African wild ass (*Equus africanus*) key resources overlap with livestock and population viability in the Danakil Ecosystem (Eritrea)

By

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any degree or any other examination in any other University.

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20 May, 2020 in Johannesburg

ABSTRACT

The African wild ass (*Equus africanus*) is the world's most endangered equid and is classified as 'Critically Endangered' by the IUCN Red List. This species faces a high risk of extinction in the wild. They persist in the Danakil desert which is one of the harshest climates and terrains in the world, where they share and potentially compete with livestock and local people for water and forage.

An important population exists on the Messir Plateau in the Danakil desert of Eritrea. Long-term data on reproduction and survival rate of the African wild ass are limited. The population's potential viability was estimated given assumptions on fecundity, survival rates and carrying capacity. The probability of persistence at the current capacity of 18 adult females was less than 50% in the worst-case scenario. A population with a potential carrying capacity of 37 females was projected to be almost 100% persistent under all scenarios. The model results indicated that the greatest threat to population viability may be livestock impacts on the vegetation resources that limit the African wild ass population size under anticipated climate change scenarios.

During the rainfall months high numbers of livestock, particularly cattle, come from the highlands and utilize the Messir Plateau daily for three to four months, depending on green forage and seasonal water availability. This may limit forage availability for African wild ass. Density, location and faecal samples of African wild ass and livestock were collected to compare the spatial and diet overlaps between the sampled herbivore species in dry vs. rainfall months. During dry months, African wild ass spatially overlapped with resident camels, domestic donkeys, goats, and sheep. During the rainfall months, African wild ass were dispersed throughout the study area, while a high number of livestock, particularly cattle, were concentrated in the northern section nearer to temporary water sources and better vegetation. The diet of the African wild ass significantly overlapped with that of domestic donkey and cattle in both dry and wet months ($p<0.0000$). The African wild ass nutrient (N, P) levels in the rainfall months were significantly lower than that found in domestic donkey faecal samples ($p<0.05$) when cattle numbers increased on Messir Plateau and African wild ass were displaced.

Access and travel distance to water is critical for lactating equid females due to energetic costs and which may affect their nutrition and the survival of their foals. Drinking behaviour (frequency, timing of visits and distance travelled to water sources) of the African wild ass on Messir Plateau was recorded and compared between lactating and non-lactating females in dry vs. rainfall months. During the dry months, female African wild ass with young foals visited permanent water once a day, travelled on average 9 km and drank only at night. Non-reproductive adult females and bachelor males travelled to water every 5-10 days. During the rainfall months, there were temporary water sources on the Messir Plateau and females with young foals drank twice a day and on average travelled 3 km to water but tended to disperse up to 7 km when livestock and people arrived on the plains area. This spatial exclusion from water sources due to livestock and people presence may reduce female African wild ass ability to provide sufficient milk to their foals.

This research indicates that the lower nutrient (N, P) level of the African wild ass than domestic donkey and their threatened population viability is due to high numbers of cattle spatially displacing them from needed forage and water resources. Therefore, any conservation strategies for this rare and endangered species in the Danakil desert should consider the impact of domestic herbivores, particularly cattle on the African wild ass nutrition and the critical issue of water sources.

Keywords: African wild ass, Danakil ecosystem, drinking frequency, faecal samples, population viability, nutrients (N, P) levels, stable carbon isotope levels, spatial overlaps.

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DEDICATION

I dedicate this work to my wife Letina Fekede Beraki and my family for their unwavering moral support and encouragement during the course of my study.

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Chapter 1. Introduction

1.1 The need for the study

The conservation status of wild equids is cause for concern since only seven wild equid species remain globally and many of these are at risk of extinction (Rosenbom et al. 2012; Moehlman et al. 2016). The African wild ass (*Equus africanus*), Grevy's zebra (*E. grevyi*), Mountain zebra (*E. zebra*), Asiatic wild ass (*E. hemionus*) and the plains zebra (*E. quagga*) have all experienced significant range reductions and population declines and are listed as 'Critically Endangered', 'Endangered' and 'Near Threatened' by the IUCN Red List (Moehlman et al. 2016; Kaczensky et al. 2016; King and Moehlman 2016). Przewalski's horse (*E. ferus przewalskii*) was 'extinct in the wild', has been re-introduced and is now listed as 'Endangered' (King et al. 2015). Only the kiang (*E. kiang*) in China and India persists in large numbers and is considered as Least Concern by the IUCN Red List (Shah et al. 2015). Wild equids (such as asses and zebras) can serve as "flagship species" for the conservation of arid habitats and their biodiversity (Moehlman 2002; Moehlman et al. 2016). The African wild ass, which is the focus of this study, is the world's most endangered wild equid (Moehlman et al. 2015, 2016) and is listed as 'Critically Endangered' by the IUCN Red List (Moehlman et al. 2015). It is listed in CITES Appendix I (CITES 1983) and CMS Appendix I (CMS 2018). Historically, the African wild ass was widespread across north-east Africa, but is currently restricted to Eritrea and Ethiopia with possible remnant populations in Somalia, Sudan, and Egypt (Moehlman et al. 2015). There are less than an estimated 600 individuals remaining within its range (Moehlman et al. 2015). The largest identified African wild ass population is on Messir Plateau in the Danakil desert of Eritrea (Moehlman et al. 2016) (Fig. 1.1). The population density throughout the global range is very low, primarily due to hunting, habitat loss and potential competition with livestock for access to water and forage

(Moehlman 2002; Moehlman et al. 2016) and in-situ conservation is critical to the survival of the species (Moehlman et al. 1998; Tesfai 2006; Kebede et al. 2014).

Since 1995, there has been a program for the research and conservation of the African wild ass and its core breeding areas (i.e. Messir Plateau) in the Danakil of Eritrea (Environment of Eritrea 1995; Department of Environment 2015). However, none of these areas has been designated as protected area for African wild ass conservation in the Danakil ecosystem. The Danakil desert and the Buri peninsula are identified by Conservation International (2005) as one of only two arid land biodiversity hotspots in Africa (Conservation International 2005). The Danakil ecosystem has low primary productivity and limited and localized surface water in the dry season. The water availability and plant biodiversity and biomass are under increasing pressure from livestock, particularly cattle coming from the highlands during the wet season (Tesfai et al. 2019). This encroachment will be further exacerbated by the development of Potash mining at Colluli in the southern part of the Danakil ecosystem (Fig. 1.1). The Colluli mine is located in one of the largest potash sites found globally (Fig.1.1). The project is still in the planning stage. The total area which will be potentially affected by the project covers about 3145 km^2, while the project footprint is around 33 km^2 (MBS Environmental 2016). The mining process requires a large amount of water, approximately 584 m^3/hr, of which 66% will be brackish and the remaining 34% desalinated seawater (MBS Environmental 2016). The groundwater in the Danakil region is largely fed by the rainfall in the highlands. Intense and simultaneous pumping by the mining company may have a negative impact on surface water which is used by the African wild ass. Transport routes and the pipeline corridor from the mining site to sea ports will create disturbances and fragmentation between foraging and breeding habitats of the African wild ass. According to the MBS Environmental (2016) document, the pipeline corridor will pass near to the Hakor, Awara and Madbaro plains (Fig. 1.1). These areas are foraging and movement corridors for African wild ass in the Danakil desert, Eritrea (Tesfai, personal observation).

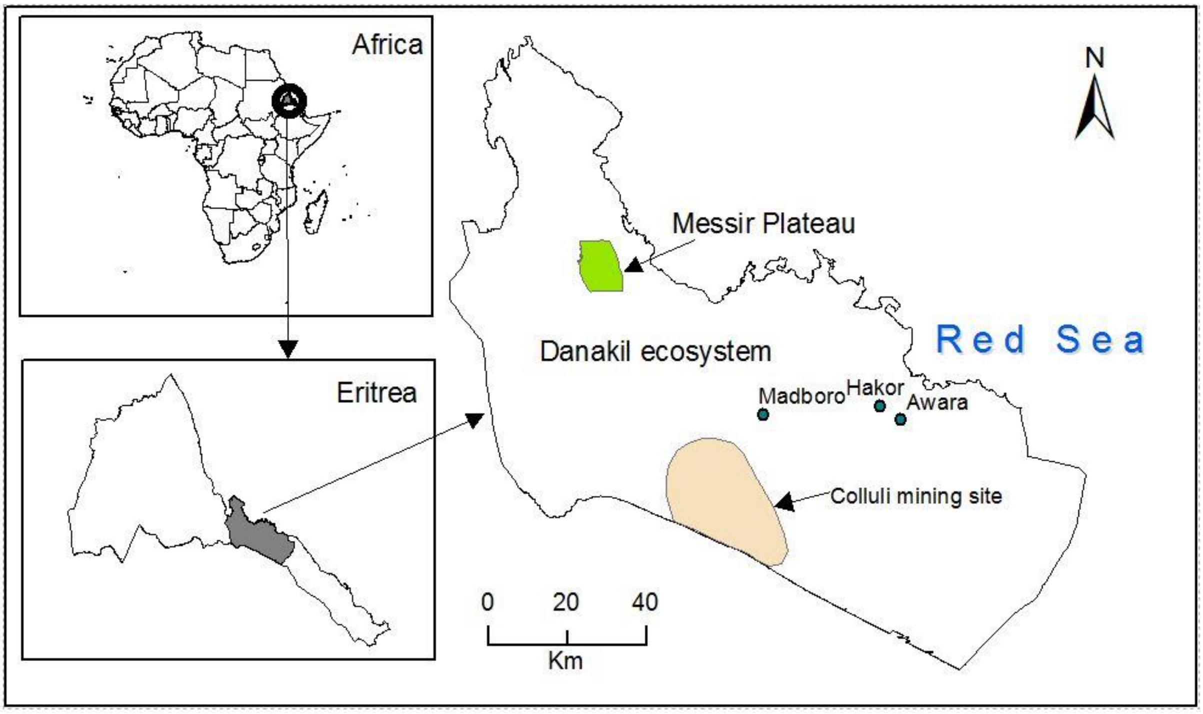


Figure 1.1 Location of the study area (Messir Plateau) in the Danakil ecosystem and location of the Danakil ecosystem in Eritrea

The local people in the Danakil desert are Afar-pastoralists who herd sheep, goats, camels and a few cattle. Afar knowledge and resource needs in these areas are critical to understanding how sustainable resource utilization and conservation could be achieved. Hence, research was needed to determine how this important area can contribute to enhance reproduction and survival of the African wild ass while maintaining the local community benefits. This research provides scientific data that will contribute to identifying and alleviating the threat from domestic livestock to the viability to the critically endangered African wild ass in the Danakil desert, Eritrea. This project also recommends future management strategies that will enhance the conservation status of the population by limiting the overlap/competition with livestock and provide options for the sustainable management of livestock based on the resource availability and drought predictions. The specific objectives of the study were as follows:

1) To assess the viability of African wild ass Messir Plateau population based on current demographic structure and rainfall scenarios using a population viability model. In the model, two estimates of carrying capacity were contrasted based either on recent population assessments, or on the potential capacity of the Messir Plateau. The model also compared realistic versus optimistic scenarios for age at first reproduction and potential longevity. Rainfall scenarios used either historic patterns or potential future rainfall with the same or amplified coefficient of variation.

2) To determine the African wild ass spatial and dietary overlap with livestock (i.e. cattle, domestic donkey, camel, goat and sheep) based on GPS location data and faecal stable carbon isotope analyses, and compare nutritional status, as indexed by percent Nitrogen and Phosphorus in faecal samples of the African wild ass compared with that of domestic donkeys in dry months vs. rainfall months.

3) To compare drinking behaviour (frequency, timing of visits and distance travelled to water sources) between lactating and non-lactating females when only one permanent water source (Asaila, Fig. 4.1 and 4.3) was available vs. when seasonal temporary water was available.

4) To make management recommendations based on the study results.

1.2 Literature review

1.2.1 Population dynamics

Theoretically, population dynamics is the result of a balance between natality and mortality and recruitment (Lebreton et al. 1993) and it is largely dependent on the relationship between age-specific birth and death rates (Eberhardt 1985). Information on population dynamics is critical in wildlife management and conservation (Caswell et al. 1997). Animal census, which is dependent on field observation data, is always a basic requirement for determining numbers and population trend predictions (Gaillard et al. 2000; Keeping and Pelletier 2014). Various studies have been conducted to assess the roles of different vital rates (such as age-specific survival and reproduction) in population dynamics (Gaillard et al. 2000). Identifying which vital rates are more variable and which ones are more likely to influence population trends over time are useful parameters in population dynamics and/or population viability studies (Caswell et al. 1997; Owen-Smith 2007).

Population dynamics in wild equids vary intraspecifically between populations as well as interspecifically (Ransom et al. 2016). All species of wild equids seem to follow the same general distribution of age-specific natality. Females are capable of conceiving at 12 months of age with the first potential foaling occurring at two years of age (Ransom et al. 2016), but most first births occur at approximately four to five years of age (Moehlman 2002; Ransom et al. 2016). However, these reproductive rates are subject to biological and ecological variation across space and time (Ransom et al. 2016). When adequate forage is available and accessible, female wild equids are more likely to give birth at an earlier age (Saltz and Rubenstein 1995; Tatin et al. 2009). Females tend to produce most foals when they are between six and seventeen years old (Penzhorn 1985; Saltz and Rubenstein 1995; Moehlman 2002). In the wild, most female equids have been reported giving birth as old as between 18 and 24 years of age (Ransom et al. 2016). Most wild equids have one offspring per year or every other year (Moehlman 2002; Grinder et al. 2006), though rare cases of twins have been reported (Vodicˇka 2010 cited in Ransom et al. 2016). The average sex ratio of foals across all wild equid species is 1.1 males to 1 female (Ransom et al. 2016).

Reports indicate that estrous, birth rates, and birth phenology have been correlated with rainfall in some populations of Grevy's zebra and Plains zebra (Williams 1998;

Georgiadis et al. 2003; Rubenstein 2010). In Laikipia, central Kenya, Plains zebra dynamics appear to be strongly affected by annually fluctuating rainfall (Georgiadis et al. 2003). The simulation model for this species indicated that Plains zebra populations continued to increase with an increase in rainfall until the next drought period, when numbers again declined (Georgiadis et al. 2003). This synchrony with rainfall and forage resources may increase female and foal survival because nutritional requirements of lactating females are elevated and higher-quality forage can result in improved body condition and nutritional support for foals (Ginsberg 1988; Ransom et al. 2016).

Different age and sex classes in a population are subject to varying mortality rates (Wolfe 1986; Owen-Smith 2007). Annual foal survival rates range from 0.53 to 0.88 and adult survival rates from 0.85 to 0.98 across all wild equids (Williams 1998; Ransom et al. 2016). Variation in annual survival rates of wild equids is affected by localized predation (Ransom et al. 2016). For example, the principal predator of the African wild ass is spotted hyena, but this carnivore is rarely observed on Messir Plateau. It is very difficult to document sub-adult survival accurately (Eberhardt 1985) as sub-adults may disperse from the study area (Georgiadis et al. 2003). Departure of sub-adult Cape Mountain zebra from their maternal family herd can influence the stable female group size (Penzhorn 1979). In arid-habitats, when forage and water becomes limited, age of first birth can be delayed and birth rates for all females can decline quickly (Ginsberg 1988). If mortality is high, due either to hunting and/or drought, the population will decline and it may be difficult or impossible for it to recover (Moehlman 2002).

Breeding season in arid habitat/resource defence equids (e.g. African wild ass, Asiatic wild ass and Grevy’s zebra) correlates with rainfall and most foals may be born after the rainy season, when the standing vegetation biomass is at its peak (Saltz et al. 2006). In resource defence polygyny, territorial males defend an area that has resources that females require and thus indirectly have access to females in estrous (Rubenstein 1994). Reproductive timing appears to be associated with the seasonal availability of forage and water. If the rains fail and forage is limited, then the survival of these young foals will be doubtful. Wild equid abortion or reabsorption of the fetus has been reported during extreme droughts (Wolfe 1986).

1.2.2 Resource competition

Domestic and wild herbivores share natural resources such as forage and water (Young et al. 2005). Among large herbivores, competition mainly occurs when grass resources are reduced during seasons of food limitations (Owen-Smith 2002). This is particularly important in arid areas (Pratt and Gwynne 1977; de Boer and Prins 1990; Madhusudan 2004); an issue alleged to be a potential reason for competition for resources between domestic and wild herbivores (Voeten and Prins 1999; Prins 2000). Livestock such as cattle and domestic donkeys potentially overlap in diet with some wild herbivores due to their similar resource requirements (Casebeer and Koss 1970; Voeten and Prins 1999; Young et al. 2005).

When populations spatially overlap this may impact individual access to resources and lead to competition (Voeten and Prins 1999; Prins 2000). Competition between domestic and wild herbivores may occur if the two species spatially overlap and are dependent on the same limited food resources at a particular period (Illius and Gordon 1987; de Boer and Prins 1990; Prins 2000). The consequence of such interaction may reduce natality, survivorship, individual and population growth rate and/or reproduction of one or both of the species concerned (Williams 1998; Prins 2000). Williams (2002) documented that due to the presence of livestock, female Grevy's zebra with foals had to travel longer distance to access both water and forage and this correlated with low foal survival.

Domestic and wild herbivores that are primarily grazers and have similar body size and resource requirements are considered to be potentially competitive (Voeten and Prins

1999; Young et al. 2005). Equids are non-ruminants and due to their digestive physiology can be sustained by consuming a larger amount of low fiber forage compared to a similar-sized ruminant, which could lead to resource partitioning in either space or time minimizing competition (Lamprey 1963). The pattern of resource partitioning can vary seasonally and also due to species-specific differences such as feeding strategy (selective versus non-selective) and digestive systems (Voeten and Prins 1999). It also varies with habitat characteristics and patterns of grazing in response to the spatial and temporal availability of forage resources (Scoones 1995; Bailey et al. 1996).

Large herbivores interact with the environment by selecting plant communities and other habitat components for feeding (Senft et al. 1987). For example, in the early wet season, wildebeests (*Connochaetes taurinus*) in Tarangire (Tanzania) selected feeding sites with a lower grass height compared to Plains zebra and cattle (Voeten and Prins 1999). Plains zebra selected feeding sites with tall grass which may be due to their digestive system that allows a higher daily food intake than ruminants of similar size (Duncan et al.1990; Bauer et al. 1994; Chege 2004). Plains zebra can compensate for low quality food by increasing intake (Demment and Van Soest 1985). However, Plains zebra can also be selective feeders and prefer higher nutrition/lower fiber greener grass species when food resources are abundant (Penzhorn and Novellie 1991). On the Ethiopian side of the Danakil ecosystem, African wild ass would arrive first to areas where it rained to take advantage of the new green grass (Kebede et al. 2014). But when pastoralists arrived with their livestock the African wild ass moved away to areas with lower plant biomass (Kebede 1999). African wild ass in the Messir Plateau (Eritrea) were observed on the plains area when new grass growth and temporary water sources were available (Tesfai 2006) but were displaced when large numbers of livestock, particularly cattle, were brought to the Messir Plateau from the highlands (Tesfai, personal observation).

1.2.3 Effects of water on herbivore distribution

Livestock and pastoralists in arid-rangelands tend to concentrate around water sources (de Leeuw et al. 2001). Travel distance to water point is a primary determinant of grazing distribution patterns that are observed at a large scale (Senft et al. 1987). Both domestic and wild grazers can optimize their uptake of water and forage, if they can minimize their travelling distance by selecting forage areas closer to water points (Sittersa et al. 2009). During dry periods, pastoralists were seen moving their herds towards the remaining water sources (Western 1975; Coppolillo 2000; de Leeuw et al. 2001). Forage quality and water availability significantly influence wild herbovores habitat use (Schoenecker et al. 2016). In northern Kenya, De Leeuw et al. (2001) observed that the majority of livestock and wildlife include Grevy's zebra, Plains zebra, giraffe (*Giraffa camelopardalis),* lesser kudu (*Tragelaphus imberbis*), oryx (*Oryx gazelle beisa*), impala (*Aephyceros melampus*), gerenuk (*Litocranius walleri*), warthog (*Phacochoerus aethiopicus*), Grant's (gazelle *Gazella granti*), and ostrich (*Struthio camelus*) within 10 km of permanent water sources. Grevy's zebra, warthog and impala were not affected by the presence of livestock and travelled to water sources regularly (De Leeuw et al. 2001).

Wild equids in arid areas are even more subject to variation in water availability (Becker and Ginsberg 1990) and need frequent access to water and suitable pasture (Kebede et al. 2014). In Samburu, Kenya, Grevy's zebra were observed travelling to water sources and staying close to the water points where they overlapped with livestock (Low et al. 2009). In Buffalo Springs protected area, non-lactating female Grevy's zebra and males were observed more than 10 km from water (Becker and Ginsberg 1990; de Leeuw et al. 2001), but lactating females were usually observed within 2 km of water (Becker and Ginsberg 1990).

The African wild ass range in arid habitats is also limited by the availability of accessible water (Moehlman 2002; Kebede et al. 2014). During the dry season, some African wild ass on the Messir Plateau (Eritrea) may move to locales with better available forage but they remain dependent on access to watering spots (Tesfai 2006). Some adult females and males stay on the plateau throughout the year (Tesfai 2006) and share the limited dry season forage and Asaila permanent water source with pastoralists and their livestock (Tesfai et al. 2019). Availability and accessibility of water is critical for African wild ass natality and survival in the extreme aridity of the Danakil ecosystem (Kebede 1999; Tesfai 2006).

1.2.4 Wild equid feeding ecology

Equids are well adapted to surviving on lower quality forage than ruminants of similar sizes because their intake is not restricted by the rate of particle-size breakdown (Demment and van Soest 1985). They can compensate by eating relatively large proportions of low quality forage to meet their protein requirements (Bauer et al. 1994; Van Soest 1996; Schoencker et al. 2016). Compared to ruminant herbivores, equids have a simpler and less efficient digestive mechanism; they are mono-gastric hindgut fermenters or cecal digesters (Owaga 1975; Janis 1976). Horses for instance, have a relatively high capacity of cecum and colon to absorb fermented products such as proteins and carbohydrates (Janis 1976). The fermentation chamber in equids is located in the colon and it is here that absorption of the cellulose-rich diet takes place (Janis 1976; Van Soest 1996). The cecum and colon allow the indigestible material to remain in contact with a commensal microbial population for digestion (Van Soest 1996).

Wild equids are predominantly grazing mammals of the grasslands and semi-desert environments of Africa and Eurasia (Rosenbom et al. 2012; Schulz and Kaiser 2013). Grevy's zebra that live in arid northern Kenya and southern Ethiopia are predominantly grazers (Schulz and Kaiser 2013) although they can browse during dry periods (Rowen and Ginsberg 1992; Williams 2002). They tend to select areas of short green grasses when available (Owaga 1975; Sundaresan et al. 2008; Low et al. 2009). Mountain zebras living in dry areas of southern African select habitats containing high abundances of grasses (Watson et al. 2005; Penzhorn and Novellie 1991). Mountain zebra browse when grass availability and quality decline during dry periods (Penzhorn and Novellie 1991). Feral asses in Death Valley feed on low-quality forage and their preferences will depend on availability (Freeland and Choquenot 1990; Moehlman 1998). Plains zebra live in mesic habitats and in the dry season graze on longer higher fiber foods than in the wet season (Arsenault and Owen-Smith 2011). Among the other equids, the kiang are classified as grazers (Schulz and Kaiser 2013) although sedges are a significant (55 %) proportion of their diets in all seasons (St-Louis and Cote 2014), while the Przewalski's horse is predominantly a grazer (Schulz and Kaiser 2013) with a diet that consists of more than 75% grasses even in dry cold winters (Sitters et al. 2009). Asiatic wild ass, adapted to arid and semi-arid environment (Kaczensky et al. 2008), are also predominantly grazers although they can browse during dry periods (Schoenecker et al. 2016).

African wild ass in Danakil desert are primarily grazers (Moehlman 2002; Tesfai 2006; Kebede et al. 2014) but also browse during the dry season (Kebede 1999; Moehlman 2002; Tesfai 2006; Schulz and Kaiser 2013). Based on the number of bite counts, *Pannicum turgidium*, a tufted perennial grass, is the main forage for the African wild ass in the Messir plateau (Tesfai unpublished data). In the Mille-Serdo Wild Ass Reserve (Ethiopia) the preferred forage for the African wild ass includes: *Aristida sp*., *Chrysopogon plumulosus, Dactyloctenium schindicum*, *Digitaria sp*., *Lasiurus scindicus*, and *Sporobolus iocladus* (Kebede 1999; Moehlman 2002; Kebede et al. 2012). African wild ass on Messir Plateau were observed to prefer the lower flatter plains portion of the area when green grass and water were available (Tesfai 2006). During the dry period, the majority of animals were observed in the ravine areas which had relatively better vegetation cover, despite being largely composed of less palatable species (Tesfai 2006). Hence over an annual cycle, the plain and ravine areas seem to be the most preferred habitats for African wild ass in the Messir plateau (Tesfai 2006).

1.3 Research design

This research project was designed to assess first the viability of the African wild ass population on the Messir Plateau given certain assumptions on fecundity, survival rates and carrying capacity. In the population viability model, carrying capacity for the female segment of the Messir Plateau population was set either at its current highest level (18 adult females), based on the long term (1998-2018) field data or at twice this number (37 adult females) to represent the potential carrying capacity. The model results indicated that there is a 50% probability of extinction at the current level of 18 adult females on Messir Plateau. If there was a carrying capacity of 37 adult females, almost 100% probability of persistence was predicted. The greatest threat to the African wild ass population viability appears to be the impact of livestock on forage availability on the Messir Plateau under anticipated climate change.

Based on the results of the population viability assessment, it was important to determine the level of spatial and dietary overlap between African wild ass and livestock (i.e. domestic donkey, cattle, camel, goat and sheep) on the Messir Plateau during dry and rainfall months. GPS location data and faecal samples were collected to determine spatial and diet overlap (African wild ass and livestock) and nutritional status (African wild ass and domestic donkeys) in dry months vs. rainfall months.

Adequate forage, especially near water sources, is critical to the survival of the African wild ass and in particular for lactating females in the Danakil desert. Therefore, drinking data were recorded to compare the drinking behaviour (frequency, the timing of visits and distance traveled to water sources) between lactating and non-reproductive females and males in dry vs. rainfall months in Messir Plateau.

Field research on the rare African wild ass in Danakil desert of Eritrea presents many physical challenges. The habitat is remote, extremely rocky and the climate is very hot (Fig. 1.2). Conventional sampling methods for monitoring a large population for an extended period of study are not possible because African wild ass are few in number and scattered in small isolated groups. To ensure that the maximum population size was sampled, all African wild ass in the study area were identified by their unique leg stripes. Individual ID sheets were drawn in the field and photos of individuals from both sides were recorded throughout the study period. This was a pre-requisite to ensure that each individual's records were independent and to avoid double counting of individuals during sampling.

In the past, births in African wild ass population on Messir Plateau peaked between December and April (1995-2007) (Tesfai 2006; Moehlman unpublished report). Hence, this field study was designed to collect faecal samples and drinking data on the African wild ass and domestic livestock in Messir Plateau during the months from October to June. Females with foals of age less than three months are at the peak of lactation and need to drink more frequently than other adults. A total of twenty-five adult females and foals (less than 3 months n=3, 4-12 months n=7 and yearlings n=3) and five adult males were recorded and monitored from October 2016 to March 2019. This is a limited sample size but provides crucial information that had not been previously documented on the diet and drinking behaviour of the critically endangered African wild ass.

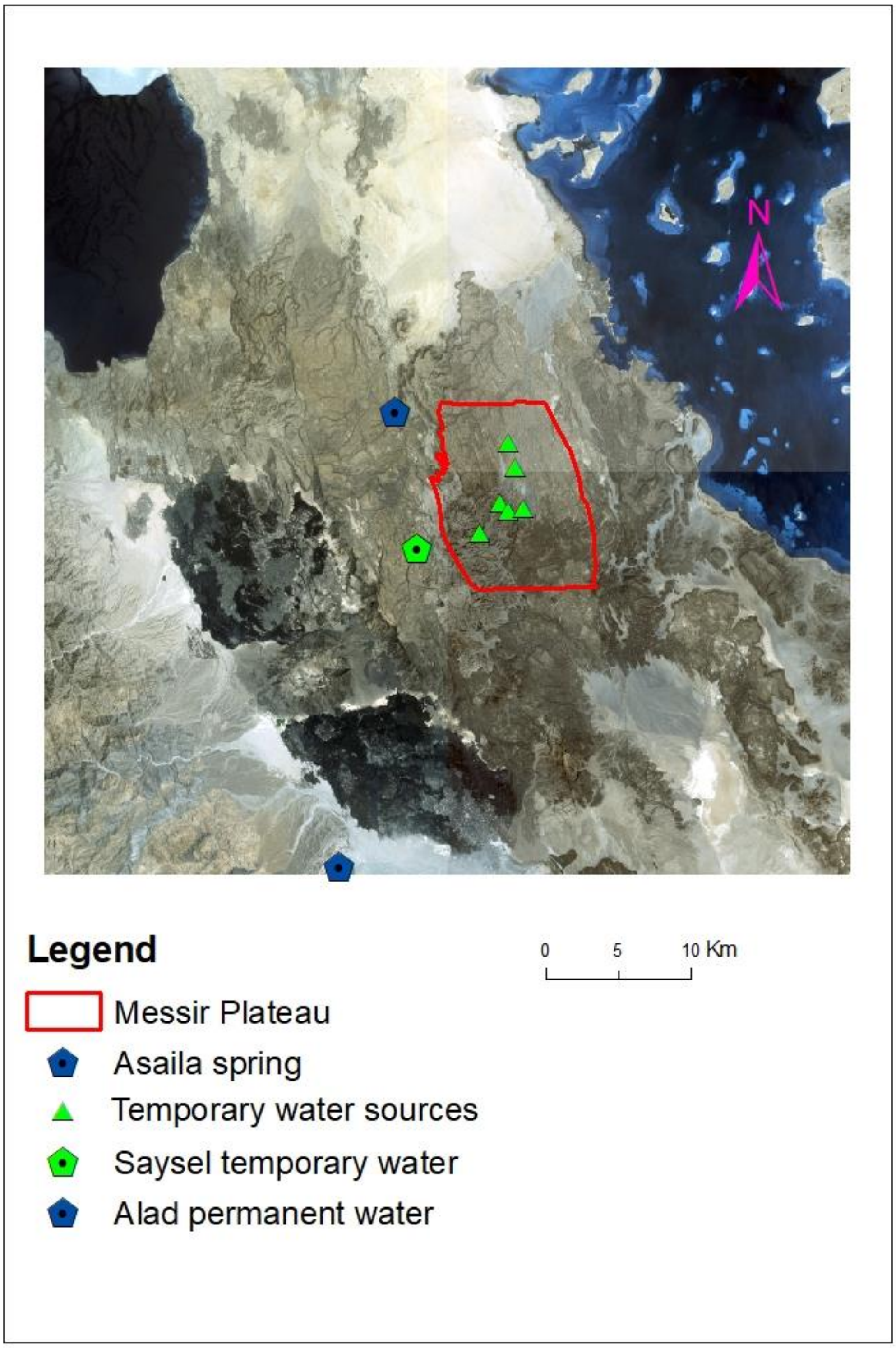


Figure 1.2 Location of the Messir Plateau showing the water sources and the rocky undulating terrain of the Danakil arid ecosystem, Eritrea.

1.4 Thesis outline

This thesis consists of 5 chapters. In the introduction (Chapter 1) I justify the need for the study, present the aim and objectives and review the relevant literature on population dynamics, wild equid feeding ecology and key resource competition between wild equids and associated livestock. The thesis is then written with three main data chapters (Chapters 2, 3 and 4), in the format of scientific publications. Since the thesis is structured for potential paper publications, there is some level of the overlap between the chapters. One of the chapters (Chapter 2) has been published in the Journal of Mammalogy (Tesfai, R.T., Owen-Smith, N., Parrini, F. and Moehlman, P.D. 2019). Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy*, Volume 100, Issue 1, 28 February 2019, Pages 185–191, https://doi.org/10.1093/jmammal/gyy164). In this paper, we assessed whether the African wild ass population on Messir Plateau is viable or not given certain assumption on vital rates (i.e. fecundity and survival rates) and carrying capacity. Vital rates and carrying capacity were based either on recent population assessments, or on the estimated potential rates. Accordingly, the probability of population persistence of the population over 50 years was estimated allowing for stochastic dynamics, density dependence, influences of rainfall on carrying capacity, and episodic disturbances reducing survival rates. Scenarios used either historical rainfall patterns or potential future rainfall with the same or amplified coefficient of variation.

In chapter 3, I investigated the spatial overlap in terms of density and location of African wild ass and livestock. Faecal samples were collected and analysed to assess the dietary overlaps between the African wild ass and associated domestic livestock. The nutritional status of African wild ass and domestic donkey were compared in dry vs. rainfall months. I presented spatial and diet overlap of the African wild ass and livestock ($\delta\ ^{13}C/^{12}C$)

on the Messir Plateau and compared the nutrient (N, P) levels between African wild ass and domestic donkeys. This was done to assess the impact of cattle on African wild ass nutrition.

In chapter 4, I documented how the drinking behaviour (frequency of visits and time of visits) and distance travelled from forage to water differed between African wild ass sex and age groups. During the dry months, Asaila was the only permanent water and during the wet months seasonal temporarily water sources were available on the Messir Plateau.

Chapter 5 is the general discussion where I review the main factors influencing the viability of the African wild ass population on Messir Plateau and recommend management intervention needed to guide effective conservation strategies in order to save the species from extinction. In this chapter I summarise and evaluate the most important findings of this research in relation to expectations based on published literature on resources competition and its impact on viability of a critically endangered wild species.

References

Arsenault, R. and Owen-Smith, N. 2011. Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa. *Canadian Journal of Zoology* **89**: 900–907.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. and Sims, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* **49**: 386–400.

Bauer, I.E., McMorrow, J. and Yalden, D.W. 1994. The historic ranges of three equid species in north-east Africa: a quantitative comparison of environmental tolerances. *Journal of Biogeography*, **21**:169–182.

Becker, C.D. and Ginsberg, J.R. 1990. Mother-infant behaviour of wild Grevy's zebra: adaptations for survival in semi-desert East Africa. *Animal Behaviour* **40**: 1111–1118.

Casebeer, R.L. and Koss, G.G. 1970. Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *African Journal of Ecology* **8**: 25–36.

Caswell H., Nisbet R.M., de Roos A.M. and Tuljapurkar S. 1997. Structured-Population Models: Many Methods, a Few Basic Concepts. In: Tuljapurkar S., Caswell H. (eds) Structured-Population Models in Marine, Terrestrial, and Freshwater Systems. Population and Community Biology Series, vol 18. Springer, Boston, MA, US.

Chege, G.K. 2004. A dissertation on the effect of livestock and forage availability on the distribution of Grevy's zebra (*Equus grevyi* oustalet) in northern Kenya. MSc in Conservation Biology, DICE, University of Kent at Canterbury, UK.

CITES Appendix I (1983): https://cites.org/eng/gallery/species/mammal/african_ass.html

Conservation International (updated 2005). Biodiversity hotspots. http://www.conservation.org

Convention on the Conservation of Migratory Species of Wild Animals (CMS) Appendix I (2018): www.cms.int. Access on 26 January 2018

Coppolillo, P.B. 2000. The landscape ecology of pastoral herding: spatial analysis of land use and livestock production in East Africa. *Human ecology* **28**: 527–560.

De Boer, W.D. and Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82**: 264–274.

De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula, H.M., Heitkönig, I.M. and Reid, R.S. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation* **100**: 297–306.

Demment, M.W. and Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist* **125**: 641–672.

Department of Environment. 2015. Revised National Biodiversity Strategy and Action Plan for Eritrea (NBSAP-E/2014-2020). Ministry of Land, Water and Environment. Asmara, Eritrea.

Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G. and Lloyd, M. 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* **84**: 411–418.

Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. The Journal of Wildlife Management **49**: 997–1012.

Environment of Eritrea. 1995. The National Environmental Management Plan for Eritrea (NEMP-E). Asmara, Eritrea.

Freeland, W.J. and Choquenot, D. 1990. Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. *Ecology* **71**: 589–597.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**: 367–393.

Georgiadis, N., Hack, M. and Turpin, K. 2003. The influence of rainfall on zebra population dynamics: implications for management. *Journal of Applied Ecology* **40**: 125–136.

Ginsberg, J.R. 1988. Social organization and mating strategies of an arid adapted equid: the Grevy's zebra *Equus grevyi* (Kenya). Doctoral dissertation, Princeton University, New Jersey, US.

Grinder, M.I., Krausman, P.R. and Hoffmann, R.S. 2006. *Equus asinus. Mammalian Species*, 794: 1–9.

Illius, A.W. and Gordon, I.J. 1987. The allomentry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**: 989–999.

Janis, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* **30**: 757–774.

Kaczensky, P., Ganbaatar, O., Von Wehrden, H. and Walzer, C. 2008. Resource selection by sympatric wild equids in the Mongolian Gobi. *Journal of Applied Ecology* **45**: 1762–1769.

Kaczensky, P., Lkhagvasuren, B., Pereladova, O., Hemami, M. and Bouskila, A. 2016. *Equus hemionus*, Asiatic wild ass. The IUCN Red List of Threatened Species. Technical Report, January 2015

Kebede, F. 1999. Ecology and conservation of the African Wild Ass (*Equus africanus*) in the Denakil, Ethiopia. MSc Thesis, University of Kent/DICE, Canterbury, UK.

Kebede, F., Bekele, A., Moehlman, P.D. and Evangelista, P.H. 2012. Endangered Grevy's zebra in the Alledeghi Wildlife Reserve, Ethiopia: Species distribution modeling for the determination of optimum habitat. *Endangered Species Research* **17**: 237–244.

Kebede, F., Moehlman, P.D., Bekele, A. and Evangelista, P.H. 2014. Predicting seasonal habitat suitability for the critically endangered African wild ass in the Danakil, Ethiopia. *African Journal of Ecology* **52**: 533–544.

Keeping, D. and Pelletier, R. 2014. Animal Density and Track Counts: Understanding the Nature of Observations Based on Animal Movements. PLoS ONE **9**(5): journal.pone. | www.plosone.org

King, S.R.B., Boyd, L., Zimmermann, W. and Kendall, B.E. 2015. *Equus ferus*. The IUCN Red List of Threatened Species 2015.

King, S.R.B. and Moehlman, P.D. 2016. *Equus quagga*. The IUCN Red List of Threatened Species 2016.

Lamprey, H.F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *African Journal of Ecology* **1**: 63–92.

Lebreton, J.D., Pradel, R. and Clobert, J. 1993. The statistical analysis of survival in animal populations. *Trends in Ecology and Evolution* **8**: 91–95.

Low, B., Sundaresan, S.R., Fischhoff, I.R. and Rubenstein, D.I. 2009. Partnering with local communities to identify conservation priorities for endangered Grevy's zebra. *Biological Conservation* **142**: 1548–1555.

Madhusudan, M.D. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* **41**: 858–869.

MBS Environmental 2016. Draft Social and Environmental Impact Assessment (SEIA) of Colluli Mining Share Company (CMSC) prepared by Martinick Bosch Sell Pty Ltd and submitted to Ministry of Energy and Mines and Ministry of Land, Water and Environment, Asmara, Eritrea. October 2016.

Moehlman, P.D. 2002. Status and Action Plan for the African wild ass (*Equus africanus*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp 2-9.

Moehlman, P.D. 1998. Behavioural Patterns and Communication in Feral Asses (*Equus africanus*). *Applied Animal Behaviour Science* **60**: 125–169.

Moehlman, P.D. Kebede, F. and Yohannes, H. 1998. The African Wild Ass (*Equus africanus*): Conservation Status in the Horn of Africa. *Applied Animal Behaviour Science* **60**: 115–124.

Moehlman, P.D., Kebede, F. and Yohannes, H. 2015. *Equus africanus*. In the IUCN Red List of Threatened Species 2015. www.iucnredlist.org.

Moehlman, P.D., King, S.R. and Kebede, F. 2016. Status and Conservation of Threatened Equids. Wild Equids: Ecology, Management, and Conservation. (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 167-186.

Owaga, M.L. 1975. The feeding ecology of wildebeest and zebra in Athi-Kaputei plains. *African Journal of Ecology* **13**: 375–383.

Owen-Smith, N. 2002. Adaptive Herbivore Ecology. From Resources to Populations Variable Environments. Student Edition. Wits University Press.

Owen-Smith, N. 2007. Introduction to modeling on wildlife and resource conservation. Blackwell Publishing. Oxford, UK. 332pp.

Penzhorn, B.L. 1979. Social organisation of the Cape Mountain zebra *Equus z. zebra* in the Mountain Zebra National Park. *Koedoe* **22**: 115–156.

Penzhorn, B.L. 1985. Reproductive characteristics of a free-ranging population of Cape mountain zebra (*Equus zebra zebra*). *Journal of reproduction and fertility* **73**: 51–57.

Penzhorn, B.L. and Novellie, P.A. 1991. Some behavioural traits of Cape mountain zebras (*Equus zebra zebra*) and their implications for the management of a small conservation area. *Applied Animal Behaviour Science* **29**: 293–299.

Pratt, D.J. and Gwynne, M.D. 1977. Rangeland management and ecology in East Africa. Robert E. Krieger Publishing Company, Huntington, New York.

Prins H.H.T. 2000. Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G., Dolan T.T. (eds) Wildlife Conservation by Sustainable Use. Conservation Biology Series, vol 12. Springer, Dordrecht. pp. 51-80.

Ransom, J.I., Lagos, L., Hrabar, H., Nowzari, H. and Spasskaya, N. 2016. Wild and Feral Equid Population Dynamics. Wild Equids: Ecology, Management, and Conservation, (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 68-83.

Rosenbom, S., Costa, V., Steck, B., Moehlman, P. and Beja-Pereira, A. 2012. Cross-species genetic markers: a useful tool to study the world's most threatened wild equid - *Equus africanus*. *European journal of wildlife research* **58**: 609–613.

Rowen, M. and Ginsberg, J.R. 1992. Grevy's zebra (*Equus grevyi Oustalet*) in: IUCN/SSC Action Plain for the Conservation of Wild Equids. IUCN, Gland, Switzerland.

Rubenstein, D.I. 1994. The ecology of female social behavior in horses, zebras, and asses. Animal societies: individuals, interactions, and organization, pp.13-28.

Rubenstein, D.I. 2010. Ecology, social behavior, and conservation in zebras. *Advances in the Study of Behavior* **42**: 231–258.

Saltz, D. and Rubenstein, D.I 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. *Ecological Applications* **5**: 327–335.

Saltz, D., Rubenstein, D.I. and White, G.C. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. *Conservation Biology* **20**: 1402–1409.

Schoenecker, K.A., King, S.R., Nordquist, M.K., Nandintsetseg, D. and Cao, Q. 2016. Habitat and Diet of Equids. Wild Equids: Ecology, Management, and Conservation. (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 41-57.

Schulz, E. and Kaiser, T.M. 2013. Historical distribution, habitat requirements and feeding ecology of the genus E quus (Perissodactyla). *Mammal Review* **43**: 111–123.

Scoones, I. 1995. Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environment* **29**: 221–237.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* **37**: 789–799.

Shah, N., St-Louis, A., Huibin, Z., Bleisch, W., van Gruissen, J. and Qureshi, Q. 2015. Equus kiang. *The IUCN Red List of Threatened Species, 723*.

Sitters, J., Heitkönig, I.M., Holmgren, M. and Ojwang, G.S. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biological Conservation* **142**: 738–750.

St-Louis, A. *and* Côté, S.D. 2014. Resource selection in a high-altitude rangeland equid, the kiang (*Equus kiang*): influence of forage abundance and quality at multiple spatial scales. *Canadian Journal of Zoology* **92**: 239–249.

Sundaresan, S.R., Fischhoff, I.R., Hartung, H.M., Akilong, P. and Rubenstein, D.I. 2008. Habitat choice of Grevy's zebras (*Equus grevyi*) in Laikipia, Kenya. *African Journal of Ecology* **46**: 359–364.

Tatin, L., King, S.R.B., Munkhtuya, B., Hewison, A.J.M. and Feh, C. 2009. Demography of a socially natural herd of Przewalski's horses: an example of a small, closed population. *Journal of Zoology* **277**: 134–140.

Tesfai, R.T. 2006. Conservation of African wild ass (*Equus africanus*) in Messir plateau (Asaila), Eritrea: the role of forage availability and diurnal activity pattern during the rainy and beginning of the dry season. MSc Thesis, University of Kent/DICE, Canterbury, UK. 85pp.

Tesfai, R.T., Owen-Smith, N. Parrini, F and Moehlman, P.D. 2019. Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy* **100**: 185–191.

Van Soest, P.J. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology* **15**: 455–479.

Voeten, M.M. and Prins, H.H. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120**: 287–294.

Watson, L.H., Odendaal, H.E., Barry, T.J. and Pietersen, J. 2005. Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. *Biological Conservation* **122**: 173–180.

Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology* **13**: 265–286.

Williams, S.D. 1998. Grevy's zebra: ecology in a heterogeneous environment, Doctoral dissertation, University College London (University of London), UK. 199pp.

Williams, S.D. 2002. Status and Action Plan for Grevy’s Zebra (*Equus grevyi*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. Pp 11-25.

Wolfe, M.L. 1986. Population dynamics of feral horses in western North America. *Journal of Equine Veterinary Science* **6**: 231–235.

Young, T.P., Palmer, T.M. and Gadd, M.E. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological conservation* **122**: 351–359.

Chapter 2. Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea)

Pulished as a journal article (Tesfai, R.T., Owen-Smith, N., Parrini, F. and Moehlman, P.D., 2019). Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy*, Volume 100, Issue 1, 28 February 2019, Pages 185–191, https://doi.org/10.1093/jmammal/gyy164).

As the first author of the published paper, I have conceptualized the research work and designed the model with the guidance of Norman Owen-Smith (co-supervisor), collected the data, analysed the data and determined the results, prepared the first draft of the manuscript and led the subsequent revisions.

Abstract

Globally, the African wild ass (*Equus africanus*) is at risk of extinction in the wild. Major threats to its survival are hunting, competition with livestock, and interbreeding with the domestic donkey. An important but rare population exists on the Messir Plateau in the Danakil ecosystem of Eritrea. Long-term data on reproduction and survival rate of African wild asses are limited, making it difficult to predict the population trend. Therefore, we assessed the population's potential viability given certain assumptions. An age-structured matrix model was used to project the population growth rate generated by assumed vital rates. The probability of population persistence over 50 years was estimated allowing for stochastic dynamics, density dependence, influences of rainfall on carrying capacity, and episodic disturbances reducing survival rates. Scenarios used either historical rainfall patterns or potential future rainfall with the same or amplified coefficient of variation. We contrasted two estimates of carrying capacity based either on recent population assessments, or on the potential capacity of the study site. Our models also compared realistic versus optimistic scenarios for age at first reproduction and potential longevity. The probability of persistence of a population of 18 females was reduced to < 50% in the worst-case scenario. With a potential carrying capacity of 37 females, persistence was projected to be almost 100% under all scenarios. The greatest threat to population viability seems to come from livestock impacts on the resources that limit the African wild ass population size under anticipated climate change scenarios. Further studies are required to assess the level of competition between African wild asses and livestock to guide effective conservation strategies.

Key words: climate change, *Equus africanus*, Danakil ecosystem, livestock competition, population survival probability

2.1 Introduction

The African wild ass (*Equus africanus*), classified as 'Critically Endangered' by the International Union for Conservation of Nature (IUCN) Red List, is at serious risk of extinction in the wild (Moehlman et al. 2015). Historically, the African wild ass was widespread across Egypt, Sudan, Eritrea, Ethiopia, Djibouti, and Somalia, but is now restricted to Eritrea and Ethiopia, and possibly Somalia, Sudan, and Egypt (Fig. 2.1), with less than an estimated 600 individuals remaining within its range (Moehlman et al. 2015). Hunting, habitat loss, and potential competition with livestock for access to water and forage are the main reasons suggested for the reduction in numbers (Moehlman 2002; Tesfai 2006; Moehlman et al. 2016).

The estimated number of African wild asses (Fig. 2.2) in Ethiopia is around 112 (Kebede 2013) and an approximate estimate for Eritrea is 400 (Moehlman et al. 2015). The

Messir Plateau, within the Danakil ecosystem of Eritrea, supports a population of approximately 50 wild asses (Moehlman et al. 1998; Moehlman 2002), consisting mainly of adult and juvenile females (Moehlman 2002; Tesfai 2006). No more than 24 individuals, including isolated male groups, have been observed elsewhere in the approximately 11,000 sq km range of the Eritrean Danakil ecosystem (Moehlman et al. 1998; Hagos 2015; Tesfai, personal observation.).

In Ethiopia, African wild asses are hunted illegally for food and traditional medicinal use (Kebede et al. 2014). The African wild ass population in the Danakil ecosystem of Eritrea is protected by the local community as part of their cultural practice (Moehlman 2002; Tesfai, pers. obs.). However, the Messir Plateau, a potentially critical breeding area for the African wild ass, currently has no protected status gazetted (Moehlman 2002; Tesfai 2006). It is therefore important to determine how conserving the Messir Plateau population may contribute to improving the survival probability of the African wild ass.

The African wild ass is primarily a grazer (Kebede 1999; Moehlman 2002; Tesfai 2006). An estimated 600 head of livestock (goats, sheep, camels, cattle, and domestic donkeys) utilize the Messir Plateau daily during the wet season for three to four months, depending on the availability of green forage and seasonal water, and potentially compete with the wild asses for food (Tesfai 2006). African wild asses tend to graze in the lower plain area of the Messir Plateau, which has more grass than higher on the plateau (Tesfai 2006). When livestock are herded onto the plains, African wild asses move to the plateau, possibly to avoid disturbance (Tesfai, personal observation).

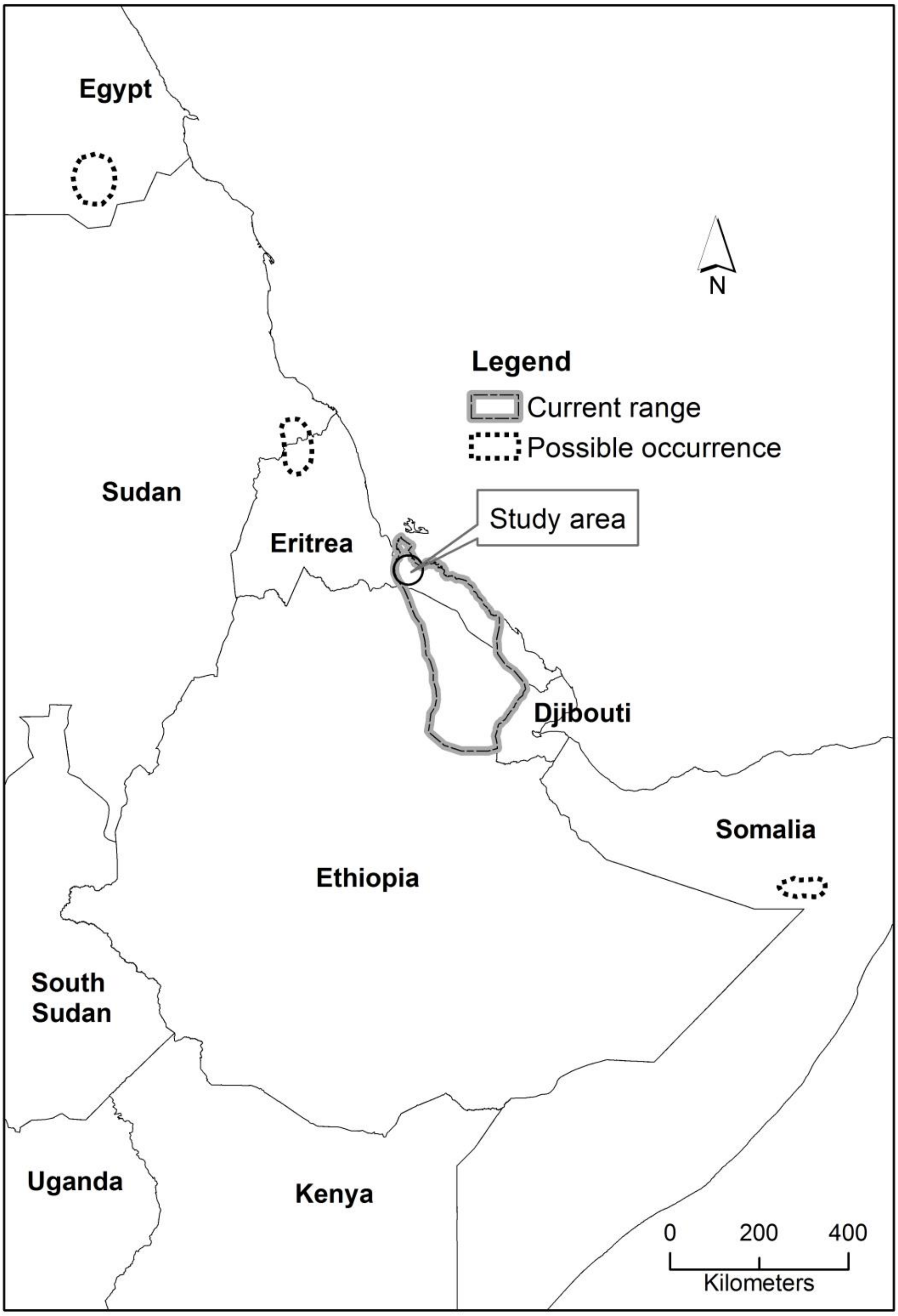


Figure 2.1 Current range of the African wild ass (*Equus africanus*). Data obtained from IUCN online portal: www.iucnredlist.org

Competition with livestock affecting access to adequate forage and water has been identified as a major threat to the African wild ass in the Danakil ecosystem (Tesfai 2006; Kebede et al. 2014; Moehlman et al. 2015, 2016). In northern Kenya, female Grevy's zebras (*E. grevyi*) with young foals travelled long distances to obtain water and forage because of the presence of people and livestock near water points (Williams 1998, 2002), adversely affecting foal survival and recruitment (de Leeuw et al. 2001; Williams 1998, 2002). On the Messir Plateau, female African wild asses occasionally travelled more than 10 km from grazing areas to drink at night, while most livestock are brought to permanent water during the day (Tesfai 2006). Female wild asses with young foals need to drink at least once per day (Moehlman 1998). Competition for resources may affect the population growth of wild equids by delaying age of first reproduction and survival rate (Garrot and Taylor 1990; Georgiadis et al. 2003).

Under ideal conditions in captivity, female African wild asses can conceive at 12 months, produce their first foal at 2-3 years of age, and subsequently give birth every other year (Moehlman 2002; Steck 2017). In the wild, they typically give birth first at 4-5 years of age, similar to most other equids (Moehlman 2002; Ransom et al. 2016). Adult females can potentially keep producing offspring until they are 18 to 24 years of age (Moehlman 2002; Ransom et al. 2016). An individually recognizable African wild ass on the Messir Plateau produced her first foal at six years of age, and another gave birth at the age of 18 years (Moehlman et al. 2013; Tesfai, personal observation).

Figure 2.2 African wild ass (*Equus africanus*) on the Messir Plateau, Eritrea (© R.T.Tesfai, 2017).

Modelling is a useful tool to address data limitations. Population viability models are widely used by conservation biologists to project the likelihood of population persistence or extinction over a future time horizon (Brook et al. 1997; Owen-Smith 2007). Hence, this study used a demographic model to assess the viability of the Messir Plateau population of African wild asses under different rainfall scenarios in order to guide future management strategies. Specifically, we used age-structured population models to project the potential population growth rate and survival probability based on assumed fecundity and survival rates under different carrying capacity and rainfall scenarios.

2.2 Materials and methods

2.2.1 Study area

The Messir Plateau (both plain and rocky plateau regions) covers about 124 km^2 and is located 15°00′ N and 40°02′ E within the Danakil ecosystem in the Northern Red Sea Zone, Eritrea (Fig. 2.1). Elevation ranges between 100 m above sea level on the plain to about 475 m on the top of the Egirale Hill. The Asaila spring, a perennial water source, is located in the northwest of the study area. The Danakil ecosystem is characterized by dissected volcanic ridges forming a very rocky landscape (Moehlman 2002; Tesfai 2006). The climate of the study area is arid with extremely hot summers (mean daily maximum temperature of 35º C). The nearest meteorological station is located at Massawa on the coast of the Red Sea 170 km to the north of the study area but within the same climate zone (Department of Land 1998). The mean annual rainfall there averaged about 160 mm over 50 years, with a high annual variability (CV 73%). Most rain usually occurs between December and February, with less rain falling in March and April. The dry season begins in May or June and lasts until October or November (Environment of Eritrea 1995). Local rainfall is highly erratic, unevenly distributed and frequently fails (Ministry of Agriculture 2002).

2.2.2 Estimating potential population growth rates

To project the potential growth rate of the African wild ass population generated by the assumed vital rates (Table 2.1), age-structured population models were constructed in Excel spreadsheets (Microsoft Excel 2013) assuming a potential longevity of either 18 or 24 years. Following convention, only the female segment of the population was represented. For a realistic growth rate, first reproduction was assumed to occur at age six and maximum reproductive longevity to be either 18 or 24 years old (Table 2.1). For an optimistic growth rate, first reproduction was assumed to be at age three with reproductive longevity either 18 or 24 years (Table 2.1). In all scenarios, it was assumed that females reproduced only every second year, consistent with their 13-month gestation period based on captive African wild asses (Moehlman 2002; Steck 2017; Kozlowski et al. 2018). Thus, the annual fecundity was 0.25 assuming a 50:50 sex ratio at birth (Ransom et al. 2016).

Table 2.1 Vital rate estimates used to project the realistic and optimistic growth rates for the African wild ass in Messir Plateau at the current density level. The realistic rates are based on observed vital rates by Moehlman et al. (2013).

	Female stage classes (years)			
Vital rate	Juvenile	Sub-adult	Prime adult	Old adult
Realistic stage ranges	0-1	1-6	6-16	16-18
Optimistic stage ranges	0-1	1-3	3-22	22-24
Annual fecundity rates	0.00	0.00	0.25	0.25
Annual survival rates	0.80	0.98	0.98	0.90

In the absence of survival estimates for African wild asses, we used those reported by Ransom et al. (2016) for wild equids in general and by Williams (1998) for Grevy's zebra. In these reports, foal survival from birth to one year of age was estimated to range between 0.53 and 0.88, and adult survival beyond one year of age to be between 0.85 and 0.98 per year, including deaths from terminal senescence. For maximum growth, adult survival up until the maximum age could approach almost 100%. Hence, we assumed maximum foal survival to be 0.8 and annual adult survival to be 0.98 during the prime age range from six to 16 years, reduced to 0.90 beyond 16 years (Table 2.1). African wild asses in the Danakil ecosystem (Eritrea) are not hunted and the incidence of predation is currently very low (Moehlman

2002; Tesfai 2006; Tesfai, personal observation). Population growth was projected over a long enough period (50 years) for the initially assigned age structure to stabilize.

2.2.3 Density-dependent population growth models

We used population viability models written in the programming language True BASIC (SMALLPOP and POPVIAB, as formulated by Owen-Smith 2007). These incorporate an Usher projection matrix, which aggregates the adult segment in one persistent stage class, because for many large ungulates the survival rate remains fairly constant after reproductive maturity is reached (Gaillard et al. 2000). Allowance was made for terminal mortality upon reaching the end of the lifespan as follows. If the adult stage extended from age six to age 16, 10% of the adult segment would die annually upon reaching the maximum age of 16 years, assuming zero prior mortality in the adult stage. If the adult stage extended over 20 years, terminal mortality would remove 5% of the adults annually, if all survived until the maximum age. Allowance was made for density-dependent reductions in survival rates as the population approached carrying capacity, defined as the population level at which the net growth rate became zero. We assumed that the maximum population growth rate generated by the assumed vital rates remained unaffected by density until the population exceeded a threshold level of one-third of its carrying capacity in a constant environment, after which survival rates decreased linearly with increasing population size relative to the carrying capacity until zero growth was attained. Fecundity, represented by annual births of female offspring by each adult female beyond some fixed age, was held constant (Table 2.2). For viability projections, the effective carrying capacity was directly dependent on the annual total rainfall relative to the mean rainfall, based on the effect of rainfall on plant growth (Nicholson et al. 1990). Accordingly, the simulated population fluctuates around a variable ceiling level. Episodic disturbances amplifying mortality occurred stochastically with a mean return interval of 10 years. Such events can have an especially severe effect on population persistence when they occur by chance in rapid succession, overriding the potentially random variation in rainfall that otherwise prevails. These events could be caused by occasional predation or hunting, enduring effects of low rainfall, severe livestock impacts on vegetation or other conditions affecting vegetation recovery. The intensified mortality was represented by amplifying survival rates by an appropriate power function; e.g., a survival rate of 0.9 became reduced to 0.81 using a power coefficient of 2. We assumed that foal survival rates over the first year would be much more sensitive to adverse conditions than adult survival rates (Eberhardt 1985; Gaillard et al. 2000), and adjusted the power coefficient appropriately (Table 2.2). We represented different options for rainfall variation and episodic disturbances in the model in addition to demographic stochasticity in survival rates and in offspring sex ratio. The effective carrying capacity (zero growth level) was set either optimistically at 37 female asses or more realistically at 18 individual females, based on repeated field observations (Moehlman et al. 1998; Moehlman 2002; Tesfai, personal observation).

Table 2.2 Vital rates assumed for realistic and optimistic growth rate for the African wild ass in Messir Plateau within the Danakil Ecosystem (Eritrea) for density-dependent population growth rate.

	Female stage classes (years)		
Vital rate	Juvenile	Sub-adult	Adult
Realistic stage ranges	0-1	1-6	6 onwards
Optimistic stage ranges	0-1	1-3	3 onwards
Annual fecundity rates	0.00	0.00	0.25
Annual survival rates:			
longevity 18 yrs (realistic)	0.81	0.98	0.91
longevity 24 yrs (realistic)	0.87	0.98	0.94
longevity 18 yrs (optimistic)	0.85	0.98	0.93
longevity 24 yrs (optimistic)	0.89	0.99	0.95

2.2.4 Modeling population viability

Potential scenarios considered in the model to assess population viability included: 1) carrying capacity of 37 adult females and optimistic vital rates (first reproduction at age three and longevity of 24 years), 2) carrying capacity of 37 adult females and realistic vital rates (first reproduction at age six and longevity of 18 years), 3) carrying capacity of 18 adult females and optimistic vital rates (first reproduction at age three and longevity of 24 years), and 4) carrying capacity of 18 adult females and realistic vital rates (first reproduction at age six and longevity of 18 years; Table 2.2). Each of the above models was run with three alternative rainfall scenarios: 1) historical rainfall pattern repeated into the future, 2) stochastic rainfall pattern with the same CV (73%) as historical pattern, and 3) stochastic rainfall pattern with widened CV (93%) due to future climate change.

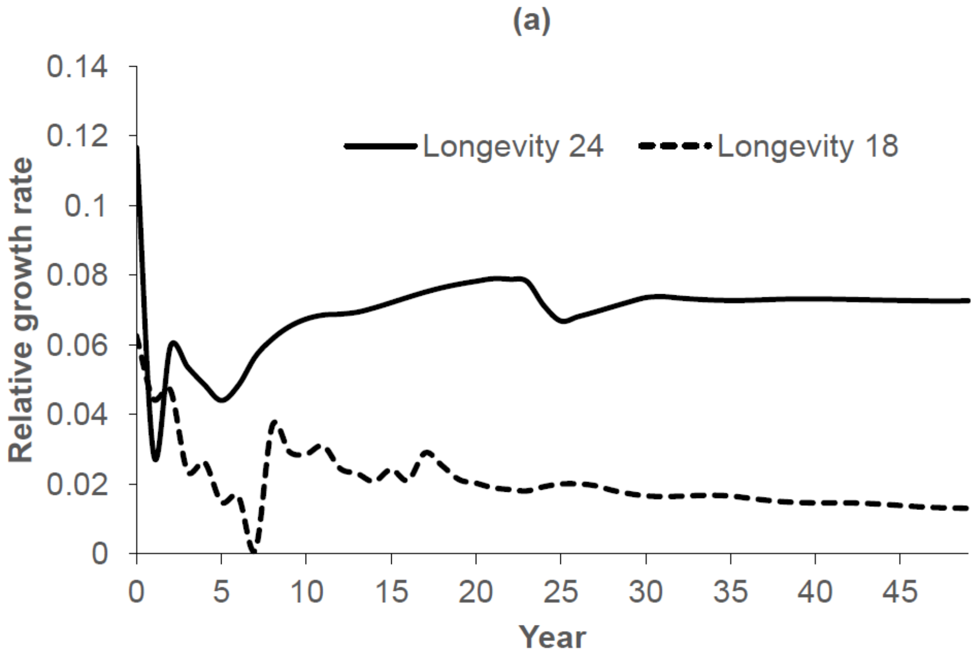
2.3 Results

2.3.1 Potential population growth rate

Population growth rates projected for realistic scenarios (age at first reproduction 6 years) were estimated to be only 1.3% annually with a longevity of 18 years, increasing to 7.2% if longevity was extended to 24 years (Fig. 2.3a). Optimistic scenarios (age of first reproduction three years) yielded higher population growth potential: 5.1% with longevity of 18 years and 10.8% with longevity of 24 years (Fig. 2.3b). The spreadsheet projection indicated how rapidly the population could recover, showing the limitation posed by the realistic demography, which then affects population viability.

2.3.2 Probability of population extinction

With carrying capacity set at a potential of 37 adult females, a 100% chance of population survival over 50 years was projected under all scenarios considered, except when a realistic growth rate was used under amplified future rainfall conditions, which generated a 96% chance of persistence (Table 2.3). The chance of population survival over 50 years was reduced to 90% if the carrying capacity was set at the current level of 18 adult females, assuming that the future rainfall pattern remained similar to that in the historical past (Table 2.3). The probability of population persistence was further reduced to < 50% with amplified variability in future rainfall (Fig. 2.4).



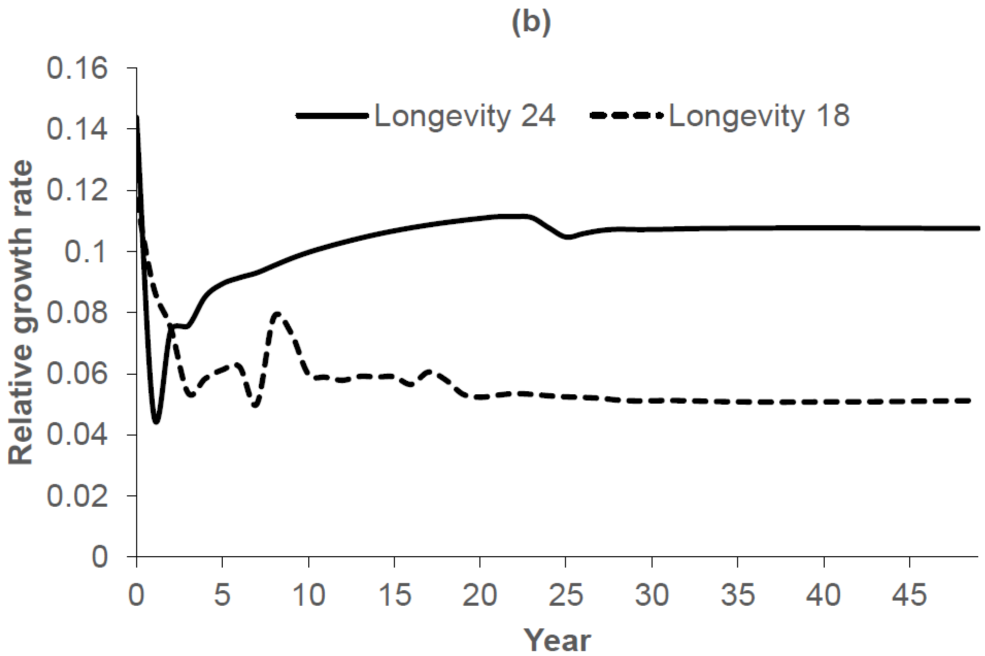


Figure 2.3 Projected population growth rate of the African wild ass (*Equus africanus*) on the Messir Plateau (Eritrea) in the absence of density dependence and rainfall variation, assuming (a) realistic growth rate with age of first reproduction set at six years and longevity either 18 or 24 years, and (b) optimistic growth rate when age of first reproduction is three years and longevity is 18 or 24 years.

Table 2.3 Population viability assessments for African wild assess on Messir Plateau (Eritrea) based on the assumed demography and effects of three alternative rainfall scenarios. Persistence probabilities (%) are estimated over a 50-year time horizon.

		Assumed rainfall condition		
Scenario	Demographic stochasticity	Historical	Random	Amplified
1.	Population size (37 adult females): optimistic vital rates (first reproduction age at three and longevity 24 years).	100	100	100
2.	Population size (37 adult females): optimistic vital rates (first reproduction age at three and longevity 18 years).	100	100	100
3.	Population size (37 adult females): realistic vital rates (first reproduction age at six and longevity 24 years).	100	100	100
4.	Population size (37 adult females): realistic vital rates (first reproduction age at six and longevity 18 years).	100	100	96
5.	Population size (18 adult females): optimistic vital rates (first reproduction age at three and longevity 24 years).	100	100	98
6.	Population size (18 adult females): optimistic vital rates (first reproduction age at three and longevity 18 years).	100	100	89
7.	Population size (18 adult females): realistic/observed rates (first reproduction age at six and longevity 24 years).	100	100	98
8.	Population size (18 adult females): realistic/observed rates (first reproduction age at six and longevity 18 years).	91	90	48

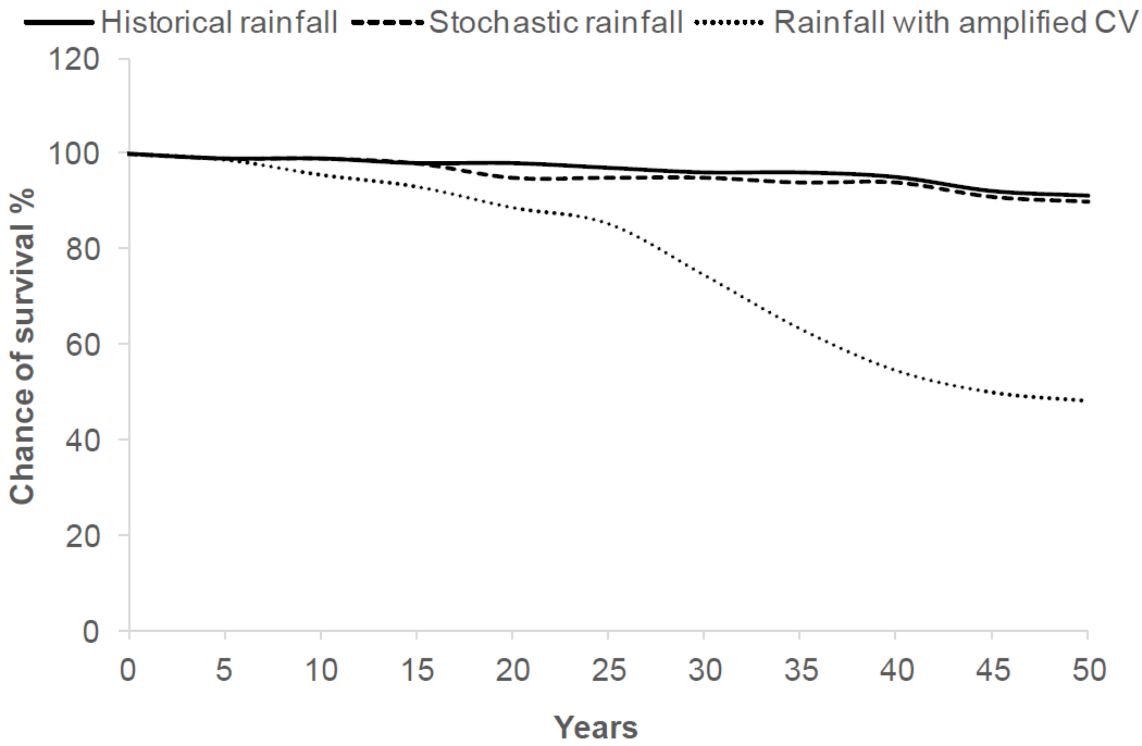


Figure 2.4 The probability of persistence for the African wild ass (*Equus africanus*) on the Messir Plateau (Eritrea) when carrying capacity is 18 adult and juveniles females. The chance of population survival is projected under three alterative rainfall scenarios (a) historical rainfall pattern repeated into the future, (b) stochastic rainfall pattern with the same CV as historical pattern, and (c) stochastic rainfall pattern with amplified CV due to future climate change.

2.4 Discussion

Competition with livestock on the Messir Plateau is thought to restrict age of first reproduction and longevity of the African wild ass. When forage is abundant, female equids are more likely to give birth at an earlier age and live longer (Saltz and Rubenstein 1995; Tatin et al. 2009) and survival rate of foals is enhanced (Ransom et al. 2016). Longevity in the African wild ass may be limited by availability of food resources. Inbreeding depression and diseases that might influence the assumed vital rates were not taken into consideration in our population viability assessments.

The model results suggest that the chance of the African wild ass population surviving over 50 years would be reduced from almost 100% to under 50% in the worst-case scenario. This outcome is projected should the population level remain at the current 18 adult and juvenile females. This finding is consistent with the IUCN Red List assessment of Critically Endangered, which under the Categories and Criteria (IUCN 2014) entails a 50% likelihood of extinction in the wild within three generations. Currently, the IUCN Red List has assessed the African wild ass as critically endangered because the total population numbers less than 250 mature individuals of both sexes, while no sub-population exceeds 50 mature individuals. The effective carrying capacity of the Messir Plateau may be undergoing a progressive decline due to the impact of livestock and drought on vegetation (Moehlman et al. 2015).

Little is known about the effect of rainfall variation on the reproductive and survival rates of African wild asses in the Danakil ecosystem. If competition with livestock additionally reduces the effective availability of forage and hence potential carrying capacity, the chances of population survival will deteriorate. The model output suggests that the probability of population survival over 50 years at its current carrying capacity (18 adult females) would be reduced from 90% to < 50%, if the historical rainfall pattern were to be replaced by amplified variability in rainfall.

Northeastern Africa, where the study area is located, is known for severe and prolonged droughts (Nicholson 2016). For instance, in 1997 and 2006 there were severe droughts in the Danakil (Ministry of Agriculture 2002; Tesfai, personal observation). Local pastoralists lost most of their goats and sheep, and some adult mortality among African wild asses occurred in 2006 (Tesfai, personal observation). Widened variation in annual rainfall as a consequence of global warming would increase the threat of population extinction. With global climate change, rainfall may become more variable and prolonged droughts in the region may occur more frequently. Repeated droughts brought about a substantial reduction in the population viability of Asiatic wild asses in the Negev Desert of Israel (Saltz et al. 2006).

The greatest threat to the viability of the African wild ass population appears to be the impact of livestock on forage availability on the Messir Plateau. This limits the population size of African wild asses below what could potentially be supported. The range of the African wild ass in Eritrea has no formally protected status. Gazetting the Messir Plateau as a "core protection area", and thereby restricting livestock use, could enhance the survival prospects of the African wild ass there. Further studies are required to assess the level of competition between African wild asses and livestock to guide effective future conservation actions to save this endangered species from extinction.

References

Brook, B. W., Lim, L., Harden, R., and Frankham, R. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen Tricholimnas sylvestris (Sclater). *Biological Conservation* **82**: 119–128.

De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula, H.M., Heitkönig, I.M., & Reid, R.S. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation* **100**: 297–306.

Department of Land 1998. Agro-Ecological Classification Map of Eritrea. Ministry of Land Water and Environment, Asmara, Eritrea.

Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* **49**: 997–1012.

Environment of Eritrea 1995. The National Environmental Management Plan for Eritrea (NEMP-E). Asmara, Eritrea. 138pp.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**: 367–393.

Garrott, R.A., and Taylor, L. 1990. Dynamics of a feral horse population in Montana. *Journal of Wildlife Management* **54**: 603–612.

Georgiadis, N., Hack, M., and Turpin, K. 2003. The influence of rainfall on zebra population dynamics: implications for management. *Journal of Applied Ecology* **40**: 125–136.

Hagos, F. 2015. Population distribution, genetics and conservation of the African wild ass *(Equus africanus somaliensis)* in Denkelia, Eritrea. MSc thesis. University of Nairobi. Nairobi, Kenya. 72pp.

IUCN Standards and Petitions Subcommittee. 2014. Guidelines for Using the IUCN Red List Categories and Criteria. Version 11. Prepared by the Standards and Petitions Subcommittee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Kebede, F. 1999. Ecology and conservation of the African wild ass (Equus africanus) in the Denakil, Ethiopia. MSc Thesis, University of Kent/DICE, Canterbury, UK. 100pp.

Kebede, F. 2013. Ecology and community-based conservation of Grevy's zebra *(Equus grevyi)* and African wild ass *(Equus africanus)* in the Afar Region. PhD dissertation University of Addis Ababa, Ethiopia. 203pp.

Kebede, F., Moehlman, P.D., Bekele, A., and Evangelista, P.H. 2014. Predicting seasonal habitat suitability for the critically endangered African wild ass in the Danakil, Ethiopia. *African Journal of Ecology* **52**: 533–542.

Kozlowski, C.P., Clawitter, H.L., Thier, T., and Asa, C.S. 2018. Characterization of estrous cycles and pregnancy in Somali wild asses (*Equus africanus somaliensis*) through fecal hormone analyses. *Zoo Biology* **37**: 35–39.

Ministry of Agriculture. 2002. The national Action Programme to Combat Desertification and mitigate the effect of Drought in Eritrea (NAP). January 2002. Asmara. 197pp.

Moehlman, P.D. 1998. Feral Asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Applied Animal Behaviour Science* **60**: 171–195.

Moehlman, P.D. 2002. Status and Action Plan for the African wild ass *(Equus africanus)* In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp 2-9.

Moehlman, P.D., Kebede, F., and Yohannes, H. 1998. The African Wild Ass (*Equus africanus*): Conservation Status in the Horn of Africa. *Applied Animal Behaviour Science* **60**: 115–124.

Moehlman, P.D., Kebede, F., and Yohannes, H. 2013. *Equus africanus*. In: J. Kingdon and M. Hoffmann (eds), The Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses, Bloomsbury Publishing, London.

Moehlman, P.D., Kebede, F., and Yohannes, H. 2015. *Equus africanus*. In the IUCN Red List of Threatened Species 2015. www.iucnredlist.org. Access on 06 September 2015

Moehlman, P.D., King, S.R., & Kebede, F. 2016. Status and Conservation of Threatened Equids. Wild Equids: Ecology, Management, and Conservation. (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 167–186.

Nicholson, S.E., Davenport M.L., and Malo A.R. 1990. A comparison of the vegetation response to rainfall in the Sahel and East Africa, using Normalized Difference Vegetation Index from NOAA AVHRR. *Climate Change* **17:** 209–241.

Nicholson, S.E. 2016. An analysis of recent rainfall condition in eastern Africa. *International Journal of Climatology* **36:** 526–532.

Owen-Smith, N. 2007. Introduction to modelling in wildlife and resource conservation. Wiley-Blackwell Publishing. Oxford, UK. 332pp.

Ransom, J.I., Lagos, L., Hrabar, H., Nowzari, H., and Spasskaya, N. 2016. Wild and Feral Equid Population Dynamics. Wild Equids: Ecology, Management, and Conservation, (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 68-83.

Saltz, D., and Rubenstein, D.I. 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus*) herd. *Ecological Applications* **5**: 327–335.

Saltz, D., Rubenstein, D.I., and White, G.C. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. *Conservation Biology* **20**: 1402–1409.

Steck B. 2017. International Studbook for the Somali wild ass 2016. Zoo Basel, Switzerland. 77pp.

Tatin, L., King, S.R.B., Munkhtuya, B., Hewison, A.J.M., and Feh, C. 2009. Demography of a socially natural herd of Przewalski's horses: an example of a small, closed population. *Journal of Zoology* **277**: 134–140.

Tesfai, R.T. 2006. Conservation of African wild ass *(Equus africanus)* in Messir plateau (Asa-ila), Eritrea: the role of forage availability and diurnal activity pattern during the rainy and beginning of the dry season. MSc Thesis, University of Kent/DICE, Canterbury, UK. 85pp.

Williams, S.D. 1998. Grevy's zebra: ecology in a heterogeneous environment. Doctoral dissertation, University College London (University of London), UK. 199pp.

Williams, S.D. 2002. Status and Action Plan for Grevy’s Zebra *(Equus grevyi)* In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. Pp 11–25.

Chapter 3. Spatial and dietary overlap between the African wild ass and livestock on Messir Plateau (Eritrea)

Abstract

Competition for forage resources with livestock has been identified as a potential threat to the survival of the African wild ass (*Equus africanus*) in the Danakil ecosystem (Eritrea). The Messir Plateau is a critical habitat for the African wild ass but it also hosts livestock (i.e. cattle, domestic donkeys, camels, goats and sheep). This study investigated the spatial and dietary overlap between African wild ass and livestock on the Messir Plateau. GPS locations and faecal samples of African wild ass and livestock were collected during dry months (October – December 2016) and rainfall months (March – June 2017). Additional faecal samples from African wild ass and domestic donkey were collected in January – March 2019. Density and location of African wild ass and livestock were recorded and faecal stable carbon isotopes ($^{13}C/^{12}C$) analyses were used to assess the dietary overlaps between the domestic and wild herbivores. The nutritional status of African wild ass and domestic donkeys was compared in both the dry and rainfall months. During the dry months, African wild ass were concentrated in the northern section of the Messir Plateau area closer to the Asaila permanent water point and they significantly overlapped spatially with resident camels, domestic donkeys, goats, and sheep. During the rainfall months, African wild ass were dispersed throughout the study area, while a high number of livestock, particularly cattle, were concentrated in the northern section near seasonal water sources. During the rainfall months, the northern section has relatively better vegetation cover and seasonal water. The diet of the African wild ass significantly overlapped with domestic donkeys and cattle. They all had relatively high $\delta\,^{13}C/^{12}C$ values indicating a grazing diet in both dry and wet months. Camels, goats and sheep had relatively low $\delta\,^{13}C/^{12}C$ values, characteristic of a browsing diet in the rainfall months. In the dry months, goats and sheep had intermediate δ $^{13}C/^{12}C$ values reflecting mixed feeding strategies, while camels had lower δ $^{13}C/^{12}C$ values indicating browsing feeding behaviour. In the rainfall months of 2017 and March 2019, the African wild ass percent faecal nitrogen was significantly lower than that found in domestic donkey samples (p=0.0254). The percent faecal phosphorus of the African wild ass was significantly lower than the domestic donkey in February 2019 (p=0.0149) and marginally in March 2019 (p= 0.0528) when cattle numbers increased on Messir Plateau. But there was no difference between the species in January (p=0.8039). The lower nutrients (N, P) level found in African wild ass faecal samples in rainfall months may be due to their displacement by the high number of cattle. This research provides pieces of evidence on how the presence of domestic herbivores, particularly cattle, may negatively impact the nutrient level of wild herbivores and threaten the survival of the critically endangered African wild ass due to their spatial displacement from needed forage and water resources.

Keywords: African wild ass, diet overlap, faecal samples, nutrients (N, P) levels, spatial overlaps, stable carbon isotope levels.

3.1 Introduction

Competition between domestic and wild herbivores may occur when they share the same limited food resources (Illius and Gordon 1987; Prins 2000). This could be revealed when an increase in domestic herbivore populations correlates with a reduction in number of wild herbivores (Illius and Gordon 1987; de Boer and Prins 1990). The most critical factor that negatively affects population growth of many wild herbivores is competition for forage with livestock (Gaillard et al. 2000). The nutritional quality and biomass of food resources are important for the reproductive performance of wild herbivores (Gedir et al. 2015; Saether 1997). Competition for limited forage between two species can have a potentially negative effect on the performance of either or both species concerned (Prins 2000). Competition for forage resources between the African wild ass (*Equus africanus*) and livestock on Messir Plateau (Eritrea) may be affecting African wild ass nutrition and reproduction (Tesfai et al. 2019).

The African wild ass lives in hot arid Danakil ecosystem where forage resources are limited (Moehlman 2002; Tesfai 2006). The presence of livestock may significantly reduce the available food resources for the African wild ass (Moehlman 2002). A study by Tesfai (2006) indicated that in the wet season the highest plant productivity occurred in the lower elevation plains of the Messir Plateau and only yielded 3.65 dry matter (DM) ton/ha. The plains area is characterized by sand-silt soil and pH = 8.6 (Tesfai 2006).

Previous research conducted on the Messir plateau indicated that during the wet season African wild ass and livestock overlap in distribution and utilize the same areas (Tesfai 2006). The pastoralists in the area own livestock, mainly camels, goats, sheep, domestic donkeys and a few cattle (Tesfai 2006). About 12 villages, collectively named the Asaila village administration area, are situated on the periphery of the study area (Tesfai 2006). However, the Messir Plateau is under increasing pressure from cattle coming from the highlands during the rainfall months. For example, an estimated 150 cattle were observed daily soon after the rains began in May 2017 (Tesfai, personal observation.). This is of great concern to the survival of the African wild ass because the presence of livestock, especially cattle, can potentially reduce available food resources and in fact, they are considered potential competitors for grazing with equids (Menard et al. 2002).

The Messir Plateau, a core breeding site for the African wild ass in Eritrea is not restricted (Moehlman 2002; Tesfai 2006; Tesfai et al. 2019) and livestock are free to utilize the area (Tesfai 2006; Tesfai, personal observation). Field observations indicate that the African wild ass disperse to the southern-most part of the plains area when high concentrations of livestock, particularly cattle, are in the northern section of the plains area (Tesfai, personal observation). Short grasses such as *Setaria incrassata* and *Setaria verticillata* offer the best quality forage (Andrews 1956; Oudtshoorn 1999) and are relatively abundant in the northern portion of the plains area in rainfall months (Tesfai, personal observation).

Stable carbon isotopes ($\delta\,^{13}C/^{12}C$) values measured from faecal samples, are commonly used in most African savannas to compare feeding behaviours and dietary overlap of herbivores (Blanchard et al. 2003; Sponheimer et al. 2003). Carbon isotopes provide information on herbivore foraging diet along a grazing-browsing gradient (Leslie et al. 2008; Schneidera et al. 2015). Plants that follow the C_3 photosynthetic pathways (dicots such as trees, shrubs, and forbs) have distinctly lower $\delta\,^{13}C/^{12}C$ values (-33 to -24‰) compared to C_4 photosynthesizing plants (grasses), which have higher values (-16 to -10‰) (Smith and Epstein 1971). Plants such as succulents that have a carbon isotopic signature intermediate between C_3 and C_4 plants are classified as having Crassulacean Acid Metabolism (CAM) (O'Leary 1988). Therefore, this study used stable carbon isotopes to assess dietary overlap between African wild ass and livestock.

Conservation management of wild herbivores generally requires knowledge of the quality and quantity of nutrients that the species can obtain from forage (Kidane et al. 2008; Gedir et al. 2015; Saether 1997). A faecal index nutrition would therefore be useful to monitor herbivore population nutritional status (Blanchard et al. 2003). Mean Faecal Nitrogen (FN) and Faecal Phosphorus (FP) were analysed to compare nutrient levels between African wild ass and domestic donkeys. FN and FP content have been commonly used to assess animal dietary quality and nutrition (Sponheimer et al. 2003; Codron et al. 2007) and indicate a positive relationship with intake and dietary dry matter digestibility (Leslie et al. 2008). Some authors have highlighted the shortcomings of the faecal index application in assessing forage quality. Precise prediction of FN can potentially be constrained by differences in species-specific digestive capacity and plant species/components consumed by the animal (Blanchard et al. 2003; Leslie et al. 2008). However, the faecal index method has been successfully used for assessing nutrient levels of wild herbivore species (Dove and Mayes 1996; Mayes and Dove 2000), and this technique is particularly useful for rare populations that are difficult to study under wild conditions (Blanchard et al. 2003; Leslie et al. 2008). Faeces are relatively easy to collect, record dietary turnover in a short time period and sampling is non-invasive (Codron et al. 2007; Leslie et al. 2008).

This research project was designed to evaluate the impact of domestic herbivores, particularly cattle, on the nutrient levels available to the African wild ass. Reduced access to good forage close to seasonal water sources may increase the distance travelled by the African wild ass to secure both water and nutrition and subsequently may reduce natality and foal survival rate (Williams 1998). The level of diet overlap and potential competition is dependent on the species of herbivores, their population numbers and foraging ecology in the same area during different months of the year. Therefore, the objectives of this study were to compare (i) spatial overlap between the African wild ass and livestock (i.e. domestic donkey, cattle, camel, goat and sheep) in dry months vs. rainfall months, (ii) diet overlap between African wild ass and livestock based on stable carbon isotope ($\delta\, ^{13}C/^{12}C$) values in dry vs. rainfall months, and (iii) nutrition (N, P) level of the African wild ass and domestic donkey in dry months vs. rainfall months. I expected that:

(1) During rainfall months, the spatial displacement of the African wild ass would intensify in the northern section of the plains area of the Messir Plateau when livestock arrive. The assumption is that during the rainfall months the northern section of the plains area has relatively better vegetation greenness and seasonal water and livestock would concentrate in the northern section. A study by Tesfai (2006) indicated that in the wet season,

surface water and the greatest percentage (98.5%) of green matter was found in the northern section of the plains area of Messir Plateau. African wild ass may be displaced to the southern section of the study area when large numbers of livestock, mainly cattle, arrive from the highlands and occupy the northern section of the plains area. During the dry months, African wild asses are expected to be found closer to the Asaila spring and will spatially overlap with camels, domestic donkey, goats and sheep. Camels, domestic donkey, goats and sheep are resident in the area throughout the year although their number fluctuates from time to time depending on the availability of forage.

(2) The diet of the African wild ass and domestic donkey should significantly overlap with that of cattle, and differ from species that are predominantly browsers (camel and goat) and mixed feeders (sheep).

(3) If African wild ass are displaced by cattle in the rainfall months and occupy the area of lower forage availability in the southern plains area, their Faecal Nitrogen percentage (FN %) and/or Faecal Phosphorus percentage (FP %) levels should be consistently lower than that of the domestic donkey, which will graze amongst the cattle. The assumption is that domestic donkeys are less constrained by other livestock and/or human disturbance because they are domestic. During the dry months both African wild ass and domestic donkeys mainly graze in the plains area and the FN % and FP % levels may be similar.

3.2 Materials and methods

3.2.1 Study area

Studies comparing spatial and dietary overlap between African wild ass and livestock were conducted on the Messir Plateau (15°00′ N, 40°02′ E) in an area of approximately 124 km^2 in the Danakil ecosystem, Eritrea. The study was conducted on the Messir Plateau because previous studies in the area indicated that livestock may compete with African wild ass for forage and water resources and threaten the survival of the African wild ass population (Moehlman 2002; Tesfai 2006; Moehlman et al. 2016; Tesfai et al. 2019). The topography of the study area is characterized by dissected volcanic ridges with a very rocky landscape (Moehlman 2002; Tesfai 2006). Elevation ranges from 100 to 475 m. The climate is arid with extremely hot summers (mean daily maximum temperature of 35º C) between July and September (Department of Land 1998). Mean annual rainfall averages about 160 mm with a high annual variability (coefficient of variation: 0.73 over 50 years) as recorded at the Massawa meteorological station (Ministry of Agriculture 2002). The dominant herbaceous plants (Appendix I) include the annuals *Cenchrus biflorus, Cyperus lavigatus, Tribulus terrestris and the perrennials Panicum turgidium and Eragrostis tenuifolia. Cenchrus biflorus* is dominant in the plains area except in the ravines (Tesfai 2006; Tesfai, personal observation). *Panicum turgidium*, a tufted perennial found mainly in the ravines, is an important forage species for the African wild ass (Tesfai 2006).

The people around the study area are predominantly pastoralists and herd goats, sheep, camels, domestic donkeys and a few cattle (20-30 animals) on the entire Plateau (Moehlman 2002; Tesfai 2006). However, during the rainfall months hundreds of cattle are brought from the highlands (up to 60-70 km away) attended by people from outside the area and remain in the area for at least two months (Tesfai, personal observation).

From a dietary perspective, three major functional groups of herbivores can be distinguished in the Messir Plateau: grazers, browsers and mixed feeders. African wild ass, domestic donkey and cattle are primarily grazers, feeding mainly on grasses (Rosenbom et al. 2012; Schulz and Kaiser 2013), but they can browse during dry periods (Kebede 1999; Moehlman 2002; Tesfai 2006; Schulz et al. 2013). Camels and goats are assumed to be predominantly browsers and largely consume leaves of trees, shrubs and forbs, although they can also feed on new green grass (Scoones 1995; Kassilly 2002); while sheep are intermediate/mixed feeders depending on the available forage and the environmental conditions (Bailey et al. 1996; Menard et al. 2002).

3.2.2 Study design

Reliable rainfall data are not available for the study area. Therefore, monthly rainfall data produced by U.S. Agency for International Development (USAID 2019) 'Climate Hazards Group Infrared Precipitation with Station data (CHIRPS) at 0.05 degrees (5 km) spatial scale' was obtained from an online portal (https://early warning.usgs.gov/fews) for the study period. The CHIRPS data are created by combining satellite data, interpolation of gauged data and topographic information of a given area. This rainfall data was used to distinguish between the dry vs. wet months during the study period. The wet season in the study area begins in December and lasts until March or April (Environment of Eritrea 1995; Department of Land 1998). However, the data obtained from CHIRPS online portal indicated that the rainfall of the Messir Plateau spikes in August during the last three years (Fig. 3.1). This is maybe due to climate change, but further research is required.

The field study was designed to collect faecal samples from the African wild ass and livestock (i.e. domestic donkey, cattle, camel, goat, and sheep) on Messir Plateau during dry months (Oct – Dec 2016) and rainfall months (Mar – Jun 2017). GPS data on the location of African wild ass and livestock were systematically collected at the same time with the faecal sample collection. A limited number of samples were collected in 2016 (dry months) and 2017 (wet months), because there were insufficient faecal drops from the targeted African wild ass adult females. Preliminary results suggested that the low nutrient levels of the African wild ass during the wet months were due to their spatial displacement by a high number of cattle in the study area. Hence, additional faecal samples were collected from African wild ass and domestic donkeys between January and March 2019, which, based on past years rainfall trends (Environment of Eritrea 1995; Department of Land 1998; Tesfai 2006), were supposed to be rainfall months during which cattle were expected in the area. However that did not prove to be the case in 2019. There was no rainfall and cattle from the highlands only arrived in the study area when isolated erratic rainfall was reported in the adjacent western escarpment in March.

The data from 2016 and 2017 were grouped as dry and wet months respectively because of the small sample sizes, while data from 2019 was treated monthly because there were a sufficient number of samples to compare the different months. The estimated number of cattle present in each period and NDVI (Normalized Difference Vegetation Index) data from CHIRPS online portal (https://early warning.usgs.gov/fews) were used to determine if high concentrations of cattle and vegetation greenness had any impact on the spatial distribution and the nutritional condition of the African wild ass on the Messir Plateau.

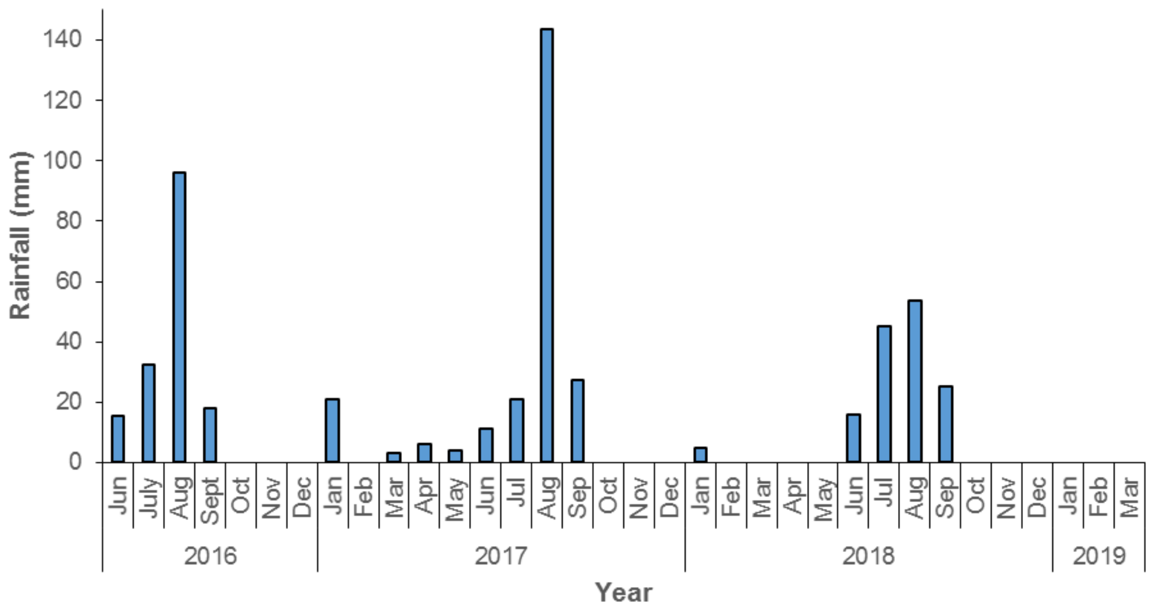


Figure 3.1 Monthly rainfall on the Messir Plateau for the study period (Oct 2016 – March 2019). Data obtained from CHIRPS online portal (https://earlywarning.usgs.gov/fews).

3.2.3 Data collection

3.2.3.1 Spatial data

The GPS coordinates of where the sampled animals were seen were collected from October to December 2016 (dry months) and March to June 2017 (rainfall months), and again from January to March 2019, which were expected to be wet months but ended up having no rainfall (Fig. 3.1). Field observations usually started by scanning the study area from the high viewpoint of the first ridge (220 meter above sea level.) using 7 x 42 binocular and/or a 25 x 75 Nikon field scope during the early morning (05:00 - 06:00 AM). This was required as a first step because the African wild ass is rare and hard to locate in the rocky undulating terrain. If no individual or group of African wild ass were spotted from the high viewpoint, I next went to the second and third ridges (201 and 150 m.a.s.l. respectively) and scanned for African wild ass. Finally, it was sometimes necessary to descend to the plains and search along the dry riverbeds and ravines. Females with their offspring and the territorial male were located at least every other day. Once individuals were located, GPS coordinates were taken where the African wild ass occurred (after they moved away) and all sampled livestock (i.e. domestic donkey, cattle, camel, goat, and sheep) that were found within 500 meters perpendicular to the walking route were recorded by triangulating their location from my position. The African wild ass were approached up to a distance of 50 meters. This was accomplished by walking slowly and by camouflaging myself behind shrubs and along the dry riverbeds and ravines so as to keep disturbance to a minimum. If other groups of livestock were spotted at a distance of greater than 500 meters, the two local scouts were properly trained to collect GPS data using a hand-held GPS device and subsequently the data were transferred to the field database. Due to the low number of African wild ass and herbivores in the study area, it was not appropriate to establish transect lines with point count stations. The locations of water sources were documented and the location of each sampled herbivore was used to determine the distance between the foraging location and the closest water point. Moderate Resolution Imaging Spectroradiometer (MODIS) 10 days NDVI images at 250 m spatial resolution produced by USAID (2019) were used to calculate NDVI value of the pixel in which the GPS location per sampled animals fell.

3.2.3.2 Diet and nutritional status

Faecal samples of African wild ass and livestock (i.e. domestic donkey, cattle, camels, goats and sheep) were collected opportunistically when the sampled animals were found associated on Messir Plateau in October to December 2016 (dry months) and March to June 2017 (rainfall months). Faecal samples were collected where the sampled animal was located. Sample collection was repeated in 2019 to substantiate the nutritional results for African wild ass and domestic donkeys obtained in the periods of 2016 and 2017. During sample collection in 2016/2017 only one sample per African wild ass female group per day was targeted. The targeted females were monitored for at least 12 hrs during the day. In 2019 (January - March), three groups of females from both African wild ass and domestic donkeys were targeted. From each targeted female African wild ass and domestic donkey group at least two faecal samples from different females per day and seven samples per month were collected. Faecal samples were air-dried over 3-5 days in the shade of a tree in the field and later stored at room temperature in sealed paper bags for subsequent analyses of stable carbon isotopes ($^{13}C/^{12}C$) and nutrient (N, P) status. To minimize any potential contamination, faecal samples were oven-dried at a minimum of 60^{o} C for at least 30 minutes at The Foot and Mouth Disease Laboratory, Onderstepoort Veterinary Institute (TAD-P, Pretoria, South Africa) prior to the carbon isotope and nutritional analyses.

Faecal stable carbon isotopes were analysed at iThemba LABS (WITS University, South Africa). Dried faecal samples were grounded into a fine material and about 0.6 mg sub-samples each were packed in a tin capsule for C isotope analysis. Ten replicates were analysed for each sample and these were repeated twice. Analyses were carried out on a Flash

HT Plus elemental analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer by a ConFloIV interface (all equipment supplied by ThermoFisher, Bremen, Germany) following the procedures used by iThemaba LABS (Dunn and Goenaga-Infante 2015). Carbon isotope values were corrected against an in-house standard (Merck Gel) and a Urea Working Standard (IVA Analysentechnik e.K., Meerbusch, Germany). Laboratory standards and blanks were run after every 24 unknown samples.

Faecal nutrient (N, P) levels of the African wild ass and domestic donkey were analysed at the Agricultural Research Council (ARC-ISCW) Laboratory (Pretoria, South Africa). Sub-samples of approximately 11.5 mg, for dry and rainfall months collected in 2016/2017 and 2019 were taken from the dried and milled faecal specimens and each were packed in a tin capsule for N and P percentage analysis. The samples for Phosphorus were analysed using the ICP-OES method and those for Nitrogen were analysed using the Carlo Erba C/N analyser technique in ARC-ISCW lab.

3.2.4. Data analysis

3.2.4.1. Spatial overlap

The spatial overlap maps were based on the location sightings of African wild ass, domestic donkeys, cattle, sheep, goats and camels on Messir Plateau during the study period. From the GPS location data for each species, spatial distribution estimates were generated by calculating density using the Kernel Density Estimation (KDE) in ArcGIS 10.5 to identify areas with high density of domestic and wild herbivores. I examined z-scores to analyze the degree of overlap/concentration using Average Nearest Neighbor (spatial statistics tools) in ArcGIS 10.5. If the average GPS location of sample species is below the average for a hypothetical random distribution, the spatial overlap/concentration being analyzed is assumed clustered. If the average GPS location of sample species is above a hypothetical random distribution, the spatial overlaps/ concentrations are assumed dispersed.

Locations of the closest permanent or seasonal temporary water sites for each sampled herbivore were estimated by measuring the distance between the foraging location and the closest water point using the ArcGIS 10.5 (ESRI 2017) distance and proximity (near) analysis tool.

I calculated the average (minimum and maximum) NDVI values across all locations for each species to correlate vegetation greenness (NDVI value) with distribution patterns of the sampled animals. I used a t-Test for independent variance to determine the difference between the mean NDVI values of the African wild ass and livestock locations.

3.2.4.2 Diet and nutritional status analysis

Individual herbivore stable carbon isotope ($\delta\,^{13}C/^{12}C$) values and Faecal N and P were compared between the dry and wet months for the 2016-2017 periods and for each month in 2019. The African wild ass faecal samples in 2016/2017 and in January, February and March 2019 were compared with samples from domestic donkeys to investigate the seasonal (2016/2017) and/or monthly (2019) Faecal N and P variations. For statistical analysis, I used one-way ANOVA to compare the stable carbon isotope ($\delta\,^{13}C/^{12}C$) values and percent of faecal nitrogen and phosphorus in diets of African wild ass and livestock (i.e. cattle, domestic donkey, camel, goat and sheep) using Fishers Least significant difference (LSD). I used a t-Test for independent variance to determine significance difference level ($P < 0.05$) of the faecal nutrient (N, P) levels between the African wild ass and domestic donkey. STATISTICA 8.0 software (Tulsa, OK: StatSoft, The USA) was used for statistical analysis.

3.3 Results

During the first fieldwork in 2016/2017, ten faecal samples for each herbivore species (Table 3.1) and a total of 236 GPS locations of the sampled herbivores (Table 3.2) were collected. In the dry months of 2016 few cattle were documented in the study area (Table 3.3). During the rainfall months of 2017 the number of cattle increased and the maximum numbers of cattle were documented in May 2017 (Table 3.3). In 2019, because of the delay in normal rainfall from January through March, the expected large numbers of cattle were not observed. The number of cattle increased in March after isolated showers in January and March (Table 3.3). In 2019 a total of 21 faecal samples each from African wild ass and domestic donkey were collected (Table 3.4) in the presence of relatively few cattle (Table 3.3) to further compare the nutrition (N, P) levels between the African wild ass and domestic donkeys. A total of 104 GPS location data of African wild ass, domestic donkey and cattle were collected in 2019 (Table 3.5) for spatial overlap analysis.

Table 3.1 African wild ass and domestic livestock faecal samples collected for dietary and nutritional analysis in the Messir Plateau, Eritrea (October 2016 – June 2017).

Sampled herbivores	**Replicate samples**		
	Dry months (n)	Rainfall months (n)	**Total**
African wild ass	4	6	10
Domestic donkey	3	7	10
Cattle	2	8	10
Camel	6	4	10
Goat	4	6	10
Sheep	4	6	10

Table 3.2 Number of GPS locations of African wild ass and domestic livestock used for spatial overlap analysis on Messir Plateau, Eritrea (October 2016 – June 2017).

Sampled species	**GPS location data**		
	Dry months (n)	Rainfall months (n)	**Total**
African wild ass	36	37	73
Domestic donkey	12	11	23
Cattle	4	22	26
Camel	17	28	45
Goat	20	24	44
Sheep	14	11	25
Total	**103**	**133**	**236**

Table 3.3 Estimated number of cattle observed on Messir Plateau, Eritrea during the field study (2016/2017 and 2019).

Year	2016			2017				2019		
Month	Oct	Nov	Dec	Mar	Apr	May	Jun	Jan	Feb	Mar
Cattle number	17	20-25	37	35-40	40-46	150	145	20-22	25-33	48-55

Table 3.4 Additional African wild ass and domestic donkey faecal samples collected in January, February and March 2019 to clarify the nutritional results (N, P) obtained in the period of 2016/2017.

Sampled herbivores	**Replicate samples**			
	January (n)	February (n)	March (n)	**Total**
African wild ass	7	7	7	21
Domestic donkey	7	7	7	21

Table 3.5 Number of GPS locations of African wild ass, domestic donkey and cattle collected in January, February and March 2019 and used for spatial overlap analysis in Messir Plateau, Eritrea.

Sampled species	**GPS location data**			
	January (n)	February (n)	March (n)	**Total**
African wild ass	11	14	21	46
Domestic donkey	13	9	19	41
Cattle	5	4	8	17
Total	**29**	**27**	**48**	**104**

3.3.1 Spatial overlap of African wild ass and livestock

During the dry months of 2016, African wild ass were concentrated towards the northern section of the Messir Plateau, approximately 9 km from Asaila permanent water (Fig. 3.2a and 3.3). Camels, domestic donkey, goats, and sheep were observed in the study area throughout the year and overlapped to some extent with African wild ass during the dry months (z-score=12.133, $p<0.001$; Fig. 3.4a). During this period, the domestic donkey and the African wild ass were located in the northern section that had a better vegetation greenness compared to the southern section where the other livestock were located (t=2.35, p=0.0206; Fig. 3.4a). During the rainfall months in 2017 there were at least six seasonal temporary water sources located in the plains area (Fig. 3.2b). During this period livestock, particularly cattle, were concentrated in the northern section of the plains area of the Messir Plateau (z-score=12.309, p<0.001), while African wild ass were dispersed throughout the study area and degree of the spatial overlap with livestock was low (z-score=2.585, p=0.009; Fig. 3.3 and 3.4b). The NDVI values where the domestic herbivores were located were similar but the African wild ass were found in relatively lower greenness areas although they were not significantly different (t=1.49, p=0.13788, Fig. 3.4b). Female African wild ass with young foals were found about 3 km from the seasonal temporary water sources but travelled up to 7 km when livestock were concentrated in the 'plains' area (N= 60, Chapter 4: Table 4.4).

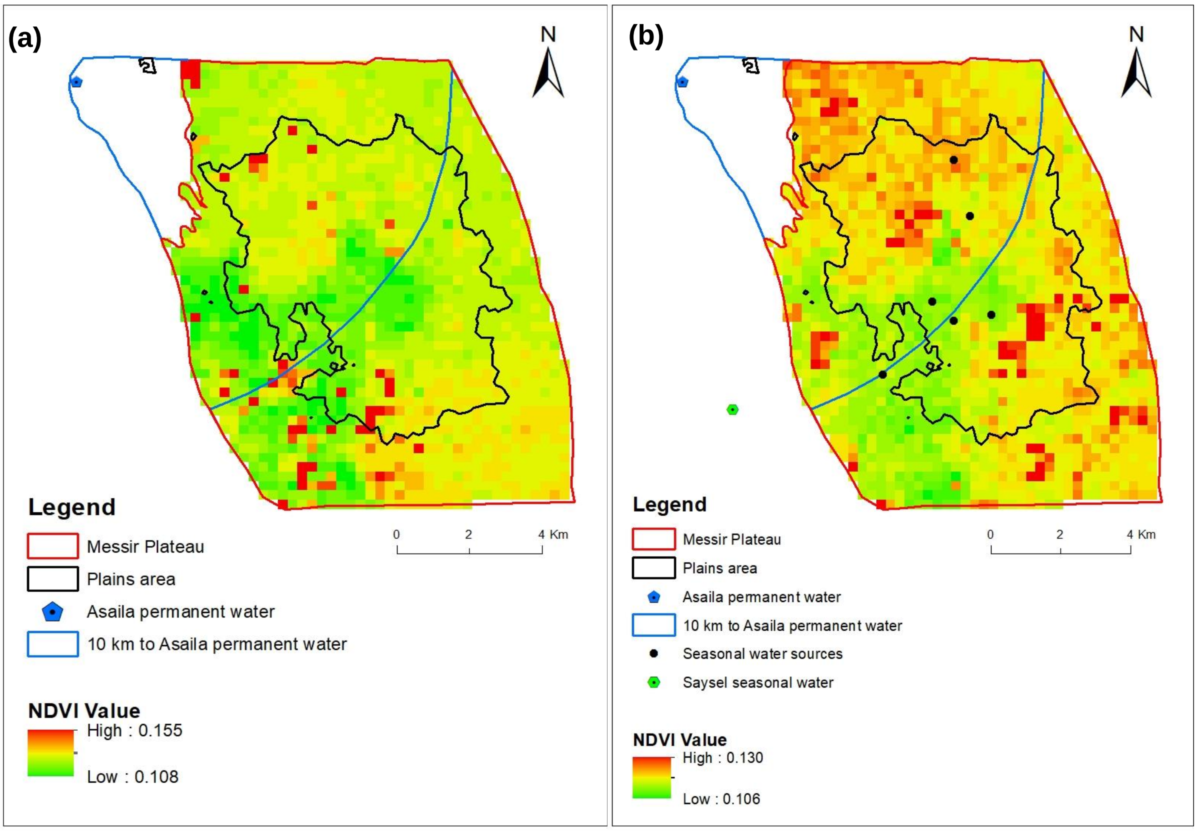


Figure 3.2 Map of the study area (Messir Plateau) showing the vegetation greenness (NDVI), location of the permanent water source Asaila, and location of at least six seasonal temporary water sources after rainfall events. (a) during dry months (Dec 2016), and (b) rainfall months (Mar 2017).

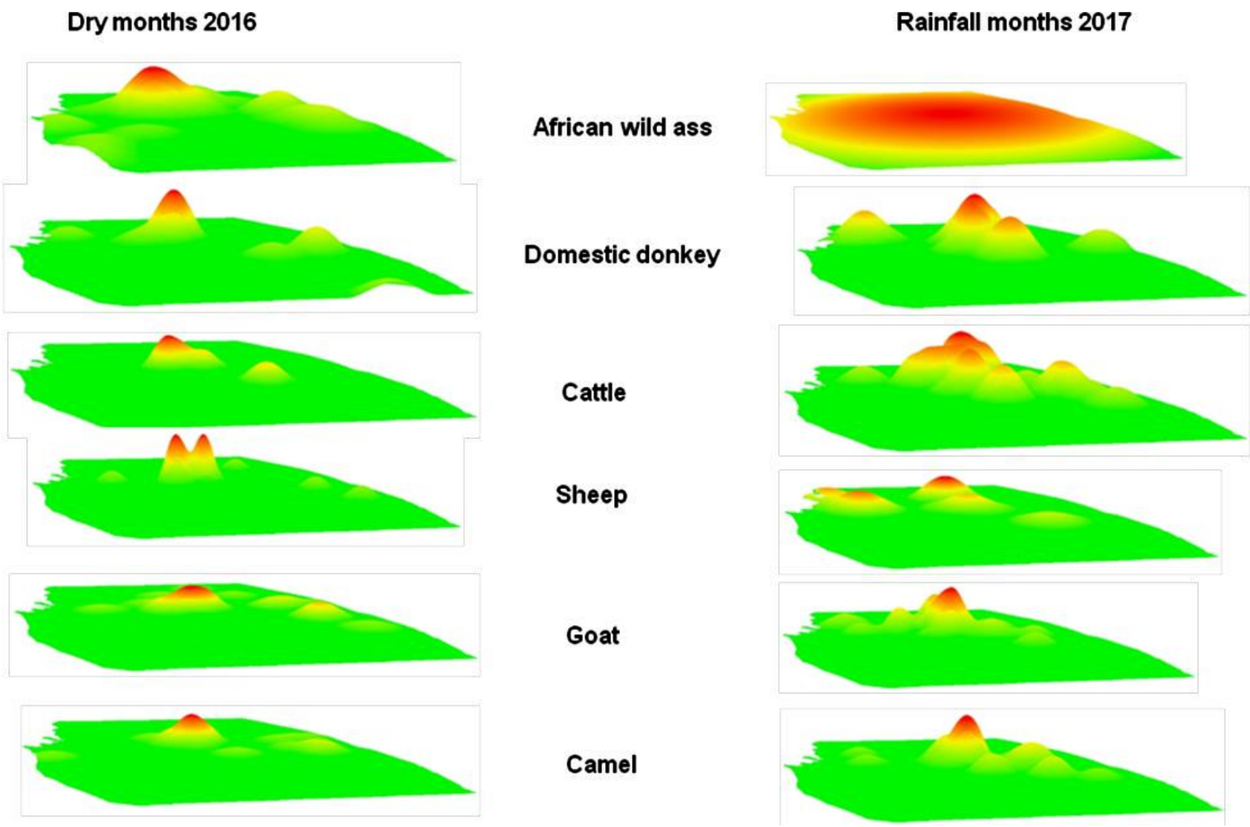


Figure 3.3 Herbivore species distribution on the Messir Plateau (Eritrea) during the dry months of 2016 vs. rainfall months of 2017. The height of the curves (red colour) indicates the highest concentration of the sampled species.

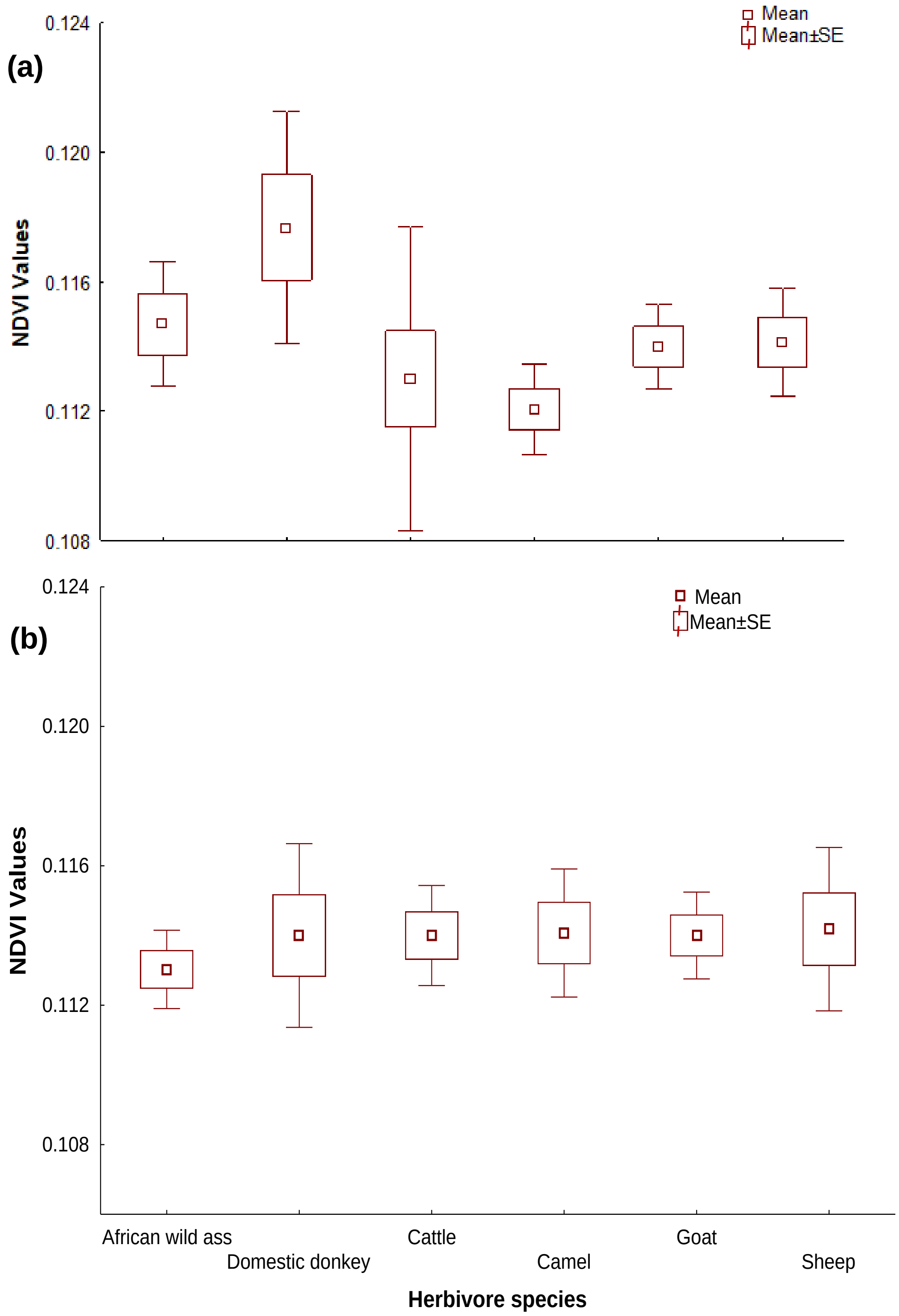


Figure 3.4 Normalized Difference Vegetation Index (NDVI) values for African wild ass and livestock locations on Messir Plateau (Eritrea). (a) During dry months of 2016, and (b) rainfall months of 2017.

In January 2019, the African wild ass were located in higher NDVI areas of the northern section areas compared to the domestic donkey and cattle (t=2.50, p= 0.0187; Fig. 3.5a and 3.7a). African wild ass were observed within 2-3 km of the Bakado seasonal water in the northern section (Number of observations= 25, Fig. 3.5a and 3.6) and were not ‘displaced’ by the few cattle present (z-score=6.088, p<0.001; Table 3.3). Bakado seasonal water was created for a few days after isolated showers in early January. In February 2019, African wild ass and the few cattle (Table 3.3) were more concentrated in the northern section of the plains area in relatively higher greenness (t=2.52, p=0.0186, Fig. 3.5b and 3.7b), while the domestic donkeys were more dispersed (z-score=0.845, p=0.397890). In February, the distribution pattern of the African wild ass and cattle appear to be random (z-score=0.768, p=0.442160). In March 2019, the distribution of these three herbivores shifted southwestof the Messir Plateau (z-score=8.294, p<0.001) when isolated erratic rainfall was reported in the adjacent western escarpment and created Sayel temporary seasonal water for few days (Fig. 3.6 and 4.1). African wild ass were observed on the top of the Egirale Hill (475 m. a. s .l), while cattle and domestic donkey were grazing on the plains (220 m.a.s.l) in an area of relatively better greenness (t=-2.29, p=0.0269, Fig. 3.6 and 3.7c). Egirale Hill is approximately 4 km from Saysel water point and about 12 km from Asaila spring (Fig. 3.5c and 4.1). Camera traps and field observation data indicated that African wild ass travelled to the plains area and towards Saysel temporary water late in the afternoon or at night.

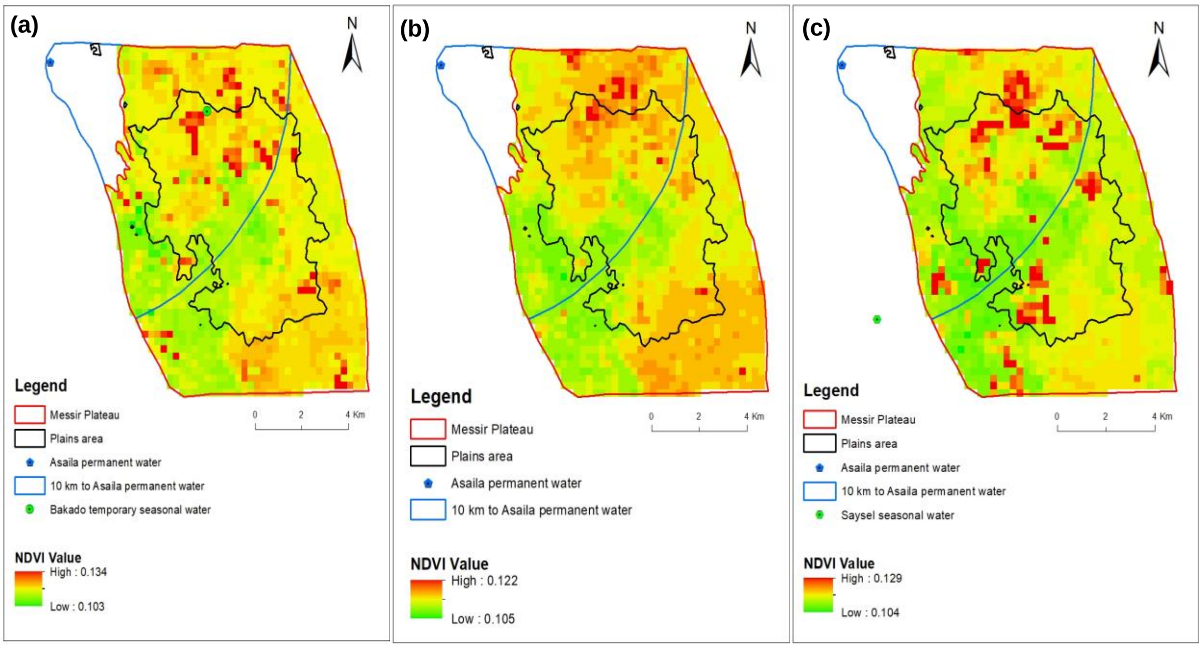


Figure 3.5 Map of the study area (Messir Plateau) showing the vegetation greenness (NDVI), location of the permanent water source Asaila, and locations of seasonal temporary water sources after rainfall events. (a) January 2019 when Bakado seasonal water occurred on the northern section of the 'plains' area, (b) February 2019, and (c) March 2019 when isolated erratic rainfall in the adjacent western escarpment created temporary seasonal water at Saysel.

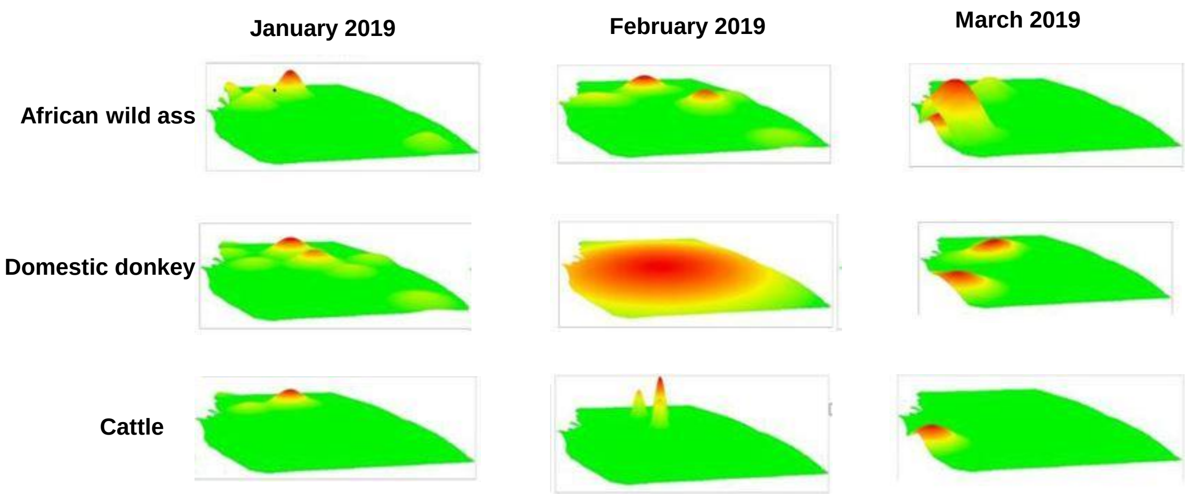


Figure 3.6 African wild ass, domestic donkey and cattle spatial distribution on the Messir Plateau in January, February and March 2019. The height of the curves (red colour) indicates the highest concentration of the sampled species.

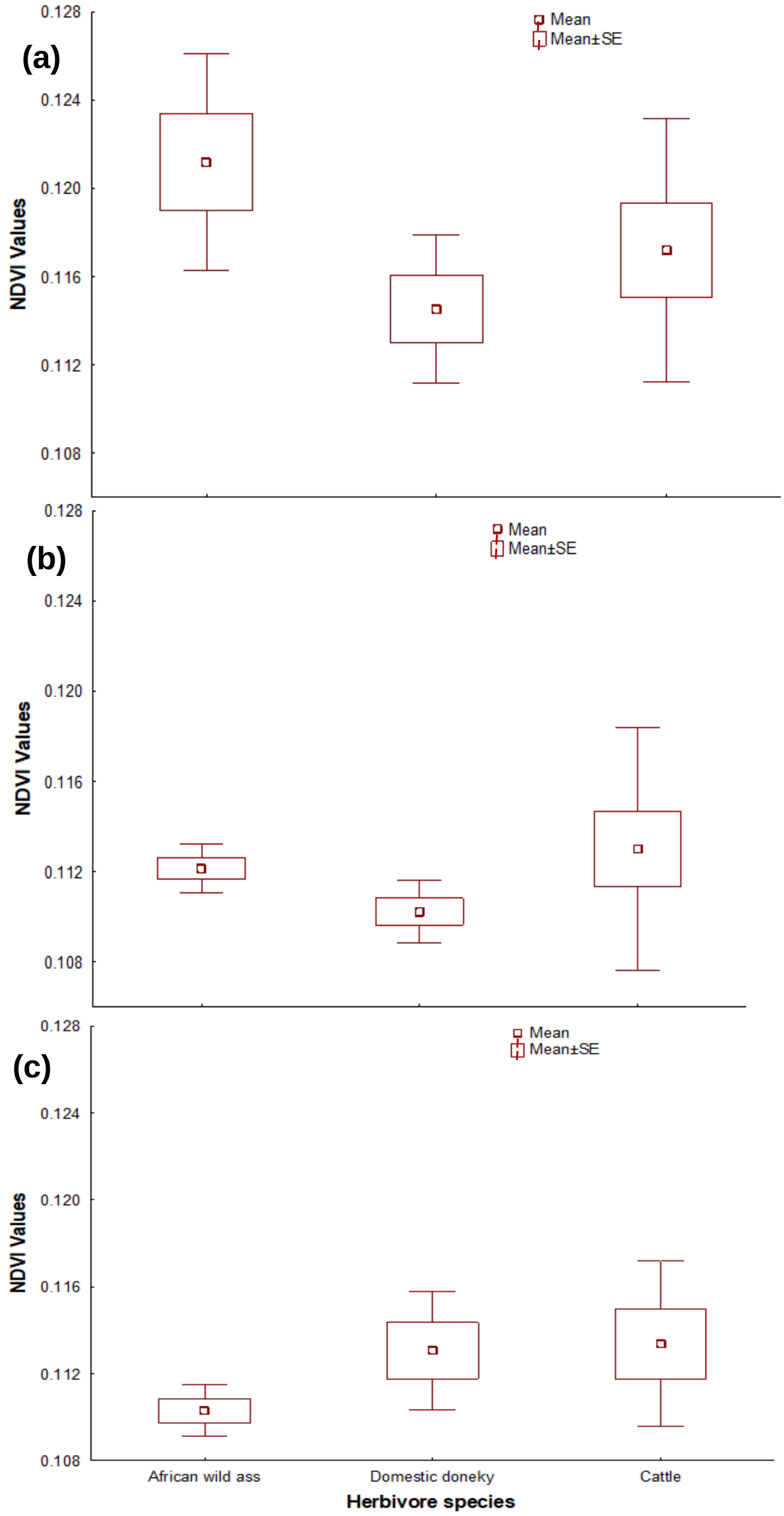


Figure 3.7 Normalized Difference Vegetation Index (NDVI) values where African wild ass, domestic donkey and cattle were located on Messir Plateau (Eritrea) during the second season of field data collection (January – March 2019). (a) January, (b) February, and (3) March 2019.

3.3.2 Diet overlaps between African wild ass and livestock

The African wild ass δ faecal $^{13}C/^{12}C$ values overlapped significantly with the domestic donkey and cattle diets in both dry and wet months ($P < 0.0000$; Fig. 3.8). All three species had relatively high δ $^{13}C/^{12}C$ values indicating a grazing diet (Fig. 3.8a and 3.8b). In the dry months, goats and sheep had intermediate δ $^{13}C/^{12}C$ values reflecting mixed feeding, while camels had lower δ $^{13}C/^{12}C$ values indicating a browse diet (Fig. 3.8a). Camels, goats and sheep had relatively low δ $^{13}C/^{12}C$ values that are characteristic of a browsing diet in the rainfall months (Fig. 3.8b).

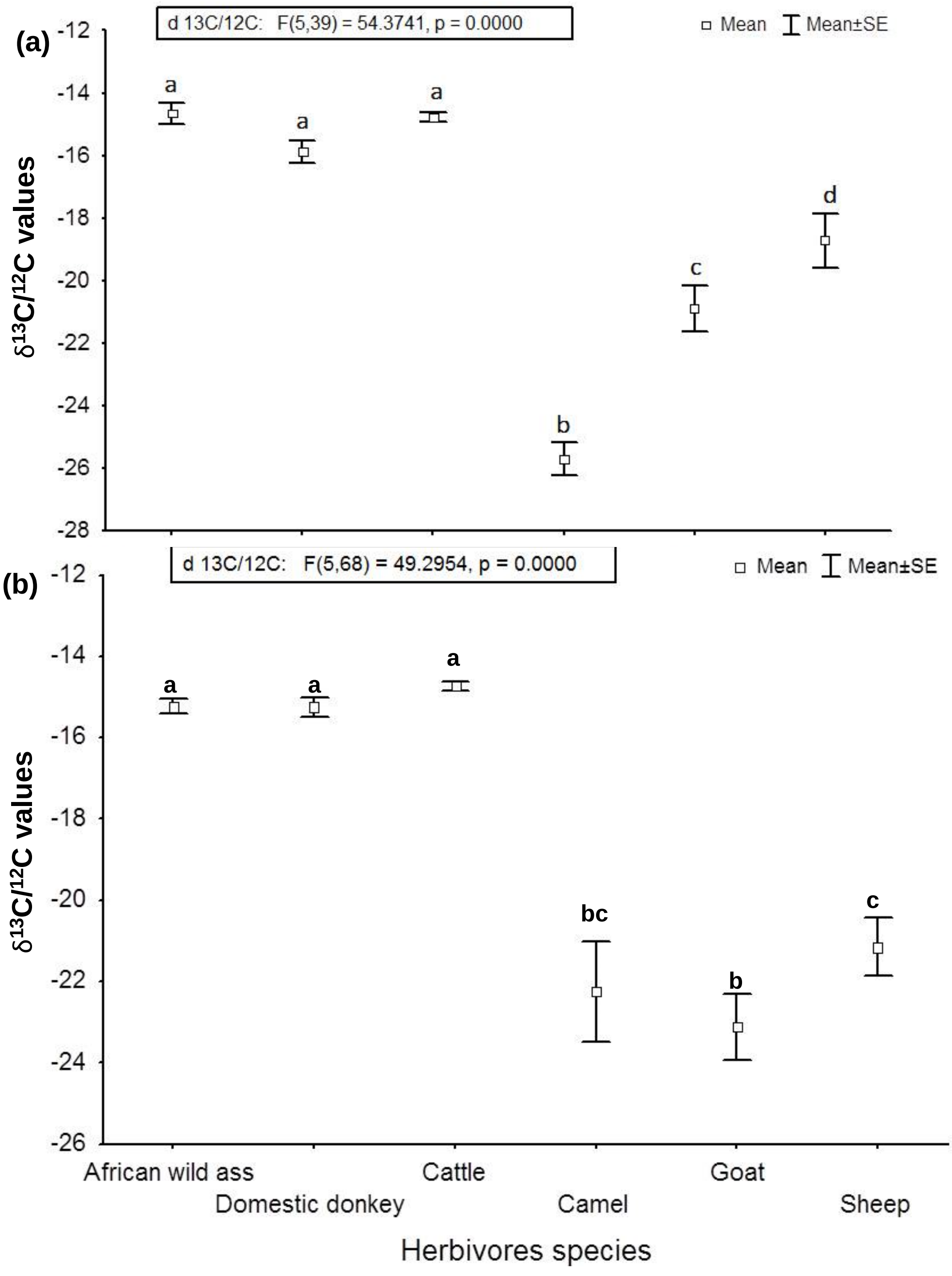


Figure 3.8 δ $^{13}C/^{12}C$ values for herbivore species on the Messir Plateau, Eritrea (a) during dry months, and (b) rainfall months. Means with the same letter indicate there is significant overlap in diet among the sampled herbivores species.

3.3.3 Comparative nutrition of African wild ass and domestic donkeys

In the wet months, the mean faecal nitrogen % of the domestic donkeys diet were significantly higher than that of the African wild ass (t=2.19, p= 0.0254, Fig. 3.9a). The faecal nitrogen % (FN %) of African wild ass did not improve significantly in the rainfall months of 2016/2017 when compared to that of dry months (t=0.13, p=0.8931, Fig. 3.9a). The mean faecal phosphorus % (FN %) of the domestic donkey was higher than that of the African wild ass although there were no significant differences in both dry and wet months (t=-1.46, p=0.1611, Fig. 3.9b). The FP % of the African wild ass in rainfall months improved, but was not significantly different from that of the dry months (t=1.36, p=0.2119; Fig. 3.9b).

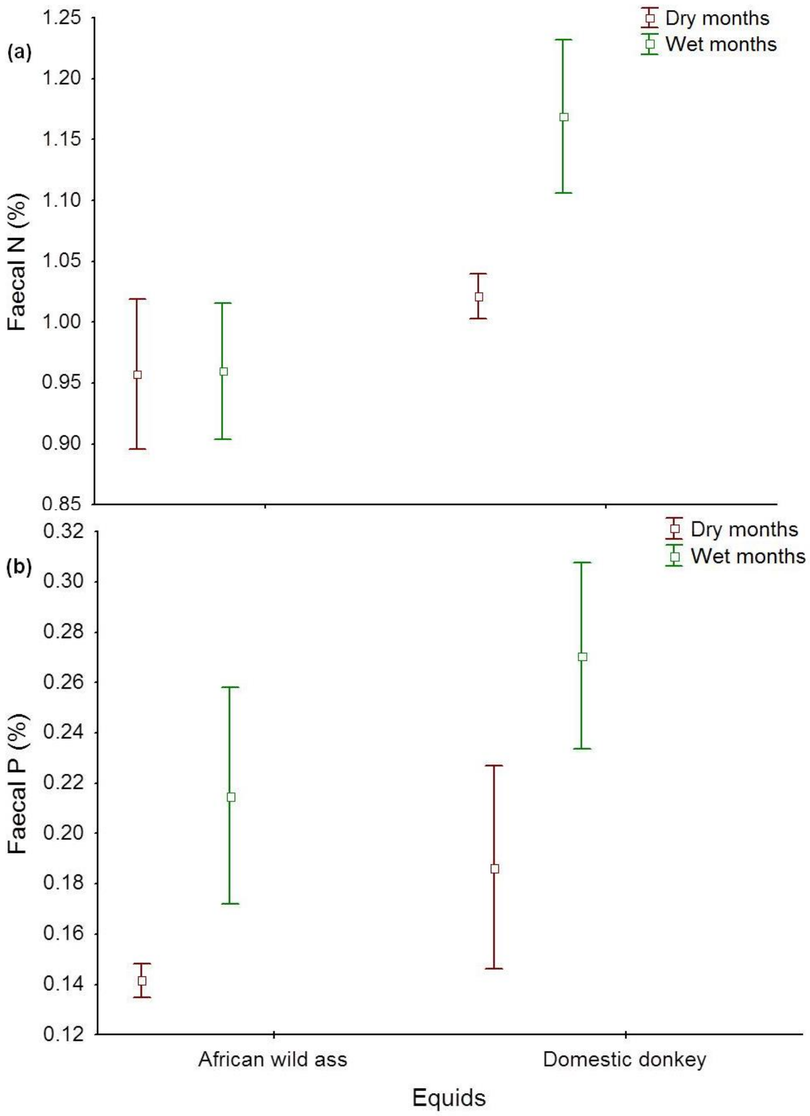


Figure 3. 9 The nutrition level of the two equids (i.e. African wild ass and domestic donkey) on Messir Plateau in dry months of 2016 vs. wet months 2017 (a) mean faecal nitrogen %, and (b) mean faecal phosphorus %.

In 2019 the mean faecal nitrogen % (FN %) of the African wild ass showed no significant difference from that of the domestic donkey in January (t= 0.24, p=0.8133, Fig. 3.10a). The FN % of the African wild ass in February was lower than that of the domestic donkey although not significantly different (t=-1.36, p=0.1987, Fig. 3.10a). But the mean FN % of the African wild ass in March 2019 was lower than that of domestic donkey (t=-2.11, p=0.0283, Fig. 3.10a) when there were about 55 cattle present on Messir Plateau (Table 3.3) and the African wild ass were spatially displaced to the southwest of the Messir Plateau and concentrated around the Hills. In January, the mean faecal phosphorus % (FP %) of the African wild ass showed no significant difference from that of the domestic donkey (t= -0.25, p=0.8039, Fig. 3.10b). But in February, the mean FP % of the African wild ass was significantly lower than that of the domestic donkey (t=-2.84, p=0.0149, Fig. 3.10b) and marginally in March (t=-2.15, p= 0.0528, Fig. 3.10b) when the cattle number was increased gradually (Table 3.3).

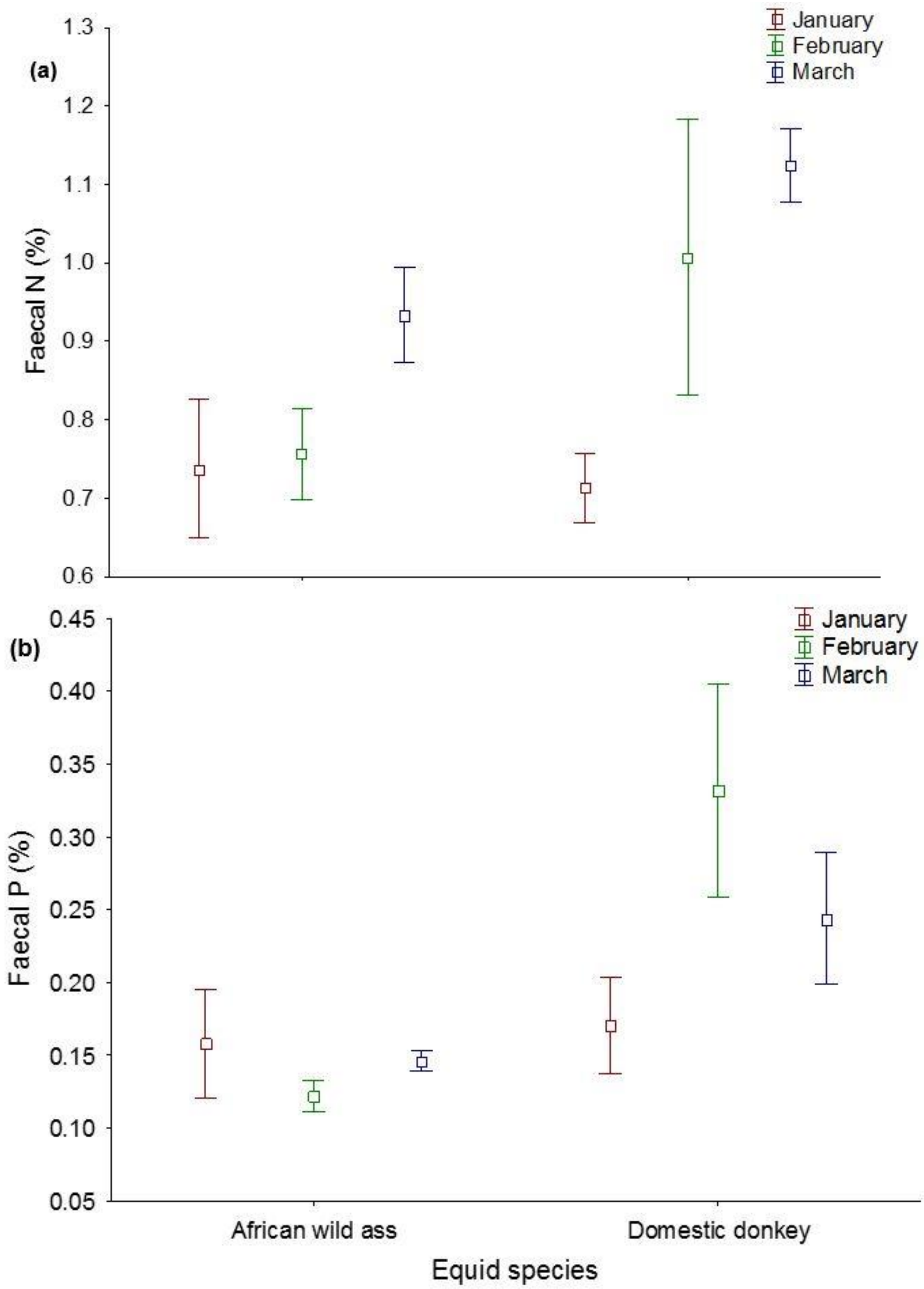


Figure 3.10 The nutrient levels of the African wild ass and domestic donkey on the Messir Plateau (Eritrea) in January, February and March 2019, (a) mean faecal nitrogen %, and (b) mean faecal phosphorus %.

3.4 Discussion

The presence of livestock, particularly cattle, appears a possible factor in the distribution pattern of the African wild ass on the Messir Plateau. During the dry months (Oct – Dec 2016), African wild ass were concentrated in the northern section when few cattle (17-37) were observed on the Messir Plateau (Fig. 3.3). This site is closer to the Asaila spring and this may minimize African wild ass travel time and distance to water. When forage and seasonal water sources were available during the rainfall months of 2017, livestock, particularly cattle, were highly concentrated in the northern section of the plains area, while the African wild ass were dispersed throughout the study area (Fig. 3.3). The northern portion of the plains area, based on NDVI, has a higher greenness index (Fig. 3.2).

In January 2019 when the study area experienced a delay in normal rainfall except for isolated showers, African wild ass were located within 2-3 km of Bakado seasonal water in the northern section (Fig. 3.5a and Fig. 3.6). They were not displaced by the few number of cattle (20-22) coming from the neighbouring villages. These local cattle were not attended by people who may add to the disturbance level (Tesfai, personal observation). The local community around Messir Plateau own few cattle (20-30), because the forage in the area is insufficient to support them throughout the year (Tesfai 2006). In February, the African wild ass and the few cattle (25-33) were still observed in the northern section of the plains area, while the domestic donkeys were more dispersed (Fig. 3.5b and Fig. 3.6). It was expected that the cattle coming from the highlands would displace the African wild ass from the northern section of the plains areas because it was supposed to be the 'wet period'. But because the study area was dry in January and February, the African wild ass distribution pattern was similar to that of the dry season. In March 2019, the domestic herbivores and African wild ass were concentrated in the southwest when isolated erratic rainfall was reported in the area (Fig. 3.5c and Fig. 3.6). During this period for nearly a week, most of the African wild ass were frequently observed on or near the Egirale Hill (475 m a.s.l) and recorded by camera traps as travelling to Saysel at night. The cattle and domestic donkeys and people were concentrated around the Saysel temporary water during the day (Tesfai, personal observation), suggesting that indeed people and cattle affected the African wild ass normal drinking behaviour (see chapter 4).

The results from faecal carbon isotope ($\delta^{13}C/^{12}C$) values suggest that the African wild ass diet requirements show similarity with that of cattle and domestic donkeys, but differed from that of the browsers (camel and goat) and mixed feeders (sheep). Cattle, and to a lesser extent sheep, potentially overlap in range use with wild equids because of their grazing feeding strategies (Menard et al. 2002). The high carbon isotope ($\delta^{13}C/^{12}C$) values of the African wild ass, domestic donkey and cattle indicate that their diet both in dry and rainfall months is largely grass. In Kenya Masai-lands (Casebeer and Koss 1970), cattle and Plains zebra (*Equus burchelli*) also had the greatest similarity in diets. However, during the dry periods, African wild ass in the Danakil desert have been observed to forage on browse (Kebede 1999; Moehlman 2002; Tesfai 2006). Research on equid dentition, including mesowear signatures, individual molar cusp shape, and relief scores indicated that African wild ass can be mixed feeders (Schulz and Kaiser 2013). Grevy's zebra inhabited in the African savannas may also have a mixed feeding strategy depending on forage resources available (Codron et al. 2007; Schulz et al. 2013).

Percentage N (reflecting crude protein content) of grazers is generally lower than that of browsers (Codron et al. 2006). The faecal nitrogen level is rapidly depleted when competition for high-quality forage is increased (Blanchard et al. 2003). The faecal sample nutritional level (N, P) analyses of the African wild ass of this study showed no significant difference between the dry and wet months of 2016/2017. The low faecal nitrogen level of the African wild ass in wet months is probably due to their displacement by high number of cattle in the study area during the rainfall months. In rainfall months, the faecal phosphorus and nitrogen percentage in African wild ass faecal samples were higher than in dry months (Fig. 3.9b). The higher phosphorus content in the wet season may also be due to their location during the data collection. During the rainfall months of 2017, African wild ass were frequently observed in the rocky areas when a high number of cattle were concentrated in the plain area (Tesfai, personal observation). A study by Tesfai (2006) indicated that soils of the rocky areas in the study area have a higher Phosphorus level (3.5 *ppm*) than the plain areas. Vegetation take up the phosphate compounds from the soil and the phosphate are then ingested when herbivores eat the plant (Filippelli 2011). To substantiate the preliminary results of the nutritional levels of the African wild ass and domestic donkeys, additional samples were collected in 2019 (January – March). The results indicated that both the mean faecal nitrogen and phosphorus percentage found in African wild ass samples improved significantly with a lower number of cattle in January and February 2019. But the mean faecal nitrogen percentage declined in March 2019 when the number of cattle increased. In the rainfall months, I expected the nutritional levels of the African wild ass to be better than in dry months because new growth forage resources are more available in the rainfall months. However, the nutritional level (N, P) of African wild ass did not improve significantly in the rainfall months compared to that of dry months. Generally, the percentage nitrogen of all plants increases from the dry to the wet season (Codron et al. 2006). Equally, the nutrients levels (N, P) in faecal samples of herbivores vary seasonally and increase in the wet period (Casebeer and Koss 1970; Macandza et al. 2004). For example, the nutritional status of Plains zebra in the Kenya Masai-lands improved during the wet season (Casebeer and Koss 1970). The mean faecal nitrogen content obtained from Plains zebra faecal samples were also consistent with higher nutritional levels in the wet months compared to the dry months (Codron et al. 2006; Miranda et al. 2014). My results do not show that trend and suggest that the African wild ass may be spatially displaced by livestock and were not able to access the higher quality forage, especially near water sources.

The efficient ruminant-digestive system in cattle may allow them to extract more digestible dry matter than equids and thus make them more competitive in the wet season (Menard et al. 2002). The equid non-ruminant stomach allows a faster passage rate in the digestive system (Janis 1976; Demment and Soest 1985; Merritt and Julliand 2013) and equids can compensate by eating relatively larger amounts of lower quality forage continuously to meet their protein requirements (Owaga 1975; Janis 1976; Bauer et al. 1994; Van Soest 1996; Schoencker et al. 2016). But, if the African wild ass are not able to access adequate forage, especially near water sources because of cattle presence, they will not be able to compensate by increasing their forage intake. Domestic donkeys are not disturbed or displaced by livestock and people and can potentially thus access the better forage available in the northern portion of the Messir Plateau.

The slow population growth of the African wild ass on the Messir Plateau might be the result of overlap and/or competition with grazers (such as cattle and domestic donkeys) for forage (Moehlman 2002; Tesfai 2006; Moehlman et al. 2016; Tesfai et al. 2019). This, however, requires further studies to assess how the nutritional wellbeing of the African wild ass is affected by livestock and also correlated with long term reproductive performance.

3.5 Management Implications

This study results suggest that the African wild ass significantly overlaps in space and diet with domestic donkeys and cattle. High concentrations of livestock, particularly cattle, were present during the rainfall months on the Messir Plateau. When cattle were present the African wild ass were spatially displaced and their nutrient levels declined. The lower nutritional status of the African wild ass may potentially have a negative impact on their reproductive biology, natality and foal survival. This study provides evidence of how the presence of domestic herbivores, particularly cattle during rainfall months may negatively affect the nutritional status and threaten the survival of this critically endangered species in a very arid ecosystem with limited resources.

References

Andrews F.W. 1956. The flowering Plants of the Anglo-Egyptian Sudan Volume (I, II, III).

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. and Sims, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* **49**: 386–400.

Bauer, I.E., McMorrow, J. and Yalden, D.W., 1994. The historic ranges of three equid species in north-east Africa: a quantitative comparison of environmental tolerances. *Journal of Biogeography* **21**:169–182.

Blanchard, P., Festa-Bianchet, M., Gaillard, J.M. and Jorgenson, J.T. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in Bighorn sheep. *Journal of Wildlife Management* **67**: 477–484.

Casebeer, R.L. and Koss, G.G. 1970. Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *African Journal of Ecology* **8**: 25–36.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R. and Fourie, N. 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology* **273**: 21–29.

Codron, D., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D. and Codron J. 2006. Inter- and intrahabitat dietary variability of Chacma Boons (Papio ursinus) in South Africa Savanna based on fecal $\delta^{13}C$ and $\delta^{15}N$ and % N. *American Journal of Physical Anthropology* **129**: 204–214.

De Boer, W.D. and Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82**: 264–274.

Demment, M.W. and Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist* **125**: 641–672.

Department of Land 1998. Agro-Ecological Classification Map of Eritrea. Ministry of Land Water and Environment, Asmara, Eritrea.

Dove, H. and Mayes, R.W. 1996. Plant wax components: a new approach to estimating intake and diet composition in herbivores. *The Journal of Nutrition* **126**: 13–26.

Dunn, P.J., Malinovsky, D. and Goenaga-Infante, H., 2015. Calibration strategies for the determination of stable carbon absolute isotope ratios in a glycine candidate reference material by elemental analyser-isotope ratio mass spectrometry. *Analytical and Bioanalytical Chemistry* **407**: 3169–3180.

Environment of Eritrea. 1995. The National Environmental Management Plan for Eritrea (NEMP-E). Asmara, Eritrea.

ESRI. 2017. ArcGIS Desktop. Ver. 10.5. Environmental System Research Institute, Inc. Redlands, California.

Filippelli, G.M. 2011. Phosphate rock formation and marine phosphorus geochemistry: the deep time perspective. *Chemosphere* **84**: 759–766.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**: 367–393.

Gedir, J.V., Cain, J.W., Harris, G. and Turnbull, T.T. 2015. Effects of climate change on long term population growth of pronghorn in an arid environment. *Ecosphere* **6**: 1–20.

Illius, A.W. and Gordon, I.J. 1987. The allomentry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**: 989–999.

Janis, C., 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* **30**: 757–774.

Kassilly, F.N. 2002. Forage quality and camel feeding patterns in Central Baringo, Kenya. *Livestock Production Science* **78**: 175–182.

Kebede, F. 1999. Ecology and conservation of the African Wild Ass (*Equus africanus*) in the Denakil, Ethiopia. MSc Thesis, University of Kent/DICE, Canterbury, UK.

Kidane, N.F., Stuth, J.W. and Tolleson, D.R. 2008. Predicting diet quality of donkeys via fecal-NIRS calibration. *Rangeland Ecology and Management* **61**: 232–259.

Leslie, D.M., Bowyer, R.T. and Jenks, J.A. 2008. Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. *The Journal of Wildlife Management* **72**: 1420–1433.

Macandza, V.A., Owen-Smith, N. and Cross, P.C. 2004. Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research* **34**: 113–121.

Mayes, R.W. and Dove, H. 2000. Measurement of dietary nutrient intake in free-ranging mammalian herbivores. *Nutrition Research Reviews* **13**: 107–138.

Menard, C., Duncan, P., Fleurance. G., Georges, J.Y. and Lila, M. 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology* **39**: 120–133.

Merritt, A.M. and Julliand, V. 2013. Gastrointestinal physiology. *Equine Applied and Clinical Nutrition E-Book: Health, Welfare and Performance,* p.1.

Ministry of Agriculture. 2002. The National Action Programme to Combat Desertification and Mitigate the Effect of Drought in Eritrea (NAP). January 2002. Asmara. 197pp.

Miranda, M., Dalerum, F. and Parrini, F. 2014. Interaction patterns within a multi-herbivore assemblage derived from stable isotopes. *Ecological Complexity* **20**: 51–60.

Moehlman, P.D. 2002. Status and Action Plan for the African wild ass (*Equus africanus*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp 2-9.

Moehlman, P.D., King, S.R. and Kebede, F. 2016. Status and Conservation of Threatened Equids. Wild Equids: Ecology, Management, and Conservation. (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 167-186.

O'Leary, H. 1988. Carbon isotopes in photosynthesis. *BioScience* **38**: 328–336.

Oudtshoorn, F. 1999. Guide to grasses of South Africa. Briza Publications, Pretoria, South Africa. First edition 1999. pp.288

Owaga, M.L., 1975. The feeding ecology of wildebeest and zebra in Athi-Kaputei plains. *African Journal of Ecology* **13**: 375–383.

Prins H.H.T. 2000. Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G., Dolan T.T. (eds) Wildlife Conservation by Sustainable Use. Conservation Biology Series, vol 12. Springer, Dordrecht. pp. 51-80.

Rosenbom, S., Costa, V., Steck, B., Moehlman, P. and Beja-Pereira, A. 2012. Cross-species genetic markers: a useful tool to study the world's most threatened wild equid - *Equus africanus*. *European journal of wildlife research* **58**: 609–613.

Sæther, B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecological Evaluation* **12**: 143–149.

Schneidera, S., Auerswalda, K., Bellof, G. and Schnydera, H. 2015. 13C discrimination between diet, faeces, milk and milk components. *Isotopes in Environmental and Health Studies* **51**: 33–45.

Schoenecker, K.A., King, S.R., Nordquist, M.K., Nandintsetseg, D. and Cao, Q., 2016. Habitat and Diet of Equids. Wild Equids: Ecology, Management, and Conservation.

(ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 41-57.

Schulz, E., Calandra, I., and Kaiser, T. 2013. Feeding ecology and chewing mechanics in hoofed mammals. 3D tribology of enamel wear. *Wea*r **300**: 169–179.

Schulz, E. and Kaiser, T.M., 2013. Historical distribution, habitat requirements and feeding ecology of the genus Equus (Perissodactyla). *Mammal Review* **43**: 111–123.

Scoones, I. 1995. Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environment* **29**: 221–237.

Smith, B.N. and Epstein, S. 1971. Two categories of 13C/12C ratios for higher plants. *Plants Physiology* **47**: 380–384.

Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E., Cerling, T., Dearing, D. and Ehleringer, J. 2003. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Can. J. Zool* **81**: 871–876.

Tesfai, R.T. 2006. Conservation of African wild ass (*Equus africanus*) in Messir plateau (Asa-ila), Eritrea: the role of forage availability and diurnal activity pattern during the rainy and beginning of the dry season. MSc Thesis, University of Kent/DICE, Canterbury, UK. 85pp.

Tesfai, R.T., Owen-Smith, N., Parrini, F. and Moehlman, P.D. 2019. Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy* **100**: 185–191.

U.S. Agency for International Development (USAID). MODIS NDVI and rainfall data accessed on 06 October 2019. (https://earlywarning.usgs.gov/fews/.

Van Soest, P.J. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology* **15**: 455–479.

Williams, S.D. 1998. Grevy's zebra: ecology in a heterogeneous environment. Doctoral dissertation, University College London (University of London), UK. 199pp.

Chapter 4. African wild ass (*Equus africanus*) drinking behaviour on the Messir Plateau, Danakil desert, Eritrea

Abstract

Access to surface water is fundamental to the survival of all wild equids. The critically endangered African wild ass (*Equus africanus*) occurs on the Messir Plateau, Danakil ecosystem (Eritrea). The area is remote, extremely rocky and the climate is very hot. Asaila spring is a permanent water source to the northwest of the Messir plateau. People, livestock and the African wild ass share this water source. Access and travel distance to water is critical for lactating females, since access to both water and sufficient forage may affect their nutrition and the survival of young foals. Direct observation and camera traps were used to collect data on drinking behaviour (frequency and time of visit) and travel distance of females with young foals vs. non-reproductive females and/or males in dry vs. rainfall months for permanent vs. temporary water points. Drinking frequency per individual per water source (permanent vs. seasonal) was obtained by calculating the number of water visits of an individual per successive days of observation. The travel distance to water was estimated by measuring the distance between the morning foraging location and the water point. The number of visits per 24 hour period (frequency) to water sources differed significantly between the eight sex and reproduction categories ($p<0.0001$), but did not differ between permanent and seasonal temporary water sources except for females with foal aged ≤ 3 months. Females with young foals daily visited the Asaila spring in dry months, while non-reproductive females and bachelor males were recorded once per five to ten successive days. When seasonal temporarily water was available on the lower elevation plains area, females with young foals (≤ 3 months) travelled to water twice as often as other adult females ($p<0.0001$). The travel distance from the forage area to the seasonal water source during wet months was significantly less than travel to the Asaila spring during the dry months ($p \leq$ 0.012). Availability of water close to forage is critical for the survival of wild equids in arid environments, particularly for lactating females and their foals. Travelling long distances to access adequate water and forage is energetically costly and may result in lower foal survival. Therefore, any conservation strategies for this rare and endangered species in the Danakil desert should consider the critical issue of water sources.

Keywords: African wild ass, Danakil ecosystem, drinking frequency, lactating females, seasonal travel distance to access water.

4.1 Introduction

Access to surface water is critical for most herbivores in arid environments (Pratt and Gwynne 1977; de Boer and Prins 1990; Sirot et al. 2016). Animals that evolved in arid environments have morphological and physiological adaptations for efficient use of water (Lillywhite and Navas 2006). However, as the physiological need for water increases and the availability of water decreases (Becker and Ginsberg 1990) there is selection for behavioural adaptations that can conserve water and reduce competition for a limited resource. Limited availability of water resources in arid areas is a potential factor for competition between domestic and wild herbivores (Voeten and Prins 1999; Prins 2000; Young et al. 2005). The need for water strongly influences the distribution and behaviour of equids (Becker and Ginsberg 1990; Schoenecker et al. 2016). Equids may reduce their movement distances (Western 1975; Pratt and Gwynne 1977) and remain closer to water (Becker and Ginsberg 1990), or alternatively may need to move long distances to find forage.

Both arid and mesic adapted equids need regular access to water. Grevy's zebra (*Equus grevyi*) live in arid environments, such as the Samburu Game Reserve, in northern

Kenya. During peak lactation (birth to 3 months) female Grevy's zebra were usually observed within 2 km of water, while non-lactating females were seen up to 15 km from water (Becker and Ginsberg 1990). Access and distance to water is particularly critical for these lactating females and the survival of their foals (Sundaresan et al. 2008). Williams (1998) documented that Grevy's zebra had lower foal survival when females with young foals made longer (more than 10 km) or more frequent movements in order to access both forage and water. Access to water and forage is crucial for a lactating female's maintenance and ability to provide milk for her foal (Loudon and Kay 1984). Lactating Grevy's zebra visited water at twice the frequency of non-lactating females and tended to remain closer to water during the foal's first three months (Ginsberg 1988; Becker and Ginsberg 1990). During this period the foal is almost entirely dependent on its mother for fluid (Ginsberg 1988). Lactating Grevy's zebra were consistently associated with two or three other lactating females and their foals and these females usually stayed on a male territory that was adjacent to a water source (Becker and Ginsberg 1990). Similarly, in Death Valley (USA), Moehlman (1998) documented that lactating feral ass (*Equus asinus*) with foals of less than 3 months of age drank daily and twice as often as other adult females during the hot summer months.

Plains zebra (*Equus quagga)* live in mesic habitats and visit water points every one or two days, but lactating females make more frequent trips to water and this may limit their access to forage (Becker and Ginsberg 1990; Sundaresan et al. 2008). Mountain zebra (*Equus zebra*) are highly dependent on daily access to water (Joubert and Louw 1976 cited in Schoenecker et al. 2016), and their home range expands when more water points are available (Novellie et al. 2002).

In over twenty years of research and survey work on the African wild ass (*Equus africanus*) in the Danakil ecosystem (Eritrea), the Messir Plateau is the only area where multiple females with young foals have been regularly observed (Moehlman 1998;

Moehlman 2002; Tesfai 2006; Tesfai, personal observation). The Messir Plateau receives 160 mm of rainfall per year on average and has very limited and localized permanent surface water during the dry months (Tesfai 2006; Tesfai et al. 2019). This critical area for females with young foals has no formal protected status (Moehlman 2002; Tesfai et al. 2019) and livestock are free to utilize the area. Field observations and interviews with local Afar pastoralists (Moehlman 2002; Tesfai et al. 2019) indicate that people, livestock and the African wild ass share the same permanent water source, Asaila spring. Livestock and/or human disturbances around water sources may affect the drinking behaviour of the African wild ass on the Messir Plateau. Given that lack of access to quality forage near to water sources may negatively affect the survival of young foals (Williams 1998, 2002), I set out to document the drinking behaviour of African wild in relation to water sources, with particular attention to females with foals. African wild ass must have access to water in order to survive and lactating females with foals are expected to drink more frequently than non-lactating females. I first confirmed that the Asaila spring is the only permanent water source for the African wild ass occurring on the Messir Plateau, and then identified the months of the year when it would be the only source of water. I then collected data on i) the frequency of visits by adults in different sex and reproductive classes, ii) the time of the day that they visited water, and iii) the distances travelled between foraging areas and water sources. I compared data between dry periods when the only available water source was the Asaila spring and wet/rainfall periods when temporary surface water was available elsewhere. I expected that:

(1). During dry months, all African wild ass occurring on the Messir Plateau would visit the Asaila spring, since it is the only available permanent water source. The next nearest accessible permanent water is ‘Alad’ at distance of 30 km from Messir Plateau to the southwest.

(2). Females with foals aged three months or less, and females with foals aged between 4 and 12 months would visit water sources more frequently than females with foals weaned older than twelve months and/or non-reproductive females and males. The hypothesis is that water and quality forage are crucial for the maintenance of a lactating female and her ability to provide milk for her foal (Loudon and Kay 1984; Becker and Ginsberg 1990).

(3). African wild ass would visit the Asaila spring only at night as it is near settlements, while they would visit seasonal water sources away from human settlements mainly during the day.

(4). Distance travelled between foraging areas and temporary water during rainfall months would be less than the distance travelled between foraging areas and the permanent water point in the dry months. The assumption is that during the rainfall months the study area has widely distributed seasonal temporary water sources associated with relatively better vegetation.

4.2 Materials and methods

4.2.1 Study area

The study was conducted on the Messir Plateau (Fig. 4.1) in the Danakil ecosystem from October 2016 to March 2019. The Danakil ecosystem is classified as a semi-desert or desert climate zone in Eritrea (Department of Land 1998). The climate of the study area is arid with extremely hot summers which have a mean daily maximum temperature of 35º C and peaks of 45 °C between June and September. During the study period, the mean daily temperature in wet/rainfall months was 27.6º C and 31.1º C in dry months. Most rain usually occurs between December and February, with less rain falling in March and April (Environment of Eritrea 1995). In rainfall months the plains area of Messir Plateau has relatively better vegetation cover than higher on the plateau and seasonal water is available (Fig. 4.1). The

Asaila spring, a perennial water source, is located approximately 9 km northwest of the plains area of the Messir Plateau (Fig. 4.1, 4.3). Reliable rainfall records were not available for the study area. Therefore, monthly rainfall data produced by CHIRPS at 0.05 degrees (5 km) spatial scale was obtained from an online portal (https://early warning.usgs.gov/fews) (Fig. 4.2) for the study period. The data was created by combining satellite data, interpolation of rain gauges data and topographic information of a given area. This rainfall data was then correlated with the field observation reports (Tesfai, personal observation). During the field work from October to December 2016 the study area was dry. From March to June 2017 there was rainfall. In 2018 (February to April) and 2019 (January to March) the area experienced no rainfall except for isolated showers (Fig. 4.2).

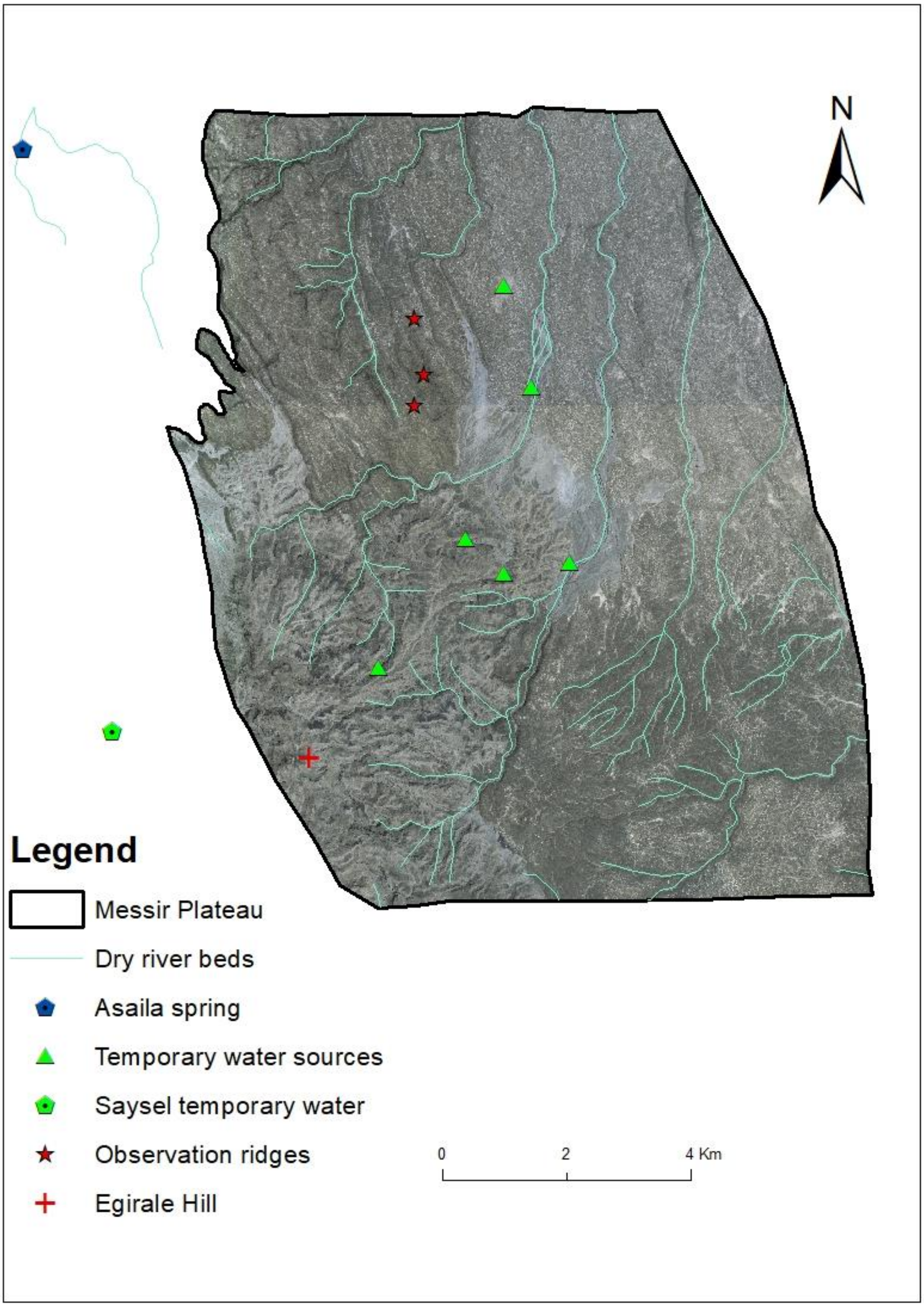


Figure 4.1 Map of study area (Messir Plateau) showing the location of the permanent water source Asaila and at least six on Messir Platea and Saysel temporary seasonal water sources that occur after rainfall events.

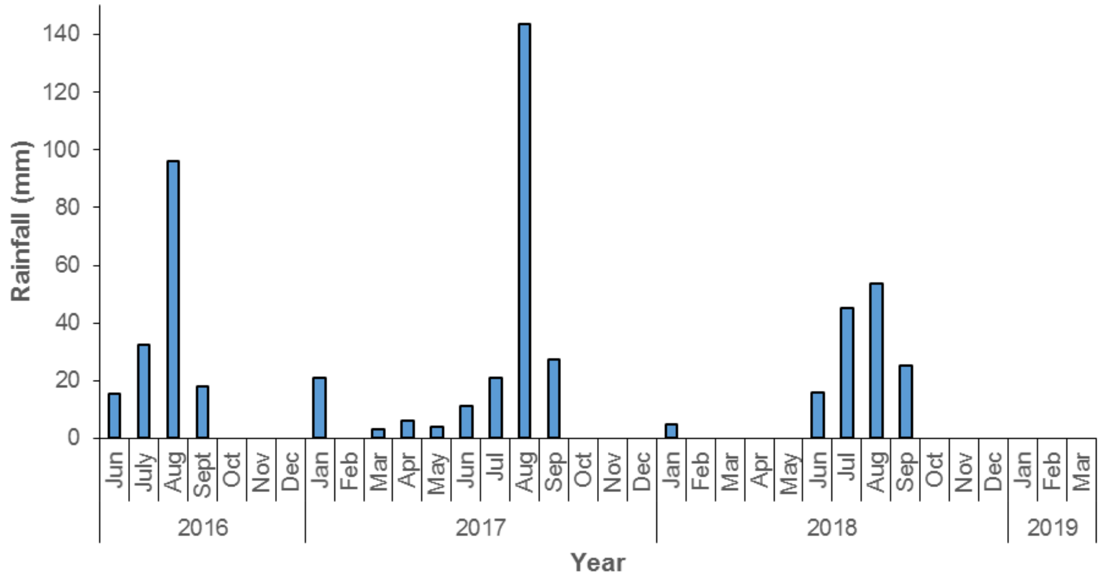


Figure 4.2 Monthly rainfall of the Messir Plateau for the study period (Oct 2016 – Mar 2019). Data obtained from CHIRPS online portal (https://earlywarning.usgs.gov/fews).

<u>4.2.2 Identifying if and when Asaila was the only water point available to the African wild ass on Messir Plateau</u>

To determine if there were any permanent water sources other than Asaila spring, an intensive survey was conducted between January and March 2019 within a radius of approximately 30 km to the west and south of Messir Plateau on foot and with camels. East and north of Messir Plateau are settlement areas, and there is no available water except some water wells and boreholes which are not accessible by wildlife. The next nearest available permanent water source (Alad) is located at a distance of 30 km southwest from Messir Plateau (Fig. 4.3). This water source is located in an extremely rocky area and the nearest source of vegetation is at a distance of approximately 15 km.

Therefore, during the field work from October to December 2016 (dry months), the only available water source for the African wild ass on Messir Plateau was the Asaila spring.

In rainfall months from March to June 2017 at least six seasonal temporary water sources were located on the lower elevation plains are of the Messir Plateau (Fig. 4.1). The following year (February to April 2018), the study area experienced no rainfall, except isolated showers in late April and the Asaila spring was again the only available water source for the African wild ass on the Messir Plateau. From January to March 2019 the area again experienced low rainfall, although there were isolated showers in January and March 2019 which created seasonal temporary water on Messir Plateau and at Saysel for a few days. Saysel temporary seasonal water was located, approximately 8 km from the plains area of the Messir Plateau and about 4 km from Egirale Hill to the southwest on the adjacent western escarpment (Fig. 4.1, 4.3). In March 2019, the distribution pattern of the African wild ass was concentrated to southwest of the Messir Plateau and they were observed travelling towards Saysel water point late in the afternoon or at night (Chapter 3, Fig. 4.1). During the day the plains area close to Saysel was monopolized by livestock and people. Therefore, during the field work in March 2019, Saysel (Fig. 4.1) was targeted for drinking data collection.

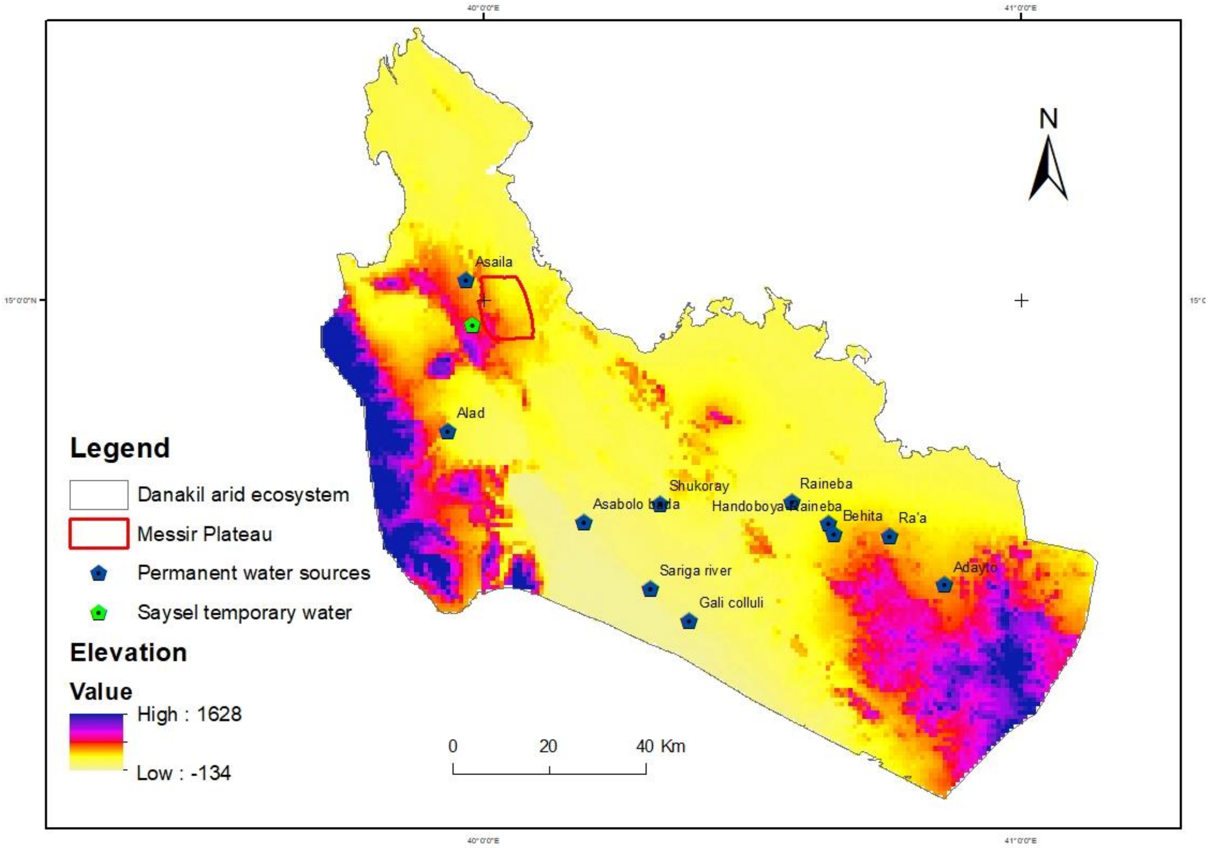


Figure 4.3 Permanent water points in the Danakil ecosystem (Eritrea). Asaila is the nearest (9 km) permanent water available for the African wild ass occurring on the Messir Plateau. The second possible permanent water source is 'Alad' at distance of 30 km to the southwest of the Messir Plateau at the bottom of the western escarpment.

4.2.3 African wild ass data collection

Direct observation and camera trap were used to collect drinking data on the African wild ass on the Messir Plateau (Table 4.1). To ensure that the maximum population size was sampled for the drinking data, all African wild ass in the study area were identified by their unique leg stripes (Fig. 4.4a). This was a pre-requisite to ensure that each individual's records were independent and to avoid double counting of individuals during sampling. Previous research indicated that births in African wild ass on Messir Platea peaked between December and

April (1995-2007) (Tesfai 2006; Moehlman unpublished report). Therefore, as described in the research design section 1.3 the drinking behaviour data collection on the African wild ass in Messir Plateau was planned during the months from December to April. Hypothetically, females with foals of age less than three months would be at the peak of lactation and need to drink more frequently than other adults. However, only two females were observed with young foals (aged ≤ 3 months) between February to March in 2017, and one in early 2018. No female was observed with a young foal (aged ≤ 3 months) between January and March 2019. A total of seven females with foals aged between 4-12 months were observed in Feb 2018 and Jan 2019. This is a limited sample size but provides crucial detailed data on drinking behaviour of lactating females. A total of twenty-five individual adult females (in each year a minimum of 10 and maximum of 18 individual adult females) and their foals and five adult males were identified (Table 4.2) and monitored. This represents the entire adult population utilizing the Messir Plateau from Oct 2016 to Mar 2019. Previous research documented approximately 18 individual adult females at any one time in the study area (Moehlman et al. 1998; Moehlman 2002; Tesfai 2006).

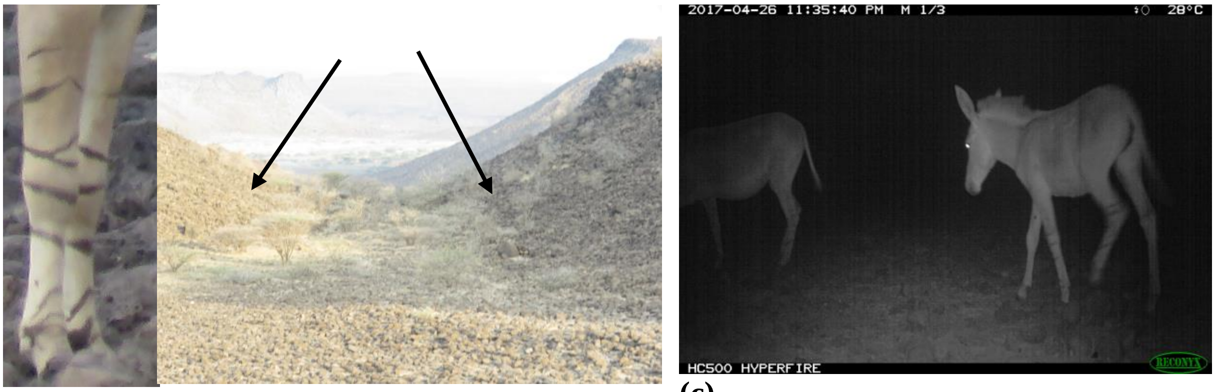
Two Reconyx Hyperfire HC500 camera traps were sited on both sides of the narrow main access path at approximately 3 km from Asaila spring (Fig. 4.4b). Camera traps were also placed closer to Asaila (10-20 m), but few data were recorded because the water point is about 25 meters by 80 meters and camera traps could not provide full coverage. The detection range of the Reconyx camera is about 60 ft (18.29 m). The camera traps recorded date and the time per photo of each individual African wild ass walking to and from Asaila (Fig. 4.4c). The narrow path site was selected based on previous observations that females with young foals and other resident females and males used this route from the Messir plateau to travel to Asaila. During March-June 2017, late April 2018 and January and March 2019 when temporary water points were available on the Messir Plateau and at Saysel for a few days, direct observations were used to document individual female visits to water during the day. A seasonal water point was selected based on the presence of fresh African wild ass faeces and hoof prints. I then waited near this water source for 3 to 5 hrs for at least three successive days to document which individuals used the selected water point. Camera traps were also placed at the selected water source throughout the day. The African wild ass hoof prints are relatively bigger than that of the domestic donkey. In addition to direct observations at the seasonal temporary water sources, camera traps were used to document individual African wild ass drinking behaviour at night. All the seasonal water points were monitored for at least three days at a time. Two camera traps were set near an observed path on both sides to seasonal water where direct observations had been made during the day. The same sampling technique was repeated at all the six seasonal water points within the study area. The two camera traps were shifted when seasonal water points were available in the study area and monitored for at least three successive days per seasonal water point for a total of 32 days of observation.

Camera traps were also deployed outside the study area at the Saysel temporary seasonal water source (Fig. 4.1) for a total of 13 successive days when isolated erratic rainfall was reported in that area in late April 2018 and March 2019. The total field days of observations (direct observation and camera traps) documenting African wild ass drinking data are provided in Table 4.1.

Table 4.1 Direct observation and camera trap data on the drinking behaviour of African wild ass on Messir Plateau, Eritrea (Oct 2016 – Mar 2019).

Year	**Month**	**Rainfall condition**	**Number of water sources**	**Method**
2016	Oct 08-11	Dry	1	Camera trap
	Nov 19-25	Dry	1	Camera trap
	Dec 17-24	Dry	1	Camera trap
Sub-total	19 days			
2017	Mar 16-21	Wet	6	Direct observation and camera trap
	Apr 26-30	Wet, but seasonal waters had dried up	1	Camera trap
	May 01-02	Wet, but seasonal waters had dried up	1	Camera trap
	May 27-31	Wet	6	Direct observation and camera trap
	Jun 01-04	Wet	6	Direct observation and camera trap
Sub-total	22 days			
2018	Feb 07-12	Dry	1	Camera trap
	Mar 14-16	Dry	1	Camera trap
	Apr 15-26	Dry, except isolated showers in late April	2	Direct observation and camera trap
Sub-total	21 days			
2019	Jan 20-28	Dry, except seasonal water for a few days.	2	Camera trap and direct observation
	Feb 18-22	Dry	1	Camera trap
	Mar 14-20	Dry, except seasonal water at Saysel for a few days.	2	Camera trap and direct observation
Sub-total	21 days			
Total	**83 days**			

Females with foals aged three or less months and females with foals aged 4-12 months and yearlings were easily identified when accessing water sources. Approximate birth dates of the foals born on Messir Plateau were known and recorded by the local scouts who monitor the study area regularly. Additionally, the African wild ass foal age classification photos supplied by the Saint Louis Zoo (USA) were used to distinguish between a foal of less than 3 months and one above three months.



(a) **(b)** **(c)**

Figure 4.4 (a) Leg stripe patterns of the African wild ass, which were used to identify all African wild ass on Messir Plateau, Eritrea, (b) Two camera traps located at the narrow path to the Asaila permanent water sources adjacent to the Messir Plateau, Eritrea to document the date and time individual African wild ass travelled to water at night, and (c) an example of a camera trap picture showing an African wild ass going to water.

To estimate the distance travelled to water sources, African wild ass were located by scanning the entire study area (approximately 124 sq km) from the highest ridge (220 m.a.s.l.), using a Nikon field scope and/or 7 x 42 binoculars during the early hours of the day (05h00 – 06h00). If any individual African wild ass were spotted foraging, I walked to those sites using GPS navigation and geographical features and recorded the individuals and their locations. If no individual was spotted from the high view point, I then walked to the 2nd and 3rd ridges (201 and 150 m.a.s.l. respectively) and scanned the whole area again (Fig. 4.1). If it was still not possible to visually locate any African wild ass, I walked to the temporary water sources on the 'plains' area (approximately100 m.a.s.l.) and followed tracks of fresh hoof prints to locate the African wild ass foraging sites. Individual African wild ass leaving the Asaila water source usually walked over the high ridges in early hours of the day and descended to forage on the plains area. They start to walk back to water from the plains late in the afternoon or evening. These movement patterns are regularly observed on the Messir

Plateau (Tesfai, personal observation). Once the African wild ass were located and confirmed foraging, individual identification (ID), date, ambient temperature and GPS location of the site were recorded using a Garmin Montana 600™ Global Positioning System (GPS). For each observed individual African wild ass the travel distance between the morning foraging location and the closest water point was calculated.

4.2.4 Data analyses

4.2.4.1 Frequency of visits to water

Drinking frequency per individual per water source (dry vs. rainfall months) was obtained by calculating the number of visits to water of an individual per successive days of observation. Drinking interval was estimated for each individual by calculating the number of hours between the 1st visit and the 2nd visit, the 2nd visit and the 3rd visit up to the last visit for successive days of observations. Subsequently, I calculated the mean, minimum and maximum drinking intervals per individual, for permanent and seasonal water points per day of observations separately. When only one drinking observation was made, the minimum interval was based on the number of successive days of observation. Scatterplots with linear regression were used to show the distribution pattern of drinking intervals for each adult female reproductive category and that of adult males. To see whether the mean number of visits (frequency) to water (dry vs. rainfall months) was affected by water sources (permanent vs. temporary) and differed between sex and reproduction categories loglinear analyses were made. Each individual was classified into one of five female reproductive categories (adult female with foal aged ≤ 3 months, adult female with foal aged 4-12 months, adult female with yearling aged 12-24 months, pregnant female with no foal and non-reproductive female) or male. For this analysis the male group was classified into three categories (territorial, bachelor adult and bachelor sub-adult males) because their drinking frequency per individual or group and their social interaction with the female group were apparent during the field study. The territorial male was usually observed on the plains area of the Messir Plateau and/or going to water with adult females. Bachelor adult males were occasionally seen on the Messir Plateau and recorded going to Asaila spring once per several days. The bachelor sub-adult male (M2016-1a) was first observed as a yearling (close to two yrs. old) in 2016 with his mother (F2016-1) as well as and daily going to water with her. The adult female F2016-1 had no young foal in 2016 and she was observed in 2017/2018 for few days, but no data were recorded from her. Drinking data for M2016-1a was collected in 2018/2019 when he became a bachelor sub-adult male.

The daily maximum and minimum temperatures of each observation day for each sex and reproduction categories (Appendix II-V) were subsequently compared with number of visits (frequency) to water using Pearson correlation coefficients to identify any significant differences at the 95% significance level ($P < 0.05$) between drinking frequency and maximum daily temperature.

4.2.4.2 Time of day and drinking behaviour

The time of the visit to water sources (permanent vs. seasonal) for each female and male category was assigned to four-time categories (18h00 – 24h00; 00h00 – 06h00; 06h00 – 12h00 and 12h00 – 18h00) and subsequently the proportion of visits in each time category was calculated for each female and male category.

4.2.4.3 Distance travelled to water

The travel distance to water was estimated by measuring the distance between the morning foraging location and the closest water point using the ArcGIS 10.5 (ESRI 2017) distance and proximity (near) analysis tool. I calculated the mean, minimum and maximum travel distances per individual for permanent and seasonal water points by day separately. Each individual was classified into one of the female or male categories as described above in section 4.2.4.1. To test if there was a significant difference in the mean distance travelled to permanent vs seasonal water points between the five female and three male categories a Generalized Liner Model (GLM) repeated measures procedure was used and the effect of the number of observations (co-variate) was controlled in order to remove/minimize a sampling bias in the data collection. Each individual observation of distance travelled to water sources (independent variable) represents one data point. All statistical analyses were carried out using STATISTICA 8.0 software (Tulsa, OK: StatSoft, USA).

4.3 Results

4.3.1 The African wild ass population and permanent water sources on the Messir Plateau

A total of 30 adult individual African wild ass (25 females and five males) were identified and monitored (Appendix II-V). Ten adult females and one territorial male were observed during the dry months of 2016 (Table 4.2). During the rainfall months of 2017, 15 adult females, one territorial male and three bachelor adult males were recorded (Table 4.2). In 2018, when the study area was dry due to a delay in normal rainfall, 18 adult females, one territorial male and one bachelor sub-adult male were observed (Table 4.2). In 2019, when the study area was again dry, 18 adult females, one territorial male, two bachelor adult males and one bachelor sub-adult male were observed (Table 4.2). In 2019 two bachelor males and two non-reproductive adult females were observed around the Alad permanent water which is approximately 30 km from Messir Plateau. However, it was difficult to determine their identity and confirm if these individuals had been observed on the Messir Plateau.

Out of the total of 25 individual adult females observed at some stage, none were identified with a foal less than three months in 2016 and early in 2019. Three females had a foal of less than three months in 2017/2018. Seven females with foals of age three to twelve months (2 in 2016, 3 in 2018 and 2 in 2019) were observed and their drinking behaviour recorded. Ten females were found with yearlings aged 12-24 months during the study period (Oct 2016-Mar 2019). Eight of these females with yearlings (3 in 2016, 2 each in 2017 and 2018 and 1 in 2019) were recorded by the two camera traps when travelling daily to the Asaila spring in dry months (Appendix II-V). No drinking behaviour was observed for the other two females (F2016-3 and F2016-11) with yearlings aged 12-24 months (Appendix III and IV) even though these two females and their yearlings were observed on Messir Plateau during the field study in 2018 and 2019. All individual African wild asses identified and monitored for the drinking behaviours are provided in Appendices II-V.

Table 4.2 Individual African wild ass observed during the field period on Messir Plateau (Oct 2016 – Mar 2019).

Reproductive status	**Observed African wild ass**			
	2016	2017	2018	2019
Female with foal aged ≤ 3 months	0	2	1	0
Female with foal aged 4-12 months	2	0	3	2
Female with yearling aged 12-24 months	3	2	3	2
Pregnant female	3	1	1	0
Non-reproductive female	2	10	10	14
Territorial male (TM)	1	1	1	1
Bachelor adult male (BM)	0	3	0	2
Bachelor sub-adult male	0	0	1	1
Total	**11**	**19**	**20**	**22**

One of the identified female individuals (F2016-8, Appendix V) in the study area was confirmed dead in February 2019. The cause of death of the female was unknown. The skeleton was collected for morphological research and to determine age at death. There was also information from the local community that two other adult females were killed by spotted hyena (*Crocuta crocuta*) around Semoti approximately 50 km southwest of the study area in early 2019, but this could not be confirmed. Spotted hyenas are rarely observed on Messir Plateau.

4.3.2 African wild ass frequency of visits to water sources

The number of visits (frequency) to water sources differed significantly between the eight sex and reproduction categories ($\chi^2 = 111.24$, df=7, $p<0.0001$), but did not differ between permanent and seasonal temporarily water sources, except for females with young foals ≤ three months. Females with young foals visited temporary water sources more frequently than Asaila spring ($t= 3.68$, $p= 0.0213$, Fig. 4.5). Frequency of visits to water sources increased when females had young foals (≤ three months) and decreased, with longer intervals, when the foal was older (Fig. 4.5). During the dry months of 2017 and 2018 (Fig. 4.5a; Table 4.3; Appendix III and IV) female African wild ass with young foals aged three months or less (n=3) were recorded by camera traps travelling daily to the Asaila water (Fig. 4.5, Table 4.3; Appendix VI). When seasonally temporarily water sources were available in 2017 females with young foals (≤ three months, n=2) travelled to water twice as often other adult females (Fig. 4.5b; $p<0.0001$). Four of the females with foals 4-12 months (i.e. F2016-6; F2016-7; F2016-10 and F2017-3) were recorded by camera traps travelling daily on successive days to the Asaila water during dry months (Appendix II, IV and VI). The other three (F2016-3; F2018-1 and F2018-2) were recorded by camera traps traveling to Asaila every two/three days when the foals were older than 10 months (Appendix IV and V).

Females with foals 4-12 months were observed visiting seasonal water every day (Fig. 4.5a; Table 4.3; Appendix V).

Out of the ten females with yearlings aged 12-24 months identified in the study, eight (3 in 2016; 2 in 2017; 2 in 2018 and 1 in 2019) were recorded by the camera traps travelling daily to the Asaila spring in dry months (Fig. 4.5a; Appendix II-V) and observed visiting temporary water every-one/two days (Fig. 4.5b; Appendix V). No drinking data were recorded for the other two females (F2016-3 and F2016-11) with yearlings aged 12-24 months (Appendix IV and V; Table 4.3) even though these two females and their yearlings were observed on Messir Plateau during the field study in 2018 and 2019.

During dry months, pregnant females were observed visiting the Asaila spring every two to ten days (Fig. 4.5a; Table 4.3; Appendix VI) and they visited temporary water sources every two to four days (Fig. 4.5b; Table 4.3; Appendix VI). Limited data indicate that non-reproductive females during the dry months visited the Asaila spring during the dry months every five to ten days (Fig. 4.5a; Table 4.3) and visited the temporary water sources every three days (Fig. 4.5b; Table 4.3).

Only one territorial male was observed in Messir Plateau throughout the study period (Oct 2016 – Mar 2019). During the dry months he was recorded travelling to the Asaila spring about every second day and he travelled daily to temporary water sources (Table 4.3; Appendix II-VI). The three bachelor adult males were occasionally observed on Messir Plateau and recorded going to Asaila spring once per seven to ten days in dry months and once per seven days to seasonal water. The M2016-1a was observed visiting both permanent and seasonal water every day with his mother (F2016-1) in dry months (Table 4.3; Appendix IV-VI). During the wet months, the F2016-1 was not observed on Messir Plateau, while M2016-1a was observed in the study area during this period. The mean temperature of the study area in wet months was 27.6 ^{0}C (n=35 days) and 31.1 ^{0}C (n=48 days) in dry months although the drinking intervals and the daily maximum temperature did not correlate significantly ($p>0.05$; Appendix II-V). More than 250 camera trap photos recorded individual females travelling to water in 2016, 2018 and 2019 when Asaila spring was the only available water source. However, not all photos provided a clear identification.

Table 4.3 Mean drinking intervals (hrs) between successive visits to water sources (dry vs. rainfall months) per each sex and reproductive category of African wild ass on the Messir Plateau, Eritrea (Oct 2016 – Mar 2019). N represents number of times each sex and reproductive category visited the water source.

Sex and reproductive category	**Drinking intervals (hrs)**							
	Permanent (dry months)				Seasonal (rainfall months)			
	N	Mean	Min	Max	N	Mean	Min	Max
Female with foal aged ≤ 3 months	36	24:57	18:32	28:24	61	15:18	9:43	21:33
Female with foal aged 4-12 months	26	40:25	24:27	67:00	14	24:27	23:10	25:00
Female with yearling aged 12-24 months	100	32:55	21:40	62:44	44	27:28	18:26	42:51
Pregnant female	12	78:28	33:16	124:44	5	73:18	30:39	141:14
Non-reproductive female	12	167:34	30:09	246:02	42	71:04	32:43	155:11
Territorial male (TM)	21	43:37	23:14	54:45	18	30:43	9:55	51:32
Bachelor adult male (BM)	6	232:33	121:03	247:03	3	194:04	168:04	246:03
Bachelor sub-adult male	10	23:59	18:22	27:39	6	18:03	16:51	24:48

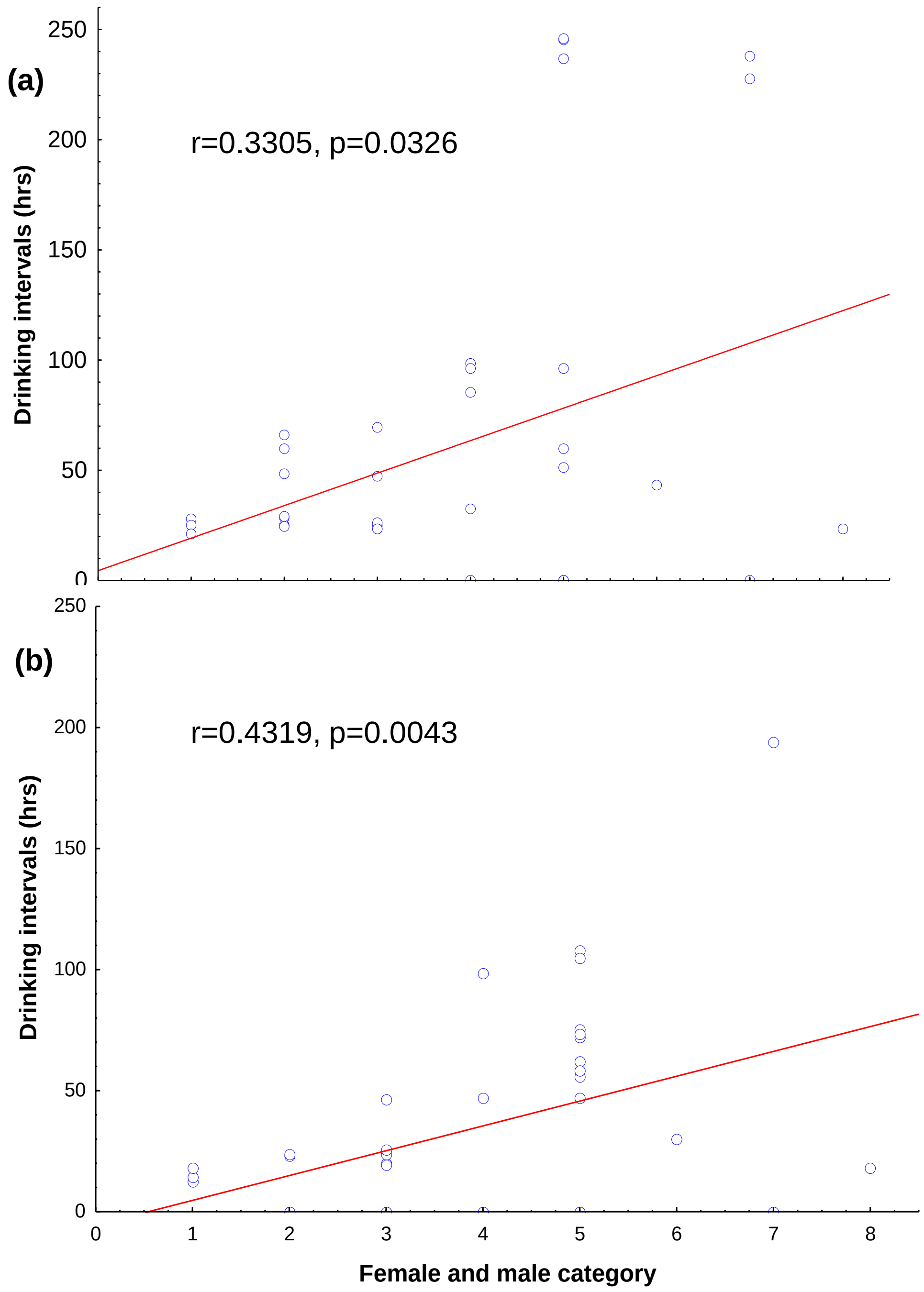


Figure 4.5 Mean drinking intervals (hrs) between visits to water sources. (a) when Asaila was the only available water sources for the African wild ass in Messir Plateau (Oct – Dec 2016, Feb – Apr 2018 and Jan – Mar 2019), and (b) when temporary water sources were available on the Messir Plateau from March to June 2017, in late April 2018 and in January

and March 2019. The regression line shows the distribution pattern of drinking intervals for each female and male category. 1) Female with foal aged ≤ 3 months, 2) Female with foal aged 4-12 months, 3) Female with yearling aged 12-24 months, 4) Pregnant female, 5) Non-reproductive female, 6) Territorial male, 7) Bachelor adult male, and 8) Bachelor sub-adult male.

4.3.3 Time of the day African wild ass visit water sources

During the dry months all female and male categories visited the permanent water point at night (between 18h00 – 06h00; Fig. 4.6a). Out of the total of 221 recordings of all female and male categories, 124 (56.1%) of the camera trap data observations occurred between 18h00 and 24h00 and the 97 (43.9 %) between 00h00 and 06h00 (Fig. 4.6a; Appendix VII).

During the wet months, females with young foals aged ≤ 3 months and other females and males were observed visiting the seasonally temporary water sources during the night and into the early hours of the day (Fig. 4.6b). Out of the total of 191 recordings of African wild ass travelling to seasonal temporary water sources, 118 (61.1%) of the observations were recorded between 18h00 and 24h00 and 36 (18.8%) between 00h00 and 06h00, and 37 (19.4%) during the day from 06h00 to 12h00 (Fig. 4.6b; Appendix VII).

Out of the total of 61 observations of females with young foals aged ≤ 3 months going to the seasonal temporarily water sources, 36 (59%) was recorded between 18h00 and 24h00 and 22 (36.1%) visits occurred between 06h00 and 12h00 and 3 (4.9%) between 00h00 and 06h00 (Fig. 4.6b; Appendix VII) and they visited seasonal waters twice a day (Table 4.3). In general, 16.5 % of females visited the temporary water sources between 06h00 and 12h00 (Fig. 4.6, Appendix VII). The territorial male also visited the temporary water sources both nocturnally and during the day (55.6% between 18h00 and 24h00, 11.1 % between 00h00 and 06h00, 33.3% between 0600 and 1200 hours) (Appendix VII). The bachelor and sub-adult males also visited water sources both night and day (50% between 18h00 and 24h00, 33.3% between 00h00 and 06h00 and 16.6% from 06h00-12h00).

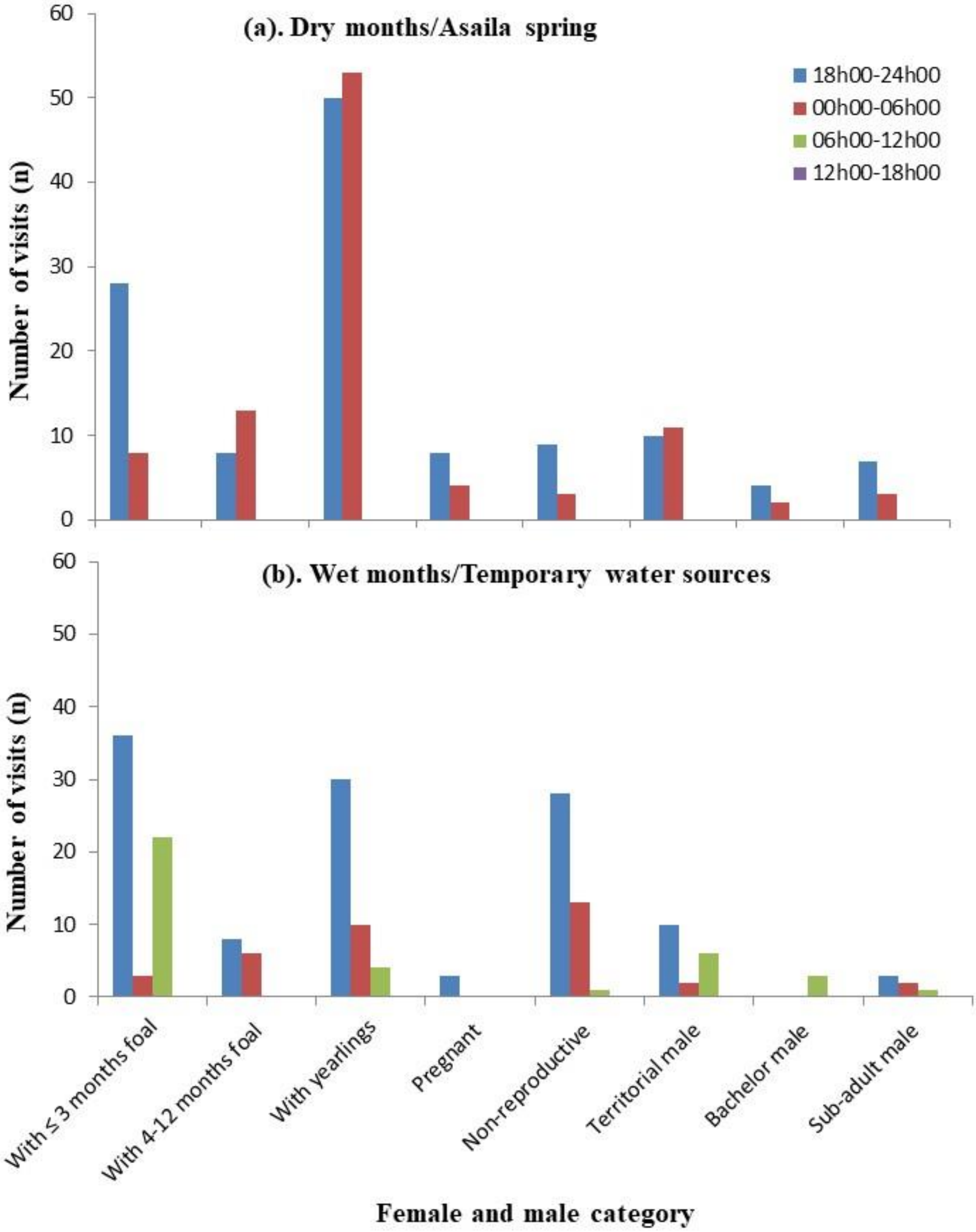


Figure 4.6 Time of visits to water sources (dry vs. rainfall months) by each sex and reproductive category of African wild ass on the Messir Plateau, Eritrea (Oct – Dec 2016;

Mar – Jun 2017; Feb – Apr 2018 and Jan – Mar 2019). (a) In dry months when Asaila was the only available permanent water and all African wild ass travelled to water at night (18h00 – 06h00), and (b) In wet months African wild ass visited seasonal waters during both diurnal and nocturnal hours.

4.3.4 The travel distance of African wild ass to water sources

The travel distances from the forage area to water sources (dry vs. rainfall months) per each individual African wild ass monitored during the study period are provided in Appendix VIII. In the rainfall months when seasonal temporary water sources were available, the travel distance from the foraging area to the seasonal water source was significantly less than the travel distance to the permanent water source during the dry months (Wilks' Lambda: H=35; df=1, $P \leq 0.012$; Table 4.4). In rainfall months from March to June 2017 when six seasonal temporary water sources were located on the Messir Plateau, two females with foals aged ≤ 3 months were observed within 3 km of the water source but tended to disperse up to 7 km when livestock arrived on the 'plains' area (N= 60, Table 4.4; Appendix VIII). During the dry months females with young foals were found on average a distance of about 9 km from Asaila permanent water (N=36, Table 4.4; Appendix VIII).

Although the field survey for drinking behavior was focused on the Messir Plateau, some individuals were observed going to Saysel temporary water source (Fig. 4.1). Hence camera traps were deployed for a total of 13 days to sample that water point in late April 2018 and March 2019. Only one female (F2018-1) with a young foal of less than 3 months were documented traveling about 4.4 km to the Saysel water point. This occurred after a brief rainfall reported in that area in late April 2018. Females with older foals and non-reproductive females and males were recorded at Saysel water point for several days in late April 2018 and March 2019 (Table 4.4; Appendix VIII).

Table 4.4 Travel distance between morning foraging and drinking sites for each sex and reproductive category of African wild ass on the Messir Plateau (Oct 2016 – Mar 2019). N represents number of times/observations each sex and reproductive category of African wild ass visited the water sources.

Sex and reproductive category	**Estimated distance to water sources (km)**							
	Permanent (dry months)				Seasonal (rainfall months)			
	N	Mean	Min	Max	N	Mean	Min	Max
Female with foal aged ≤ 3 months	36	9.0	7.2	11.1	61	3.18	1.85	5.91
Female with foal aged 4-12 months	26	8.76	8.03	10.97	14	4.75	0.54	8.27
Female with yearling aged 12-24 months	100	10.21	7.79	12.98	44	3.12	0.712	5.86
Pregnant female	12	10.24	9.33	10.92	3	4.56	0.26	6.69
Non-reproductive female	12	10.74	10.40	11.05	42	4.00	1.78	6.15
Territorial male (TM)	21	9.34	7.63	14.73	18	3.65	0.2	7.85
Bachelor adult male (BM)	6	6.67	5.185	7.78	3	2.68	1.56	4.36
Bachelor sub-adult male	10	8.32	5.54	11.64	6	6.85	2.77	9.27

4.4 Discussion

Asaila spring was confirmed as the nearest permanent water available in dry months for the African wild ass occurring on the Messir Plateau. The frequency of visits to water sources for individual African wild ass on Messir Plateau differ significantly between sex and reproductive status categories. During the dry months females with foals aged ≤ 3 months, and females with foals aged between 4 and 12 months visited water sources more frequently than females with offspring older than twelve months and/or non-reproductive females and males (Table 4.3). Females with young foals aged ≤ 3 months and between 4 and 12 months are lactating and physiological constraints would select for more frequent drinking behaviour in order to provide sufficient milk for their foals (Loudon and Kay 1984; Becker and Ginsberg 1990). Females with such young foals would be at peak lactation (Becker and Ginsberg 1990). During the wet months females with foals aged ≤ 3 months were documented visiting seasonal water sources more frequently than they had visited the Asaila spring during the dry months and twice as often as other females and males (Table 4.3). The more frequent visits to water sources during the wet period, when it is cooler than the dry the period is perhaps due to their closer proximity to grazing areas. The frequency of visits by individual females with older foals, plus non-reproductive female and male categories did not differ statistically between dry and rainfall/wet months. African wild ass with older foals and non-reproductive females and males may not need to visit water more frequently during the wet seasonal period compared to dry season because forage provides more water in the wet season, temperatures are cooler and they are less physiologically stressed.

Out of the total of 25 individual adult female African wild ass observed on Messir Plateau at some stage, 13 females (5 with foals 4-12 months, 3 with yearlings aged 12-24 months, 3 pregnant and 2 non-reproductive) were not recorded drinking at seasonally available water in wet months (Table 4.3; Appendix VI). Non-reproductive females, some pregnant females and females with yearlings aged 12-24 months plus bachelor adult males were not recorded visiting at Asaila spring for several days at a time in dry months. The possible reasons for some individuals travelling to the Asaila spring at long intervals include (a) they were 'photographed' by the camera trap, but not identified. African wild asses with young foals on the Messir Plateau do not leave their foals behind (i.e. crèched) when travelling to water during the night. The presence of the young foal with the mother in the camera trap photo provides additional verification of the adult female individual identification, (b) they travelled to water by another path, and (c) non-reproductive females and bachelor males are often not seen on the Messir plateau and did not need to travel frequently to water. It may be that they are less water-dependent and can forage farther from the Messir plateau and are utilizing other permanent water sources such as Alad, Asabolo-bada and Shukoray (Fig. 4.3). This finding is consistent with information on another arid wild equid occupying arid habitat, Grevy's zebra. Rubenstein (2010) and Sundaresan et al. (2012) documented in Laikipia, Kenya that Grevy's zebra would not go to water for up to five days, but females with young foals were observed drinking daily.

In this field study, African wild ass visited the permanent water source 'Asaila' only at night, probably because it is in an area with settlements and livestock (Fig. 4.6a). In dry months, livestock and people were usually observed near Asaila during the day (Tesfai, personal observation). Previous studies in the Danakil ecosystem both in Eritrea and Ethiopia have indicated that African wild ass visit water points nearness to human settlements and their domestic livestock only during the night when these localities are free from disturbance by people and livestock (Kebede 1999; Tesfai 2006). Travel at night when temperatures are cooler may be less costly energetically and physiologically, but may result in an increased risk of predation. However, the incidence of predation on African wild ass by spotted hyena on Messir Plateau is currently very low or non-existent (Tesfai et al. 2019).

When water sources are monopolised by domestic livestock, Grevy's zebra in Kenya are forced to drink at night (Williams 2002). This is in direct contrast to those in protected areas, where the Grevy's zebra drink during a brief window of time during the middle of the day, probably as an adaptive response to reduce the risk of predation (Williams 1998, 2002).

During wet months when seasonally temporary water sources were available and distant from human settlements and livestock, lactating female African wild ass on the Messir Plateau sometimes visited temporary water sources during the day (06h00-12h00). In rainfall months, African wild ass, particularly females with young foals, were observed within 3 km of the nearest seasonal water point, but were found at a greater distance (up to 7 km) when there were high concentrations of livestock, particularly cattle, on the plains area. This was apparent soon after the rains began in May 2017 when an estimated 150 cattle arrived in the area (Tesfai, personal observation).

In dry months, lactating females foraged at mean distance of approximately 9 km from the only available water source (Table 4.4). Kebede et al. (2014) observed African wild ass within a radius of 10-25 km from permanent water sources in an area of high livestock abundance in northern Afdera (Ethiopia). In the Danakil African wild ass live in an arid environment where grass occurs in widely dispersed patches and displacement by livestock may limit access to water and quality forage. This spatial exclusion from water sources due to livestock presence may reduce the ability of African wild ass ability to provide sufficient milk to their foals. Availability and accessibility of adequate and quality forage closer to water can affect nutrition and energetic costs. Becker and Ginsberg (1990) suggested that wild equids in arid areas may reduce lactation costs by reducing milk production when females are denied access to water sources and adequate forage. Lactating females with foals (≤ 3 months, 4-12 months) travelled to water daily. In rainfall months, the study area had widely distributed seasonally temporary water sources associated with relatively better vegetation in the plains area. Females with foals went more frequently to water and travelled shorter distances.

During rainfall months, the territorial male (M2016-1) was usually observed in the plains area close to seasonal water. This may increase optimize his access to females in estrus that are located near the seasonal water sources. Females with young foals were usually seen in association with other females and the territorial male in plains area. Non-reproductive females and bachelor males were seldom observed in the plains area, especially when livestock were present in dry months. Non-reproductive females and bachelor males may be less dependent on access to water and can travel farther to find better foraging areas not used by livestock.

Availability of water near forage areas strongly influences the distribution and drinking behaviours of wild equids. This is evident in arid ecosystems such as the Danakil desert (Kebede 1999; Tesfai 2006). In dry months, African wild asses, particularly lactating females on the Messir Plateau, were more frequently observed within 9 km of Asaila spring and travelled to water at night. Travelling long distances to access forage and water may result in low foal survival (Williams 1998). Therefore, any conservation strategies for this rare and endangered equids on the Messir Plateau in the Danakil desert should consider the critical issue of water source placement in relation to foraging areas and potential conflict with livestock that results in longer travel distances between forage and water.

References

Becker, C.D. and Ginsberg, J.R. 1990. Mother-infant behaviour of wild Grevy's zebra: adaptations for survival in semi-desert East Africa. *Animal Behaviour* **40**: 1111–1118.

De Boer, W.D. and Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82**: 264–274.

Department of Land (1998). Agro-Ecological Classification Map of Eritrea. Ministry of Land Water and Environment, Asmara, Eritrea.

Environment of Eritrea 1995. The National Environmental Management Plan for Eritrea (NEMP-E). Asmara, Eritrea. 138pp.

Ginsberg, J.R. 1988. Social organization and mating strategies of an arid adapted equid: the Grevy's zebra *Equus grevyi* (Kenya). Doctoral dissertation, Princeton University, New Jersey, US.

Kebede, F. 1999. Ecology and conservation of the African Wild Ass (*Equus africanus*) in the Denakil, Ethiopia. MSc Thesis, University of Kent/DICE, Canterbury, UK.

Kebede, F., Moehlman, P.D., Bekele, A. and Evangelista, P.H. 2014. Predicting seasonal habitat suitability for the critically endangered African wild ass in the Danakil, Ethiopia. *African Journal of Ecology* **52**: 533–542.

Lillywhite, H.B. and Navas, C.A. 2006. Animals, energy, and water in extreme environments: perspectives from Ithala 2004. *Physiological and Biochemical Zoology* **79**: 265–273.

Loudon, A.S.I. and Kay, R.N.B. 1984. Lactational constraints on a seasonally breeding mammal: the red deer. In Symposia of the Zoological Society of London, **51,** 233-252). Published for the Zoological Society by Academic Press.

Moehlman, P.D. 1998. Feral Asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Applied Animal Behaviour Science* **60**: 171–195.

Moehlman, P.D. 2002. Status and Action Plan for the African wild ass (*Equus africanus*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp 2-9.

Moehlman, P.D. Kebede, F. and Yohannes, H. 1998. The African Wild Ass (Equus africanus): Conservation Status in the Horn of Africa. *Applied Animal Behaviour Science* **60**: 115–124.

Novellie, P., Lindeque, M., Lindeque, P., Lloyd, P. and Koen, J. 2002. Status and action plan for the mountain zebra (*Equus zebra*). Equids: Zebras, Asses, and Horses: Status, Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp. 28-42.

Prins H.H.T. 2000. Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G., Dolan T.T. (eds) Wildlife Conservation by Sustainable Use. Conservation Biology Series, vol 12. Springer, Dordrecht. pp. 51-80.

Pratt, D.J. and Gwynne, M.D. 1977. Rangeland Management and Ecology in East Africa. Robert E. Krieger Publishing Company, Huntington, New York.

Rubenstein, D.I. 2010. Ecology, social behavior, and conservation in zebras. In Advances in the Study of Behaviour. Academic Press. **42**: 231–258.

Schoenecker, K.A., King, S.R., Nordquist, M.K., Nandintsetseg, D. and Cao, Q. 2016. Habitat and Diet of Equids. Wild Equids: Ecology, Management, and Conservation. (ed by: Jason I. Ransom and Petra Kaczensky). Johns Hopkin University Press, USA. pp. 41-57.

Sirot E.E., Renaud, P.C. and Pays, O. 2016. How competition and predation shape patterns of waterhole use by herbivores in arid ecosystem. *Animal Behaviour* **118**: 19–26.

Sundaresan, S.R., Fischhoff, I.R., Hartung, H.M., Akilong, P. and Rubenstein, D.I. 2008. Habitat choice of Grevy's zebras (*Equus grevyi*) in Laikipia, Kenya. *African Journal of Ecology* **46**: 359–364.

Sundaresan, S., Bruyere, B., Parker, G., Low, B., Stafford, N. and Davis, S. 2012. Pastoralists' perceptions of the endangered Grevy's Zebra in Kenya. *Human Dimensions of Wildlife* **17**: 270–281.

Tesfai, R.T. 2006. Conservation of African wild ass (*Equus africanus*) in Messir plateau (Asaila), Eritrea: the role of forage availability and diurnal activity pattern during the rainy and beginning of the dry season. MSc Thesis, University of Kent/DICE, Canterbury, UK. 85pp.

Tesfai, R.T., Owen-Smith, N. Parrini, F and Moehlman, P.D. 2019. Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy* **100**: 185–191.

U.S. Agency for International Development (USAID), 2019. MODIS NDVI and rainfall data accessed on 06 October 2019. https://earlywarning.usgs.gov/fews/.

Voeten, M.M. and Prins, H.H. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120**: 287–294.

Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology* **13**: 265–286.

Williams, S.D. 1998. Grevy's zebra: ecology in a heterogeneous environment, Doctoral dissertation, University College London (University of London), UK. 199pp.

Williams, S.D. 2002. Status and Action Plan for Grevy’s Zebra (*Equus grevyi*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. Pp 11-25.

Young, T.P., Palmer, T.M. and Gadd, M.E. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation* **82**: 351–359.

Chapter 5. General discussion

This research project was designed to investigate the factors influencing the viability of the African wild ass population on the Messir Plateau in the Danakil desert of Eritrea. The African wild ass has lost about 90 percent of its historic range (Moehlman 2002) and is classified as 'Critically Endangered' by the IUCN Red List (Moehlman et al. 2015). It is thought that this is mainly due to hunting, competition with livestock and habitat loss. A small but important population persists on the Messir Plateau, in the Danakil desert of Eritrea (Moehlman 2002; Tesfai et al. 2019). The Messir Plateau is remote, extremely rocky and the climate is very hot, thus presenting many physical challenges for data collection. To ensure that the maximum population size was sampled, all African wild asses in the study area were individually identified and monitored. A total of twenty-five adult females and their offspring (less than 3 months n=3, 4-12 months n=7 and yearlings n=3) and five adult males were located and monitored. This is a small population but provides crucial information that previously has not been documented on the diet and drinking behaviour of the African wild ass.

The African wild ass population in Eritrea is protected by the local community as part of their cultural practice (Moehlman 2002; Tesfai et al. 2019) and the incidence of predation by spotted hyenas is currently minimal (Tesfai, personal observation). There is no evidence of gene flow from domestic donkeys to the African wild ass (Beja-Pereira unpublished report). The fundamental question behind this research was why the population is not increasing if there is no poaching, relatively low predation, and no evidence of hybridization? Understanding the environment and the resource use that influence the population's natality and survival is crucial for developing effective conservation strategies (Zeller et al. 2012; Ripple et al. 2016; Muntifering et al. 2019). This is particularly important for threatened species such as the African wild ass in the Danakil desert ecosystem where forage and permanent water sources are limited (Moehlman 2002; Tesfai et al. 2019).

Long-term data on reproduction and survival rate of the African wild ass on the Messir Plateau are limited. Population viability was assessed given certain assumptions about fecundity, survival rates and carrying capacity. The present population consists of maximum 18 adult females utilizing the Messir Plateau at any one time (Moehlman et al. 1998; Moehlman 2002; Tesfai 2006). Small populations are more susceptible to extinction than large populations and have a lower probability of persistence (Berger 1990; Owen-Smith 2007). The risk of population extinction can be further exacerbated by the stochastic events and natural catastrophes (Owen-Smith 2007). Model results indicated that there is a 50% probability of extinction at the current level of 18 adult females on Messir Plateau. If there was a carrying capacity of 37 adult females, almost 100% probability of persistence is predicted. The greatest threat to the viability of the African wild ass population appears to be the impact of livestock on forage availability on the Messir Plateau under anticipated climate change. During the rainfall months, high numbers of livestock, particularly cattle come from the highlands to the Messir Plateau and this may limit forage availability for African wild ass.

During the rainfall months, African wild ass were spatially displaced by cattle from the northern plains area of the Messir Plateau. During this period, the northern plains area had seasonal water sources and the highest NDVI greenness index. During the dry months, African wild ass were concentrated towards the northern section of the Messir Plateau that had better vegetation greenness than the southern section and was closer to the permanent Asaila waterpoint. They were not spatially displaced by the few (17-37) cattle present during the dry months.

The diet of the African wild ass overlaps significantly with that of cattle and domestic donkeys both in dry and wet periods, but differs from other herbivore species that are predominantly browsers (camel and goat) and mixed feeders (sheep). In rainfall months, the domestic donkeys were not spatially displaced by cattle and hence had access to better forage and had higher nutrition than African wild ass. In dry months, when African wild ass were not displaced by the few local cattle they had better nutrition compared to the rainfall months. Generally, herbivore nutrition tends to improve in the wet months due to increased availability of forage (Casebeer and Koss 1970; Macandza et al. 2004). The lower nutrient level characteristic of African wild ass in rainfall months was thought to be due to their spatial displacement by the high number of cattle.

During the dry months, African wild ass females with young foals on the Messir Plateau visited water once a day, travelled on average 9 km to get there, and drank only at night. Non-reproductive adult females travelled to water every 5-7 days. During the rainfall months, there were seasonal water sources and females with young foals drank twice a day and on average only need to travel 3 km to water. African wild ass females with foals must travel to water every day and may have to travel long distances to access available forage because of the presence of cattle. Lactating females must have both water and forage and it is energetically costly for both mother and foal to travel long distances. These findings demonstrate how the distribution of water sources close to foraging, which changes with seasonal rainfall, can affect the travel distance of the African wild ass in the Danakil desert particularly, for lactating females because of the presence of cattle. Grevy's zebra also live in an arid habitat and lactating females travel to water more frequently than non-lactating females and tend to remain closer to water when the foals are ≤ three months in a protected area (Ginsberg 1988; Becker and Ginsberg 1990). Adequate forage near water sources is critical for lactating females' maintenance and ability to provide milk for their foals (Loudon and Kay 1984; Becker and Ginsberg 1990).

5.1 Conclusion

African wild ass have dietary overlap with cattle and domestic donkeys and are displaced by high numbers of cattle on the Messir Plateau during rainfall months. Higher forage quantity in both the dry and wet seasons has the potential to provide better nutrition and lower energetic costs for the African wild ass. This could result in an earlier age of first reproduction and higher natality and foal survival. Improving vegetation near water is needed to increase the carrying capacity (to at least 37 adult females) of this endangered species on the Messir Plateau. Discussion is underway with local communities and government administration to designate the Messir Plateau and its dispersal range (foraging and movement corridors) as an African wild ass sanctuary. The local community supports the establishment of a 124 km^2 protected area on the Messir Plateau. Equally, they want to be involved fully and benefit from the establishment of the African wild ass sanctuary. Adjacent to the Messir Plateau there are 12 villages which are home to about 1400 Afar pastoralists who depend on livestock production for their livelihoods. The total area used by this population covers about 500 km^2. During the dry period, the majority of the villages depend on the Asaila spring for human and livestock use (Tesfai, personal observation). Therefore, all conservation programs in this area should be closely linked to local pastoralists being able to participate in, and benefit from the protected area.

The specific recommendations stemming from this research include:

1) The future viability of this species appears to be dependent on the establishment of a small African wild ass sanctuary (124 km^2) on the Messir Plateau. If the communities are committed and government conservation policies are supported, livestock, particularly cattle from the highlands should be excluded from the Messir Plateau. My research results suggest that the low nutrient level of the African wild ass results from by their displacement by the high number of cattle coming to the plateau from the highlands in rainfall months. The local

community close to the Messir Plateau owns few cattle (20-30) because the grass biomass in the area is insufficient to support them throughout the year. Most of the cattle observed in rainfall months are coming from the highlands. Hence, excluding livestock, especially cattle, from the area is likely to be supported by the local community. The local people in the area herd mainly camel, goats, and sheep.

2) This study and a previous study by Tesfai (2006) demonstrated that Asaila spring is the nearest permanent water available for the African wild ass occurring on the Messir Plateau in dry months. Hence, future conservations management should consider sustainable use of Asaila for human and wildlife. Artificial water points are often constructed to attract wildlife in a protected area (Owen-Smith 1996). However, the establishment of water points for the African wild ass on Messir Plateau is not an option because of potential major negative repercussions as it may attract more livestock.

3) Community elders from the 12 villages, local administrators, pastoralists at the local political level (sub-zoba Ghelalo administration) and wildlife experts should discuss and determine what area should be selected for the conservation of African wild ass on the Messir Plateau. This research will provide scientific data and maps for the discussion. The discussion in the meeting should also include the needs of the local people before and after the establishment of the protected area. The issue of water sources and improving grassland productivity should be discussed. The Ministry of Agriculture (Eritrea) has a plan for re-seeding the Messir Plateau and adjacent areas to improve the grass quality once the African wild ass sanctuary is established.

4) Once established, the boundaries of the protected area will be demarcated and legalised. Then, further research would be required to monitor and compare African wild ass carrying capacity and population viability before and after the establishment of the protected area. Vegetation biomass and African wild ass nutrition status on the Messir Plateau should be

measured at the beginning of the study and monitored at regular intervals. This research will provide a scientific basis for conservation management strategies.

References

Becker, C.D. and Ginsberg, J.R. 1990. Mother-infant behaviour of wild Grevy's zebra: adaptations for survival in semi-desert East Africa. *Animal Behaviour* **40**: 1111–1118.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* **4**: 91–98.

Casebeer, R.L. and Koss, G.G. 1970. Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *African Journal of Ecology* **8**: 25–36.

Ginsberg, J.R. 1988. Social organization and mating strategies of an arid adapted equid: the Grevy's zebra *Equus grevyi* (Kenya). Doctoral dissertation, Princeton University, New Jersey, US.

Loudon, A.S.I. and Kay, R.N.B. 1984. Lactational constraints on a seasonally breeding mammal: the red deer. In Symposia of the Zoological Society of London, **51,** 233-252). Published for the Zoological Society by Academic Press.

Macandza, V.A., Owen-Smith, N. and Cross, P.C. 2004. Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research* **34**: 113–121.

Moehlman, P.D. 2002. Status and Action Plan for the African wild ass (*Equus africanus*) In: Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan (ed Patricia D. Moehlman). IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge UK. pp 2-9.

Moehlman, P.D. Kebede, F. and Yohannes, H. 1998. The African Wild Ass (*Equus africanus*): Conservation Status in the Horn of Africa. *Applied Animal Behaviour Science* **60**: 115–124.

Moehlman, P.D., Kebede, F. and Yohannes, H. 2015. *Equus africanus*. In the IUCN Red List of Threatened Species 2015. www.iucnredlist.org.

Muntifering, J.R., Ditmer, M.A., Stapleton, S., Naidoo, R. and Harris, T.H. 2019. Hartmann's mountain zebra resource selection and movement behavior within a large unprotected landscape in northwest Namibia. *Endangered Species Research* **380**: 159–170.

Owen-Smith, N. 1996. Ecological guidelines for water points in extensive protected areas. *South African Journal of Wildlife Research-24-month delayed open access* **26**: 109–112.

Owen-Smith, N. 2007. Introduction to modeling on wildlife and resource conservation. Blackwell publishing. Oxford, UK. 332pp.

Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A. and Corlett, R.T. 2016. Saving the world's terrestrial megafauna. *Bioscience* **66**: 807–812.

Tesfai, R.T. 2006. Conservation of African wild ass (*Equus africanus*) in Messir plateau (Asaila), Eritrea: the role of forage availability and diurnal activity pattern during the rainy and beginning of the dry season. MSc Thesis, University of Kent/DICE, Canterbury, UK. 85pp.

Tesfai, R.T., Owen-Smith, N. Parrini, F and Moehlman, P.D. 2019. Viability of the critically endangered African wild ass (*Equus africanus*) population on Messir Plateau (Eritrea). *Journal of Mammalogy* **100**: 185–191.

Zeller, K.A., McGarigal, K. and Whiteley, A.R. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* **27**: 777–797.

Appendix I. Dominant herbaceous plants identified on Messir Plateau, Danakil desert, Eritrea (Oct 2016 – Mar 2019)

S.N	**Scientific name**	**Family name**	**Life form**
1.	*Amanranthus viridis*	Amaranthaceae	Herb
2.	*Abutilon hirtum*	Malvaceae	Herb
3.	*Barleria hildebrandtii*	Acanthaceae	Herb
4.	*Barleria lanceata*	Acanthaceae	Herb
5.	*Blepharis linariifolia*	Acanthaceae	Herb
6.	*Cleome gynandra*	Cleomaceae	Herb
7.	*Caralluma acutangula*	Asclepiadaceaea	Herb
8.	*Commelina latifolia*	Commelinaceae	Herb
9.	*Cometes abyssinica*	Caryophyllaceae	Herb
10.	*Corchorus olitorius*	Tiliaceae	Herb
11.	*Cucumis prophetarum*	Cucurbitaceae	Herb
12.	*Crotalaria impressa*	Fabaceae	Herb
13.	*Crepis foetida*	Asteraceae	Herb
14.	*Fagonia indica*	Zygophyllaceae	Herb
15.	*Glossonema nubicum*	Asclepiadaceae	Herb
16.	*Heliotropium longiflorum*	Boraginaceae	Herb
17.	*Heliotropium strigosum*	Boraginaceae	Herb
18.	*Indigofera articulate*	Fabaceae	Herb
19.	*Indigofera hochstetteri*	Fabaceae	Herb
20.	*Leucas martinicensis*	Lamiaceae	Herb
21.	*Melilotus albus*	Fabaceae	Herb
22.	*Ochradenus baccatus*	Resedaceae	Herb

23.	*Orthosiphon pallidus*	Lamiaceae	Herb
24.	*Podostelma schimperi*	Asclepiadaceae	Climber
25.	*Pulicaria undulate*	Asteraceae	Herb
26.	*Polygala erioptera*	Polygalaceae	Herb
27.	*Reichard tingitara*	Asteraceae	Herb
28.	*Solanum incanum*	Solanaceae	Herb
29.	*Reseda amblycarpa*	Resedaceae	Herb
30.	*Aristida adoensis*	Poaceae (Gramineae)	Grass
31.	*Brachiaria ramose*	Poaceae (Gramineae)	Grass
32.	*Cenchrus setigerus*	Poaceae (Gramineae)	Grass
33.	*Chloris pycnothrix*	Poaceae (Gramineae)	Grass
34.	*Cyperus rubicumdus*	Cyperaceae	Grass
35.	*Chrysopogon aucheri*	Poaceae (Gramineae)	Grass
36.	*Dichanthium annulatum*	Poaceae (Gramineae)	Grass
37.	*Eragrostis papposa*	Poaceae (Gramineae)	Grass
38.	*Eleusine compresaa*	Poaceae (Gramineae)	Grass
39.	*Paspalidium desertorum*	Poaceae (Gramineae)	Grass
40.	*Pennisetum setaceum*	Poaceae (Gramineae)	Grass
41.	*Phalaris paradoxa*	Poaceae (Gramineae)	Grass
42.	*Setaria incrassata*	Poaceae (Gramineae)	Grass
43.	*Setaria verticillata*	Poaceae (Gramineae)	Grass
44.	*Stipagrostis hirtigluma*	Poaceae (Gramineae)	Grass
45.	*Stipagrostis plumose*	Poaceae (Gramineae)	Grass
46.	*Sporobolus helvolus*	Poaceae (Gramineae)	Grass
47.	*Sporobolus spicalius*	Poaceae (Gramineae)	Grass

Appendix II. Individual African wild ass identified and monitored and recorded by camera traps travelling to the Asaila water during dry months. No females with foals less than 3 months were observed between Oct and Dec 2016.

Individual ID	Reproductive status	**Field observation days 2016**																		
		Oct (dry)				Nov (dry)							Dec (dry)							
		08	09	10	11	19	20	21	22	23	24	25	17	18	19	20	21	22	23	24
	Temperature max/min	35.6/ 23.3	35.7/ 28.2	33.5/ 21.9	33.1/ 24.8	32.6/ 21.4	32.1/ 24.6	34.4/ 19.7	34.7/ 20.7	32.9/ 22.7	33.9/ 22.3	33.1/ 22.3	34.5/ 25.4	31.1/ 25.3	35/ 21.8	34.4/ 23.7	34.4/ 22.7	33.7/ 21.5	36.2/ 23.7	35/ 24.6
F2016-1	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
F2016-2	With yearling aged 12-24 months	√	√	√	√	×	√	√	√	√	√	√	√	√	√	√	√	√	√	√
F2016-3	Pregnant	×	√	√	√	ø	ø	×	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	×	ø
F2016-4	Non-reproductive	×	×	√	×	×	×	×	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-6	With foal aged 4-12 months	×	√	√	√	×	×	×	×	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø
F2016-7	With foal aged 4-12 months	ø	ø	ø	ø	×	×	×	×	×	×	×	√	√	√	×	√	×	√	√
F2016-8	Non-reproductive	ø	ø	√	√	×	ø	ø	ø	ø	×	ø	ø	×	×	×	ø	ø	ø	ø
F2016-9	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
F2016-10	Pregnant	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×	√	√	√	√	√
F2016-11	Pregnant	ø	ø	ø	ø	ø	ø	×	ø	×	ø	ø	×	×	×	√	×	×	×	×
M2016-1	Territorial male	×	√	×	√	√	×	√	×	√	×	√	√	×	√	×	√	×	×	√

Key:
√ - Drinking data collected for successive days
× - Identified individual observed, but no drinking data collected
Ø - Identified individual were not seen during the study period

Appendix III. Individual African wild ass identified and monitored and recorded by direct observation and camera traps to water sources during rainfall months (March – June 2017).

Individual ID	Reproductive status	Field observation days 2017																					
		Mar (rain)						Apr (dry)					May (rain)							Jun (rain)			
		16	17	18	19	20	21	26	27	28	29	30	01	02	27	28	29	30	31	01	02	03	04
	Temperature max/min	34.1/ 22	30/ 19.7	35/ 20.1	33.3/ 19.5	30.2/ 21.4	31.8/ 22.1	36.1/ 28	40.5/ 21.8	37.6/ 24.3	37.9/ 27	36.1 / 29	36.9/ 23.5	40.1/ 27.1	27.5/ 23.3	33.5/ 22.2	31.5/ 21.2	35.8/ 24.2	31/ 23.8	38/ 24.7	37.9 / 21	35.6 / 23	35.3 25.3
F2016-1	Non-reproductive	ø	ø	ø	ø	ø	ø	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×
F2016-4	Non-reproductive	ø	ø	ø	ø	ø	ø	×	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-6	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	×	×	√	√	√	√
F2016-7	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	×	√	√	√	√
F2016-8	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	×	ø	ø	×	ø	√	×	×	×	√	×	ø	ø	ø	ø
F2016-9	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	ø	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-11	With foal aged ≤ 3 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
F2017-1	Non-reproductive	√	√	×	×	×	×	ø	ø	ø	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	×	×
F2017-2	Non-reproductive	√	√	√	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2017-3	Pregnant	√	√	√	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2017-4	Non-	ø	ø	ø	ø	ø	ø	×	√	√	√	√	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø

	reproductive																						
F2017-5	Non-reproductive	Ø	Ø	Ø	Ø	Ø	Ø	Ø	√	Ø	Ø	Ø	×	×	Ø	Ø	Ø	Ø	Ø	×	×	×	×
F2017-6	Non-reproductive	Ø	Ø	Ø	Ø	Ø	Ø	Ø	√	×	×	×	×	×	×	×	×	×	×	×	×	×	×
F2017-7	Non-reproductive	√	√	√	Ø	Ø	Ø	Ø	Ø	Ø	×	×	√	×	×	×	×	×	×	×	√	√	×
F2017-9	With foal aged ≤ 3 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√
M2016-1	Territorial male	×	√	×	√	×	√	×	√	×	√	√	√	×	√	×	√	√	×	×	√	×	√
M2017-1	Bachelor adult male	√	×	×	√	×	√	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø	Ø
M2017-2	Bachelor adult male	Ø	Ø	Ø	Ø	Ø	Ø	×	×	×	×	√	×	×	Ø	Ø	√	Ø	Ø	Ø	√	×	×
M2017-3	Bachelor adult male	Ø	Ø	Ø	Ø	Ø	Ø	×	×	×	×	√	×	×	Ø	Ø	√	Ø	Ø	Ø	√	×	×

Key:
√ **-** Drinking data collected for successive days
× **-** Identified individual observed, but no drinking data collected
Ø **-** Identified individual was not seen on this day

Appendix IV. Individual African wild ass identified and monitored and recorded by camera traps travelling to the Asaila water during dry months (Feb – April 2018).

Individual ID	Reproductive status	**Field observation days 2018**																				
		Feb (dry)						Mar (dry)			Apr (dry, except isolated showers)											
		07	08	09	10	11	12	14	15	16	15	16	17	18	19	20	21	22	23	24	25	26
	Temperature max/min	37.7/ 27	36/ 22.8	33.9/ 28.1	35.7/ 21.3	37.8/ 23.2	38.7/ 24	37.5/ 25.3	35.4/ 26	37.2/ 26	33.6/ 26.2	36.6/ 27.3	34.8/ 21.9	34/ 22.9	37.6/ 29.5	35.7/ 28.3	32.2/ 29	29.4/ 23.1	30.2/ 21.8	33.9/ 21.8	34.6/ 22.2	35.5/ 21.8
F2016-1	Non-reproductive	×	ø	ø	ø	ø	×	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-2	Non-reproductive	ø	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-3	With foal aged 4-12 months	×	×	×	×	×	√	√	×	×	×	×	×	×	×	×	×	×	×	×	×	×
F2016-6	Non-reproductive	×	ø	ø	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-7	Non-reproductive	×	ø	ø	×	ø	×	ø	ø	ø	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-9	Non-reproductive	×	ø	ø	×	×	×	ø	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2016-10	With foal aged 4-12 months	×	√	√	√	√	√	√	×	√	×	×	×	×	×	×	×	×	×	×	×	×
F2016-11	With yearling aged 12-24 months	×	×	×	×	×	×	ø	ø	ø	×	×	×	×	×	×	×	×	×	×	×	×
F2017-2	Non-reproductive	×	×	×	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2017-3	With foal aged 4-12 months	√	√	×	√	×	×	ø	×	×	×	×	×	×	×	×	×	ø	ø	ø	ø	ø
F2017-4	Non-reproductive	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø

F2017-5	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×	×	×
F2017-6	Non-reproductive	ø	ø	ø	×	ø	ø	ø	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2017-7	Non-reproductive	ø	ø	ø	ø	ø	×	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
F2017-8	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	×	×	×	×	×
F2017-9	With yearling aged 12-24 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	×	×	×
F2018-1	With foal aged ≤ 3 months	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	√	×	√	×
F2018-2	Pregnant	ø	ø	ø	ø	√	√	√	×	×	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
M2016-1	Territorial male	√	×	×	√	√	×	√	×	√	×	√	×	√	×	√	×	×	×	×	×	×
M2016-1a	Bachelor sub-adult male	√	×	×	√	√	√	√	×	√	√	×	√	×	×	√	√	×	√	×	×	×

Key:
√ - Drinking data collected for successive days
× - Identified individual observed, but no drinking data collected
Ø - Identified individual was not seen on this day

Appendix V. Individual African wild ass identified and monitored and recorded by camera traps travelling to the Asaila water during dry months (Jan – Mar 2019).

Individual ID	Reproductive status	**Field observation days 2019**																				
		Jan (dry, except isolated showers)									Feb (dry)					Mar (dry, except isolated showers)						
		20	21	22	23	24	25	26	27	28	18	19	20	21	22	14	15	16	17	18	19	20
	Temperature max/min	33.1/ 30	32.7/ 25.2	29.6/ 19.8	32.2/ 23	30.9/ 23.5	35.5/ 27.7	33.5/ 23	34.5/ 22.6	31.5/ 23	30.8/ 19.5	32.5/ 20.3	34.4/ 19.2	21.1/ 20.9	29.6/ 19.8	43.6/ 27.1	39.2/ 25.5	38/ 28.2	37.2/ 27.1	36/ 27	40.2/ 27	44.7/ 25.3
F2016-3	With yearling aged 12-24 months	×	×	×	×	×	×	×	×	×	×	×	×	×	×	ø	ø	ø	ø	ø	ø	ø
F2016-4	Non-reproductive	ø	ø	ø	√	√	ø	ø	√	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×
F2016-6	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×	ø	ø	ø	×
F2016-7	Non-reproductive	ø	ø	ø	√	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×	ø	ø
F2016-8	Non-reproductive	ø	ø	ø	√	ø	ø	√	ø	ø	Confirmed dead											
F2016-10	With yearling aged 12-24 months	×	√	×	×	√	√	×	×	√	√	×	×	×	×	√	×	×	√	×	√	√
F2016-10a	Non-reproductive	ø	ø	ø	ø	√	×	×	×	√	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×
F2016-11	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	ø	ø	ø	ø	×	×	ø	ø
F2017-1	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	ø	ø	ø	ø	ø	×
F2017-2	Non-reproductive	×	×	×	√	×	×	×	√	×	×	×	√	×	×	×	×	ø	ø	ø	ø	ø

F2017-4	Non-reproductive	ø	ø	ø	ø	ø	ø	ø	√	×	√	×	×	√	×	×	×	×	√	×	×	×
F2017-8	Non-reproductive	×	×	×	×	×	√	×	×	√	×	×	√	×	×	×	×	×	×	√	×	×
F2017-8a	Non-reproductive	×	×	×	×	×	√	×	×	√	×	×	√	×	×	×	×	×	×	√	×	×
F2017-9	Non-reproductive	×	×	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	×	×	√	×	√	×	×
F2018-1	With foal aged 4-12 months	√	×	×	×	√	×	√	×	√	√	×	×	√	×	√	×	√	×	√	×	√
F2018-2	With foal aged 4-12 months	×	√	×	×	√	√	√	×	×	√	×	×	×	×	×	√	×	√	×	√	√
F2019-1	Non-reproductive	×	√	×	√	×	×	√	×	×	ø	ø	ø	ø	ø	√	×	×	×	√	×	√
F2019-2	Non-reproductive	×	√	×	×	√	×	√	×	√	×	ø	ø	ø	ø	√	×	×	×	×	×	√
M2016-1	Territorial male	√	×	×	√	×	×	×	√	√	√	×	×	√	×	√	×	×	√	×	×	√
M2017-2	Bachelor adult male	ø	ø	ø	ø	ø	×	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø
M2017-3	Bachelor adult male	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	ø	×	×	×	×	×	×	×
M2016-1a	Bachelor sub-adult male	×	×	√	×	×	×	√	×	×	×	×	√	×	×	×	×	√	×	√	×	×

Key:
√ - Drinking data collected for successive days
× - Identified individual observed, but no drinking data collected
Ø - Identified individual was not seen on this day

Appendix VI. Mean drinking intervals (hrs) between successive visits to water sources (dry vs. rainfall months) per each female adult reproduction category and each male category of African wild ass on the Messir Plateau, Eritrea (Oct 2016 – Mar 2019). N represents number of times an individual visited the water source.

		Drinking intervals (hrs)							
		Permanent (dry months)				Seasonal (rainfall months)			
Individual ID	Sex and reproduction categories	N	Mean	Min	Max	N	Mean	Min	Max
F2016-11	Female with foal aged ≤ 3 months	9	28:14	18:32	30:16	29	12:48	09:37	19:06
F2017-9	Female with foal aged ≤ 3 months	9	25:06	18:17	27:09	31	14:19	09:48	24:15
F2018-1	Female with foal aged ≤ 3 months	18	21:31	18:48	27:48	1	18:48	-	-
F2016-3	Female with foal aged 4-12 months (older)	2	48:16	22:04	96:13	-	-	-	-
F2016-6	Female with foal aged 4-12 months	3	28:54	24:01	52:45	-	-	-	-
F2016-7	Female with foal aged 4-12 months	6	25:16	19:35	34:32	-	-	-	-
F2016-10	Female with foal aged 4-12 months	7	24:59	21:53	32:16	-	-	-	-
F2017-3	Female with foal aged 4-12 months	3	29:19	23:16	48:05	-	-	-	-
F2018-1	Female with foal aged 4-12 months (older)	2	59:51	28:27	91:15	8	23:49	23:07	24:12
F2018-2	Female with foal aged 4-12 months (older)	3	66:14	32:19	112.2	6	24:08	23:13	26:12
F2016-1	Female with yearling aged 12-24 months	19	24:43	23:21	30:45	-	-	-	-
F2016-2	Female with yearling aged 12-24 months	18	25:12	23:03	30:56	-	-	-	-
F2016-6	Female with yearling aged 12-24 months (older yearlings)	4	47:20	23:03	87:34	16	20:45	12:56	26:12
F2016-7	Female with yearling aged 12-24 months	5	26:23	19:19	120:4	16	19:54	12:26	25:56
F2016-9	Female with yearling aged 12-24 months	20	23:23	19:59	25:53	-	-	-	-
F2016-10	Female with yearling aged 12-24 months (older yearlings)	3	69:24	23:57	152:2	6	24:01	23:13	27:12
F2017-8	Female with yearling aged 12-24 months	16	23:19	23:16	26:05	2	46:51	22:27	71:15

F2017-9	Female with yearling aged 12-24 months	15	23:38	17:19	28:36	4	25:50	21:06	63:38
F2016-3	Pregnant female	3	85:48	27:00	158:0	2	47:43	22:25	72:22
F2016-10	Pregnant female (10+ months)	5	32:53	23:58	72:10	-	-	-	-
F2016-11	Pregnant female	1	98:52	-	-	-	-	-	-
F2017-3	Pregnant female	-	-	-	-	3	98:52	38:52	210:5
F2018-2	Pregnant female	3	96:17	48:49	144:3	-	-	-	-
F2016-4	Non-reproductive female	1	96:29	-	-	3	56:23	36:15	75:17
F2016-8	Non-reproductive female	2	59:59	23:56	96:02	2	62:41	49:19	76:03
F2017-1	Non-reproductive female	-	-	-	-	2	72:03	22:56	120:1
F2017-2	Non-reproductive female	-	-	-	-	6	47:20	23:03	72:34
F2017-4	Non-reproductive female	5	51:23	36:19	144:4	2	62:50	49:22	76:18
F2017-5	Non-reproductive female	1	237:0	-	-	-	-	-	-
F2017-6	Non-reproductive female	1	237:1	-	-	-	-	-	-
F2017-7	Non-reproductive female	-	-	-	-	5	72:48	23:09	240:3
F2017-8	Non-reproductive female	-	-	-	-	4	58:17	25:30	190.3
F2017-8a	Non-reproductive female	-	-	-	-	4	58:19	27:11	189.2
F2017-9	Non-reproductive female	-	-	-	-	2	108:1	46:32	168:5
F2016-10a	Non-reproductive female	-	-	-	-	2	105:2	36:33	173:3
F2019-1	Non-reproductive female	1	245:3	-	-	5	75:18	25:30	236:3
F2019-2	Non-reproductive female	1	246:2	-	-	5	73:48	27:11	240:3
M2016-1	Territorial male	21	43:37	23:14	54:45	18	30:43	09:55	51:32
M2017-1	Bachelor adult male	-	-	-	-	3	194.4	168:4	246:3
M2017-2	Bachelor adult male	3	227.5	119.5	247.5	-	-	-	-
M2017-3	Bachelor adult male	3	238.1	123.1	248.1	-	-	-	-
M2016-1a	Bachelor sub-adult male	10	23:59	18:22	27:39	6	18:03	16:51	24:48

Appendix VII: Time of visit to water sources (permanent vs seasonal) of individual African wild ass in the Messir Plateau, Eritrea (Oct-Dec 2016; Mar-June 2017; Feb-Apr 2018 and Jan- Mar 2019). In dry months the time was recorded by camera traps when African wild ass were traveling to Asaila and during the rainfall months data were recorded at the seasonal water sources. N represents number individual visits to water sources.

	Permanent (dry months)										**Seasonal (rainfall months)**									
	18h00-24h00		00h00-06h00		06h00-12h00		12h00-18h00		**Total**		18h00-24h00		00h00-06h00		06h00-12h00		12h00-18h00		**Total**	
Reproduction categories	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Females with foals aged ≤ 3 months (n=3)	28	77.8	8	22.2	0	0.0	0	0.0	36	100	36	59.0	3	4.9	22	36.1	0	0.0	61	100
Females with foals aged 4-12 months (n=6)	8	38.1	13	61.9	0	0.0	0	0.0	21	100	8	57.1	6	42.9	0	0.0	0	0.0	14	100
Females with yearlings aged 12-24 months (n=9)	50	48.5	53	51.5	0	0.0	0	0.0	103	100	30	68.2	10	22.7	4	9.1	0	0.0	44	100
Pregnant females (n=5)	8	66.7	4	33.3	0	0.0	0	0.0	12	100	3	100	0	0.0	0	0.0	0	0.0	3	100

Non-reproductive female (n=14)	9	75.0	3	25.0	0	0.0	0	0.0	12	100	28	66.7	13	31.0	1	2.4	0	0.0	42	100
Territorial male (n=1)	10	47.6	11	52.4	0	0.0	0	0.0	21	100	10	55.6	2	11.1	6	33.3	0	0.0	18	100
Bachelor adult male (n=3)	4	66.7	2	33.3	0	0.0	0	0.0	6	100	0	0.0	0	0.0	3	100	0	0.0	3	100
Bachelor sub-adult male (n=1)	7	70.0	3	30.0	0	0.0	0	0.0	10	100	3	50.0	2	33.3	1	16.6	0	0.0	6	100

Appendix VIII: Travel distance between morning foraging and drinking sites for each African wild ass individual on the Messir Plateau (Oct 2016 – Mar 2019). N represents number of times an individual visited the water sources.

		Estimated distance to water sources (km)							
		Permanent (dry months)				Seasonal (rainfall months)			
Individual ID	Sex and reproduction categories	N	Mean	Min	Max	N	Mean	Min	Max
F2016-11	Female with foal aged ≤ 3 months	9	9.32	7.78	10.88	29	3.18	0.97	6.68
F2017-9	Female with foal aged ≤ 3 months	9	9.31	7.78	10.88	31	3.19	0.2	6.69
F2018-1	Female with foal aged ≤ 3 months	18	8.5	6.14	11.64	1	4.37	4.37	4.37
F2016-3	Female with foal aged 4-12 months	2	6.58	5.54	7.63	-	-	-	-
F2016-6	Female with foal aged 4-12 months	3	10.09	8.99	12.24	-	-	-	-
F2016-7	Female with foal aged 4-12 months	6	10.8	8.11	13.44	-	-	-	-
F2016-10	Female with foal aged 4-12 months	7	8.39	6.24	11.72	-	-	-	-
F2017-3	Female with foal aged 4-12 months	3	4.56	8.05	8.84	-	-	-	-
F2018-1	Female with foal aged 4-12 months	2	10.67	9.63	11.72	8	4.83	0.54	8.2
F2018-2	Female with foal aged 4-12 months	3	10.21	9.63	11.2	6	4.66	0.54	8.33
F2016-1	Female with yearling aged 12-24 months	19	11.92	8.11	15.62	-	-	-	-
F2016-2	Female with yearling aged 12-24 months	18	11.46	8.11	14.67	-	-	-	-
F2016-6	Female with yearling aged 12-24 months	4	9.15	7.78	10.88	16	3.23	0.3	6.69
F2016-7	Female with yearling aged 12-24 months	5	10.48	8.79	12.03	16	3.38	1.31	6.53
F2016-9	Female with yearling aged 12-24 months	20	11.73	8.11	15.62	-	-	-	-
F2016-10	Female with yearling aged 12-24 months	3	10.33	9.63	11.72	6	5.02	0.23	10.3
F2017-8	Female with yearling aged 12-24 months	16	8.35	6.24	11.64	2	1.65	0.86	2.45

F2017-9	Female with yearling aged 12-24 months	15	8.22	5.53	11.64	4	2.32	0.86	3.33
F2016-3	Pregnant female	3	9.75	9.05	10.11	-	-	-	-
F2016-10	Pregnant female	5	10.57	8.11	12.55	-	-	-	-
F2016-11	Pregnant female	1	12.55	12.55	12.55	-	-	-	-
F2017-3	Pregnant female	-	-	-	-	3	4.56	0.26	6.69
F2018-2	Pregnant female	3	8.08	7.61	8.47	-	-	-	-
F2016-4	Non-reproductive female	1	11.59	11.59	11.59	3	1.08	0.23	1.98
F2016-8	Non-reproductive female	2	9.65	8.99	10.33	2	2.06	1.02	3.1
F2017-1	Non-reproductive female	-	-	-	-	2	5.74	5.56	5.92
F2017-2	Non-reproductive female	-	-	-	-	6	4.39	1.45	6.97
F2017-4	Non-reproductive female	5	10.53	8.79	12.03	2	4.58	1.98	7.18
F2017-5	Non-reproductive female	1	12.07	12.07	12.07	-	-	-	-
F2017-6	Non-reproductive female	1	12.07	12.07	12.07	-	-	-	-
F2017-7	Non-reproductive female	-	-	-	-	5	4.78	2.61	6.69
F2017-8	Non-reproductive female	-	-	-	-	4	5.02	1.49	8.2
F2017-8a	Non-reproductive female	-	-	-	-	4	5.02	1.49	8.2
F2017-9	Non-reproductive female	-	-	-	-	2	3.46	3.43	3.5
F2016-10a	Non-reproductive female	-	-	-	-	2	1.01	0.54	1.49
F2019-1	Non-reproductive female	1	9.63	9.63	9.63	5	6.05	1.02	10.3
F2019-2	Non-reproductive female	1	9.63	9.63	9.63	5	4.82	0.54	10.3
M2016-1	Territorial male	21	9.34	7.63	14.73	18	3.65	0.2	7.85
M2017-1	Bachelor adult male	-	-	-	-	3	2.68	1.56	4.36
M2017-2	Bachelor adult male	3	6.23	3.93	7.78	-	-	-	-
M2017-3	Bachelor adult male	3	7.11	6.44	7.78	-	-	-	-
M2016-1a	Bachelor sub-adult male	10	8.32	5.54	11.64	6	6.85	2.77	9.27