian mongoose. This may reflect a more significant effect of anthropomorphic change on the Egyptian mongoose or its penchant to create and follow permanent paths (Ben-Yaacov and Yom-Tov, 1983), supported by personal observations of an Egyptian mongoose (believed to be the same individual due to loss of part of the tail) seen following the same trail in front of a camera multiple times. Detection probability increased with increasing village-level maximum NDVI for both primates and decreased for the Egyptian mongoose and pale fox. This agreed with our hypothesis that mesopredators would be harder to detect with taller grasses. Both primates may have had increased detection probability due to abundant food resources. All species showed an increased detection probability with increasing maximum (tantalus and Egyptian mongoose) or average (patas and pale fox) monthly temperature. This effect was especially significant with the pale fox and may relate to its adaptations to a warmer arid environment. Increased primate detections are likely due to resource availability. For example, tantalus monkeys were observed foraging fruit, a preferred energy source especially for tantalus males, in April which is the month with the hottest average maximum temperature (Nakagawa, 2000). Additionally, this is also why tantalus monkey detection probability decreased as trapping length increased, as tantalus were more active during the beginning of the study period.

Other species detected that could be exposed to infections due to their diet include genets, civets, marsh mongooses, side-striped jackals, African wildcats, servals, caracals, and ratels. Of these, African wildcats and servals are the only species known to have natural *D. medinensis* infections in Chad (Hopkins et al., 2021, 2018). Most of these species are dietary generalists with the ability to adapt to changes in resources. However, the marsh mongoose is more of a specialist species, feeding primarily on crustaceans, with the addition of amphibians, fish, mollusks, terrestrial arthropods, and rodents (Baker and Ray, 2013). The marsh mongooses' aquatic dietary preference and riparian habitat needs may increase their risk of exposure.

There are several important limitations to note with this study. Home range sizes used for landcover and NDVI analysis were estimated based on the best available research. However, there may be differences in this environment. Home range estimates for both patas and tantalus monkeys were taken from Nakagawa (1999), as their study site (a seasonally flooded Sahelo-Sudanian prairie beside the Chari river in Northern Cameroon) seemed to resemble ours most similarly. However, patas monkey home range size has been recorded to be large in Laikipia, ranging from 23.4 km^2 - 32 km^2 and increasing with group size (Chism and Rowell, 1988). If patas in our area do have this large of a home range, it would violate the spatial independence assumption, though patas were only detected in one village (Gongo). Egyptian mongoose are understudied in Africa, so the home range estimate used in this study is of males (slightly larger than females) from populations in SW Spain (Palomares, 1994). As stated previously, the pale fox is understudied and the only home range estimate comes from populations in TTT, which may or may not be similar in our study area. Additionally, while villages needed to be accessible for practicality purposes, it is possible that more accessible villages also have less wildlife.

CONCLUSIONS

The Guinea Worm Eradication Program has been widely successful at reducing infections of dracunculiasis in people. However, high infections in domestic dogs and cats in Chad, combined with sporadic detections in wildlife, threatens the eradication initiative and highlights the need for a One Health approach. There is no doubt that the CWEP volunteers and supervisors do an excellent job at health education and responding to rumors, however a recent survey on the surveillance system has noted some areas of improvement. There was a disconnect between how often villagers reported being visited by volunteers and how often volunteers reported visiting villagers, with some villagers reporting they had never been visited by volunteers. Dog-owners reported being visited by volunteers more frequently than those who did not own dogs, suggesting that volunteers may be biasing their searches towards dog owners in hopes of discovering worms rather than equally searching the entire village (Rubenstein et al., 2021). Recent epidemiological modeling has highlighted several important environmental and anthropogenic variables predicting infections (Richards et al., 2020). The continuing implementation and strengthening of health education to villagers on both human and animal infections, preventative measures, signs and symptoms, and treatment, combined with utilizing knowledge of geographic, topographic, and environmental predictors for infections is paramount.

This study aimed to help bridge the deficient in knowledge on the wildlife side by providing baseline information on species present near villages around Sarh, Chad, a hotspot for *D. medinensis* transmission. We discovered higher biodiversity in endemic villages, specifically of primate species and mesopredators. While it is unknown if tantalus and patas monkeys are able to act as hosts for *D. medinensis* in the wild, experimental infections do show susceptibility (Leiper, 1907; Muller, 1972). Similarly, little is known on host competency of herpestids, specifically the

Egyptian mongoose, but dietary preferences and confirmed presence around endemic villages suggest they could be exposed to infection. Dogs with multiple emerging worms frequently also exhibit multiple maternal parasite lineages (Thiele et al., 2018), and it is possible wildlife infections are contributing to the contamination of water sources. However, whether wildlife are competent enough hosts are able to sustain transmission of *D. medinensis* if human and dog infections are eliminated remains unknown. The Ethiopia Dracunculiasis Eradication Program has been tracking several baboon troops over recent years through radio telemetry in an effort to increase knowledge on troop movement, locate potentially contaminated water sources, and treat them with Abate before they are able to infect people or domestic animals. While this research may be time and labor intensive, an adaptation of this program into Chad may shed additional light on natural wildlife hosts. Ultimately, increasing the comprehension of transmission pathways and alternative hosts will provide a broader perspective into the management of *Dracunculus medinensis*.

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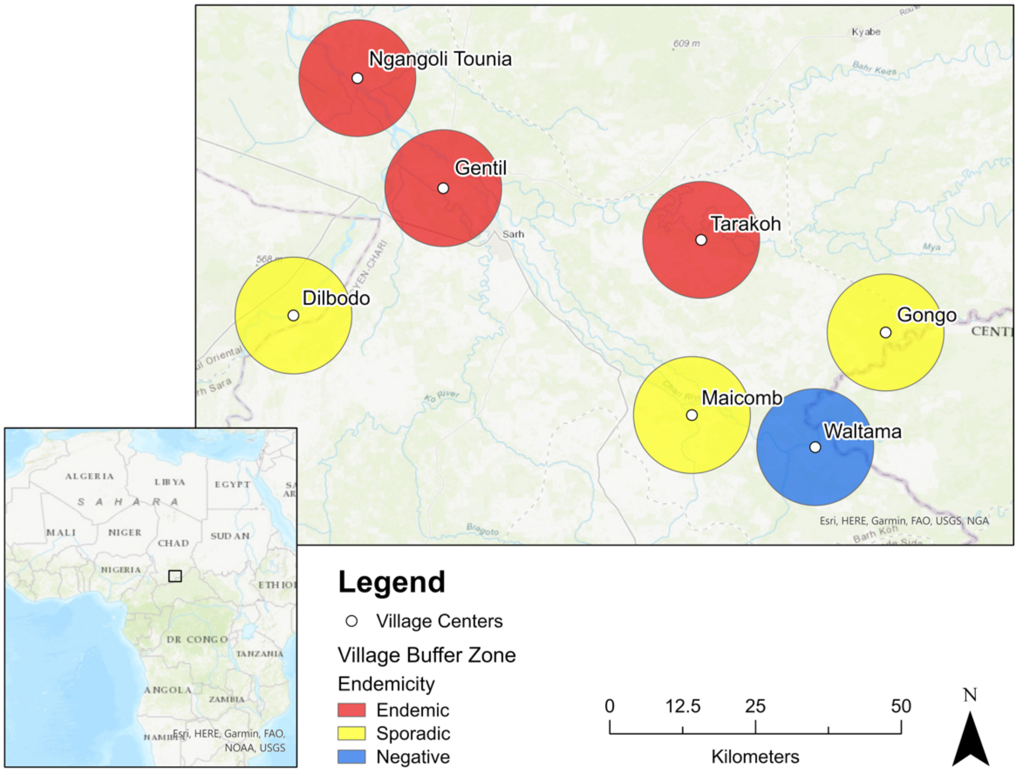

FIGURE 2.1. Map of villages where game cameras were deployed. Buffers show the non-overlapping 10 km radial buffer zone around each village. Three villages (Tarakoh, Ngangoli Tounia, and Gentil) were classified as endemic, three villages (Dilbodo, Maicomb, and Gongo) were classified as sporadic transmission, and Waltama was the only negative village in the region that met all criteria for inclusion.

TABLE 2.1. Home range size of each species used for analysis of landcover and NDVI statistics

Species	**Home range (km^2)**	**Reference**
Tantalus monkey *(Chlorocebus tantalus)*	0.43	Nakagawa, 1999
Patas monkey *(Erythrocebus patas)*	3.62	Nakagawa, 1999
Egyptian mongoose *(Herpestes ichneumon)*	3.52	(Palomares, 1994)Palomares, 1994
Pale fox *(Vulpes pallida)*	6.79	Sillero-Zubiri et al., 2016

TABLE 2.2. Days of game camera trapping effort and detections for each village around Sarh, Chad

Village	**Endemicity**	**Trapping effort (days)**	**Total detections (% Mammalia)**	
Tarakoh	Endemic	1,578	759	(78.8)
Ngangoli Tounia	Endemic	1,514	942	(74.0)
Gentil	Endemic	1,162	1,171	(76.4)
Gongo	Sporadic	964	303	(79.5)
Maicomb	Sporadic	1,497	350	(64.9)
Dilbodo	Sporadic	1,341	1,220	(61.1)
Waltama	Negative	1,224	833	(84.4)
Total	--	**9,280**	**5,578**	**(73.6)**

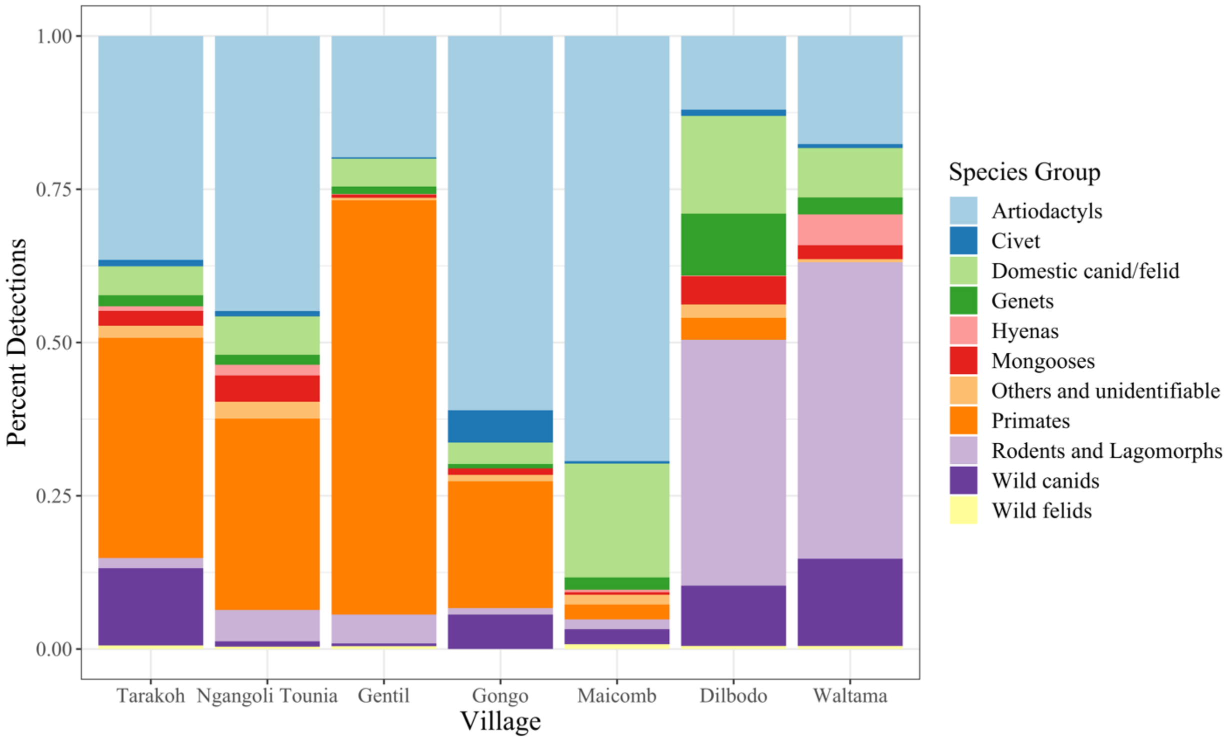

FIGURE 2.2. Percent of mammalian detections in each village separated into species groups

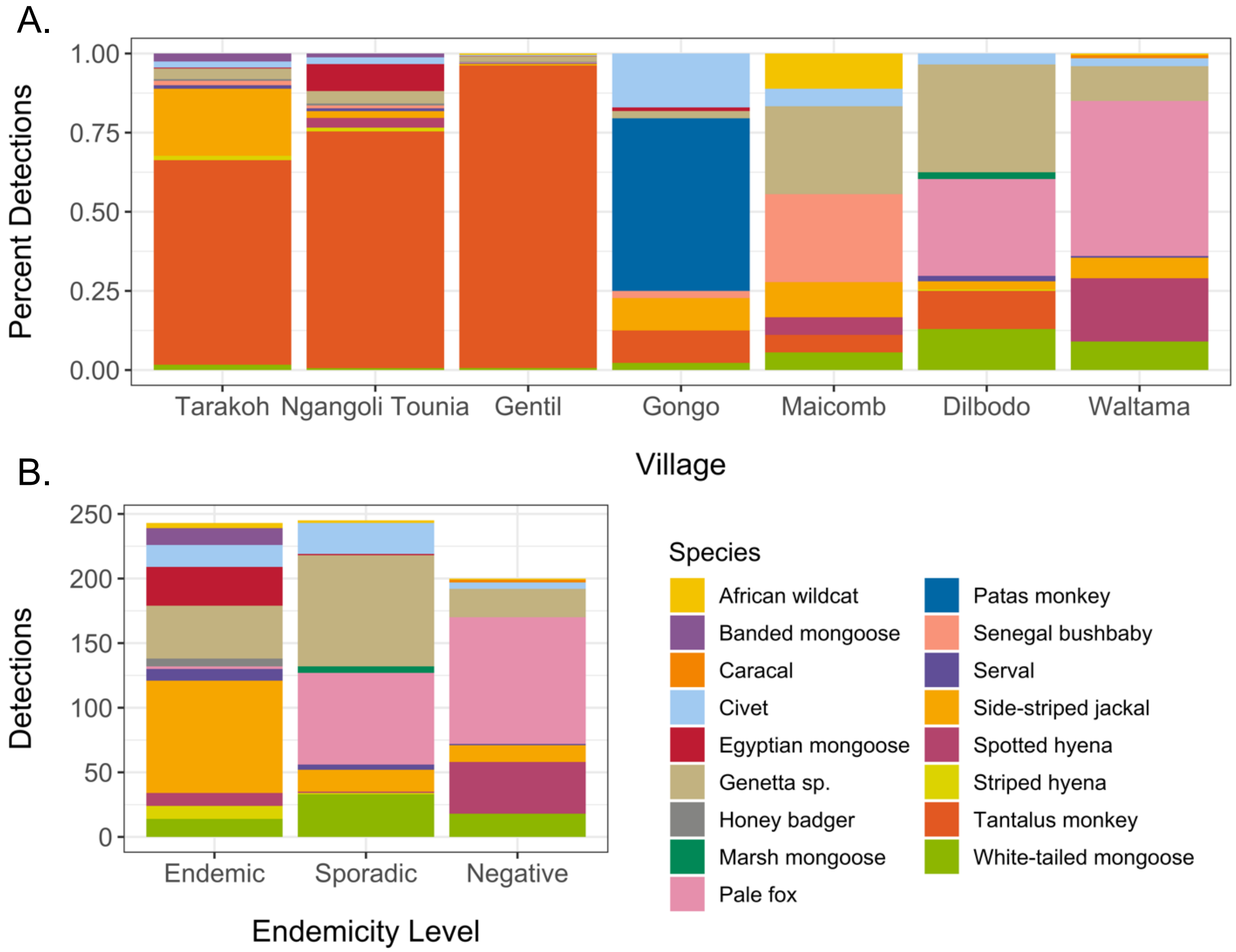

FIGURE 2.3. (A) Percent total primate and carnivore detections in each village. (B) Count of total carnivore detections summed across village endemicity levels

TABLE 2.3. Best fit models for each species chosen for occupancy modeling. Models were compared based on Akaike's Information Criterion, relative Akaike model weights (w_i), and ΔAIC. Models were tested for goodness-of-fit using parametric bootstrapping of the sum of squared residuals with 1,000 simulations.

Species	**Best fit model**
Tantalus monkey *(Chlorocebus tantalus)*	psi(percent_water + percent_range + minimum_NDVI + Infection_level) p(maximum_temperature + distance_to_center + distance_to_path + maximum_NDVI + camera_trapping_length)
Patas monkey *(Erythrocebus patas)*	psi(Infection_level) p(average_temperature + distance_to _center + distance_to_path + maximum_NDVI)
Egyptian mongoose *(Herpestes ichneumon)*	psi(percent_built_area + Infection_level) p(maximum_temperature + distance_to_center + distance_to_water + distance_to_path + maximum_NDVI)
Pale fox *(Vulpes pallida)*	psi(percent_water + percent_tree + Infection_level) p(precipitation + average_temperature + distance_to_center + maximum_NDVI + camera_trapping_length)

TABLE 2.4. Results of conditional occupancy and detection estimates for each species chosen for occupancy modeling from their best-fit model

	Conditional Occupancy Estimate							**Detection Estimate (camera-level)**
	Endemic			Sporadic			Negative	
	Tarakoh	Ngangoli Tounia	Gentil	Gongo	Maicomb	Dilbodo	Waltama	
Tantalus monkey *(Chlorocebus tantalus)*	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	6.9 x 10^{-7} ± 0.0	0.06 ± 0.005
Patas monkey *(Erythrocebus patas)*	2.4 x 10^{-3} ± 0.05	2.5 x 10^{-3} ± 0.05	1.7 x 10^{-3} ± 0.04	1.0 ± 0.0	0.99 ± 0.01	0.99 ± 0.01	2.6 x 10^{-5} ± 0.005	3.5 x 10^{-6} ± 8.3 x 10^{-5}
Egyptian mongoose *(Herpestes ichneumon)*	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	5.4 x 10^{-8} ± 0.0	0.04 ± 0.02
Pale fox *(Vulpes pallida)*	0.0 ± 0.0	3.8 x 10^{-8} ± 0.0	1.0 ± 0.0	0.0 ± 0.0	1.7 x 10^{-9} ± 0.0	1.0 ± 0.0	1.0 ± 0.0	0.04 ± 0.005

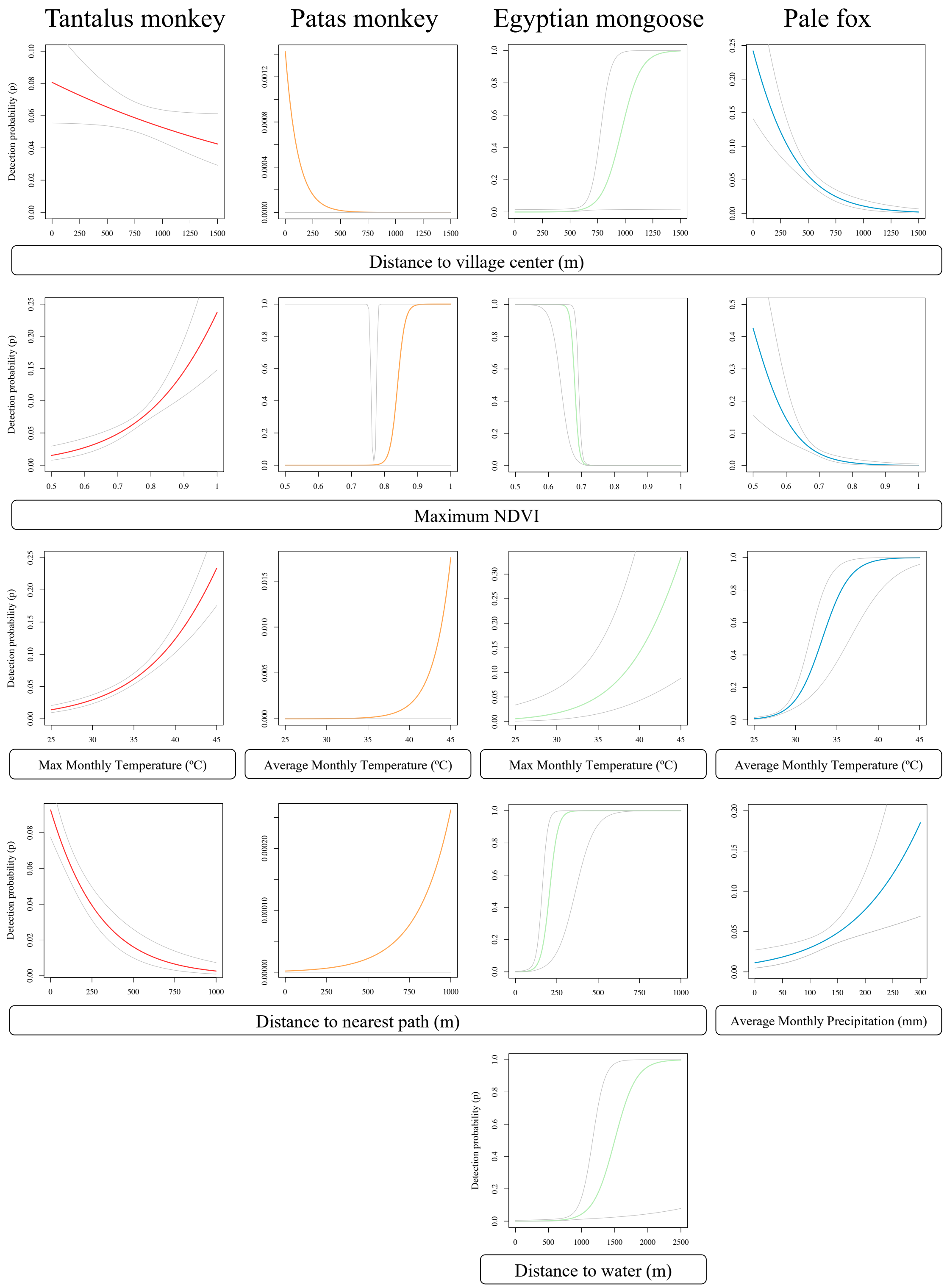

FIGURE 2.4. Change in detection probability (*p*) of each modeled species over their respective important covariates from their best-fit model

CHAPTER 3

SPATIOTEMPORAL INTRAGUILD INTERACTIONS OF CARNIVORES AROUND VILLAGES IN CHAD, AFRICA[2]

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[2] Korns, Avery L., Morin, Dana J., Chandler, Richard B., Yabsley, Michael J., Cleveland, Christopher A., To be submitted to *African Journal of Ecology*

ABSTRACT

Ecological overlap and intraguild competition can be reduced by spatial, temporal, or dietary partitioning of resources. African carnivore guilds are diverse, but research focuses on larger predators, and mesopredators are relatively understudied. We collected data from 52 game cameras across seven villages in the Sarh region of southern Chad as part of ongoing research into potential wildlife reservoirs of *Dracunculus medinensis*. We aimed to increase understanding of carnivore community structure in this area by investigating potential competitive interactions and indications of niche partitioning among six species: spotted hyaena, side-striped jackal, pale fox, African civet, genets, and white-tailed mongoose. We estimated kernel density estimates of the time of activity of subordinate predators when a dominant predator was detected compared to when one was not detected. We observed temporal partitioning between civets and genets, and civets and spotted hyaenas. Genets appeared to shift to crepuscular activity in the presence of nocturnal civets, and civets shifted to two activity peaks in the presence of spotted hyaenas. We calculated a relative activity index (RAI) to test for evidence of spatial niche partitioning in relation to anthropogenic features, including distance to the village center, the nearest water source, and the nearest path. Spotted hyaenas exhibited higher activity at camera traps closer to the village center, while side-striped jackals used areas farther away. Pale foxes used areas closer to the village center but shifted their relative space use in areas of high hyaena activity. Our results provide insight into how carnivores may interact in human-altered landscapes and guide future studies into community dynamics.

INTRODUCTION

Ecosystem dynamics and development are influenced by an interplay of bottom-up and top-down processes, and their importance may vary in different habitats (Elmhagen & Rushton, 2007; Heath, Speirs, & Steele, 2014; Pace, Cole, Carpenter, & Kitchell, 1999; Ritchie & Johnson, 2009; Wang et al., 2020). Niche theory proposes that species in competition must segregate on at least one axis (typically spatial, temporal, or dietary) to coexist without declines in one population (Brown, 1989; Schoener, 1974). Many previous studies have demonstrated niche partitioning within Africa's carnivore guild (Brown, 1989; Dröge, Creel, Becker, & M'soka, 2017; Durant, 1998; Hayward & Slotow, 2009; Mills, 1984; Ramesh, Kalle, & Downs, 2017). However, much research has focused on interactions between Africa's largest carnivores, with less focus on the interaction between large predators and mesopredators and between different mesopredators (but see Easter, Bouley, & Carter, 2020; Rich, Miller, Robinson, McNutt, & Kelly, 2017; Schuette, Wagner, Wagner, & Creel, 2013; Vissia & van Langevelde, 2022). Anthropogenic influences, including increasing human consumption of resources, can have wide-ranging effects, including altering community structure and species interactions (Estes et al., 2011; Foley et al., 2005). Outcomes can vary across ecosystems depending on the type and severity of disturbance and may inhibit, destabilize, or facilitate niche partitioning (Sévêque, Gentle, López-Bao, Yarnell, & Uzal, 2020).

Fragmented landscapes and habitat loss can reduce apex predator activity or increase interactions with mesopredators that typically avoid apex predators (Ritchie & Johnson, 2009; Schuette et al., 2013). Local extirpation of apex predators can result in biodiversity losses (Sergio, Newton, Marchesi, & Pedrini, 2006; J. Terborgh et al., 2001; J. W. Terborgh, 2015), including "trophic downgrading" (Estes et al., 2011) and "mesopredator release" (Soulé et al., 1988), increasing the activity or distribution of smaller predators. These potential outcomes can impact the dynamics and competition among carnivores and may favor generalist species (Clavel, Julliard, & Devictor, 2011).

While interspecific competition can occur among many species, the effects may be felt far greater by carnivores due to their morphological and behavioral killing adaptations (Creel, Spong, & Creel, 2001). According to Creel (2001), carnivore interspecific competition is usually asymmetric and can affect the subordinate species in three main ways: intraguild predation (where the dominant predator kills the subordinate with or without consuming), food stealing by the dominant species resulting in a fitness loss to the subordinate, and avoidance of the dominant species to reduce risk from direct encounters. Additionally, interspecies killing is most common among canids, felids, and mustelids (Palomares & Caro, 1999). Adverse competitive interactions can result in behavioral changes (e.g., changing activity times), moving to suboptimal habitat, reducing prey availability or food intake, limiting distribution range, and/or increasing mortality. Physical traits, such as body size, play a large role in the dietary preferences of large carnivores (Owen-Smith & Mills, 2008; Sinclair, Mduma, & Brashares, 2003) and thus can affect the type of competition experienced. Exploitative competition may occur among species of similar size and diet, while aggressive interference competition and interspecies killing may occur among species with a greater difference in body size (Donadio & Buskirk, 2006; Palomares & Caro, 1999). African carnivores may be especially prone to exploitative and interference competition, as the average African carnivore shares its geographic range, habitat type, and dietary habit with 22.4 other carnivore species (Caro & Stoner, 2003).

In Chapter 2, we discovered diverse carnivore communities within our studied villages. The abundance of data collected from that study allows us the opportunity to increase knowledge on understudied mesopredators, gather preliminary insight into competitive interactions, and investigate potential niche partitioning that may be used to guide future studies. As several species had few detections, we have limited our analysis to six species: spotted hyaena (*Crocuta crocuta),* side-striped jackal (*Lupulella adustus*), pale fox (*Vulpes pallida*), African civet (*Civettictis civetta*), common genet rusty-spotted genet (*Genetta genetta* and *G. maculata*, respectively), and white-tailed mongoose (*Ichneumia albicauda*). We estimated pair-wise temporal overlap and calculated a relative activity index (RAI) across different anthropogenically-influenced covariates, including distance to the village center, nearest water source, and nearest path. Given previous research (Cozzi et al., 2012; Easter et al., 2020; Ramesh et al., 2017; Vissia & van Langevelde, 2022) and the fact that all species investigated are predominately nocturnal, we expected to observe a relatively high temporal overlap between carnivores. However, we expected to potentially observe potential fine-scale temporal partitioning by discerning if activity peaks differed when dominant predators were detected compared to when they were not. We expected relative activity to increase or decrease closer to the village centers, depending on the species' sensitivity to anthropomorphic change. Similarly, those sensitive to human-related activity may avoid paths frequently traveled by humans, livestock, and domestic dogs (*Canis lupus familiaris*). Denser vegetation associated with riparian habitats may provide cover and benefit several species, particularly larger carnivores such as spotted hyaenas.

METHODS AND STUDY AREA

Site Selection and Study Area

Villages for game camera deployment were chosen as part of a research study into potential wildlife reservoir hosts of *Dracunculus medinensis*, a parasitic nematode causing a painful and debilitating disease in humans called Guinea worm disease or dracunculiasis. The Sarh region in southeastern Chad was targeted as it is a hotspot for *D. medinensis* transmission (Eberhard et al., 2014; Guagliardo et al., 2020). Seven villages were chosen for game camera placement based on several factors: surveillance intensity, accessibility, spatial independence, and Guinea worm endemicity. More information on village selection criteria can be found in Chapter 2.

Cameras were deployed surrounding villages located along the Chari River or its tributaries and to the southeast of the Salamat floodplain (Figure 3.1). This area is in the Sudan-Savanna biotic zone, where abundant rainfall supports larger human populations and increased cultivation. Agriculture, alongside livestock grazing and browsing, has converted the area into broadleaf shrubby savanna (Keith & Plowes, 1997). Cattle and goats are the most commonly raised livestock, and peri-domestic dogs roam freely in every village. From WorldClim data collected from 1970-2000, the area's average annual minimum and maximum temperature ranges from 15°C - 39°C. Average annual precipitation is around 990 mm, with the majority of rain falling from May-September (Fick & Hijmans, 2017). The average elevation for village centers was 368 meters (range 359.26-377 m) ("Airbus World DEM 24m," n.d.).

Game camera deployment

Eight Browning Dark Ops HD cameras (Forestry Suppliers, Inc., Jackson, MS) were deployed around each village for a total of 56 cameras (Appendix E). The plan was to deploy four game cameras at the cardinal position (north, south, east, and west) 500 meters from the village center. The other four game cameras would be set up at the offset cardinal positions (northeast, southeast, southwest, and northwest) 1,000 meters away from the village center. However, in some cases, adjustments in placement were necessary because of landowner requests or geographic factors. Cameras were placed in a security box on a tree 24 in off the ground and secured with a nylon strap and locking cable. Cameras were triggered by motion with a 60-second delay and used an infrared flash. Cameras were deployed from 2/27- 3/5/2019 and picked up 11/4- 11/9/2019, with exact dates varying based on travel to villages. Cameras were checked at the end of May and August 2019 to replace batteries and SD cards.

Data analysis

All species seen on the cameras were identified to the most specific taxonomic group possible. Independent detections (defined as being $\geq$ 30 minutes apart) for each species were summarized across cameras. Temporal overlap was estimated through kernel density estimates using package ‘overlap’ in R version 4.1.1 (R Core Team, 2021; Ridout & Linkie, 2009). Estimates are calculated on a 0 to 1 scale, with 0 meaning no overlap and 1 meaning complete overlap. The mean estimate and 95% confidence intervals were calculated after generating 10,000 bootstrap iterations. Typically, $\widehat{\Delta_1}$ was used to account for smaller sample sizes (< 50 independent detections), though $\widehat{\Delta_4}$ was used when appropriate ($\geq$ 50 independent detections). The subordinate species were separated into two groups to look at small-scale changes in temporal activity: detections at a camera where a dominant predator was detected and detections at a camera where a dominant predator was not detected during the study period. To estimate differences in temporal activity overlap between a subordinate species and a dominant species, we estimated temporal overlap in detections at cameras where the dominant predator was not detected and compared to overlap at cameras where the dominant predator was detected. We calculated the difference in mean overlap by subtracting the overlap estimate with the dominant predator from the overlap estimate without the dominant predator. If a species changed their activity to avoid a dominant predator, the difference between the two estimates will be > 0.

Three covariates associated with human influence were calculated using ArcGIS Pro version 2.9.0 to look at partitioning in relative space use: distance from each camera to the village center, the nearest water source, and the nearest path. Independent detections were summarized across cameras, and data were fit using a negative binomial generalized linear model to account for overdispersion. The number of trapping days was added as a covariate into each model to account for differences in trapping effort due to battery failure or human disturbance. Predictions were made of a relative activity index (RAI) for 100 trapping days. Distance to the village center was chosen to account for sensitivity to anthropomorphic change, as areas closer to villages are assumed to have increased human activity. Distance from the camera to the nearest path was calculated by digitizing paths surrounding villages and cameras using the satellite base map in ArcGIS Pro. These study sites contain many paths traveling from village centers to crop fields, water sources, or other villages and may be frequented by people, livestock, and domestic dogs. Therefore, species sensitive to human activity may avoid these areas. Distance to the nearest water source was calculated by extracting the water layer from 2019 landcover data downloaded from Esri (Karra et al., 2021). We assumed denser vegetation associated with riparian habitats may be beneficial to several species by providing cover.

RESULTS

Four cameras were lost for the entire study due to damage and/or theft. Days were excluded from analysis if cameras were deemed inoperable for the following reasons: cameras died before battery replacement, human interaction moved the camera to point at the ground, or dense vegetation obstructed camera view (generally occurred in August after high rainfall) (n=1,396). In total, cameras were fully operable for 9,280 trapping days, and 1,070,891 pictures were acquired, from which there were 5,578 detections of mammals (Table 3.1).

A total of 32 mammalian species were identified, encompassing seventeen families and eight orders (Figure 3.2). Additionally, 70 avian and three reptile species were observed (Appendix D). The most frequently observed orders were Primates (n=1,547), Artiodactyla (n=1,436), and Carnivora (n=1,094). Of the Carnivora, fifteen species were detected: side-striped jackal (*Lupulella adustus*), pale fox (*Vulpes pallida*), serval (*Leptailurus serval*), caracal (*Caracal caracal*), African wildcat (*Felis lybica lybica*), spotted hyaena (*Crocuta crocuta*), striped hyaena (*Hyaena hyaena*), ratel/honey badger (*Mellivora capensis*), African civet (*Civettictis civetta*), common genet (*Genetta genetta*), rusty-spotted genet (*Genetta maculata*), marsh mongoose (*Atilax paludinosus*), Egyptian mongoose (*Herpestes ichneumon*), white-tailed mongoose (*Ichneumia albicauda*), and banded mongoose (*Mungos mungo*) (Figure 3.3).

The common genet (*Genetta genetta*) and rusty-spotted genet (*Genetta maculata*) are the two genet species whose range falls in southern Chad. They can be differentiated by the length of the pelage, shape/size of dorsal spots, and coloration of the tail tip (Angelici & Gaubert, 2013; Delibes & Gaubert, 2013). However, both species are nocturnal and were typically photographed too far from the camera to determine pelage characteristics and make a specific species identification. Both species were observed in the few close-up pictures captured but were included together for further analysis. They are hereafter referred to as genets.

The most widespread species detected in every village were the side-striped jackal, white-tailed mongoose, African civet, and genets. However, the pale fox was the most frequently detected species (n=154 independent detections), followed by genets (n=141 independent detections) and side-striped jackals (n=103 independent detections). Due to a low number of detections for several species, temporal and spatial analysis could only be done on the following: spotted hyaena, side-striped jackal, pale fox, civet, white-tailed mongoose, and genet.

Temporal partitioning

All species exhibited nocturnal activity and high temporal overlap (Table 3.2, Figure 3.4). Some species did show decreased mean temporal overlap when the dominant species was present. However, the 95% confidence intervals between the two estimates (with and without the dominant species) overlapped. The species relationships exhibiting the least change were: spotted hyaena and side-striped jackal, side-striped jackal and pale fox, and all relationships between the white-tailed mongoose and the dominant species. While side-striped jackals had high temporal overlap with spotted hyaenas, they did show a slight shift to a more distinct nocturnal peak (Figure 3.4). The species relationships exhibiting the greatest change were: civet and genet, spotted hyaena and civet, and spotted hyaena and pale fox. At cameras where civets were detected, genets shifted their activity from nocturnal to more crepuscular activity, displaying higher activity peaks at dawn and dusk. Similarly, at cameras where spotted hyaenas were detected, civets were observed to shift their activity from one peak centered over midnight to two distinct peaks around 22:00 and 6:00, directly following the spotted hyaena activity peak. Pale foxes were observed to have an extended activity time with no distinct peak in the presence of spotted hyaenas. Conversely, genets were observed to have greater temporal overlap at cameras where side-striped jackals were detected. Any relationship between the white-tailed mongoose and a dominant or subordinate predator showed little change.

Spatial partitioning

Distance to the village center was a significant predictor variable (p-value < 0.05) for spotted hyaenas and side-striped jackals. Spotted hyaenas had a higher RAI closer to the village center, while side-striped jackals' activity was higher farther from the village center (Figure 3.5). Distance to the village center was not significant for all pale fox detections. However, a relatively even split of pale fox detections between villages Dilbodo (which detected no spotted hyaenas) and Waltama (which accounted for ~78% of spotted hyaena detections) allowed us to look at differences with and without a dominant predator. Distance to the village center was a significant predictor for pale foxes in Dilbodo but not in Waltama (Figure 3.6). Civets, genets, and white-tailed mongooses had a relatively stable RAI across distances from the village center.

Distance to water was a significant predictor variable for spotted hyaenas and pale foxes, though all species except jackals showed decreasing RAI farther from water (Figure 3.5). Distance to the path was not a significant variable for any species, and most species exhibited a stable RAI across distances. Pale foxes did show a decreasing RAI farther from paths, and civets showed an increased RAI farther from paths.

DISCUSSION

Our objective was to provide insight into carnivore interactions and indications of niche partitioning in human-altered landscapes. This research is the first attempt to increase the overall understanding of the community structure around Sarh, Chad. At our study site, some species exhibited a degree of either temporal or spatial partitioning. Temporal partitioning was most apparent between civets and genets and spotted hyaenas and civets. Spatial partitioning was most evident between spotted hyaenas and side-striped jackals and between spotted hyaenas and pale foxes. White-tailed mongooses appeared to be least affected by the presence of any other dominant species.

As concluded in several other studies (Cozzi et al., 2012; Easter et al., 2020; Ramesh et al., 2017, 2017; Vissia & van Langevelde, 2022), all species exhibited high temporal overlap. Similar to previous research between black-backed jackals (*Lupulella mesomelas*) and spotted hyaenas in Botswana (Vissia & van Langevelde, 2022), our study reports high temporal overlap between side-striped jackals and hyaenas. However, we did observe side-striped jackals shifting to a stronger nocturnal activity peak in the presence of hyaenas.

We found evidence supporting fine-scale temporal avoidance between several species. The largest difference was observed between civets and genets, where genets shifted to crepuscular activity peaks in the presence of strictly nocturnal civets. These results are in contrast to previous studies in Mozambique and Botswana, where high temporal overlap ($\hat{\Delta} > 90$) between civets and genets was observed, and there was little change in genet activity in response to civets (Easter et al., 2020; Vissia & van Langevelde, 2022). Common genets, *G. genetta*, are believed to be the most vulnerable African carnivore to both exploitative competition and interspecific killing due to their small size, wide distribution, and generalist feeding habits (Caro & Stoner, 2003). Genets appear to be very adaptable to their specific environment. Differences in their interactions across their range may be due to their community structure (e.g., the presence and abundance of larger carnivores), environmental differences (e.g., an abundance of trees allows for easier avoidance as genets are more arboreal), anthropogenic change, or other unknown factors. The second largest temporal difference was observed between spotted hyaenas and civets, indicating potential avoidance behavior. Civets changed their activity from one distinct nocturnal peak to two peaks- one before midnight and one after the hyaena activity peak before dawn. Additionally, pale foxes showed reduced temporal overlap in the presence of hyaenas by delaying their activity peak until after the hyaena activity peak.

Additionally, we found evidence of spatial avoidance relating to human activity and anthropomorphic change. Notably, side-striped jackals avoided village centers where hyaenas had the highest activity, and avoidance may be amplified by human and domestic dog activity (though dogs were observed evenly at all distances from the village center). This agrees with previous studies that found spotted hyaena occupancy increased closer to human settlements in Kenya while black-backed jackal occupancy decreased (Schuette et al., 2013). Conversely, black-backed jackal occupancy and activity were positively associated with relative human abundance in South Africa, although the larger predators detected here were caracals and servals, not hyaenas (Ramesh & Downs, 2015). Therefore, differences may reflect community structure and fear responses from top predators. Furthermore, a strong relationship was observed in spatial avoidance between pale foxes and spotted hyaenas. Pale foxes preferred areas closer to the village center in Dilbodo, where hyaenas were not detected. However, they utilized all distances from the village center in Waltama, a village with high hyaena activity. This result suggests a change in preferred areas to avoid hyaenas. Pale foxes are one of the least studied canids in the world, and very little is known about competitive interactions (Sillero-Zubiri, 2013), so this finding has not been reported previously.

A previous study has reported increased civet abundance farther from human settlements in Mozambique (Easter et al., 2020), but we did not find evidence of increased relative activity to support this in our study. Distance to the village center was also not observed to be a significant predictor of relative activity for genets, which agrees with a previous study finding *G. maculata* abundance was not affected by distance to permanent settlement in Mozambique (Easter et al., 2020). Other genet species appear to tolerate human disturbance well, as large-spotted genet (*Genetta tigrina*) occupancy across farmlands in South Africa was positively associated with human abundance (Ramesh & Downs, 2014), and they have been observed to take advantage of food resources in urban environments (Widdows & Downs, 2015).

Closer distances to water were a significant predictor variable for spotted hyaena and pale fox activity in our study. Similarly, spotted hyaenas occupancy was higher near permanent water in Kenya (Schuette et al., 2013). It is likely denser vegetation surrounding water provides beneficial cover to spotted hyaenas and pale fox. Denser vegetation surrounding water likely provides beneficial cover to spotted hyaenas and pale foxes. However, seasonal rains creating temporary ponds could have reduced the effect of activity near water sources for other species.

White-tailed mongooses showed the least change in response to all dominant predator detections and did not show spatial avoidance. Likewise, Schuette et al. (2013) found that distance to the nearest water permanent water source and human settlement was not a significant predictor for white-tailed mongoose occupancy. White-tailed mongooses at our study site may face less competition as they are the only insectivorous, nocturnal carnivore detected in this area.

While this study offers valuable insight on how understudied mesopredators may co-occur around human-altered landscapes, it was not designed for this purpose and has several limitations. After splitting subordinates into two groups, sample sizes were small for kernel density estimation of temporal overlap reducing precision of estimates. Additionally, the group with the dominant predator present was typically smaller than without the dominant predator. For example, there were 99 independent detections of pale foxes at cameras where spotted hyaenas were not detected, but there were only 55 detections where spotted hyaenas were detected. However, this could also indicate smaller-scale spatial avoidance. Other potentially important environmental factors that could predict spatial partitioning, such as habitat type and agriculture use, were not evaluated. The long trapping period from the end of the dry season to the end of the wet season meant the environment changed considerably throughout the study. More work would be required to accurately quantify environmental factors remotely due to seasonal flooding increasing vegetation growth and planting seasonal crop fields. Future studies could also improve the temporal part of this work by adding a factor that measures how much time it takes for a subordinate species to be detected after detecting a dominant predator, which could provide more information on competitive interactions.

We investigated the spatial and temporal interactions between co-occurring carnivores around villages in Sarh, Chad. We provide support for previous findings (e.g., high temporal overlap between jackals and hyaenas) and report novel findings (e.g., genets shifting activity patterns in the presence of civets). Additionally, we provide more research into intraguild interactions among Africa’s smaller carnivores, an understudied area of research. Bottom-up and top-down processes both regulate ecosystem dynamics, and differences in interactions between species in the literature may be explained by the relative importance of each of these processes in that individual species’ environment. However, competitive interactions in this area are likely asymmetrical and may be a glimpse into competitive exclusion. Competitive exclusion is a slow process occurring over broad temporal scales (Yackulic, 2017), so longer-term studies are required to determine if these interactions represent coexistence or exclusion over time. The growth of human, livestock, and domestic animal populations may increase land disturbance, habitat fragmentation, and human-wildlife conflict. It is difficult to predict how this may impact the carnivore guild because consequences of human disturbance vary across ecosystems (Sévêque et al., 2020). Human-wildlife conflict may be particularly risky for spotted hyaenas, who were observed to have increased activity close to villages. Furthermore, removing or disrupting the apex predator in this system may have far-reaching effects down trophic levels. We hope insights provided here into carnivore interactions can be used to guide future studies on the stability of the carnivore community in this area and their response to anthropomorphic change.

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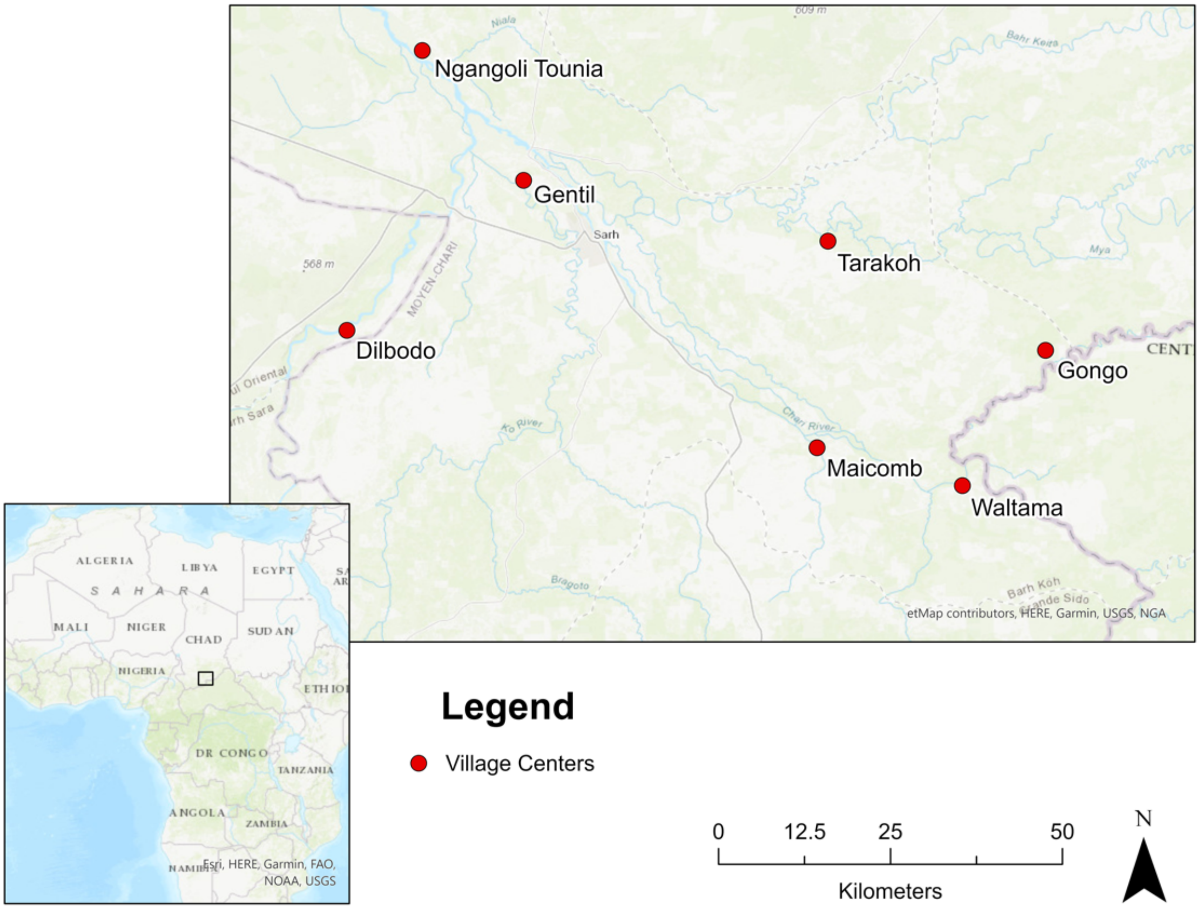


FIGURE 3.1. Map of village locations where game cameras were deployed. Villages were located around the Chari River near Sarh, Chad. Villages were chosen as part of ongoing research into potential wildlife reservoirs of *Dracunculus medinensis*

TABLE 3.1. Days of game camera trapping effort and detections for each village around Sarh, Chad

Village	Trapping effort (days)	Total pictures	Total detections (% Mammalia)
Tarakoh	1,578	92,549	759 (78.8)
Ngangoli Tounia	1,514	58,438	942 (74.0)
Gentil	1,162	121,024	1,171 (76.4)
Gongo	964	155,747	303 (79.5)
Maicomb	1,497	147,843	350 (64.9)
Dilbodo	1,341	163,291	1,220 (61.1)
Waltama	1,224	331,999	833 (84.4)
Total	9,280	1,070,891	5,578 (73.6)

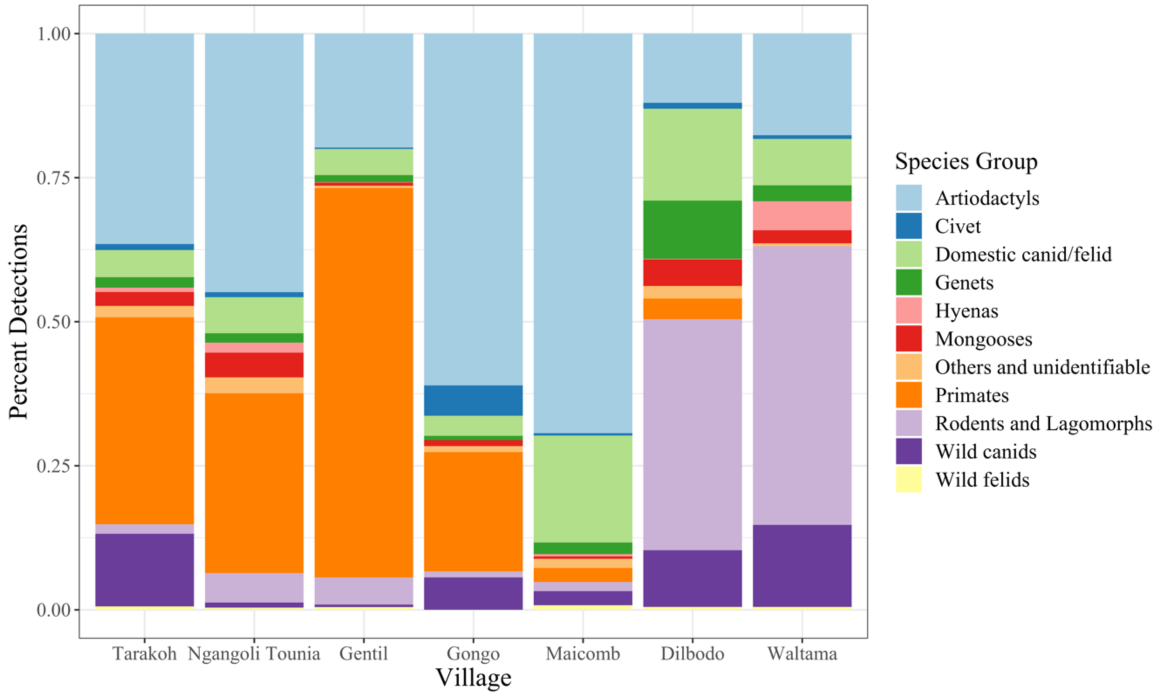


FIGURE 3.2. Percent of mammalian detections in each village separated into species groups

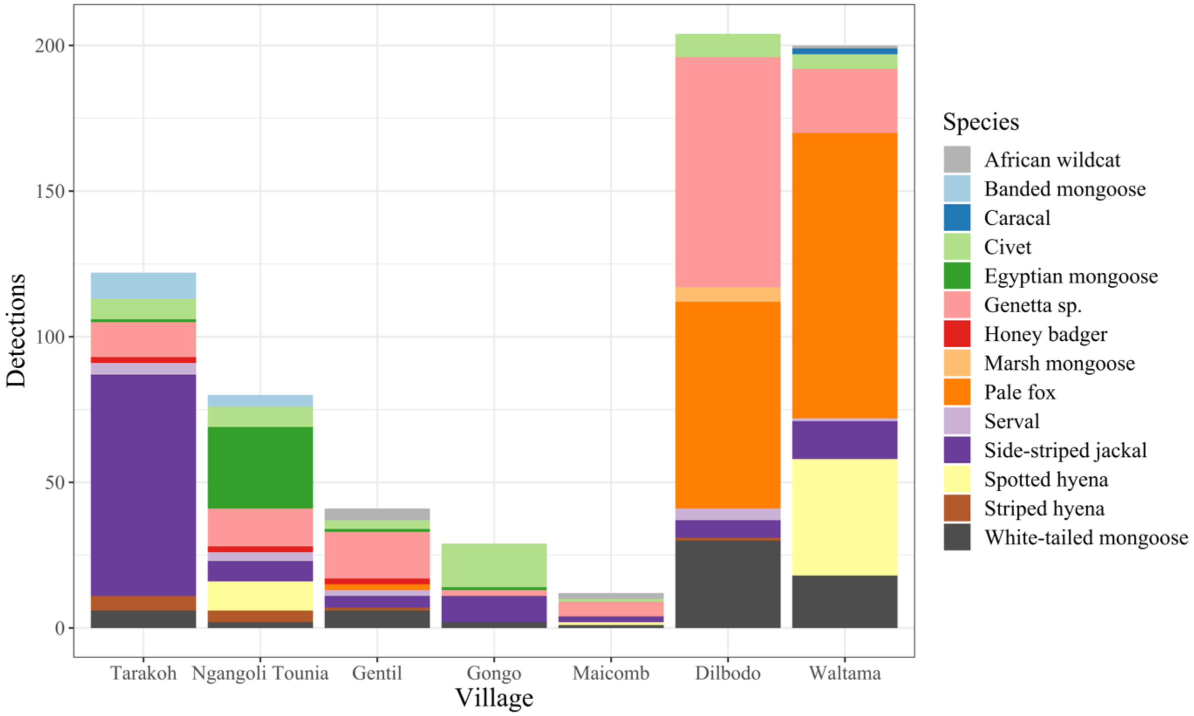


FIGURE 3.3. Total count of carnivore detections separated by village

TABLE 3.2. Temporal overlap estimates of subordinates species with and without dominant predators

Dominant-Subordinate	**Without dominant (95% CI)**	**With dominant (95% CI)**	$\mathbf{\Delta\,\widehat{\Delta}}$ **Change in overlap when dominant was detected**
HY-JA	$\widehat{\Delta_1} = 0.76$ (0.65-0.88)	$\widehat{\Delta_1} = 0.74$ (0.59-0.95)	0.02
HY-PF	$\widehat{\Delta_1} = 0.74$ (0.60-0.84)	$\widehat{\Delta_1} = 0.65$ (0.48-0.72)	0.09
HY-CI	$\widehat{\Delta_1} = 0.77$ (0.62-0.90)	$\widehat{\Delta_1} = 0.67$ (0.47-0.90)	0.10
HY-WM	$\widehat{\Delta_1} = 0.77$ (0.64-0.90)	$\widehat{\Delta_1} = 0.78$ (0.66-0.95)	-0.01
HY-GEN	$\widehat{\Delta_1} = 0.77$ (0.66-0.84)	$\widehat{\Delta_1} = 0.72$ (0.54-0.89)	0.05
JA-PF	$\widehat{\Delta_4} = 0.81$ (0.74-0.91)	$\widehat{\Delta_4} = 0.82$ (0.74-0.93)	-0.01
JA-CI	$\widehat{\Delta_1} = 0.71$ (0.49-0.86)	$\widehat{\Delta_1} = 0.79$ (0.66-0.90)	-0.08
JA-WM	$\widehat{\Delta_1} = 0.83$ (0.75-0.95)	$\widehat{\Delta_1} = 0.78$ (0.67-0.93)	0.05
JA-GEN	$\widehat{\Delta_4} = 0.73$ (0.59-0.81)	$\widehat{\Delta_4} = 0.85$ (0.77-0.96)	-0.12
CI-WM	$\widehat{\Delta_1} = 0.83$ (0.77-0.99)	$\widehat{\Delta_1} = 0.81$ (0.70-0.95)	0.02
CI-GEN	$\widehat{\Delta_1} = 0.80$ (0.66-0.90)	$\widehat{\Delta_1} = 0.67$ (0.48-0.75)	0.13
WM-GEN	$\widehat{\Delta_1} = 0.78$ (0.66-0.97)	$\widehat{\Delta_4} = 0.80$ (0.68-0.89)	-0.02

HY: Spotted hyaena; JA: Side-striped jackal; PF: Pale fox; CI: African civet; WM: White-tailed mongoose; GEN: Genet

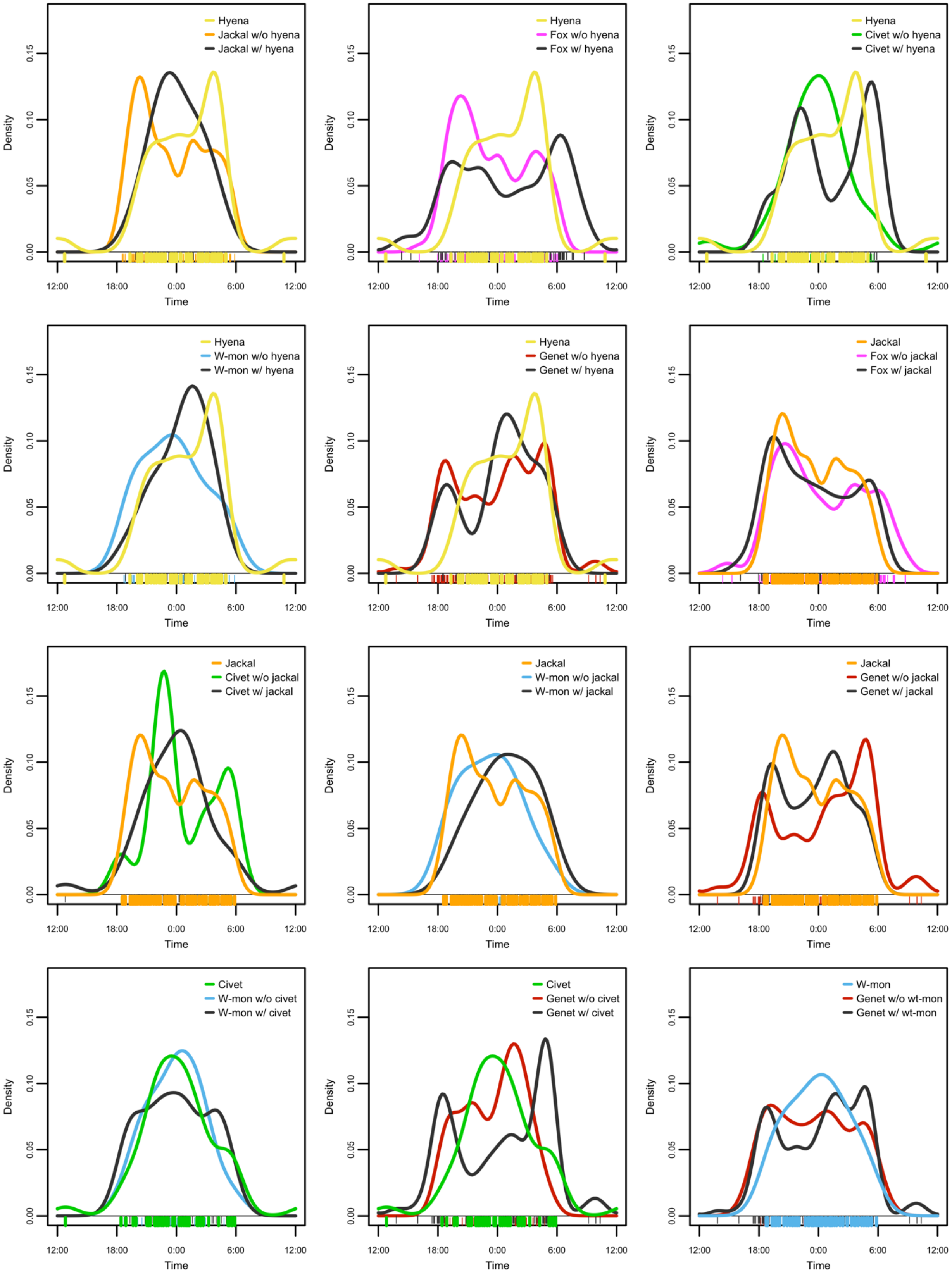

Hyena
Jackal w/o hyena
Jackal w/ hyena
Hyena
Fox w/o hyena
Fox w/ hyena
Hyena
Civet w/o hyena
Civet w/ hyena
Hyena
W-mon w/o hyena
W-mon w/ hyena
Hyena
Genet w/o hyena
Genet w/ hyena
Jackal
Fox w/o jackal
Fox w/ jackal
Jackal
Civet w/o jackal
Civet w/ jackal
Jackal
W-mon w/o jackal
W-mon w/ jackal
Jackal
Genet w/o jackal
Genet w/ jackal
Civet
W-mon w/o civet
W-mon w/ civet
Civet
Genet w/o civet
Genet w/ civet
W-mon
Genet w/o wt-mon
Genet w/ wt-mon
Density
0.00
0.05
0.10
0.15
Time
12:00
18:00
0:00
6:00
12:00

FIGURE 3.4. Daily temporal activity patterns and overlap among species for when they were detected without their dominant predator and with the dominant predator (black line). Lines on the x-axis indicate the time stamps used to calculated activity patterns.

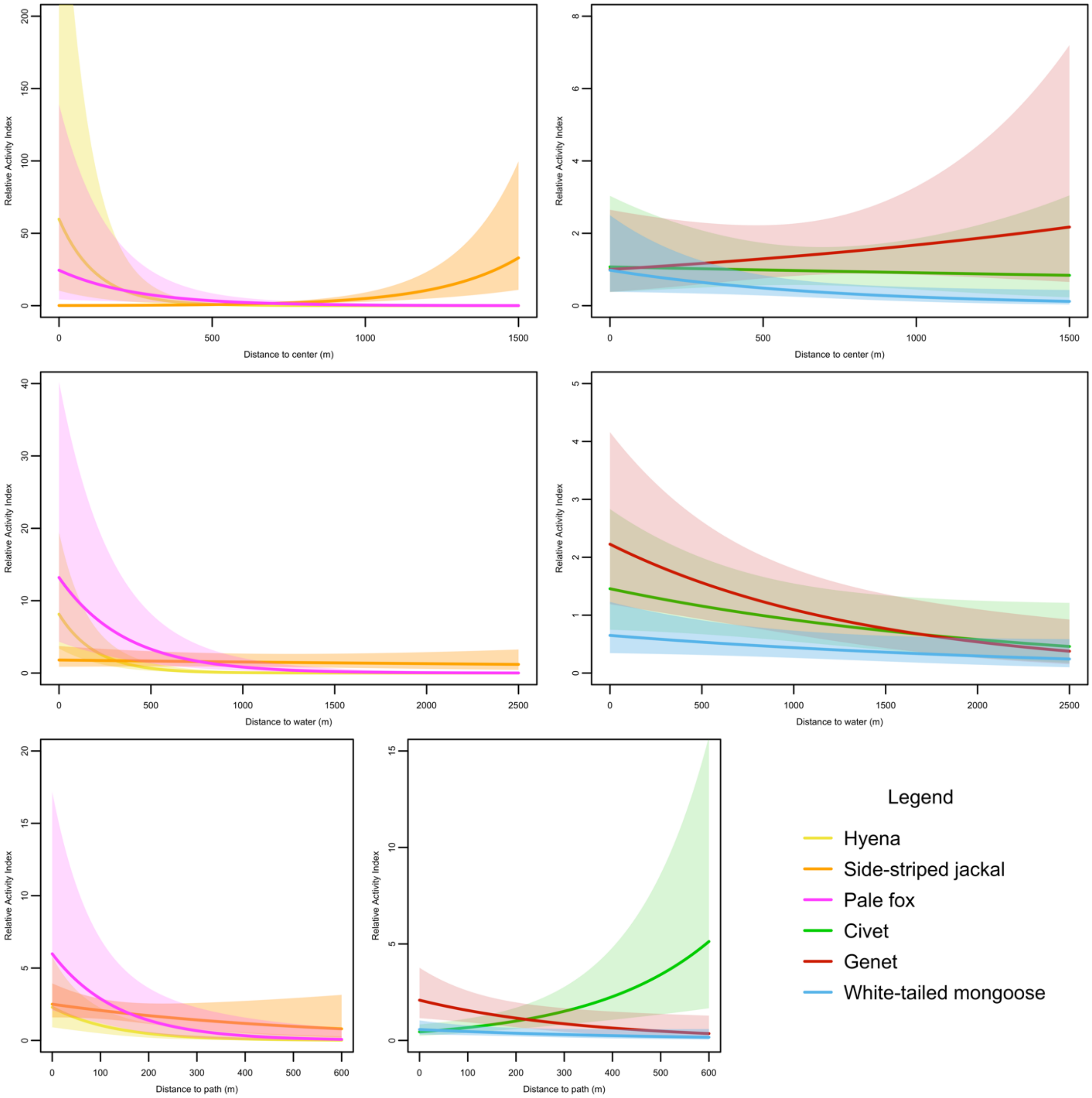


FIGURE 3.5. Predicted Relative Activity Index (RAI) and standard error among species across different spatial predictors.

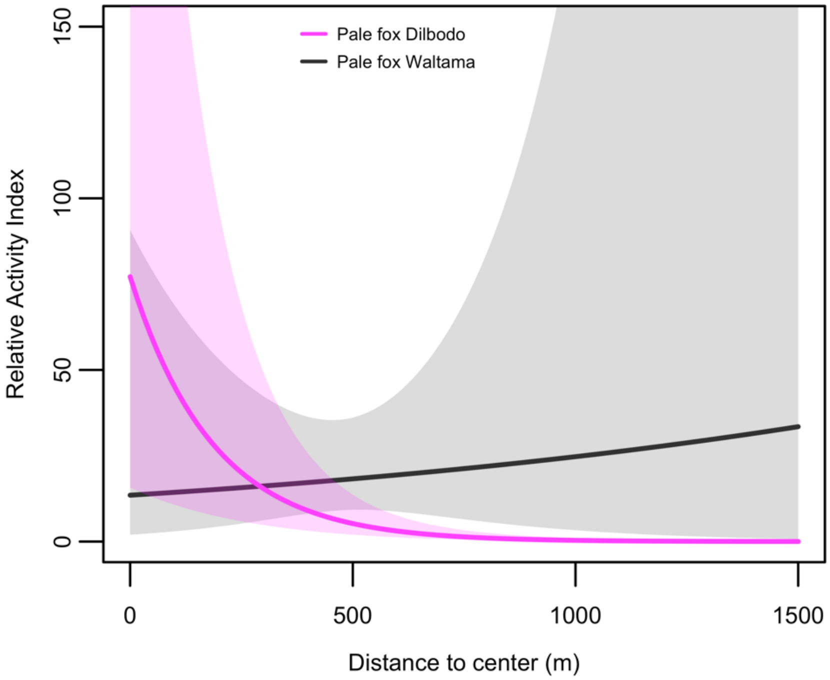


FIGURE 3.6. Relative pale fox activity near village centers in Dilbodo (a village with no spotted hyaena detections) versus Waltama (a village with high spotted hyaena activity)

CHAPTER 4

CONCLUSIONS

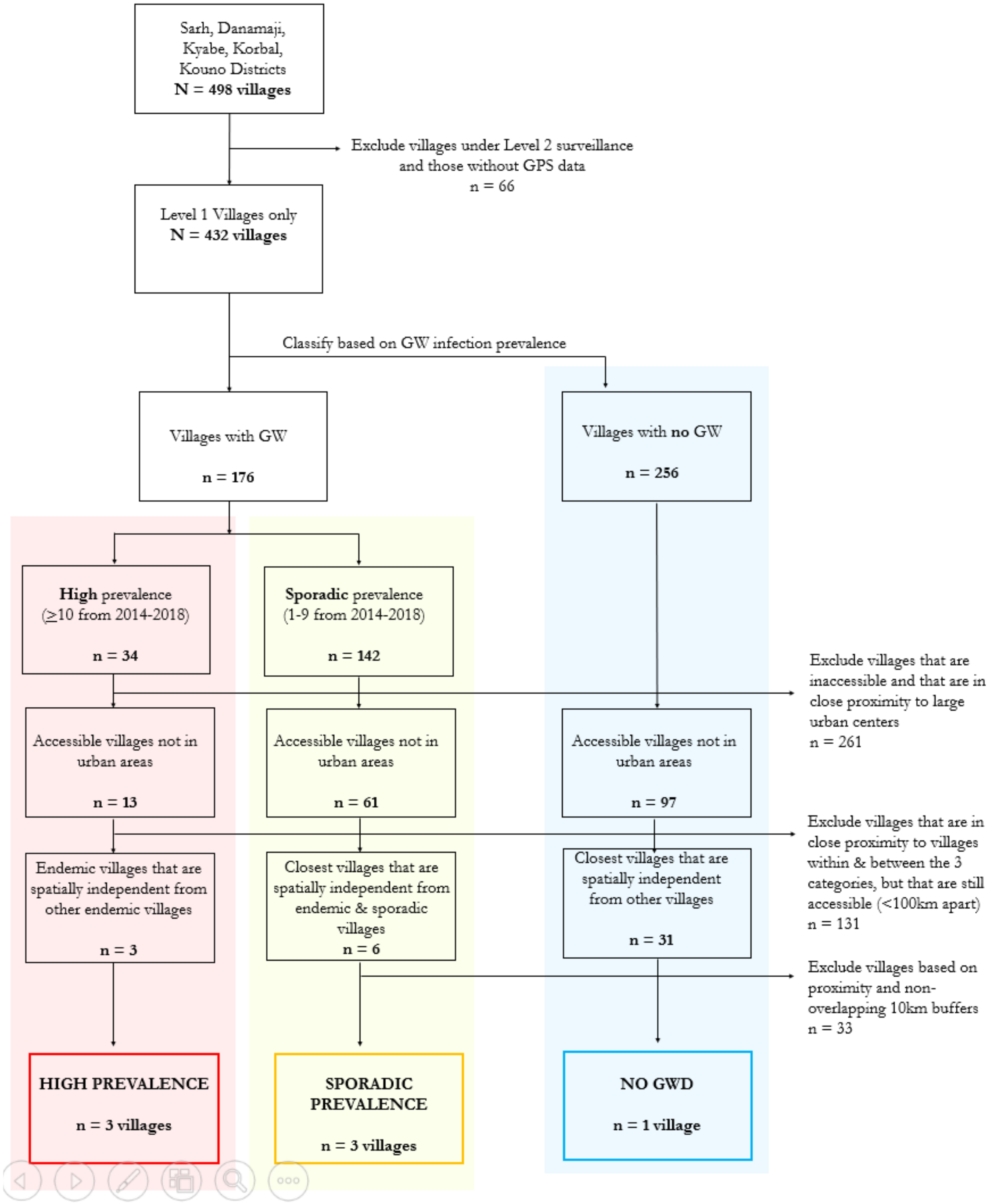
Guinea worm disease (dracunculiasis) is a painful infection caused by the filarial nematode *Dracunculus medinensis*. The Guinea Worm Eradication Program (GWEP) has reduced human cases from 3.5 million across 21 countries in 1986 to only 15 human cases across 4 countries in 2021. Since 2012, Guinea worm (GW) infections have increased in domestic dogs and cats and have been confirmed in baboons and wild felids. Laboratory and field research support the belief that an aquatic paratenic and/or transport host is now an alternative transmission pathway. Natural wildlife infections have been found in olive baboons (*Papio anubis*) in Ethiopia and wild felids in Chad. Little is known on the wildlife diversity surrounding villages in Chad, Africa, complicating our understanding of potential wildlife definitive hosts. The objectives of this study were to determine the occupancy of wildlife species, particularly wild carnivores and primates, as it relates to villages with differing levels of GWD endemicity, increase understanding on community structure in this area by investigating potential competitive interactions and indications of niche partitioning, and document wildlife diversity in and around villages in the Sarh region of Chad.

To address this knowledge gap, we conducted a game camera study in Chad. Seven villages were chosen for game camera deployment based on GWEP surveillance intensity, accessibility, spatial independence, and GW endemicity (3 endemic, 3 sporadic, and 1 negative village). Eight game cameras were deployed per village and recorded from February-November 2019. All wildlife detected were identified to the most specific taxonomic level possible. Villages with GW had higher levels of wildlife diversity. Specifically, we found a higher detection of primates and mesopredators surrounding endemic villages. Single-season occupancy models were fit for the following species: tantalus monkeys (*Chlorocebus tantalus*), patas monkeys (*Erythrocebus patas*), Egyptian mongoose (*Herpestes ichneumon*), and pale fox (*Vulpes pallida*), which supported that tantalus monkeys, patas monkeys, and Egyptian mongoose were present in endemic and/or sporadic villages. By providing valuable knowledge on the wildlife species present around villages in Chad, our results are a key step towards increasing the understanding wildlife may play in transmission and sylvatic maintenance of GW. *Dracunculus medinensis* infections in dogs threaten the eradication program and call for a One Health approach, and this study helps bridge the gap of knowledge on the wildlife side.

Partitioning of resources spatially, temporally, or dietarily can reduce ecological overlap and intraguild competition. Several species were chosen to analyze intraguild interactions: spotted hyaena, side-striped jackal, pale fox, African civet, genets, and white-tailed mongoose. Kernel density estimation was used to analyze changes in activity of a subordinate predator when a dominant predator was detected. In the presence of nocturnal civets, genets were observed to shift to crepuscular activity. In the presence of spotted hyaenas, civets shifted to two distinct activity peaks. Spatial partitioning was analyzed using distance to the village center, nearest water source, and nearest path. A relative activity index (RAI) was constructed for predicted species counts over 100 trapping days. Spotted hyaenas utilized areas closer to the village center, while side-striped jackals utilized areas farther away. Pale foxes preferred areas closer to the village center, but shifted their space use in areas of high hyaena activity. Both wildlife in this area and African mesopredators as a whole are understudied, and this research provides insight into how carnivores may interact in human-altered landscapes to guide future studies into community dynamics.

APPENDICES

APPENDIX A. Village selection criteria flowchart for game camera selection



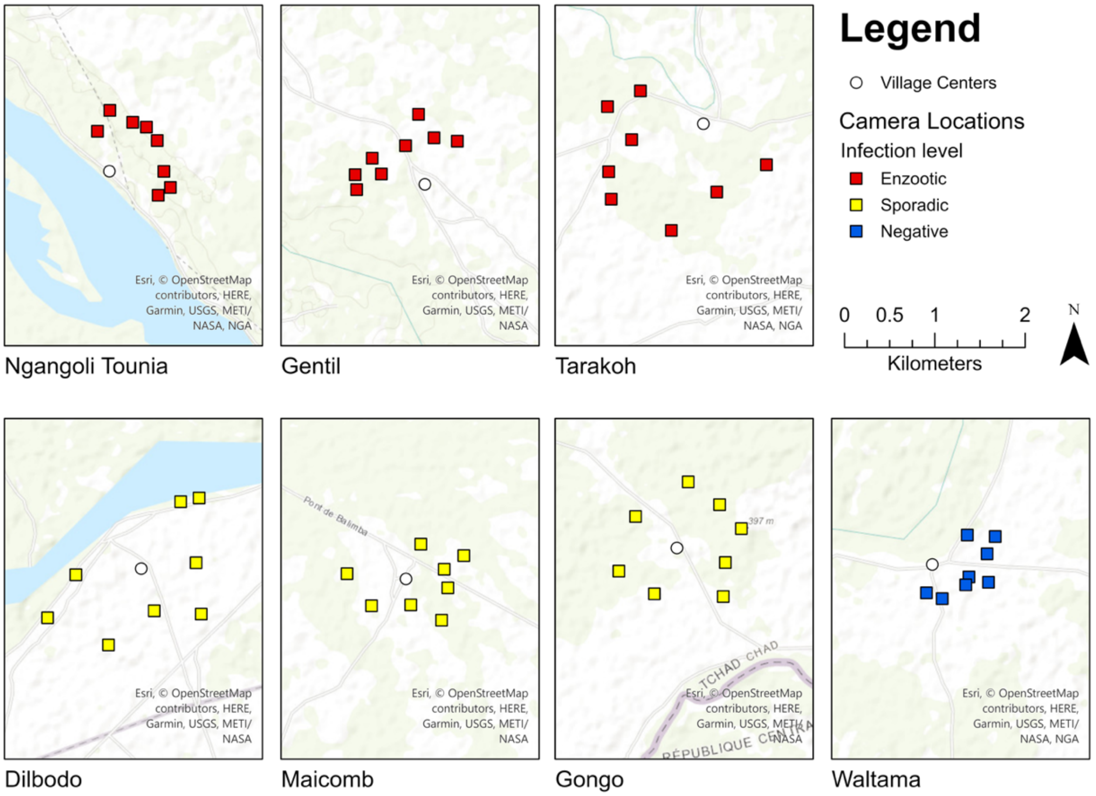
APPENDIX B. Population size and total infections for villages chosen for camera placement

Village	Endemicity	Human population 2018[1]	Dog population 2018[1]	Total infections 2014-2018[2]	Prevalence in Dogs per 1000 population, 2018
Tarakoh	Endemic	717	121	88	214.9
Ngangoli Tounia	Endemic	473	31	22	225.8
Gentil	Endemic	570	37	11	54.1
Gongo	Sporadic	343	65	2	15.4
Maicomb	Sporadic	491	35	6	29.0
Dilbodo	Sporadic	384	32	2	31.3
Waltama	Negative	700	15	0	0

[1] Estimate based on annual census conducted by the Chad National Guinea Worm Eradication Program.

[2] Includes infections in humans, dogs, and cats.

APPENDIX C. Map of game camera placement inside each village and endemicity level



APPENDIX D. Full species catalogue grouped by mammals (A) and birds and reptiles (B)

A.

	Tarakoh	**Ngangoli Tounia**	**Gentil**	**Gongo**	**Maicomb**	**Dilbodo**	**Waltama**	**Grand Total**
Artiodactyla	**241**	**358**	**257**	**174**	**172**	**94**	**140**	**1436**
Bovidae	**241**	**317**	**257**	**174**	**172**	**94**	**140**	**1395**
Bohor reedbuck	8			12		1		21
Cape bushbuck	79	280	52	27		37		475
Common duiker	142	34	200	108	172	51	140	847
Lelwel hartebeest				3				3
Oribi				13				13
Unidentifiable Bovid	12	3	5	11		5		36
Suidae		**41**						**41**
Common warthog		41						41
Carnivora	**161**	**127**	**100**	**46**	**64**	**331**	**265**	**1094**
Canidae	**114**	**54**	**64**	**25**	**52**	**202**	**176**	**687**
Side-striped jackal	76	4	4	9	2	6	13	114
Pale fox			2			71	98	171
Domestic dog	31	50	58	9	46	125	63	382
Unidentifiable Canid	7			7	4		2	20
Felidae	**4**	**3**	**7**	**1**	**2**	**4**	**4**	**25**
Serval	4	3	2			4	1	14
Caracal							2	2
African wildcat			4		2		1	7
Domestic cat			1	1				2
Hyaenidae	**5**	**14**	**1**		**1**	**1**	**40**	**62**
Spotted hyaena		10			1		40	51
Striped hyaena	5	4	1			1		11
Mustelidae	**2**	**2**	**2**					**6**
Honey badger	2	2	2					6
Herpestidae	**16**	**34**	**7**	**3**	**1**	**36**	**18**	**115**
Marsh mongoose						5		5
Egyptian mongoose	1	28	1	1				31
Banded mongoose	9	4						13
Unidentifiable mongoose						1		1
White-tailed mongoose	6	2	6	2	1	30	18	65
Viverridae	**19**	**20**	**19**	**17**	**6**	**87**	**27**	**195**
Civet	7	7	3	15	1	8	5	46

Rusty-spotted genet	1	4	3			9	7	24
Northern small-spotted genet						3		3
Unidentifiable genet	11	9	13	2	5	67	15	122
Unidentifiable Carnivora	**1**				**2**	**1**		**4**
Primates	**237**	**249**	**878**	**59**	**6**	**28**		**1457**
Cercopithecidae	**232**	**246**	**878**	**57**	**1**	**28**		**1442**
Patas monkey				48				48
Tantalus monkey	232	246	878	9	1	28		1394
Galagidae	**5**	**3**		**2**	**5**			**15**
Senegal bushbaby	5	3		2	5			15
Tubulidentata		**16**						**16**
Orycteropodidae		**16**						**16**
Aardvark		16						16
Rodentia	**11**	**41**	**39**	**3**	**4**	**288**	**384**	**770**
Hystricidae		**1**		**2**		**1**		**4**
Crested porcupine		1		2		1		4
Muridae		**2**				**9**	**5**	**16**
Muridae spp.		2				9	5	16
Nesomyidae	**2**		**12**		**2**	**153**		**169**
Gambian pouched rat	2		12		2	153		169
Sciuridae	**9**	**38**	**27**	**1**	**2**	**124**	**379**	**580**
African striped ground squirrel	7	20	20		1	108	379	535
Gambian sun squirrel	2	18	7	1	1	16		45
Unidentifiable Rodentia						**1**		**1**
Unidentifiable Rodentia						1		1
Erinaceomorpha					**2**	**16**		**18**
Erinaceidae					**2**	**16**		**18**
Four-toed hedgehog					2	16		18
Lagomorpha			**22**			**26**		**48**
Leporidae			**22**			**26**		**48**
Lepus spp.			22			26		48
Chiroptera		**3**	**1**	**1**	**2**	**7**	**7**	**21**
Chiroptera spp.		3	1	1	2	7	7	21
Unidentifiable Mammalia	**10**	**4**	**3**	**3**			**4**	**24**

Grand Total	**660**	**798**	**1300**	**286**	**250**	**790**	**800**	**4884**

B.

	Tarakoh	**Ngangoli Tounia**	**Gentil**	**Gongo**	**Maicomb**	**Dilbodo**	**Waltama**	**Grand Total**
Accipitriformes	**17**	**3**	**1**	**10**	**7**	**8**		**46**
Accipitridae	**17**	**3**	**1**	**10**	**7**	**8**		**46**
African Harrier Hawk		1						1
Banded snake-eagle	1					4		5
Black Kite				1				1
Grasshopper buzzard	16		1	5				22
Wahlberg's eagle				2				2
Dark-chanting goshawk		1			2			3
Pallid harrier					1			1
Circus spp.					1			1
Unidentifiable accipiter		1		2	3	4		10
Bucerotiformes	**29**	**23**	**19**	**11**	**6**	**45**	**6**	**139**
Bucerotidae	**8**	**21**	**17**	**3**	**5**	**42**	**6**	**102**
African gray hornbill	2		2		2	3	2	11
Northern red-billed hornbill	6	21	15	3	3	37	4	89
Unidentifiable hornbill						2		2
Bucorvidae	**21**	**2**	**2**	**8**	**1**	**2**		**36**
Abyssinian ground-hornbill	21	2	2	8	1	2		36
Phoeniculidae						**1**		**1**
Green woodhoopoe						1		1
Caprimulgiformes					**2**		**2**	**4**
Caprimulgidae					**2**		**2**	**4**
Caprimulgus spp.							2	2
Long-tailed nightjar					2			2
Charadriiformes						**11**		**11**
Burhinidae						**11**		**11**
Senegal Thick-knee						10		10
Spotted Thick-knee						1		1

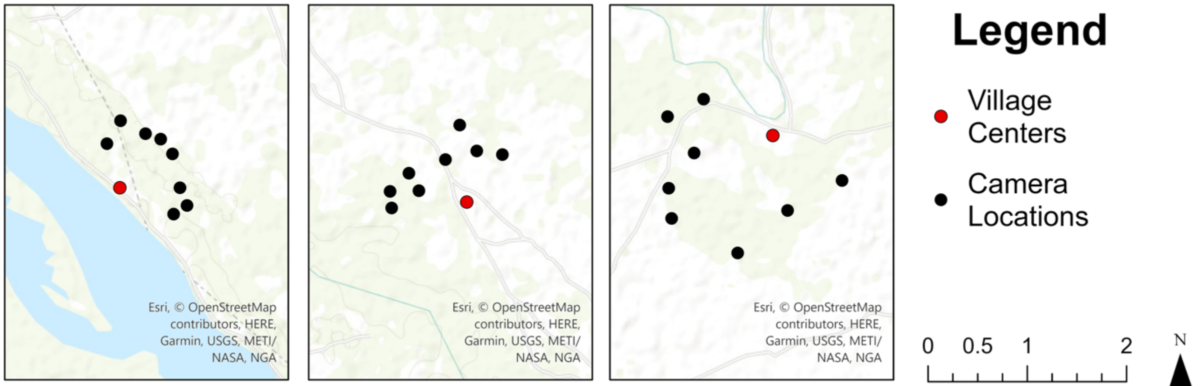
Ciconiiformes	**3**	**9**		**12**		**2**		**26**
Ciconiidae	**3**	**9**		**12**		**2**		**26**
Abdim's stork				6		2		8
Woolly-necked Stork	3			6				9
Unidentifiable stork		9						9
Columbiformes	**8**	**46**	**6**	**1**	**13**	**125**	**15**	**214**
Columbidae	**8**	**46**	**6**	**1**	**13**	**125**	**15**	**214**
African collared dove						1		1
Mourning collared dove		3	1			12		16
Red-eyed dove			1					1
Vinaceous Dove	2	2				4	2	10
Laughing dove		4			1	10		15
Streptopelia spp.						66	3	69
Black-billed wood dove	5	16	1		9	14	6	51
Blue-spotted wood dove			1					1
Turtur spp.	1	15			2	15	4	37
Unidentifiable dove		6	2	1	1	3		13
Coraciiformes	**1**	**2**	**2**		**1**	**16**	**3**	**25**
Alcedinidae	**1**	**1**	**1**		**1**	**6**		**10**
Gray-headed kingfisher						3		3
Woodland Kingfisher	1	1	1		1	3		7
Coraciidae						**1**		**1**
Abyssinian roller						1		1
Meropidae		**1**	**1**			**9**	**3**	**14**
Green bee-eater							3	3
Merops spp.						2		2
Red-throated bee-eater		1				7		8
Swallow-tailed bee-eater			1					1
Cuculiformes						**4**	**1**	**5**
Cuculidae						**4**	**1**	**5**
Pied cuckoo							1	1
Senegal Coucal						4		4
Galliformes	**163**	**156**	**215**	**40**	**53**	**176**	**42**	**845**
Numididae	**154**	**143**	**201**	**40**	**48**	**172**	**42**	**800**

Helmeted Guineafowl	154	143	201	40	48	172	42	800
Odontophoridae	**7**	**3**	**14**		**2**	**4**		**30**
Stone partridge	7	3	14		2	4		30
Phasianidae		**10**						**10**
Clapperton's francolin		10						10
Unidentifiable Galliformes	2				3			5
Musophagiformes						**2**		**2**
Musophagidae						**2**		**2**
Violet turaco						2		2
Otidiformes				**1**	**1**			**2**
Otididae				**1**	**1**			**2**
Black-bellied bustard				1	1			2
Passeriformes	**60**	**60**	**153**	**12**	**22**	**105**	**22**	**434**
Campephagidae	**3**							**3**
White-breasted cuckooshrike	3							3
Cisticolidae		**4**	**9**			**1**		**14**
Green-backed camaroptera		4	9			1		14
Corvidae			**1**			**6**	**11**	**18**
Piapiac			1			6	11	18
Estrildidae	**1**	**9**	**30**		**1**	**7**		**48**
Red-cheeked Cordonbleu	1	7	30		1	7		46
Lagonosticta spp.		2						2
Fringillidae							**1**	**1**
Yellow-fronted canary							1	1
Laniidae						**6**		**6**
Yellow-billed shrike						6		6
Leiothrichidae		**3**	**4**	**1**		**15**		**23**
Blackcap babbler						2		2
Brown babbler		3	4	1		13		21
Malaconotidae		**2**			**1**	**1**	**2**	**6**
Black-crowned tchagra		1					2	3
Black-headed gonolek		1				1		2
Gray-headed bushshrike					1			1
Motacillidae		**1**						**1**

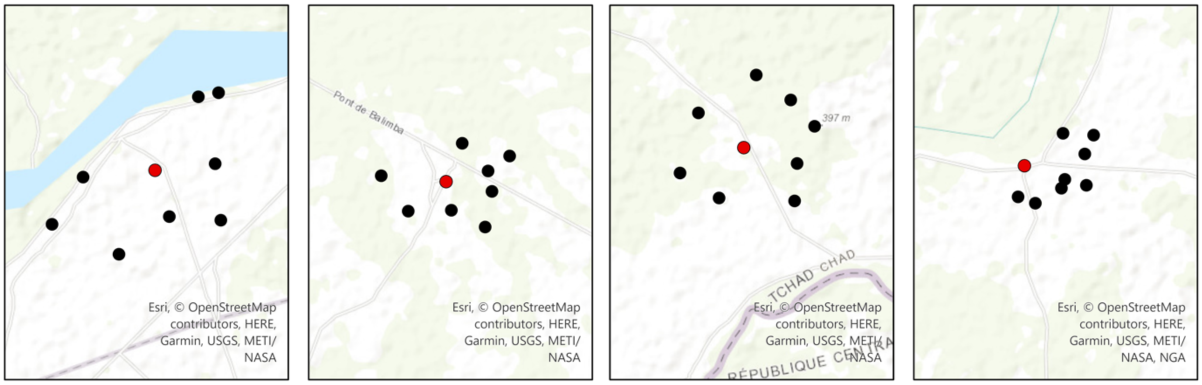
Western yellow wagtail		1						1
Muscicapidae	**1**		**47**		**1**	**9**		**58**
Snowy-crowned robin-chat			39		1	2		42
White-browed Robin-Chat						7		7
Cossypha spp.			4					4
Muscicapidae spp.	1		4					5
Nectariniidae		**1**		**2**	**1**	**1**	**2**	**7**
Beautiful sunbird							1	1
Copper sunbird		1		2		1	1	5
Eastern Olive-Sunbird					1			1
Passeridae						**4**		**4**
Northern gray-headed sparrow						4		4
Ploceidae		**3**	**2**	**3**		**3**	**1**	**12**
Black-headed weaver		2				1	1	4
Black-winged bishop				3				3
Chestnut-crowned sparrow-weaver			1					1
White-billed buffalo weaver						2		2
Unidentifiable weaver		1	1					2
Pycnonotidae			**21**		**1**	**8**		**30**
Common bulbul			21		1	8		30
Sturnidae	**55**	**33**	**19**	**6**	**11**	**33**	**5**	**162**
Long-tailed Glossy Starling	46	27	10	2	5	21	1	112
Purple starling	4			3	1	2	2	12
Violet-backed Starling					1			1
Lamprotornis spp.	5	6	9	1	4	10	2	37
Turdidae		**4**	**20**		**4**	**11**		**39**
African thrush		4	20		4	11		39
Vangidae					**2**			**2**
White Helmetshrike					2			2
Pelecaniformes	**17**	**43**	**6**	**1**	**102**	**71**	**34**	**274**
Ardeidae	**17**	**30**	**6**	**1**	**102**	**62**	**34**	**252**
Black-headed heron		8	6	1	16	27	33	91

Cattle egret	17	21			86	31	1	156
Dwarf bittern		1						1
Unidentifiable egret						4		4
Threskiornithidae		**13**				**9**		**22**
African Sacred Ibis						9		9
Hadada ibis		13						13
Piciformes		**1**				**1**		**2**
Picidae		**1**				**1**		**2**
Unidentifiable woodpecker		1				1		2
Pterocliformes							**2**	**2**
Pteroclidae							**2**	**2**
Four-banded sandgrouse							2	2
Strigiformes	**1**					**4**	**2**	**7**
Unidentifiable owl	1					4	2	7
Unidentifiable bird	**13**	**35**	**52**	**13**	**10**	**94**	**30**	**247**
Reptilia					**1**	**1**		**2**
Unidentifiable snake					1	1		2
Squamata		**1**	**2**				**2**	**5**
Scincidae			**2**					**2**
African 5-lined Skink			1					1
Fire-sided skink			1					1
Varanidae		**1**					**1**	**2**
Nile monitor		1						1
Varanus spp.							1	1
Unidentifiable lizard							1	1
Grand Total	**312**	**379**	**456**	**101**	**218**	**665**	**161**	**2292**

APPENDIX E. Map of game camera placement inside each village



Ngangoli Tounia   Gentil   Tarakoh



Dilbodo   Maicomb   Gongo   Waltama