Conservation and ecology of nocturnal primates: night monkeys, galagos, pottos and angwantibos as case studies

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This dissertation is the result of my own work, and includes nothing which is the outcome of work done in collaboration except where specifically stated in the text.

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Abstract

Nocturnal primates are generally understudied compared to their diurnal cousins, and in some geographical areas there is an almost complete dearth of knowledge on nocturnal primates, for example in Angola and the Gambia. Also well-studied species are less known in part of their distribution, thick-tailed greater galago (*Otolemur crassicaudatus*) in Uganda and the Panamanian night monkey (*Aotus zonalis*) are both a case in point. Further there are topics where African nocturnal primates in particular previously have been overlooked: trade and ethnozoological usage. My publications included in this PhD by Published Work document the results of field surveys carried out between 2006 and 2016 across Africa (Uganda, the Gambia and Angola) as well as Central and South America (Panama and Argentina). They further include results of desk based studies conducted between 2014 and 2016. My research has focused on the conservation and ecology on often little known nocturnal primates, namely night monkeys (*Aotus* spp.), galagos (*Galago* spp., *Galagoides* spp. and *Otolemur* spp.), pottos (*Perodicticus* spp.) and angwantibos (*Arctocebus* spp.). The overall goal of my studies was to fill the large information gaps on the ecology, biogeography and conservation status of nocturnal primates. Using systematic methods, conducting transects and behavioural observation I have collected data on previously understudied nocturnal primates, including data on their distribution, densities and ecology. These field studies were then combined with data I extracted from the literature, questionnaires and online databases adding to what we know on domestic and international trade in nocturnal primates. I have with my research showed that nocturnal primates of Africa occur more frequently than previously thought within both the bushmeat and pet trades. I was also able to give an overview of the extent of international trade in the Neotropical nocturnal primates. Through my research and subsequent publications I have managed to create baselines for further studies and hopefully it will aid in promoting conservation of these nocturnal primates.

Dedication

I want to dedicate this PhD to my late great aunt Stina Hermansson who always been my greatest motivator to get this PhD and an inspiration to me in so many ways. And also to the late Ingalill Aldén for putting the idea of doing a PhD in my head, many years ago.

”Man ska vara rädd om det man vill bevara och älska sin nästa”

Stina Hermansson

1913 - 2016

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Abbreviations

CITES – Convention on International Trade in Endangered Species

ha – Hectares

IUCN – International Union for Conservation of Nature

kg – Kilograms

kHz – Kilohertz

km – Kilometers

m asl – Meters above sea level

mm – Millimeter

NGO – Non-governmental Organization

NP – National Park

NPRG – Nocturnal Primate Research Group

CHAPTER 1:

INTRODUCTION

1.1 General introduction

Of the currently 504 recognised primate taxa, more than 60% are now categorised under the Threatened categories (Vulnerable, Endangered and Critically Endangered) on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species 2016 (Estrada *et al.,* 2017). Although primates are fortunate in that no species has gone extinct during the last four centuries (Cowlishaw, 1999), an increasing number of primate species are on the brink of extinction with ~75% of the species having declining populations (Cotton *et al*., 2016; Estrada *et al*., 2017). The threats to their survival include habitat destruction, climate change, hunting, ethnozoological use, trade and infectious diseases (Wich & Marshall, 2016). Forest loss is most severe in the Neotropics (Central and South America) with >5,000 km^2 forest having been lost annually between 1990 and 2015 (FAO, 2016). The forest within the Neotropics are especially rich in primate biodiversity, as with 171 recognized species they are home to the highest number of primate taxa of any primate regions (the regions being: Neotropics, Asia, Africa and Madagascar) (Estrada *et al*., 2017). Mainland Africa (hereafter referred to as Africa) hosts the third largest primate diversity with 111 recognised species and subspecies (Estrada *et al*., 2017), but the African forests are also disappearing at alarming rates with 2,500 - 5,000 km^2 lost annually in the same time period (FAO, 2016). Even though the global net forest loss has decreased by 50% since 1990 the trends in both these areas are going in the opposite direction (FAO, 2016). This rampant habitat destruction is mainly due to growing human population, logging, fuelwood production, cattle ranching, and infrastructural projects (Contreras-Hermosilla, 2000; Fearnside, 2005; Gibbs *et al.,* 2010; FAO, 2016).

Habitat loss combined with the fragmentation of the remaining forests and increased hunting due to accessibility are together forming the largest threat to primate conservation (Fa *et al.,* 2002; Strier, 2011). Hunting and trade of primates is occurring at unsustainable levels in many primate range countries, and especially in West and Central Africa, and in South East Asia the trade of primates, both live individuals and body parts, is considered a major threat to primate populations (Brashares, 2003; Milner-Gulland & Bennet, 2003; Nijman *et al.*, 2011; Mittermeier *et al.,* 2012). Also in areas where bushmeat trade was not previously thought to be a threat to primates evidence are now accumulation to prove the opposite, as with the protected lemurs in Madagascar (Razafimanahaka *et al*., 2012).

Primate conservation is a complex challenge that is becoming increasingly important. The necessity to conserve primates is multifaceted. Not only do primates have key ecological functions, such as being important for their habitats as seed dispersers and pollinators (Corlett, 2002; Russo & Chapman, 2011; Peres *et al*., 2016), they also serve as umbrella/flagship species as by conserving primates and their habitats we are also conserving other species living within the same environment (Marshall & Wich, 2016a). Further, primates are important to the human population, by enabling economic benefits for communities in their vicinity by providing revenue from eco-tourism (Kirkby *et al.,* 2010) and as they are our closest relatives, by studying the behaviour, ecology and sociology of primates we can learn more about our own evolution (Marshall & Wich, 2016a).

For a proper understanding of the evolution and ecology of primates, and indeed their conservation, it is vital to include representative samples of all primate taxa (Nekaris & Nijman, 2013). And for conservation efforts and strategies to be meaningful a proper understanding of the distribution and ecology of also lesser-known species is crucial. There is an increasing amount of primatological research being conducted globally, but the majority of primate studies focus on diurnal species (Chapman & Peres, 2001; Nekaris & Nijman, 2013). Due to the cryptic nature of nocturnal primates, and specialised techniques needed to study them, hitherto these taxa have been underrepresented in the primate literature, also in publication regarding their conservation (Fig. 1).

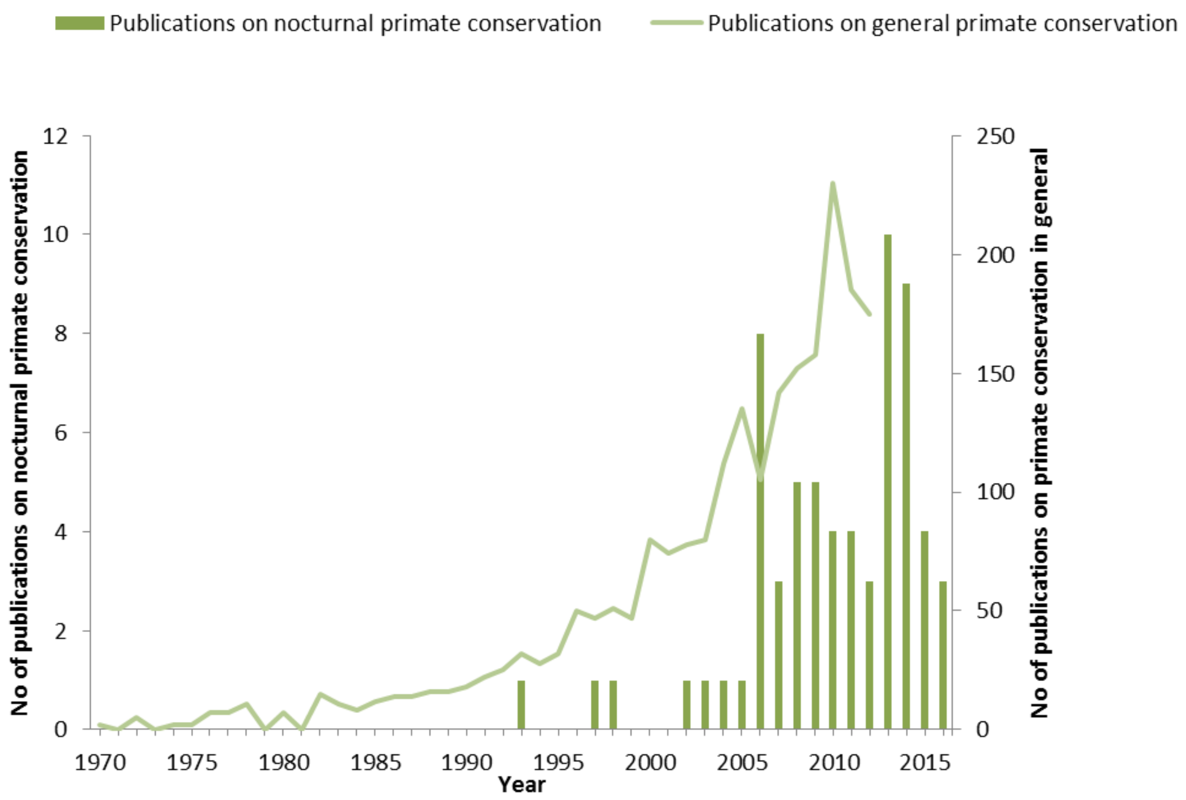

Figure 1. *First Y axis:* The number of scientific publications on nocturnal primate conservation annually from 1970 – 2016. Data reflect the numbers returned using key words in Web of Science (https://login.webofknowledge.com) where all key words were present in the result of the search ('nocturnal' + 'primate' + 'conservation'). Search was done 07/12/16. *Second Y axis:* The number of publications on primate conservation in general between 1970 and 2012. Source: Wich & Marshall, 2016.

Nocturnal primates are found in all primate range areas; Neotropics (N = 11 species), Asia (N = 22), Africa (N = 26) and Madagascar (N = 65). The majority of nocturnal primates fall under the suborder Strepsirrhini, as does the Lemuroidea of Madagascar with more than half of them being nocturnal or cathemeral (Gould *et al*., 2011). The Strepsirrhini in Africa are the Galagidae and the Lorisidae, the latter also ranging in Asia (Nekaris & Bearder, 2011). Under the suborder Haplorrhini the nocturnal primates are Tarsiidae which occurs in Asia, and the Aotidae in the Neotropics (Campbell *et al*., 2011). This dissertation will focus on the distribution, ecology and trade of the nocturnal primates of the Neotropics and Sub-Saharan

Africa to contribute to the long-term conservation of these nocturnal primates and to create a baseline for further studies.

1.1.1 Distribution and ecology

Mapping geographical ranges of primates, collecting data on their habitat use and abundance in different ecosystems are important when defining the conservation status and planning conservation initiatives of species and populations (Cowlishaw & Dunbar, 2000; Campbell *et al*., 2011). Knowing whether these patterns are changing with time is perhaps even more critical, to increase our awareness about the current conservation status of primate species, as well as making population viability predictions considering future environmental changes. Geographic and climatic shifts affect primate distributions via changes in vegetation composition and habitat connectivity. Ecological barriers, including mountain ranges, rivers, different habitat types, and habitat disturbance, cause species to colonise different areas and leading to new species interactions, adaptations and speciation (Butynski & de Jong, 2007; Aquino *et al*., 2009, Harcourt & Wood, 2012). Primate species are limited by geographic barriers such as rivers like the Amazon River in the Neotropics (Gascon *et al*., 2000) or mountain ranges, for example the Eastern Rift Valley and the Angolan Escarpment (Butynski & de Jong, 2007; Svensson & Bersacola, 2013, Bersacola *et al*., 2015).

Geographical ranges are also determined by the primate species' ecological adaptation abilities and flexibility (i.e. opportunity to exploit new niches during environmental changes). Understanding ecological adaptations (e.g. habitat use, diet, the relationship between habitat and density of primates) help us understand their ecological requirements and therefore predict their distribution patterns and develop appropriate conservation management plans (Campbell *et al*., 2011).

1.1.2 Trade in nocturnal primates

Wildlife trade, be it for consumption, biomedical purposes, use of body parts or as pets, occurs both domestically, regionally and internationally and represents one of the leading threats to tropical biodiversity conservation (Nijman *et al*., 2011; Linder *et al*., 2013). International trade of primates have been estimated to include about 40,000 live primates annually (Karesh *et al.,* 2005). When including domestic trade, the trade in live primate involves even more, and including body parts or dead specimens this number is in the millions each year (Fa *et al*., 2006; Nijman *et al.,* 2011).

The reason primates, and other mammals, are traded varies depending on where in the world the trade occurs, and on what species of animal it is. Bushmeat trade is particularly rampant in Central and West Africa and primates are, along with duikers the most commonly hunted and traded animals (Bowen-Jones *et al*., 2003). Medium and large bodied species are more common in the bushmeat trade (Robinson, 1995; Fa *et al.,* 2006) but smaller species are being targeted in increasing numbers due to overhunting of larger species (Anadu *et al.,* 1988). Pet trade of primates is mostly occurring in South East Asia and the Neotropics (Fuentes, 2006). Using primates in traditional practices is most common in Asia, followed by Africa where 59% and 32% of all primate species occurs in this type of trade respectively (Alves *et al*., 2010; Starr *et al.,* 2010). Before the of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) came into force in 1975 trade in primates for the biomedical trade was rampant, but subsequently breeding centres became more popular, leading to the legal international trade numbers in many species has gone down (Gozalo & Montoya, 1990; Rappold & Eckert, 1994; Málaga *et al.,* 1997; Obaldía III, 2001; Linder *et al*., 2013).

With the majority of individuals in the trade being wild caught, many primate populations are in danger of not being able to sustain heavy exploitation (Cowlishaw & Dunbar 2000; Schwitzer *et al*., 2012). Trade of wildlife greatly affects their conservation as it can cause biodiversity loss, introduce invasive species into new areas and spread diseases (Baker *et al*., 2013).

Prior to my studies no studies had focussed on trade in nocturnal primates in Africa, although nocturnal primates are sometimes included in data from bushmeat market surveys (e.g. Fa *et al.,* 2006; Gaubert *et al*., 2014). In Asia, the Neotropics and Madagascar more research has been conducted on trade, especially in the slow lorises (*Nycticebus* spp.), lemurs and in the Neotropical diurnal primates (Duarte-Quiroga & Estrada, 2003; Nekaris & Nijman, 2007; Ratsimbazafy, 2009; Nekaris *et al.,* 2010; Starr *et al.,* 2010; Maldonado & Peck, 2014; Reuter *et al.,* 2016). As seen in these primates, and especially the Asian lorises, the more research that has been conducted on these species the more apparent it has become that trade is one of the major threats to their survival (Svensson & Friant, 2014; KAI Nekaris, pers. comm.).

1.2 Background

As a research member of the Nocturnal Primate Research Group (NPRG) at Oxford Brookes University since 2008 I have been conducting research throughout the Neotropics and Africa. My research has focused on the conservation and ecology on often little known nocturnal primates, namely night monkeys (*Aotus* spp.), galagos (*Galago* spp., *Galagoides* spp. and *Otolemur* spp.), pottos (*Perodicticus* spp.) and angwantibos (*Arctocebus* spp.). In the subsequent text I abbreviate *Galagoides* as *Gd*. to distinguish it from the abbreviation of *Galago* (*G*.).

I have chosen to focus my case studies in geographical areas with an almost complete dearth of knowledge on nocturnal primates, and on species that has previously been neglected or understudied in part of their range. The fieldwork in Panama was conducted on the then newly acknowledged species *Aotus zonalis* (Defler & Bueno, 2007; Rylands *et al*., 2012). I chose to focus on this species as it had not been subject to any long-term research prior to mine and I had the opportunity to study the northernmost *Aotus* species in a national park with a wide range of habitats at different altitude (Estrada *et a*l., 2005; Fondo Chagres, 2009). I then followed this research up with research on the southernmost *Aotus* species in Argentina, *A. azarae*, when I joined the longest running project focussing on night monkeys, the Owl Monkey Project in norther Argentina (Juarez *et al*., 2011).

The fieldwork in Angola was arranged as no studies previously had been conducted previously on nocturnal primates in the country (Bersacola *et al*., 2015; Svensson *et al*., 2017d). The study sites on the Angolan Escarpment were chosen due to the landscape characteristics, with differences in elevation gradients and habitat mosaics creating an uniquely biodiverse region (Figueiredo, 2010; Clark *et al*., 2011; Romeiras *et al*., 2014). I had also been made aware that a possible new species of galago occurred in the area, based on museum specimens, and wanted to survey the area to confirm this (Svensson *et al.*, 2017d).

Galago senegalensis is one of the most studied nocturnal primates in Africa, however the research has been focussed in the eastern part of their range (Ambrose, 2002; Off *et al.,* 2008; Butynski & de Jong, 2012; Nash *et al*., 2013). I therefore chose to study the westernmost subspecies *G. s. senegalensis* in the Gambia to enable comparisons with the eastern subspecies regarding their ecology and behaviour (Svensson & Bearder, 2013). *Otolemur crassicaudatus* is another well studied species, but it is still unconfirmed in parts of its range (de Jong & Butynski, 2012). I therefore chose to focus my research on this species in Uganda where it has previously been highlighted as possibly occurring but confirmation was needed (de Jong & Butynski, 2012; Svensson & Bersacola, 2013).

I have also chosen to conduct research on topics where African, and to some degree Neotropical, nocturnal primates previously have been overlooked: trade and the ethnozoological utilisation (Svensson & Friant, 2014; Svensson *et al.,* 2015; Svensson *et al*., 2016). In Asia it has become apparent through an increase in research that trade in nocturnal primates is a bigger threat to their survival than previously thought (Nekaris & Nijman, 2007; Nekaris *et al*., 2010; Starr *et al.*, 2010), I therefore became interested in exploring if this was the case also for the African and Neotropical nocturnal primates (Svensson & Friant, 2014; Svensson et al., 2015; Svensson *et al*., 2016). Throughout this dissertation I will be referring to the research as conducted by myself, however by using "I" I am also referring to all the colleagues that I have worked with throughout the research stages and writing of the publications included in this dissertation, all listed in the acknowledgements.

1.3 Aim and objectives of this research programme and dissertation outline

The overall goal of my studies was to fill the large information gaps on the ecology and biogeography of nocturnal primates and thus aiding their conservation. The objectives set for the work included in this dissertation were to create a baseline for further studies and promote conservation of these species. Specific aims are presented in the publications that form this dissertation, but can be summarised as follows:

- To confirm presence of little studied nocturnal primate species in Neotropics and Sub-Saharan Africa.
- To provide density estimates or distribution data to aid with conservation initiatives.
- To provide habitat assessments and to get a better understanding of the ecology of nocturnal primate species in the Neotropics and Sub-Saharan Africa.
- To find out if trade and ethnozoological usage in nocturnal primates are on the increase, as well as where and how it is occurring.
- To assess possible conservation threats to nocturnal primate populations.

1.4 A list of the publications in this research programme

As all the publications included in this dissertation (Annexes 1-8) are multi-authored work, I here describe the extent and scope of my contribution in relation to the other authors. Co-author statements on my contribution on the Publications included in this dissertation can be found in Annex 10.

DISTRIBUTION & ECOLOGY

Svensson MS, Samudio R, Bearder SK, Nekaris KAI (2010). Density estimates of Panamanian owl monkeys (*Aotus zonalis*) in three habitat types. *American Journal of Primatology,* 72: 187-192.
I initiated this study, and was thereafter involved in all parts of finalising the paper, including collecting the data, analysing the data and writing the paper.

Svensson MS, Bearder SK (2013). Sightings and habitat use of the northern lesser galago (*Galago senegalensis senegalensis*) in Niumi National Park, the Gambia. *African Primates,* 8: 51-58.
I initiated this study along with SK Bearder, and was thereafter involved in all parts of finalising the paper, including collecting and analysing the data and writing the paper.

Svensson MS, Bersacola E (2013). Sightings of thick-tailed greater galago *Otolemur crassicaudatus monteiri* (Bartlett in Gray, 1863) near Lake Mburo National Park, south Uganda. *African Primates,* 8: 63-66.
I initiated this study, and was thereafter involved in all parts of finalising the paper, including collecting the data and writing the paper.

Bersacola E, Svensson MS, Bearder SK (2015). Niche partitioning and environmental factors affecting abundance of strepsirrhines in Angola. *American Journal of Primatology,* 77(11): 1179-1192.
I initiated this study along with E Bersacola and SK Bearder, and was thereafter involved in most parts of finalising the paper, including collecting the data and writing the paper.

Svensson MS, Bersacola E, Mills MSL, Munds RA, Nijman V, Perkin A, Masters JC, Couette S, Nekaris KAI & Bearder SK (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. *American Journal of Physical Anthropology*, 163(1): 30-43.
I initiated this study along with E Bersacola and SK Bearder, and was thereafter involved in most parts of finalising the paper, including collecting the data and writing the paper.

TRADE IN NOCTURNAL PRIMATES

Svensson MS, Friant SC (2014). Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. ***Endangered Species Research,*** **23(2): 107-114.**
I initiated this study and was thereafter involved in all parts of finalising the paper, including collecting and analysing the data and writing the paper.

Svensson MS, Ingram D, Nekaris KAI, Nijman V (2015). Trade and ethnozoological use of African lorisiforms in the last 20 years. ***Hystrix- Italian Journal of Mammology,*** **26(2): 153-161.**
I initiated this study and was thereafter involved in most parts of finalising the paper, including collecting the data and writing the paper.

Svensson MS, Shanee S, Shanee N, Bannister FB, Cervera L, Donati G, Huck M, Jerusalinsky L, Juarez CP, Maldonado AM, Mollinedo JM, Méndez-Carvajal PG, Argandoña MAM, Mollo Vino AD, Nekaris KAI, Peck M, Rey-Goyeneche J, Spaan D, Nijman V (2016). Disappearing in the night: an overview on trade and legislation of night monkeys in South and Central America. ***Folia Primatologica,*** **87(5):332-348.**
I initiated this study and was thereafter involved in all parts of finalising the paper, including collecting and analyzing the data and writing the paper.

CHAPTER 2:

METHODS

2.1 The study regions and timeline

The work included in this dissertation describes my research on nocturnal primates in the Neotropics and Sub-Saharan Africa between 2006 and 2013, as well as desk based studies conducted in the UK between 2013 and 2016 (Table 1; Table 2; Fig. 2 & 3). I studied night monkeys (Panama in 2008 and Argentina in 2009-2010), galagos (the Gambia in 2012, Uganda in 2006 and 2011, Angola in 2013) and pottos (Angola in 2013) *in situ*. These field studies were then combined with data I extracted from the literature, online questionnaires and online databases on these species as well as angwantibos. These studies combined allowed me to obtain an overview of their conservation and ecology in parts of the range of nocturnal primates.

Table 1. Timeline of the research programme, including fieldwork not presented in this thesis. In grey are publications and conference abstracts that are outcomes of the fieldwork but not part of this dissertation.

Field trips	Topic	Duration (days)	Year	Publications
Uganda	Occurrence of nocturnal predators and galagos, as well as play behaviour in warthogs.	30	**2006**	**Svensson, MS (2008).** A comparative study of play behaviour in wild and captive warthogs. *Journal of the Association of British and Irish Wild Animal Keepers*, **35 (1):** 3-7. Also see below (Uganda 2011)
Panama	Distribution and population density of night monkeys (*Aotus zonalis*)	92	**2008**	**Svensson MS, Samudio R, Bearder SK & Nekaris KAI (2010).** Density estimates of Panamanian owl monkeys (*Aotus zonalis*) in three habitat types. *American Journal of Primatology*, **72:** 187- 192. **Svensson MS, Samudio R & Bearder SK (2009).** Assessing the distribution and abundance of owl monkeys (*Aotus zonalis*) in Chagres National Park, Panama. 78th Annual Meeting of AAPA, Chicago, USA.

				Svensson MS & Bearder SK (2008). Improving management of nocturnal primates: assessing the distribution and abundance of owl monkeys (*Aotus zonalis*) in Alto Chagres, Panama. International Journal Primatology Suppl (abstract.). International Primatological Society meetings, Edinburgh Scotland. **Svensson MS, Samudio R & Bearder SK (2008).** Population densities and geographic distribution of Panamanian night monkeys (*Aotus zonalis*) in central Panama. Winter meeting of PSGB, England.
Argentina	Demography, behaviour, ecology and distribution of night monkeys (*Aotus azarae*)	365	2009 – 2010	**Juárez CP, Svensson MS, Huck M & Fernandez-Duque E (2010).** Effects of a naturally fragmented habitat on the population biology of night monkeys (*Aotus azarae*) in the humid Chaco of Argentina. MSc Primate Conservation 10th Anniversary Conference at Oxford Brookes University, England. **Svensson MS, Shanee S, Shanee N, Bannister FB, Cervera L, Donati G, Huck M, Jerusalinsky L, Juarez CP, Maldonado A, Martinez Mollinedo J, Méndez-Carvajal PG, Molina Argandoña MA, Mollo Vino AD, Nekaris KAI, Peck M, Rey-Goyeneche J, Spaan D & Nijman V (2017).** Disappearing in the night: an overview on trade and legislation of night monkeys in South and Central America. *Folia Primatologica*, **87(5):** 332-348.

Uganda	Distribution and behaviour of galagos (*Otolemur* sp.)	10	**2011**	**Svensson MS & Bersacola E (2013).** Sightings of thick-tailed greater galagos *Otolemur crassicaudatus monteiri* (Barlett in Gray, 1863) near Lake Mburo National Park, south Uganda. *African Primates, **8:** 63-66.*
The Gambia	Behaviour and habitat use of galagos (*Galago senegalensis*)	19	**2012**	**Svensson MS & Bearder SK (2013).** Sightings and habitat use of the northern lesser galago (*Galago senegalensis senegalensis*) in Niumi National Park, the Gambia. *African Primates, **8:** 51-58.* **Svensson MS., Bearder SK., Perkin, A. De Jong Y. & Butynski T (2012).** Biological variation across the range of *Galago senegalensis*. Winter meeting of Primate Society of Great Britain, England **De Jong YA, Butynski TM & Svensson MS (2017).** *Galago senegalensis*. IUCN Red List.
Angola	Occurrence and habitat use of nocturnal primates, as well as the bushmeat trade	17	**2013**	**Svensson MS, Bersacola E & Bearder SK (2013).** Assessing occurrence and distribution of nocturnal primates in Angola. Winter meeting of PSGB, England. **Bersacola E, Svensson MS & Bearder SK (2013).** Are primates in Angola threatened by the bushmeat trade? Winter meeting of PSGB, England. **Bersacola E, Svensson MS, Bearder SK, Mills M & Nijman V (2014).** Hunted in Angola: surveying the bushmeat trade. *SWARA*, January-March: 31-36. **Svensson MS, Bersacola E & Bearder SK (2014).** Pangolins in Angolan bushmeat markets. *IUCN/SSC Pangolins Specialist Group Newsletter.*

Bersacola E & Svensson MS (2014). Reporting on the ivory trade in Angola: will the nation's entry to CITES make a difference? *National Geographic Daily News: a Voice for Elephants*.

Svensson MS, Bersacola E, Bearder SK, Nijman V & Mills M (2014). Open sale of elephant ivory in Luanda, Angola. *Oryx*, **48(1):** 13-14.

Bersacola E, Svensson MS, Bearder SK (2015). Niche partitioning and environmental factors affecting abundance of strepsirrhines in Angola. *American Journal of Primatology,* **77(11):** 1179-1192.

Bersacola E, Svensson MS & Bearder SK (2015). Habitat use and spatial niche partitioning of five nocturnal primates in Angola. 6th EFP Meeting, Rome Italy.

Svensson MS, Bersacola E, Mills MSL, Munds RA, Nijman V, Perkin A, Masters JC, Couette S, Nekaris KAI & Bearder SK (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. *American Journal of Physical Anthropology*, **163(1):** 30-43.

Svensson MS, Bersacola E & Bearder SK (2017). *Galagoides demidovii*. IUCN Red List.

Svensson MS & Bearder SK (2017). *Galagoides thomasi*. IUCN Red List.

Svensson MS, Bersacola E, Nijman V, Mills MSL & Bearder SK (2017). *Galagoides kumbirensis*. IUCN Red List.

Desk based study	Occurrence in trade and use of pottos (*Perodicticus* spp.) and angwantibos (*Arctocebus* spp.) throughout Africa, including comparison to the trade and use of the slow lorises (*Nycticebus* spp.) in Asia, using questionnaires and through literature review.	**2014**	**Svensson MS & Friant SC (2014).** Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. *Endangered Species Research*, **23(2):** 107-114. **Bearder SK, Bersacola E, Svensson MS & Nekaris KAI (2014).** About faces- please help us test an identification key for nocturnal primates. Winter meeting of Primate Society of Great Britain, England. **Svensson MS & Nekaris KAI (2017).** *Arctocebus aureus.* IUCN Red List. **Oates JF & Svensson MS (2017).** *Arctocebus calabarensis. IUCN* Red List. **Svensson MS & Pimley E (2017).** *Perodicticus edwardsi*. IUCN Red List. **Svensson MS, Pimley E, Gonedelé Bi S & Oates JF (2017).** *Perodicticus potto*. IUCN Red List.
Desk based study	Trade and ethnozoological use of all mainland African lorisiforms (galagos, pottos and angwantibos) using questionnaires, existing databases and through literature review.	**2015**	**Svensson MS, Ingram D, Nekaris KAI, Nijman V (2015).** Trade and ethnozoological use of African lorisiforms in the last 20 years. *Hystrix- Italian Journal of Mammology,* **26(2):** 26(2): 153-161. **Bearder SK, Svensson MS & Butynski TM (2017).** *Galago moholi.* IUCN Red List. **De Jong YA, Butynski TM, Perkin AW, Svensson MS & Masters J (2017).** *Otolemur garnettii*. IUCN Red List.

Table 2. Study sites characteristics

	Chagres NP	Estancia Guaycolec	Lake Mburo NP	Niumi NP	Kumbira/ Bimbe/ NScarp/ Calandula
Country	Panama	Argentina	Uganda	The Gambia	Angola
Nocturnal primates studied	*Aotus zonalis*	*Aotus azarae*	*Otolemur crassicaudatus*	*Galago senegalensis*	*Perodicticus edwardsi, Otolemur crassicaudatus, Galago moholi, Galagoides demidovii, Gd. kumbirensis*
Coordinates	9.4297° N 79.4254° W	25.983° S 58.183° W	0.5968° S 31.0106° E	13.5591° N 16.5260° W	11.15449° S 14.29289° E
Protected area	Yes	No	Yes	Yes	No
Area (km^2)	1,296	50	260	49.4	N/A
Habitat type	Semi-deciduous / Secondary gallery / Lowland moist-wet forest / Higher-elevation cloud forest	Semi-deciduous gallery forest/ Forest fragments in palm savannah	Hilly woodland, wetland system of swamps & lakes	Open woodland savannah	Moist forest, primary and secondary / Miombo woodland, gallery forest / Semi-arid baobab savannah woodland
Altitude (m asl)	100 - 800	700	1,200	0 - 15	285 - 1,180
Average annual rainfall (mm)	2,400	1,400	750	609	762 - 1,343
Average annual temperature (°C)	25.5	22.6	21.1	28	21.1 - 24
Sympatric diurnal primate species	*Alouatta palliata*, *Ateles geoffroyi*, *Cebus capucinus, Saguinus geoffroyi*	*Alouatta caraya*	*Papio Anubis*, *Chlorocebus pygerythrus*	*Erythrocebus patas*, *Chlorocebus sabaeus*	*Cercopithecus mitis mitis*, *Miopithecus talapoin*
References	Fondo Chagres, 2009; Robinson *et al*., 2004; Candanedo & Samuido, 2005	Juarez *et al*., 2011; Fernandez-Duque, 2016; Worldbank, 2015	Snelson & Wilson, 1994; Kagoro-Rugunda, 2004; Averbeck *et al*., 2012; UWA, 2016	Nije *et al*., 2011; Worldbank, 2015	Mills *et al*., 2011; Bersacola *et al*., 2015; Worldbank, 2015

Figure 2. Ranges of study species and field sites in the Neotropics (Map created in ArcGIS, base layer from US National Park Service (available from http://services.arcgisonline.com/ArcGIS/services) and species range shape files from IUCN, 2008)

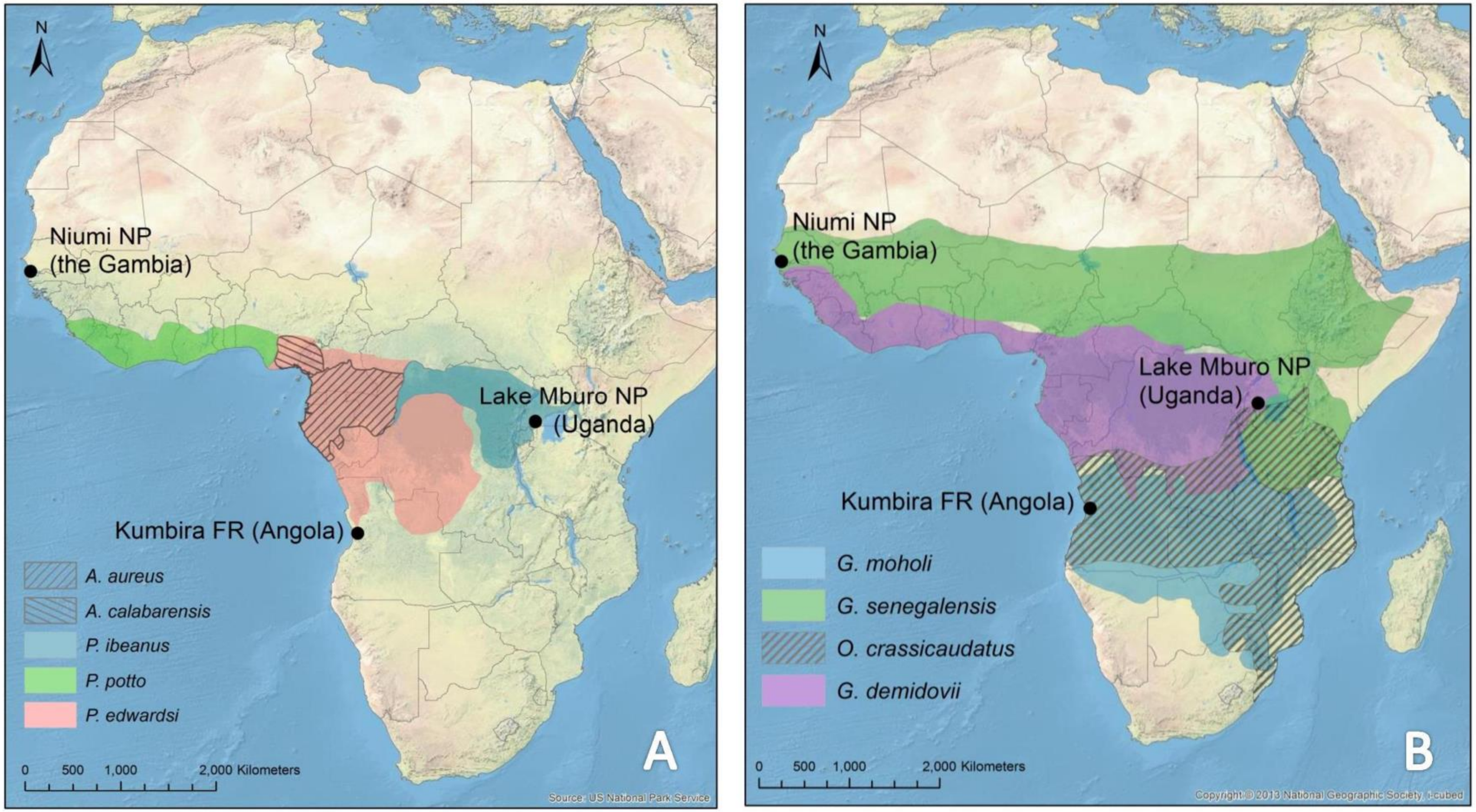

Figure 3. Range of study species (A – galagos; B - pottos and angwantibos) and field sites in Africa (Map created in ArcGIS, base layer from US National Park Service (available from http://services.arcgisonline.com/ArcGIS/services) and species range shape files from IUCN, 2008)

2.2 Study species

2.2.1 Taxonomy

The taxonomy of nocturnal primates is constantly evolving, with an increasing number of species and genera being recognised (Masters & Brothers, 2002; Fernandez-Duque *et al*., 2013; Nekaris 2013a, 2013b; Pozzi *et al*., 2014, 2015; Masters *et al.,* 2017). In the Neotropics 11 species of night monkeys (*Aotus* spp.) are currently recognised (Fernandez-Duque *et al.,* 2013). In Africa the nocturnal primates consists of three species of potto (*Perodicticus* spp.), two of angwantibo (*Arctocebus* spp.), 18 species of galagos (*Euoticus* spp., *Galago* spp., *Galagoides* spp., *Otolemur* spp., *Sciurocheirus* spp., *Paragalago* spp.) (Nekaris 2013a, 2013b; Masters *et al.,* 2017).

2.2.2 Aotidae

Night monkeys, also referred to as owl monkeys or douroucoulis, are the only nocturnal primate in the Neotropics, although the night monkey species in Argentina and Paraguay; Azara's night monkey (*A. azarae*), is cathemeral (Erkert *et al.,* 2012). Night monkeys are one of the few primates being socially monogamous (Fernandez-Duque, 2011) and to display paternal care (Huck *et al.,* 2014). They live in small groups of up to six individuals, but normally the grouping consists of an adult female, and adult male and their offspring(s) (Wright, 1994). The species range from the Chaco plains of Argentina in the south to Coclé del Norte in Panama's rainforests in the north (Fig. 2) (Fernandez-Duque *et al*., 2013). Although mainly frugivorous the night monkeys also feed on leaves, flowers, fungi and insects (Fernandez-Duque *et al.,* 2013). The species can be found in both primary and secondary forests, in habitats including dry forests, deciduous seasonal forests, riparian gallery forests, flooded forests and tropical rain forests (Fernandez-Duque *et al.,* 2010;

Table 3. Study species

Species	**Common Name**	**Range Countries**	**IUCN Red List Category**
Aotus azarae	Azara's night monkey	Argentina; Bolivia; Brazil; Paraguay; Peru	Least Concern
A. zonalis	Panamanian night monkey	Colombia; Panama	Near Threatened
Galagoides demidovii	Demidoff's dwarf galago	Angola; Benin; Burkina Faso; Burundi; Cameroon; CAR; Congo; DRC; Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Liberia; Mali; Nigeria; Rwanda; Senegal; Sierra Leone; Tanzania; Togo; Uganda	Least Concern
Gd. kumbirensis	Angolan dwarf galago	Angola	Suggested Vulnerable
Galago senegalensis	Northern lesser galago	Benin; Burkina Faso; Cameroon; CAR; Chad; DRC; Côte d'Ivoire; Eritrea; Ethiopia; Gambia; Ghana; Guinea; Guinea-Bissau; Kenya; Mali; Niger; Nigeria; Rwanda; Senegal; Sierra Leone; Somalia; South Sudan; Sudan; Tanzania; Togo; Uganda	Least Concern
G. moholi	Southern lesser galago	Angola; Botswana; DRC; Malawi; Mozambique; Namibia; South Africa; Swaziland; Tanzania; Zambia; Zimbabwe	Least Concern
Otolemur crassicaudatus	Thick-tailed greater galago	Burundi; DRC; Kenya; Malawi; Mozambique; Rwanda; South Africa; Swaziland; Tanzania; Zambia; Zimbabwe	Least Concern
Arctocebus calabarensis	Calabar angwantibo	Cameroon; Nigeria	Near Threatened
A. aureus	Golden angwantibo	Angola; Cameroon; CAR; Congo; Equatorial Guinea; Gabon	Least Concern
Perodicticus potto	West African potto	Benin; Côte d'Ivoire; Ghana; Guinea; Kenya; Liberia; Nigeria; Senegal; Sierra Leone; Togo	Vulnerable
P. edwardsi	Milne-Edward's potto	Angola; Cameroon; CAR; Congo; DRC; Equatorial Guinea; Gabon; Nigeria	Least Concern
P. ibeanus	East African potto	Burundi; DRC; Kenya; Rwanda; Uganda	Least Concern

Information from the 2016 IUCN Red List (IUCN, 2017).

Svensson *et al*., 2010; Shanee & Shanee, 2011; Maldonado & Peck, 2014). Since the night monkey was first described in 1802 by Félix de Azara (Goldman, 1914) until 1983, when nine species were suggested, they were thought to comprise of only one species, *A. trivirgatus* (Hershkovitz, 1983). The taxonomy and suggested arrangements of the number of species and subspecies continues to be debated (Defler and Bueno, 2007; Rylands *et al*., 2012). For this dissertation I follow the taxonomy used by Fernandez-Duque *et al.* (2013), recognizing 11 species. Two of these are listed as Least Concern on the most recent 2016 assessment (*A. azarae* and *A. trivirgatus*), three as Near Threatened (*A. nigriceps, A. vociferans* and *A. zonalis*), four as Vulnerable (*A. brumbacki, A. griseimembra, A. lemurinus* and *A. nancymaae*), one as Endangered (*A. miconax*) and one as Data Deficient (*A. jorgehernandezi*) (IUCN, 2017).

The night monkey species studied throughout this research programme were the northernmost species *A. zonalis*, ranging in Panama and Colombia, and the southernmost species *A. azarae*, ranging in Argentina, Bolivia, Brazil, Paraguay and Peru (Fig. 2).

2.2.3 Galagidae

Galagos occur over most of Sub-Saharan Africa and in varied habitats depending on species. The species focussed on in this dissertation was the northern lesser galago (*Galago senegalensis*), the southern lesser galago (*G. moholi*), thick-tailed greater galago (*Otolemur crassicaudatus*), Demidoff's dwarf galago (*Galagoides demidovii*) and we further describe a new species of galago; the Angolan dwarf galago (*Gd. kumbirensis*) (Svensson *et al*., 2017c), also referred to as *Galagoides* sp. nov. 4 in Bersacola *et al.* (2015).

Galago senegalensis has the widest range of all the galagos, ranging 7,000 km from the Gambia in the west to Ethiopia in the east (Fig. 3; Table 3) (Nash *et al*., 2013). They occur in open woodland, savannah and thorn bush as well as riverine woodland and in some parts in more closed forest habitats, using all strata (Bearder *et al.,* 2003; Nash *et al*., 2013). The social organisation of *G. senegalensis* is small groups or non-gregarious; foraging solitarily but exhibit a social network (Bearder *et al.,* 2003). The species is omnivorous, with their diet consisting of insects and other animal matter, as well as gum, nectar and fruits (Haddow & Ellice, 1964; Nash & Whitten, 1989; Svensson & Bearder, 2013; Kingdon, 2015). *Galago senegalensis* consist of four known subspecies: *G. s. senegalensis, G. s. braccatus, G. s. sotikae* and *G. s. dunni* (Nash *et al.,* 2013; Nekaris 2013a). The species is listed as Least Concern on the 2016 IUCN Red List (de Jong *et al*., 2017a).

Galago moholi was long thought to be the same species as *G. senegalensis*, but has since been raised to its own species based on vocalisation and morphology (Olson, 1979; Zimmermann *et al.,* 1988). The species ranges from South Africa northwards to southern Tanzania (Fig. 3), using all strata in open woodland, savannah, forest edges and other semi-arid habitats (Bearder *et al*., 2003; Pullen & Bearder, 2013). *Galago moholi* lives in small groups or non-gregarious, similar to *G. senegalensis* (Bearder *et al*., 2003) and they feed on gum and invertebrates (Pullen & Bearder, 2013; Kingdon, 2015). The species is listed as Least Concern on the 2016 IUCN Red List (Bearder *et al.*, 2017).

Otolemur crassicaudatus belongs to the greater galagos, and they range over large parts of southern Africa, from South Africa to Kenya in the north, and from Angola in the west to Mozambique in the east (Fig. 3) (Bearder & Svoboda, 2013). *Otolemur crassicaudatus* can be found in open woodland and savannah habitats as well as in forests edges and thickets, using mid to high strata (Bearder *et al*., 2003; Bearder & Svoboda, 2013). The species tends to be restricted to areas with well-defined seasons (Bearder & Svoboda, 2013). *Otolemur crassicaudatus* are omnivorous and their diet is comprised of invertebrates, gum and fruits (Bearder & Doyle, 1974; Bearder & Svoboda, 2013). Their social organisation is non-gregarious or in small groups of up to four individuals (Bearder *et al.,* 2003). The species is listed as Least Concern on the 2016 IUCN Red List (IUCN, 2017).

Galagoides demidovii is the smallest of all the galagos and range from Sierra Leone in the west, through to Tanzania in the east and Angola in the south (Fig. 3). The species occurs in many types of forests, including deciduous and semi-deciduous forests, evergreen and gallery forests, mainly in the edge and understory habitats (Bearder *et al*., 2003; Ambrose & Butynski, 2013). *Galagoides demidovii* are omnivorous, with their diet consisting of insects and other animal matter such as caterpillars, and as well as gum, fruits, buds and leaves (Charles-Dominique, 1977; Ambrose & Butynski, 2013). They live in groups of two to ten individuals (Bearder *et al*., 2003). The species is listed as Least Concern on the 2016 IUCN Red List (Svensson *et al.,* 2017a).

I am also describing a new dwarf galago (*Gd. kumbirensis*) in Angola (Svensson *et al*. 2017d). The species is so far only known to range in north western Angola, and an IUCN Red List assessment is submitted suggesting to list *Gd. kumbirensis* as Vulnerable, based on the species' extrapolated an extent of occurrence, the known habitat destruction trends and situation in Angola (Svensson *et al*., 2017c).

As part of my desk based research all galago species were included.

2.2.4 Lorisidae

My studies have also included the African Lorisidae, related to the Lorisidae of Asia (*Nycticebus* spp. and *Loris* spp.) (Pozzi *et al*., 2015). In the field based part of my research I have focussed on one of the three potto species, *Perodicticus edwardsi*, which is endemic to western Central Africa (Fig. 3) and is the largest of the potto species (Pimley & Bearder, 2013). Both the other potto species (*P. ibeanus* and *P. potto*) were also included in the desk based part of my research. Pottos occur in both primary and secondary forests, from low altitude to montane forests (Butynski & de Jong, 2007; Pimley, 2009; Oates, 2011; Pimley & Bearder, 2013). They are non-gregarious and their diet is omnivorous, including insects, snails, gum and fruits (Bearder *et al*., 2003; Pimley & Bearder, 2013; Kingdon, 2015).

Perodicticus edwardsi and *P. ibeanus* are listed as Least Concern and *P. potto* as Vulnerable on the 2016 IUCN Red List (Svensson & Pimley, 2017; Svensson *et al*., 2017b; de Jong *et al*., 2017b).

During fieldwork I never encountered angwantibos, but I did include both species in my desk based research (*Arctocebus aureus* and *A. calabarensis*). Angwantibos range is limited to western Central Africa (Fig. 3), and they can be found in habitats such as evergreen forest and tree fall zones, both primary and secondary forests (Oates, 2011; Ambrose, 2013; Oates & Ambrose, 2013). Both species are non-gregarious and their diets insectivorous (Ambrose, 2013; Oates & Ambrose, 2013). *Arctocebus aureus* is classed as Least Concern and *A. calabarensis* as Near Threatened on the 2016 IUCN Red List (Oates & Svensson, 2017; Svensson & Nekaris, 2017).

2.3 Data acquisition

2.3.1 Overall research approach

I provide a detailed account in each of the publications included in this dissertation, on methods used within each study (Table 3; Annexes 1-8), as well as discussing their limitations. I will here outline the methods used and further elaborate on their advantages and limitations, as well as discuss any adaptations needed to make methods work for my studies and chosen study sites. I will also discuss why methods were chosen and how they are useful for primate conservation.

2.3.2 Field surveys

The majority of my publications are based on fieldwork conducted *in situ*, throughout the Neotropics and Sub-Saharan Africa (Table 1). I collected data at all sites using standardized methods. During nocturnal surveys and behavioural observations I used red light sources as much as possible. This to not disturb the nocturnal animals, as they can't see red light, and therefore also allowed me to observe their natural behaviour (Nekaris, 2003). I also used halogen light sources as LED has been found to be harmful to the eyes of nocturnal mammals (Plumptre *et al*., 2013). Only when identification was difficult in the slightly dimmer red light did I use a torch with white light. All the nocturnal primates in Africa have the light reflecting layer *tapetum lucidum* behind their retina and are therefore easy to spot due to their eye shine (Bearder *et al*., 2006). This was more problematic in Panama and Argentina as night monkeys are lacking a *tapetum lucidum*. However, I did find that their eyes do often reflect lights well enough to sight them, and I rapidly learnt other ways of detecting their presence, such as their vocalisations and by using the silhouette survey method as their silhouettes can easily be seen against the sky as they jump and move along branches during twilight hours (Perkin, 2012). At all times during my fieldwork was I accompanied by either research assistants and/or colleagues and we conducted these surveys and observations in groups of two to four people.

2.3.3 Transect surveys

To enable effective conservation strategies it is vital to know basic parameters such as density and distributions of the primate species in question (Cowlishaw & Dunbar, 2000; Plumptre *et al*., 2013; Campbell *et al*., 2016). The most common way to estimate primate densities is to use transects; line and strip/quadrat transects. The advantages using this method are that you can cover a large survey area in relatively short time, and there are well developed methods to analyse this kind of data, e.g. the computer program Distance (Buckland *et al*., 2001; Ross & Reeve, 2011; Plumptre *et al*., 2013; Campbell *et al.,* 2016). When using line transects there are several assumptions that needs to be met; animals directly on the transect cannot be missed, animals are counted before they move, animals are not counted twice on the same transect, angles and distances are measured accurately, each sighting is an independent event and finally, to be able to run analyses with Distance your data a minimum of 40 individual sightings are necessary for an accurate estimate of detection (Buckland *et al*., 2001; Ross & Reeve, 2011). The usual caveats for line transect surveys apply for both diurnal and nocturnal surveys, including differential detection distances depending on habitat type, level of disturbance and habituation of the primates (Duckworth, 1998).

In Panama (Svensson *et al*., 2010) I repeatedly walked line transects already established in the study area, with a total effort of 69 km of transects. The transects were walked in a randomised order, in straight lines, avoiding human paths, thus avoiding sampling bias (Plumptre *et al*., 2013). I was therefore able to calculate densities of *A. zonalis,* but due to small sample size (33 individuals in 16 groups) we could not conduct analyses using Distance (Buckland *et al*., 2001).

In Angola (Bersacola *et al*., 2015) due to time constraints, the fact that hunting was known to occur in the area and to avoid further habitat disturbance, I did not create new transects. I used an adaptation of reconnaissance surveys (recces), using existing trails and paths, with a total effort of 22 km of transects. Only encounter rates (animal/km) could be obtained when using this method as recces are biased due to sampling not being stratified and random (Plumptre, 2000; Plumptre *et al*., 2013). However studies have found that there is a positive correlation between densities and encounter rates from using reconnaissance surveys (Plumptre, 2000; Plumptre *et al*., 2013). Encounter rates allows for comparison between sites (Wallace *et al*., 1998). When analysing the relative abundance of primates in Angola I divided the paths into 1 km-long tracks, this to decrease variance and obtain a sufficient sample size for statistical comparison. I also discarded ~200 m of effort between each track to ensure independence of sampling units. Differences in visibility are a possible caveat when comparing relative abundance of primates in different habitat types. However, Rovero *et al.* (2006) found no significant differences in sighting distances when surveying diurnal primates in different habitats in Tanzania. Additionally, nocturnal primates are relatively easy to detect due to their reflecting eye shine.

In both countries I walked at an average speed of 800 m/hour. At each sighting of primates I collected time of sighting, species, group size and structure, height above ground, response behaviour, GPS location and perpendicular distance of the animal to the transect (Brockelman & Ali, 1987; Ross & Reeve, 2011).

Table 4. Overview of methods used in publications included in this dissertation

Publication	Transect surveys	Reconnoissance surveys	Distribution mapping	Behavioural observations	Vegetation sampling	Questionnaires (incl. online)	Literature Review	Researching online databases	Acoustic analysis	Statistical analysis
Svensson *et al*., 2010	√		√		√					√
Svensson & Bersacola, 2013			√							
Svensson & Bearder, 2013				√	√				√	
Bersacola *et al*., 2015		√	√	√	√					√
Svensson *et al*., 2017d		√	√	√	√		√		√	√
Svensson & Friant, 2014						√	√	√		√
Svensson *et al*., 2015						√	√	√		√
Svensson *et al*., 2016							√	√		√

2.3.4 Distribution mapping

As previously mentioned, it is important to know a primate species' distribution if conservation efforts are to be successful. We need to know where the primates occur and how they might be affected by anthropogenic and environmental factors (Plumptre *et al*., 2013; Campbell *et al.,* 2016). When field studies are limited by time and economic constraints presence-absence surveys can be used, as this method allows greater coverage of a species' range in a short amount of time. However, caution should be taken when interpreting absence data, as to get a true absence of a primate in an area lots of time and resources are needed (Phillips *et al.,* 2009).

One of the aims of my research in Panama (Svensson *et al.*, 2010) was to confirm the presence of *A. zonalis* in Chagres NP and to map their distribution within the national park, and in Uganda to confirm the presence of *O. crassicaudatus* in the country (Svensson & Bersacola, 2013). In Angola (Bersacola *et al*., 2015) I aimed to confirm what nocturnal primates were occurring in that part of Angola, as nothing was previously known regarding the primate populations in the area. The mapped primate distributions in Angola are mainly based on museum specimens (Nash *et al*., 1989; Nekaris, 2013a,b)

2.3.5 Behavioural data collection

To better understand primates' relationship with their anthropogenic and natural environments data on their behaviour and ecology is necessary (Cowlishaw & Dunbar, 2000). If not using indirect methods, such as camera traps, this kind of data can best be collected once animals are habituated to human presence. Nocturnal primates such as galagos and pottos are relatively easy to habituate to researchers presences; sometimes it only takes a few hours (Williamson & Feistner, 2011; Svensson & Bearder, 2013). Behavioural observations are however more difficult at night. Techniques, such as radio telemetry is aiding in following nocturnal primates (Kaplin & William, 2013). In Argentina I did use radio tracking to find and follow the night monkeys. Studying the Argentinean night monkeys is easier as the species is cathemeral (Fernandez-Duque *et al.,* 2010) and therefore their behaviour can be studied both at night and in the day. I conducted demographic studies, where I collected data on group sizes and age of individuals. I also carried out behavioural observations, using instantaneous sampling method, where every 2 minutes I would record social, locomotary and foraging behaviours (Bateson & Martin, 2007).

I also conducted behavioural observations in the Gambia (Svensson & Bearder, 2013) where I followed the *G. senegalensis* for as long as possible, recording their height use and group sizes to get a better understanding of their habitat use and social groupings. I also recorded other behaviours *ad libitum*, including behaviour such as social interactions, mating, locomotion, feeding and foraging, as well as recording their vocalisation.

In Angola (Bersacola *et al*., 2015) I observed the behaviours of the nocturnal primates during transects, recording their height use and behaviour on first sighting as well as their vocalisation. I studied these behaviours to collect data on their habitat/strata use and to add to our knowledge on galago vocalisation.

2.3.6 Vegetation sampling

To be able to understand the interaction between the nocturnal primates and their habitat vegetation sampling is essential. Primate ecology is partly influenced by habitat quality (undisturbed vs. disturbed), vegetation species composition and food availability (Cowlishaw & Dunbar, 2000). There are many standardised methods to generate variables to test hypotheses and the point-quarter sampling method enables sampling of large areas in a time efficient manner (Ganzhorn *et al*., 2011). I used this method at all study site where I conducted habitat surveys, measuring DBH, basal area, canopy cover, tree density, and species composition (Svensson *et al*., 2010; Svensson & Bearder, 2013; Bersacola *et al*., 2015), to get the vegetation structure of each site and to be able to understand the relation to the ecology of the nocturnal primates.

2.3.7 Market surveys and interviews

To assess trade, consumption and harvest of primates increasingly market surveys are being used as they provide a rapid and non-invasive way of quantifying demand, supply and utilisation of wildlife and their derivatives (Linder *et al*., 2013). As with any research methods involving human participants it is important to conduct the market surveys with sensitivity and ensure confidentiality to all involved (Newing, 2011; Linder *et al*., 2013). Market surveys are often presented in combination with methods such as hunter or household interviews (Linder *et al*., 2013).

In Nigeria (Svensson & Friant, 2014) my colleague S. Friant conducted interviews in communities in and around the Cross River National Park. Inhabitants of the communities were hunters and/or farmers. These data was then combined with data gathered from online questionnaires (see below) to provide a clearer view of the scale of trade in and use of African nocturnal primates, and to see if this trade is presenting a threat to their conservation.

2.3.8 Online questionnaires

Questionnaires are increasingly being distributed and conducted online and this has both its advantages and limitations. It allows for rapid assessments as well as being an inexpensive, anonymous and rapid way of collecting data (Couper *et al*., 2007). However, using an Internet-based method will preclude those without access to the Internet. For my two publications where I conducted overview on the utilisation and trade of African nocturnal primates (Svensson & Friant, 2014; Svensson *et al*., 2015) I conducted the online survey using the Survey Monkey website (www.surveymonkey.com), including ten questions on observations of African nocturnal primates in trade or used for ethnozoological purposes. The questions focused on locations, amount of traded animals observed and in what circumstance the observations were made. I distributed the online questionnaires using self-selecting (non-probability) sampling whereby respondents volunteer themselves to partake in the research. The target audience was people who had lived or worked for a minimum of one month in African countries, and the questionnaires were distributed via email, Facebook and Twitter. Both questionnaires are available in Annex 9.

2.3.9 Using the CITES database

For three of my publications, all focusing on trade and usage of nocturnal primates, (Svensson & Friant, 2014; Svensson *et al*., 2015; Svensson *et al.,* 2016) I conducted the main part of the research online (Table 3). Part of it involved me downloading and analysing trade data reported to the database CITES (https://trade.cites.org/). The CITES database consists of reports made by importing and exporting countries party to the convention and is readily available for anyone to download. This allowed me to analyse international trade data of nocturnal primates, from 1975, when the Convention was established, until 2015. All primate species are listed in CITES appendix II (which means all commercial trade is regulated), if not specified to be listed otherwise (Nijman *et al.,* 2011).

2.3.10 Literature review

I also conducted extensive literature reviews for all my publications relating to trade of nocturnal primates (Svensson & Friant, 2014; Svensson *et al*., 2015; Svensson *et al*., 2016). This allowed me to collect historical data on the trade and usage of the nocturnal species. This was done by searching the online databases Web of Science and Google Scholar in a systematic manner, using a set of key search words specific to each publication. To not miss out on trade/usage data that sometimes occur in grey literature I also included unpublished reports by for example Non-Governmental Organisations, as well as dissertations available online (both MSc and PhD dissertations). Books not available online were accessed in Oxford libraries.

2.3.11 Acoustic analysis

We made recordings of galago vocalisation using a Fostex Field Recorder equipped with a Sennheiser K6-ME67 directional microphone. Vocalisation recordings were digitalised using Avisoft SASLab Pro software (R. Specht, Berlin; version 5.2) and measured following method described in detail in Anderson *et al.,* (2000). Recordings were converted into spectrograms with a frequency resolution of 48 kHz (FFT length 512; 50% overlap; Hamming window). The call parameters chosen for analysis were [A] formant (dominant frequency, measured in kHz), [B] fundamental frequency (first harmonic, measured in kHz), [C] unit length (basic element of a call that is represented as a continuous tracing along the temporal axis of a sonogram, measured in s) and [D] unit interval length (the time interval between two consecutive units, measured in s) (Fig. 4). The calls were only analysed after visual inspection of sonogram, to ensure only recordings with all important parts present were included and then converted into spectograms.

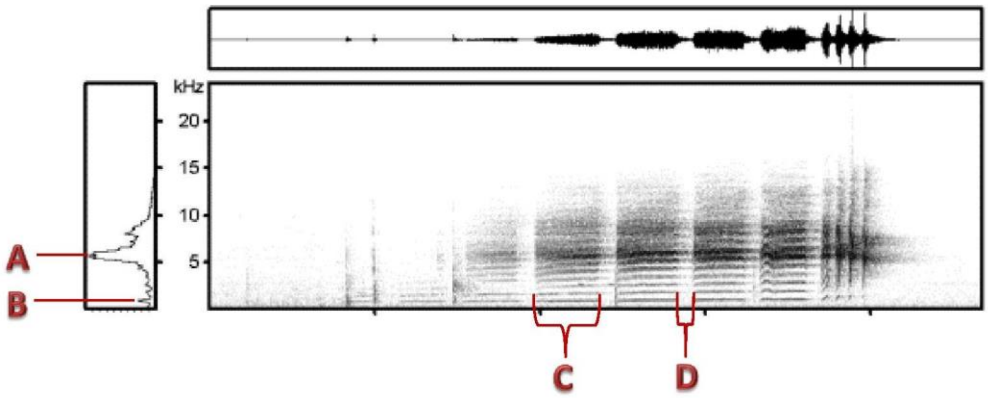

Figure 4. Example of spectrogram (vocalisation: crescendo-twitter by *Gd. kumbirensis*). [A] formant, [B] fundamental frequency, [C] unit length,[D] unit interval length.

2.3.12 Statistical analysis

Due to the small sample sizes and limited duration of my fieldwork I present the majority of my research using descriptive statistics, and non-parametric statistics where possible. The non-parametric tests used in this dissertation were Kruskal-Wallis one-way analysis of variance by rank, Chi-Squared test, Mann-Whitney U test, Binomial test and Fisher's exact probability test. I also used Spearman rank correlation coefficient, Principal Component Analysis and Discriminant analysis. To test and correct data I used Barlett's test of sphericity and Bonferroni corrections.

CHAPTER 3:

DISCUSSION

3.1 General discussion

The main aim of my research was to contribute to the long-term conservation of nocturnal primates in Africa and the Neotropics and create a baseline for further studies. The exploratory approaches of most of my studies have provided me with opportunities to gather descriptive data on primates rarely studied, and in areas where few or no studies have been undertaken. The publications contribute to our understanding of the conservation status of these cryptic, nocturnal primate species; the threats that they face, and will hopefully contribute to conservation prioritisation at national, regional and global levels.

I have chosen to divide my discussion into two sections, reflecting the main research areas of my studies; biogeography/ecology studies and wildlife trade. These subjects are intertwined and depend on each other, all important to study in order to understand and be able to conduct successful conservation work. I will discuss each subject in the different sections and then argue their relevance to each other.

In each section I outline the research conducted and its relevance to the research aims of the individual publications. I will also discuss the original contributions to conservation of nocturnal primates represented in each publication included in this PhD by Published Work.

3.2 Distribution and ecology

Five of the publications (Annexes 1 - 5) in this dissertation include data on the distribution and ecology of nocturnal primate species, in Panama, Uganda, the Gambia and Angola (Svensson *et al.,* 2010; Svensson & Bearder, 2013; Svensson & Bersacola, 2013; Bersacola *et al*., 2015; Svensson *et al*., 2017d).

In Panama our research confirmed the presence of *A. zonalis* in the Chagres NP for the first time, at 3 locations, as well as provided data on density and ecology data on this newly described species in an area that was previously unstudied (Svensson *et al.,* 2010). Night monkeys are known to range in a wide range of habitats and their distribution is partly well known. I found densities of *A. zonalis* being dependent on habitat structure, with densities of 14.3/km^2 in secondary gallery forests in the highlands to 19.7/km^2 in semi-deciduous lowland forests (Svensson *et al.,* 2010). Density estimates of *Aotus* spp. varies greatly between species, but there is also great variation within species. Night monkeys tend to have higher densities in areas with high plant species diversity and dense canopies (Aquino & Encarnación, 1994; Kinzey, 1997; van der Heide *et al.,* 2012). Green (1978) found *A. griseimembra* to have a density of 1.5/km^2 in the humid tropical forests of northern Colombia. Aquino and Encarnación (1986; 1988) found that in northern and north-eastern Peru *A. nancymaae* have a density of between 24.2/km^2 in highland forests and 46.3/km^2 in lowland forest and *A. vociferans* between 7.9/km^2 in highland forests and 33/km^2 in lowland forests. Maldonado and Peck (2014) found that in the Amazonian border area of Peru and Colombia densities of *Aotus* spp. ranged from 3.2/km^2 (*A. nancymaae*) to 44/km^2 (*A. vociferans*). My density estimates of *A. zonalis* fall within the mid to upper range of the density estimates of *Aotus* spp. in the northern part of the genus' range, and mirrors previous finding with higher densities in lowland forests. However, in Panama the density estimates did not follow the predicted trends regarding differences in densities in different habitat types. I observed no *A. zonalis* in the habitat we predicted would be the most suitable for them, based on the densest canopy cover and high tree species diversity. The highest density of *A. zonalis* was instead found in the more disturbed semi-deciduous lowland forest with smaller trees and the lowest percentage canopy cover, indicating possible flexibility to habitat disturbance. The apparent absence of *A. zonalis* in the more suitable forest habitat could have been due to the high presence of hardwood trees, as northern night monkey species has a strong selectivity towards using tree holes as sleeping sites, and hardwood trees may present fewer opportunities for this (Hershkovitz, 1983; Aquino & Encarnación, 1988). Sleeping sites determining distribution is observed in other nocturnal primate species, such as the Milne Edward's sportive lemurs (*Lepilemur edwardsi*) (Rasoloharijaona *et al.,* 2003). The distribution pattern in Chagres NP might also have been due to food tree distribution, with the semi-deciduous forest containing high diversity of preferred night monkey food trees, including *Inga* spp. and *Calycophyllum* spp. (Garcia & Braza, 1993; van der Heide *et al.,* 2012; Shanee *et al.,* 2013).

Galago senegalensis is well studied in East Africa (Nash & Whitten, 1989; Ambrose, 2002; Off *et al.,* 2008; Butynski & de Jong, 2012), but very limited research has been conducted throughout the species' distribution west of Uganda (Nash *et al*., 2013). Svensson & Bearder (2013) provides a first study from the westernmost part of the *G. senegalensis* distribution, from Niumi NP in the Gambia. There are few detailed studies of dietary preferences in *G. senegalensis*, but it is thought to be similar to that of *G. moholi* (Nash *et al.,* 2013). In Kenya vegetable matter and insects has been found in their stomach contents (Haddow & Ellice, 1964), Kingdon (1971) reports on fruits in their diet, whilst Nash and Whitten (1989) reports on gum eating in *G. senegalensis*. I was able to contribute to this knowledge through my studies in Niumi NP where *G. senegalensis* were observed to forage and feed on insects, gum and fruits, coinciding with previous studies. *Galago senegalensis* in Niumi NP were found to use mainly tree tangles as sleeping sites, but also utilised tree holes to a lesser extent. This, again, is in line with what is seen in other *G. senegalensis* populations (Bearder *et al*., 2003; Off *et al*., 2008). Sleep sites in this type of dense vegetation might be to gain protection from the sun and from predators in the area (Bearder *et al.,* 2003; Burnham *et al*., 2013). Burnham *et al*. (2013) discuss the benefits of nocturnal primates, including *Galago* spp., being predominantly non-gregarious throughout the night as a mean of avoiding being detected by predators, whilst sleeping in groups will protect them during the day. The *G. senegalensis* of Niumi NP were considerably more gregarious during night than other *G. senegalensis* populations (Haddow & Ellice, 1964; Ambrose, 2002; Off *et al.,* 2008). This could be due to the lack of predators in the Niumi NP, as with high levels of anthropogenic disturbance in the national park less of the typical predators of *Galago* spp. are present. These findings support the hypothesis of Burnham *et al.* (2013). Habitat use of *G. senegalensis* in Niumi NP coincided with their eastern conspecifics, being observed in open woodland savannah. The height use was however predominantly in lower strata compared to other *G. senegalensis* populations (Ambrose, 2002; Off *et al*., 2008). Vegetation height in Niumi NP is lower due to the anthropogenic pressure, and many larger trees have been cut down. This use of lower strata by *G. senegalensis* could however also be due to the number of nocturnal terrestrial predators within the park being low (Nije *et al.,* 2011).

The field surveys in Uganda (Svensson & Bersacola, 2013) generated new range records for *O. crassicaudatus,* a species that was previously not confirmed to range further than the boarder of Tanzania and Uganda (Kingdon, 1971; de Jong & Butynski, 2012). Ambrose (2002) surveyed protected areas in Uganda and provided a report on the nocturnal primates present in these parks and reserves. Ambrose findings were in line with previous research, observing *Gd. thomasi, Gd. demidovii, G. matschiei* and *P. potto* (now classified as *P. ibeanus*) in Uganda (Bearder & Harcourt, 1989; Ambrose, 2002). Ambrose did also add *G. senegalensis* to the list of nocturnal primate species, but did not observe any *O. crassicaudatus*. This absence of *Otolemur* spp. in Uganda was highlighted as unexpected as there is plenty of suitable habitats for the species throughout the country (Kingdon, 1971; de Jong & Butynski, 2012; L Ambrose, pers. comm.).

I provided evidence that this indeed is the case, and *O. crassicaudatus* range at least as far north as to Lake Mburo NP. With suitable habitats such as Acacia savannah and bushy thickets extending further north and west it is very probable that the species distribution is even larger (Snelson & Wilson, 1994; Kigyagi, 2002).

In Angola I confirmed the presence of *G. moholi, Gd. demidovii, P. edwardsi* and *O. crassicaudatus*, as well as generated new range records for *Gd. demidovii* and *P. edwardsi* (Bersacola *et al*., 2015). I further described the new dwarf galago species; the Angolan dwarf galago (*Galagoides kumbirensis*) based on the fieldwork in Angola, in combination with research conducted in museums (Svensson *et al.,* 2017d). *Galagoides kumbirensis* is distinguished from other *Galagoides* species by its species-typical loud call; the crescendo-twitter, as well as by differences in the skull morphology, pelage colour, facial markings and larger body size, similar to that of *Galago moholi*, which is not known to be sympatric (Svensson *et al.,* 2017d).

In Angola I found more nocturnal primate species coexisting than in many other locations, with three species in most of the four study sites (Bersacola *et al.,* 2015). I also observed unusual sympatries between species, such as *P. edwardsi* and *O. crassicaudatus*, which has previously only been seen in the Rift Valley (Butynski & de Jong, 2007; Kamilar *et al.,* 2014) and *G. moholi* coexisting with *O. crassicaudatus* and *Gd. demidovii*. I hypothesised that these sympatries are due to the heterogeneous forest compositions, and species throughout the study sites showed a strong partitioning using different vertical strata or using different habitat within the same locations, and therefore enabling their coexistence.

Encounter rates of *O. crassicaudatus* ranged between 0.20/km in miombo woodland, gallery forest to 0.83/km in semi-arid baobab savannah woodland. My encounter rates for *O. crassicaudatus* falls within the range of other studies on the species; 0.06/km in the Loita Hills in Kenya (Butynski & de Jong, 2012) and 0.49/km in Shire Highlands, Malawi (Wallace, 2005). *Otolemur crassicaudatus* is believed to range throughout most parts of Angola based on museum specimens and preferred habitat, i.e. savannah habitat and miombo woodland (Bearder *et al*., 2003; Bearder & Svoboda, 2013). My research confirms that the species is present in the north western parts of Angola and it was indeed observed most frequently in savannah habitat as well as miombo woodland. *Otolemur crassicaudatus* have been described to be flexible in their ecological adaptations (Bearder & Svoboda, 2013), and my findings mirror this with the relative abundance of the species not varying significantly between different habitats and altitudes in Angola.

Galago moholi were observed at a relatively high encounter rate of 4.40/km in miombo woodland, gallery forest. This contrasts reports on *G. moholi* being less common in habitats dominated by miombo trees (Skinner & Smithers, 2005). My findings do however support previous studies that report the species ranging in habitats close to human settlements (Pullen & Bearder, 2013).

In Angola *P. edwardsi* was found at encounter rates ranging from 0.80 individuals/km in secondary, moist tall forests to 1.8/km in highland moist forest (both primary and secondary). This is considerably higher than abundance estimates of the sister species *P. ibeanus* in Kibale NP in Uganda where they were observed in moist, evergreen forest at 0.03 – 0.16/km (Weisenseel *et al.,* 1993), and 0.04/km (Off, 2003). Pimley (2002) reports on density estimates of *P. edwardsi* in Cameroon, same potto species as in Angola, to be 4.7/km^2, with them occurring in highland secondary forest and farm bush. Charles-Dominique (1977) reports on *P. edwardsi* being more common in the flooded forests of Makokou, Gabon, with a density estimate of 28/km^2, than in primary forests where they occur at 8-10/km^2. Pottos are known to range in a wide variety of habitats and altitudes, and that was seen in Angola as well. *Perodicticus edwardsi* mainly utilise the upper strata of its habitat, and as a quadrupedal climber, that do not jump, a continuous canopy is important (Oates, 2011). In Angola the highest density of *P. edwardsi* was indeed observed in the site with the densest canopy coverage. Pimley (2002) and Weisenseel *et al.* (1993) did also observe higher densities of pottos in primary forests. Forest disturbance with logging of larger trees therefore has great conservation implication for this species. With my data I was able to update the distribution records of *P. edwardsi* as I observed the species ~320 km south/west of its currently known range (Oates *et al.,* 2008).

Galagoides demidovii was the most frequently encountered species in north western Angola, at a rate of between 0.3/km in semi-arid baobab savannah woodland and 6.8/km in highland moist forest (both primary and secondary). Stokes (2011) did similarly observe *Gd. demidovii* more frequently than any other galago species present on Bioko Island, Equatorial Guinea, with an encounter rate of 1.54/km. Other studies of *Gd. demidovii* on Bioko Island reports on lower encounter rates of 0.3/km (Croce, 2009). In Korup NP in Cameroon *Gd. demidovii* was encountered at a rate of 1.9/km (Bearder & Honess, 1992), and in Okomu NP in Nigeria it was encountered at 3.0/km (Bearder & Oates, 2009). *Galagoides demidovii* tend to be more abundant in lower elevation forests (Ambrose & Butynski, 2013). I report on a considerably higher encounter rate than previously recorded, and the highest encounter rates were observed at higher altitude. This might indicate that *Gd. demidovii* is more adaptable than previously thought, and therefore its distribution may well be larger than reported, with many parts of the distribution of *Gd. demidovii* still to be surveyed (Bearder *et al.,* 2003). The high abundance of *Gd. demidovii* correlated positively with the density of the undergrowth, in line with other studies on this species (Charles-Dominique, 1977; Ambrose, 1999) but also with canopy cover. Laurance *et al*. (2008) on the contrary did not find that canopy cover was positively associated with abundance of galagos and pottos, but found slope levels to be the determining factor for *Gd. demidovii*. There are big advantages for *Gd. demidovii* to utilise undergrowth that is denser as it provides shelter and protection against predators. Further, using the undergrowth does provide food opportunities as *Gd. demidovii* has been observed to feed on insects on the forest floor (A. Perkin. pers. comm). I was able to do expand the known distribution for *Gd. demidovii* as I observed the species ~190 km south/west of its previous distribution records (Bearder, 2008). My data therefore represent new southern limits for both the *P. edwardsi* and *Gd. demidovii*.

The new species I have described in Angola, *Galagoides kumbirensis* is so far only known to range in four locations in north western Angola, where it seems to replace *Gd. thomasi*. *Galagoides kumbirensis* was observed at a rate of between 0.17/km in semi-arid baobab savannah woodland to 2.67/km in secondary moist tall forests. Based on these habitat types and the altitudinal distribution of where *Gd. kumbirensis* was observed (285-910 m asl), as well as taking into account geographical barriers, such as the steep escarpment, we extrapolated an extent of occurrence of 20,000 km^2. It may be possible that the species range further north as the suitable habitats extends in to small parts of the Democratic Republic of Congo. Recently the *Galagoides* genus was divided in two, where the western dwarf galagos (*Gd. demidovii*, *Gd. thomasi* and now also *Gd. kumbirensis*) still belongs to *Galagoides*, and the remaining eastern dwarf galagos now falls under *Paragalago* (Masters *et al*., 2017). The division of the genus was based on differences in morphologies, vocal repertoires and on molecular genetic evidence (Masters *et al*., 2017). This split highlights the need of studying and conserving dwarf galagos as the *Paragalago* spp. and *Galagoides* spp. are now even more unique and geographically restricted than previously thought, and conservation strategies planned for one genus or species will no longer be suitable as they consists of several, very different species (Groves, 2016).

The results of my studies in Africa have further provided a valuable data set on the distribution and densities of galagos and pottos in Uganda and Angola. The data from these publications have already aided in the reassessments of the IUCN Red List accounts for *Gd. thomasi* (Svensson & Bearder, 2017), *G. moholi* (Bearder *et al*., 2017), *Gd. demidovii* (Svensson *et al*., 2017a) and *P. edwardsi* (Svensson & Pimley, 2017).

3.3 Trade in nocturnal primates

Three of the publications (Annexes 6 - 8) included in this dissertation focussed on the trade and use of nocturnal primates and other wildlife (Svensson & Friant, 2014; Svensson *et al.,* 2015; Svensson *et al.*, 2016). Although the utilisation of and trade in primates is known to be one of the main threats to the survival of primate populations the research has previously mainly been focussed on diurnal primates, which in many locations are hunted at unsustainable rates (Fa & Yuste, 1995; Juste *et al*., 1995; Nekaris & Nijman, 2013). My research on trade was mainly desk based (Svensson & Friant, 2014; Svensson *et al.*, 2015; Svensson et al., 2016), but also included our fieldwork in Nigeria conducting interviews with hunting communities (by S. Friant). I aimed through my research to quantify the trade in nocturnal primates, and explore whether the trade represents a conservation threat to the Neotropical and African nocturnal primates, as seen in diurnal primates and the Asian lorises (Nekaris & Nijman, 2007; Starr *et al.,* 2010). In Svensson and Friant (2014) I focussed on trade in pottos and angwantibos to enable a comparison with their Asian cousins; the slow lorises. From online questionnaires I found that respondents from over half of the potto and angwantibo range countries knew of trade in these species (including for consumption, traditional medicine and as pets). Of the interviewees in Nigeria 64% reported to have eaten these species and of these people about half were eating them on a weekly basis. This indicates that trade, and more specifically hunting of angwantibos and pottos is occurring in greater numbers than previously thought (Ntiamoa-Baidu, 1992; Juste *et al.,* 1995; Hofmann *et al*., 1999; Fa & Yuste, 2001; Fa *et al.,* 2006; Olupot *et al.,* 2009; Mbete *et al*., 2011). Based on the findings in this first study I decided to broaden my scope to include also the galagos and a broader geographical area (Svensson *et al*., 2015). The follow up study showed that this trade is even more widespread, both in regards to type of trade and regions. Further I found that galagos are also being traded, both domestically and internationally, and was especially prevalent in the pet trade.

Previously it has been thought that smaller bodied animals are less threatened by hunting as economically it makes more sense to hunt larger prey species. However this pattern seems to be changing. In Svensson & Friant (2014) I report on angwantibos being targeted by hunters in Republic of Congo due to lack of more commonly targeted, and larger, species. In Angola we frequently observed small bodied squirrels being sold as bushmeat (Bersacola *et al.,* 2014). These findings mirrors results from other recent studies. For example, in Madagascar the grey mouse lemur (*Microcebus murinus*) and the grey-brown mouse lemur (*M. griseorufus*) are hunted as bushmeat despite having the body size of *Galagoides* spp. and they are eaten locally as well as being sold in markets (Nekaris, 2013a; Gardner & Davies, 2014). Anadu *et al*. (1988) also found that smaller species, such as nocturnal primates, were being targeted in increasing numbers due to overhunting of larger species. It might be possible that we can use prey choice as a proxy to show that larger species are becoming rarer in areas where population surveys are difficult to conduct. We could through market surveys assess the amount of small bodied species to give an indication of the hunting patterns.

As pointed out in Svensson *et al*. (2015) there is a paucity of trade data from some African range countries, including Angola. We concluded that the absence of reports from these areas does not necessarily indicate an absence of trade, but rather reflecting the general low levels of focused research conducted in these countries, mostly due to political instabilities. My research area was limited to urban areas and trade occurring along the main roads (Bersacola *et al.,* 2014), whereas previous findings has shown that small bodied animals such as nocturnal primates tend to be consumed by hunters and their families or traded in more rural settings (Svensson & Friant, 2014; Svensson *et al*., 2015). During my fieldwork in

Angola I did not observed any nocturnal primates in neither the bushmeat trade nor the pet trade, however colleagues in Angola have since reported on *O. crassicaudatus* occurring in the bushmeat trade (Fig. 5). Although the increasingly growing commercial bushmeat trade is having an obvious effect on wild primate populations, smaller scale subsistence hunting has also been found to locally have an effect on primate populations (Fitzgibbon *et al.*, 1995). It is therefore important to monitoring this local trade and to study the wild populations of nocturnal primates to keep an eye on population trends.

This figure has been removed due to copyright restrictions

Figure 5. *Otolemur crassicaudatus* (and *Miopithecus talapoin*) sold as bushmeat in the Province of Bengo, Angola (February 2017) © Christopher Hines

As discussed in Svensson & Friant (2014) the trade and usage of nocturnal primates has been covered by much more research in South East Asia (Nekaris & Nijman, 2007; Nekaris *et al.*, 2010; Starr *et al.*, 2010; Musing *et al.*, 2015). It has with the increase in research over the last few decades become apparent that trade is a much larger threat to the nocturnal primates in Asia than previously thought (Nekaris & Nijman, 2007; Nekaris *et al.*, 2010; Starr *et al.*, 2010; Musing *et al.*, 2015). The bushmeat and pet trade is becoming an emerging threat to the lemurs of Madagascar as well, especially after the political upheaval in

2009 (Barrett & Ratsimbazafy, 2009; Schwitzer *et al*., 2014; Reuter *et al.,* 2016). As taboos are degrading in many areas lemur species are becoming more common in the pet and bushmeat trade, including as a luxury meat in the urban areas (Barrett & Ratsimbazafy, 2009; Jenkins *et al*., 2011; Reuter *et al.,* 2016). This might well be the case in Africa and the Neotropics as well and, again, monitoring of wild populations is therefore imperative.

It became apparent from my research on trade in African nocturnal primates that Japan is one of the major importers of African strepsirrhines (Svensson & Friant, 2014; Svensson *et al*., 2015). Japan as a major importer of wildlife and specifically trade in nocturnal primates has been highlighted in other studies as well (Nijman *et al.,* 2011; Musing *et al*., 2015). Musing *et al.* (2015) found from the CITES database that between 1985 and 2013 Japan was the biggest importer of slow lorises (*Nycticebus* spp.). The numbers of traded strepsirrhines may be small in comparison to other wildlife, but it is important to monitor trade numbers, especially to import countries where demand is higher, such as Japan. It is also important that we monitor population trends of the nocturnal primates in the exporting countries.

I have also broadened my online trade research further and the most recent study on nocturnal primate trade focussed on the night monkeys in the Neotropics (Svensson *et al.,* 2016). In the Neotropics regional and domestic trade in night monkeys has previously been covered in detail but only in parts of the species' distribution: Colombia, Peru and Brazil (Maldonado *et al.,* 2009; Rojas Briñez, 2011; Ruiz-García *et al.,* 2013; Maldonado & Peck, 2014). My research of mainly the international trade of night monkeys provided an overview of the current situation, as well as looking at trends over the last four decades (Svensson *et al.,* 2016). It was found that the legal trade is still ongoing, but in decreasing numbers with only Peru still trading live individuals in significant numbers. My findings did however show that although there is national legislation in place in all range countries, they are often not following CITES regulations and are rarely enforced. Illegal pet and bushmeat trade is still occurring in night monkeys (Maldonado *et al.,* 2009; Maldonado & Peck, 2014; Svensson *et al.,* 2016), and in other primate species such as squirrel monkeys (*Saimiri* spp.) and capuchin monkeys (*Cebus* spp.) (Ceballos-Mago *et al.,* 2010; Shanee, 2012). Maldonado and Peck (2014) provide evidence of wild populations of night monkeys still being affected negatively by the trade for biomedical research. It seems that the major problem regarding trade in night monkeys is one of enforcement.

With the findings from the studies included in this dissertation I have been able to add to the knowledge on trade in primate species that were previously known little about. We now have more of an insight into the trade and usage of African nocturnal primates and it is clear that there is an occurring trade of nocturnal primates throughout mainland Africa, in all types of trade, but varying over geographical areas. I have also been able to contribute to a better understanding of the international trade in night monkeys. Although the numbers of traded nocturnal primates are seemingly small it is obvious that this trade is still ongoing and is occurring throughout their distribution.

CHAPTER 4:

CONCLUSION AND RECOMMENDATIONS FOR FUTURE STUDIES

4.1 Conclusion and recommendations for future studies

Even though publications on nocturnal primate conservation are becoming more common the nocturnal primates are still under-represented in conservation research. As discussed throughout this dissertation nocturnal primates are severely under studied in many parts of their distribution (Nekaris & Nijman, 2013; Svensson & Friant, 2014) and there is also a big gap in publications coming out of research on nocturnal primates. The representation within nocturnal primates is however also skewed with more research being published on lemurs than any of the Lorisiformes (Galagos, pottos, angwantibos and lorises) (Setchell, 2012). Primates are one of the most studied mammal groups (Marshall & Wich, 2016a) but there are still large gaps in our understanding of many primate species, nocturnal and diurnal, including information missing on their population statuses, distribution and what threats they face (Marshall & Wich, 2016b). Without a good understanding of the distribution and densities we cannot implement successful conservation plans, and equally important is the knowledge about their ecology and how this affects their distribution. As Nekaris and Nijman (2013) points out, we have an ethical obligation to include all species in our research as far as we are able to, diurnal and nocturnal. It is also of great importance to conduct follow up studies, especially on density and ranges of species so that we can monitor population and distribution trends. I hope that the studies included in this dissertation will provide a useful baseline for further studies on distribution, species' ecology and trends in trade.

Although many nocturnal primates are extensively distributed across Sub-Saharan Africa and the Neotropics, many species continue to be only partially described throughout their range (Bearder *et al.,* 2003; Nekaris & Bearder, 2011; Rylands *et al.,* 2012). In many cases, information regarding species-specific abundance, behaviour, ecology and conservation status is incomplete or non-existent (Dinesen *et al.,* 2001; Bearder *et al*., 2003; Defler &

Bueno, 2007; Rylands *et al.,* 2012; Shanee *et al*., 2013). The Gambian *G. senegalensis* I studied is a case in point, as it is well studied in the easternmost, and to some extents in the western parts of its distribution, but nothing is known about the species in the area in between which covers 1000s of km. Niumi NP would be ideal as a field site for long-term research, such as radio-tracking studies, of the western *G. senegalensis* as the habitat is accessible and the animals were easy to habituate.

Other nocturnal primates that we still know very little about, and where detailed studies should be a priority, are the angwantibos and to some extent the pottos. Focussed research of these species is especially urgent in Central Africa where very limited research has been done as discussed in Svensson *et al*. (2015).

Reviews of galago, potto and night monkey diversity highlight a lack of data for acknowledged species as well as potential new forms. Morphological and genetic evidence suggest that a far greater number of cryptic species may yet be revealed within these species (Groves, 2001; Grubb *et al*., 2003; Pimley, 2009; Rylands *et al.,* 2012; Nekaris, 2013a; 2013b; Oates, 2011; Pozzi *et al.,* 2014; 2015). It is important to be aware of the possibility of new species being present within populations. The cryptic nocturnal species may have very similar appearances but studies have shown that similarly looking species can actually differ strongly in parameters such as reproduction and social organisation, as seen in squirrel monkeys (*Saimiri* spp.) (Boinski & Cropp, 1999). The new Angolan *Gd. kumbirensis* is also a case in point, as it previously based on museum specimens was believed to be *Gd. thomasi*. If future systematic research reveals more species then increased conservation attention will be urgently needed to create new conservation strategies for each individual species (Nekaris 2013a, b). Further long-term research on the ecology, behaviour and conservation needs of *Gd. kumbirensis* is urgently needed. The forests of Angola are being logged at an alarming rate and there is a risk of the newly described galago to be more threatened than we think

(Hansen *et al*., 2013; Bersacola *et al*., 2015; Cáceres *et al.,* 2016; Svensson *et al*., 2017d). I suggest the Kumbira Forest on the Angolan Escarpment as a possible long-term field site to study this new galago in more detail.

The trade and ethnozoological uses of nocturnal primates may appear to be small-scale but its impact may nevertheless be significant in certain areas, especially when trade is considered in conjunction with other anthropogenic pressures. Increasing our knowledge and understanding of nocturnal primate taxonomy is important also when it comes to fighting the trade of these species, especially the international trade. If the traded primates are not consistently and accurately identified to species level the reporting of for example CITES will not reflect our current understanding of species richness and distribution, and thus will hamper the traceability and assessment of the scale and impact of the trade. It will also make re-introduction of rescued primates problematic. The morphological similarities between many nocturnal primate species present the possibility of confusion or even laundering of rarer species under the guise of commoner ones. Where possible protocols for rapid genetic testing of traded primates by wildlife authorities and border personnel should be implemented, to determine species.

It is evident through my research that even if legislation is in place to hinder the illegal international trade it is often a case of lack of enforcement. I recommend that research conducted on nocturnal primate trade, where possible, should be shared with the government agencies responsible for natural resource management in the range countries, as well as academic institutions. This is important to raise awareness and encourage enforcement of legislation regarding wildlife trade.

It became apparent when conducting the literature reviews, but also when comparing abundance estimates, that there is a lack of consistency in research methods when surveying nocturnal primates, both between continents, but also between research groups in the same locations. Fieldwork focussing on the ecology and behaviour of nocturnal primates are often collected opportunistically and not in a systematic manner that would enable more rigorous statistical analysis (Bearder *et al*., 2003; Plumptre *et al.,* 2013). It should be a priority to develop standardised techniques and survey methods for nocturnal primates. The Best Practice Guidelines for Great Ape Conservation, set up by the great ape section of the IUCN Primate Specialist Group could be used as models. A great example is their guidelines on surveying and monitoring great ape populations (Kühl *et al.,* 2008).

Because nocturnal primates in Africa and the Neotropics occur in increasingly fragmented and threatened forest habitat (Butynski *et al*., 1998; Bearder, 1999; Dinesen *et al*., 2001; Shanee *et al.,* 2013; Shanee *et al.,* 2105) it is likely that without urgent research and intervention some species may disappear from parts of their range before sufficient information and correct identification has been gathered to implement effective conservation strategies. With this dissertation I hope I have contributed to this knowledge bank and that my data will be used in the future to build on, by myself and others.

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ANNEXES

Publications submitted, with statement scope of the candidate's contribution in relation to the other authors in the case of multi-authored work.

THE PUBLICATIONS HAVE BEEN
REMOVED FROM THIS THESIS DUE
TO COPYRIGHT CONCERNS

Annex 1

Svensson MS, Samudio R, Bearder SK, Nekaris KAI (2010). Density estimates of Panamanian owl monkeys (*Aotus zonalis*) in three habitat types. ***American Journal of Primatology*** 72: 187- 192.

Author contributions: Initiated the study: MSS, SKB, KAIN; collected data: MSS; analysis: MSS; wrote the paper: MSS, KAIN, RS, SKB; all authors approved the final submission.

Annex 2

Svensson MS, Bearder SK (2013). Sightings and habitat use of the northern lesser galago (*Galago senegalensis senegalensis*) in Niumi National Park, the Gambia. ***African Primates,*** 8: 51-58.

Author contributions: Initiated the study: MSS, SKB; collected data: MSS, SKB; analysis: MSS; wrote the paper: MSS, SKB; both authors approved the final submission.

Annex 3

Svensson MS, Bersacola E (2013). Sightings of thick-tailed greater galago *Otolemur crassicaudatus monteiri* (Bartlett in Gray, 1863) Near Lake Mburo National Park, South Uganda. ***African Primates**,* 8: 63-66.

Author contributions: Initiated the study: MSS; collected data: MSS, EB; analysis: MSS; wrote the paper: MSS; both authors approved the final submission.

Annex 4

Bersacola E, **Svensson MS,** Bearder SK (2015). Niche partitioning and environmental factors affecting abundance of strepsirrhines in Angola. ***American Journal of Primatology,*** 77(11): 1179-1192.

Author contributions: Initiated the study: MSS, EB; collected data: MSS, EB, SKB; analysis: EB; wrote the paper: MSS, EB; all authors approved the final submission.

Annex 5

Svensson MS, Bersacola E, Mills MSL, Munds RA, Nijman V, Perkin A, Masters JC, Couette S, Nekaris KAI & Bearder SK (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. ***American Journal of Physical Anthropology***, 163(1): 30-43.

I initiated this study along with E Bersacola and SK Bearder, and was thereafter involved in most parts of finalising the paper, including collecting the data and writing the paper.

Annex 6

Svensson MS, Friant SC (2014). Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. ***Endangered Species Research,*** 23(2): 107-114.

Author contributions: Initiated the study: MSS; collected data: MSS, SCF; analysis: MSS, SCF; wrote the paper: MSS, SCF; both authors approved the final submission.

Annex 7

Svensson MS, Ingram D, Nekaris KAI, Nijman V (2015). Trade and ethnozoological use of African lorisiforms in the last 20 years. ***Hystrix- Italian Journal of Mammology***, 26(2): 153-161.

Author contributions: Initiated the study: MSS; collected data: MSS, DI, VN; analysis: VN; wrote the paper: MSS, DI, VN, KAIN; all authors approved the final submission.

Annex 8

Svensson MS, Shanee S, Shanee N, Bannister FB, Cervera L, Donati G, Huck M, Jerusalinsky L, Juarez CP, Maldonado AM, Mollinedo JM, Méndez-Carvajal PG, Argandoña MAM, Mollo Vino AD, Nekaris KAI, Peck M, Rey-Goyeneche J, Spaan D, Nijman V (2016). Disappearing in the night: an overview on trade and legislation of night monkeys in South and Central America. ***Folia Primatologica,*** 87(5): 332-348.

Author contributions: Initiated the study: MSS; collected data: MSS, SS, NS, FBB, LC, GD, MH, LJ, CPJ, AMM, JMM, PGCM, MAMA, ADMV, KAIN, MP, JRG, DS, VN; analysis: MSS, VN; wrote the paper: MSS, SS, NS, MH, KAIN, VN; all authors approved the final submission.

Annex 9

Questionnaires distributed in Nigeria by S. Friant

and

Online questionnaires created in surveymonkey.com

The following supplement accompanies the article

Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia

Magdalena S. Svensson[1,*], Sagan C. Friant[2]

[1]Nocturnal Primate Research Group, Oxford Brookes University, Oxford OX3 0BP, UK
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Endangered Species Research 23: 107–114 (2014)

SUPPLEMENT. Oral questionnaire used in the survey (July to December 2012) of 327 hunters in the Oban Division of Cross River National Park, southeast Nigeria

Questionnaire

DATE ___ ___ / ___ ___ / ___ ___ PARTICIPANT ID NUMBER _________________

A1	What is your preferred bushmeat?	NAME ANIMAL ____________________________
A2	Which bushmeat do you eat most often?	NAME ANIMAL ____________________________
B1	Are there any medicinal practices in your village that involve live or dead wild animals?	YES 1 NO 2 DESCRIBE:
B2	Have you **ever** touched a wild animal (dead or alive) for any of the following reasons? *MARK ALL THAT APPLY*	NO 1 HUNTING 2 TRAPPING 3 BUTCHERING 4 SELLING 5 KEEPING AS PET 6
B3	Which animal do you prefer to hunt?	ANIMAL: WHY:

Use the following questions to fill the chart below.

C1-C4	*For EACH animal, ask : Do you hunt, consume butcher or sell:* *How often?*	NEVER (N) 1-5 TIMES EVER (R) 1-3 TIMES/ YEAR (Y) EVERY MONTH (M) EVERY WEEK (W) EVERY DAY (D)
C5	Have you ever kept a wild animal as a pet? If yes, which ones & how many?	

	C1	**C2**	**C3**	**C4**		**C5**		
SPECIES NAME	**HUNT**	**CONSUME**	**BUTCH**	**SELL**		**PET**		**COMMENTS**
					Price	**#**		
28. Potto/ Angwantibo (fox)								

Trade in African nocturnal primates

*** 1. In which African country are you currently working / have you been working?**

Please specify location, length of stay and main occupation

*** 2. Have you ever seen pottos, angwantibos and/or bushbabies for sale?**

- ◯ Yes
- ◯ No

If yes, please give details on species, number of individuals and location of sighting:

*** 3. If you saw pottos, angwantibos and/or bushbabies for sale, where was this?**

- ☐ Small village market
- ☐ City/town market
- ☐ Road side
- ☐ N/A (you have never seen them for sale)
- ☐ Other (please specify below)

Comments (please give details on species and number of individuals if possible):

*** 4. How often have you observed pottos, angwantibos and/or bushbabies for sale?**

- ◯ Once a week or more
- ◯ Once a month
- ◯ Less regulary (please give details below)
- ◯ Never

Comments (please give details on species and number of individuals if possible):

*** 5. How often did/do you visit the location where you observed these species for sale?**

- ◯ Once a week or more
- ◯ Once a month
- ◯ Less regularly (please give details below)
- ◯ N/A

Comments:

*** 6. If you have seen pottos, angwantibos or bushbabies for sale, how were they displayed?**

- ☐ Live
- ☐ Fresh whole carcasses
- ☐ Smoked whole carcasses
- ☐ Smoked body parts
- ☐ Other (please comment below)
- ☐ N/A

Comments (please give details on species and number of individuals if possible):

*** 7. Apart from seeing carcasses/individuals of pottos, angwantibos and/or bushbabies being sold, have you heard of any of these species being hunted?**

- ◯ Yes
- ◯ No

If yes, please give details on species and number of individuals if possible:

*** 8. When pottos, angwantibos and/or bushbabies were observed in markets, in which season did the observation/s occur, and during which season were you in the location?**

- ◯ During the wet season - I was there during the wet season only
- ◯ During the wet season - I was there during both seasons
- ◯ During the dry season - I was there during the dry season only
- ◯ During the dry season - I was there during both seasons
- ◯ During both season - I was there both season
- ◯ N/A

Comments:

*** 9. What usage of pottos, angwantibos and/or bushbabies do you know about?**

- ☐ Bushmeat
- ☐ Kept as pet
- ☐ Traditional medicine
- ☐ Witchcraft
- ☐ None
- ☐ Other (please give details below)

Comments:

10. Thank you for taking time to fill in this survey. If you have more comments please email me at svensson_magdalena@hotmail.com or use the space below.

Trade in African nocturnal primates

Annex 10

Co-author statements on the contribution of Magdalena S Svensson on the Publications included in this PhD by Published Work

28 April 2016

To whom it may concern,

Magdalena Svensson and I have worked together for several research projects, including surveying nocturnal primates in Uganda and Angola. Here I include details of mine and Magdalena's contribution to the work:

Svensson MS & Bersacola E (2013) Sightings of thick-tailed greater galagos *Otolemur crassicaudatus monteiri* (Barlett in Gray, 1863) near Lake Mburo National Park, south Uganda. *African Primates* 8: 63-66

The research concept and was Magdalena's, while my role was to assist her during data collection and review the draft of the manuscript she wrote before submission.

With my full support, Magdalena submitted two publications which I am co-author, and confirm that the information regarding each contributions she provided in her thesis is correct. The publications are the following:

Bersacola E, Svensson MS, Bearder SK, Mills M & Nijman V (2014) Hunted in Angola: Surveying the bushmeat trade. *SWARA* (January - March): 31-36

Conceived and designed the study: MSS, EB, SKB; Conducted fieldwork: MSS, EB, SKB, MM; Entered and analysed data: MSS, EB, VN; Wrote first draft of the manuscrupt: EB, Helped with writing: MSS

Bersacola E, Svensson, M & Bearder, SK (2015) Niche partitioning and environmental factors affecting abundance of nocturnal primates in Angola. *American Journal of Primatology*, 77(11): 1179-1192

Conceived and designed the study: MSS, EB; Conducted fieldwork: MSS, EB, SKB; Entered and analysed data: EB, MSS; Wrote first draft of the manuscrupt: EB, Helped with writing: MSS

Sincerely

Elena Bersacola

MPhil/PhD Student
Anthropological Centre for Conservation, the Environment and Development (ACCEND)
Oxford Brookes University, Oxford, UK

OXFORD BROOKES UNIVERSITY

28th of April 2016

Re: Confirmation of authorship

Dear Sir / Madam,

Svensson MS, Samudio R, Bearder SK, Nekaris KAI (2010). Density estimates of Panamanian owl monkeys (Aotus zonalis) in three habitat types. American Journal of Primatology 72: 187- 192.
I hereby confirm that Magdalena Svensson initiated this study and conducted the fieldwork in Panama. She took the lead in writing the paper and carried out the most part of the analysis of the data.

Nekaris KAI, Arnell AP, Svensson MS (2015). Selecting a conservation surrogate species for small fragmented habitats using ecological niche modelling. Animals 5(1): 27-40.
As the first author I hereby confirm that Magdalena Svensson was involved in the analysis and writing of the above publication.

Yours sincerely,

Prof Anna Nekaris
Director Little Fireface Project
Course Tutor MSc Primate Conservation

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OXFORD BROOKES UNIVERSITY

School of **Social Sciences** and **Law**

Oxford 28 April 2016

Dear Members of the PhD committee

I write this letter at the request of Magdalena S Svensson who is enrolled as a PhD-by-Published-Work student, with me as her Director of Studies. We have co-authered the following two papers and Magda has been involved in all stages of the process.

Bersacola E, **Svensson MS**, Bearder SK, Mills M, Nijman V (2014). Hunted in Angola: surveying the bushmeat trade. *Swara* January-March: 31-36.

The contributions of the different authors: Initiated the study: **MSS**, EB, SKB; collected data: **MSS**, EB, SKB, MM; analysis: **MSS**, EB, VN; wrote the paper: **MSS**, EB; all authors approved the final submission.

Svensson MS, Ingram D, Nekaris KAI, Nijman V (2015). Trade and ethnozoological use of African lorisiforms in the last 20 years. *Hystrix- Italian Journal of Mammology* 26(2): Online First.

The contributions of the different authors: Initiated the study: **MSS**; collected data: **MSS**, DI, VN; analysis: **MSS**, VN; wrote the paper: **MSS**, DI, VN, KAIN; all authors approved the final submission.

I confirm that Magdalena indeed did make the contributions to the papers as indicated above.

Professor Vincent Nijman

29 April 2016

Letter of confirmation regarding contribution to publications: Magdalena Svensson

Magdalena and I have conducted several fieldwork projects over the years throughout Africa, surveying the occurrence of nocturnal primates (specifically *Galago* spp. and *Perodicticus* spp.) and their ecology. I am happy to confirm her contribution to the following paper:

Svensson MS, Bearder SK (2013). Sightings and habitat use of the northern lesser galago (Galago senegalensis senegalensis) in Niumi National Park, The Gambia. African Primates 8: 51-58.

The study was initiated by the two of us and we conducted the fieldwork in the Gambia together in 2013. I aided Magdalena in the writing of the manuscript but she was the main author, doing the bulk of the writing up.

Kind regards,

S. K. Bearder

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10 January 2017

Research Degrees Panel
Oxford Brookes University

Dear Research Degrees Panel,

PhD candidate: **Magdalena Svensson**

I am writing as one of the co-authors on the publication;

Svensson, M., Shanee, S., Shanee, N., Bannister, F.B., Cervera, L., Donati, G., Huck, M., Jerusalinsky, L., Juarez, C.P., Maldonado, A., Martinez Mollinedo, J., Mendez-Carvajal, P.G., Molina Argandoña, M.A., Mollo Vino, A.D., Nekaris, K.A.I., Peck, M., Rey-Goyeneche, J., Spaan, D. & Nijman, V. (2017). Disappearing in the Night: An Overview on Trade and Legislation of Night Monkeys in South and Central America. *Floia Primatologica*. 87: 332-358.

This paper details the legal trade of South American night monkeys, genus Aotus, over the period 1975-2015 using data from the CITES database. The paper showed a decrease over time in international trade in the different species; however results suggest that even current levels of trade could still pose a threat to certain species, particularly the rarer ones. I can confirm that Ms Svensson initiated the study and took the lead in data collection analysis as well as writing the paper.

Please do not hesitate to contact me if you have specific questions.

Yours sincerely,

Dr Sam Shanee

THE UNIVERSITY of WISCONSIN MADISON

To whom it may concern,

I hereby, as a co-author, confirm Magdalena S Svensson's involvement in the following paper: Svensson MS & Friant SC (2014). Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. Endangered Species Research 23(2): 107-114.

Magdalena invited me to contribute to this publication with my data from Nigeria. We then worked together to analyse and finalise the manuscript, with Magdalena acting as the lead author.

Sincerely,

4/28/2016

Sagan Friant

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