**BSc. thesis:**
Predator-primate occupation and co-occurrence in the Issa Valley, Katavi Region, western Tanzania.

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Student Applied Biology, Aeres University of Applied Sciences, Almere, The Netherlands
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In association with the Ugalla Primate Project
Edam, 2 June 2017

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Front page images, top to bottom:
Top: Eastern chimpanzee and leopard at the same location, different occasions.
Middle: Researcher and leopard at the same location, different occasions.
Bottom: Red-tailed monkey and researchers at the same location, different occasions.
All: Camera trap footage from the Issa Valley, provided by the Ugalla Primate Project. Edited: combined, gradient created and cropped.

Acknowledgements

Contents

Summary

Studies of predator-primate dynamics are scarce and often face difficulties when it comes to data collection. For this reason, the effects of predation on primate ecology are still partially unknown. As some studies on the subject have revealed that anthropogenic factors such as habitat destruction, hunting or encroachment can influence species interactions, there is a need for a better understanding of predator-primate dynamics to allow for more effective protection of species against such threats. However, a lack of knowledge about these dynamics currently prevents their inclusion in conservation policy development, which may result in counterproductive conservation methods in which time, resources and labour are negated by unpredictable circumstances. Therefore, the study reported here attempted to uncover patterns in the co-occurrence of primates and their likely predators in the Issa Valley of western Tanzania, a representative for the Miombo woodland ecosystem. To study these patterns, camera trap data collected in a year-long period (October 2014 to September 2015) and PRESENCE software were used to model single-species occupancy and two-species interactions. Single-species occupancy was modelled to find which covariates influence species occupation, and two-species interactions were modelled to find patterns in species co-occurrence. The principal findings of these models are that: 1) the occupation of most species is high, as most included species – except red-tailed monkey – were estimated to occupy more than half of the 14 included camera locations; 2) primates' occupation and detection (chimpanzee, baboon and red-tailed monkey) were mostly influenced or – in red-tailed monkey – even limited by habitat type, which may be the result of the species' adaptations to (perceived) predation risk; 3) baboons may shun areas of high leopard occupation, whereas red-tailed monkey occupation does not seem to be influenced by leopard occupation. However, data selection methods led to a set of data that limited the conclusions on species interactions to those two-species interactions mentioned above. Despite these limitations, the method for data analysis was found to fit the objective of this study. Therefore, these methods are recommended for use in further studies of co-occurrence patterns when the recommendations of this study this study are considered. Most importantly – to prevent encountering the same limitations as this study – future studies are recommended to 1) select locations systematically to represent the study area as a whole and prevent biases caused by possible location preferences of other studies (e.g. termite mound locations in chimpanzee studies), and 2) analyse species interactions using detection probability as well as occupation probability to incorporate (patterns in) the frequency with which species visit locations.

Résumé

Les études de la dynamique prédateur-primate sont rares et rencontrent souvent des difficultés en méthodes de collecte de données. Pour cette raison, les effets de la prédation sur l'écologie des primates sont encore partiellement inconnus. Parce que quelques études de la matière ont révélé que des facteurs anthropiques comme la destruction de l'habitat, la chasse ou l'empiètement humain peuvent influencer les interactions entre espèces, c'est nécessaire de mieux comprendre la dynamique prédateur-primate pour permettre une protection des espèces plus efficace contre ces facteurs. Cependant, le manque de connaissances sur ces dynamiques empêche actuellement leur inclusion dans le développement des mesures de conservation de la nature, ce qui peut entraîner des méthodes de conservation contre-productives dans lesquelles le temps, les ressources et le travail sont compromis par des circonstances imprévues. C'est pour cette raison que cette étude a essayé de découvrir des modèles dans la cooccurrence de primates et leurs prédateurs potentiels dans la vallée d'Issa de la Tanzanie de l'Ouest, un représentant possible pour l'écosystème des savanes boisées de Miombo. Pour étudier ces modèles, les données des camera pièges sont recueillies au cours d'une période d'un an (octobre 2014 à septembre 2015) et de logiciel PRESENCE est utilisé pour la modélisation d'occupation d'une seule espèce et les interactions entre deux espèces. L'occupation d'une seule espèce est modélisée pour déterminer les facteurs qui affectant l'occupation de l'espèce, et les interactions entre deux espèces sont modélisées pour déterminer des modèles de cooccurrence d'espèces. Les résultats principaux de ces modélisations sont: 1) l'occupation de la plupart d'espèces est élevée, car la plupart d'espèces incluses - à l'exception de le cercopithèque ascagne – ont été estimées à occuper plus de la moitié des 14 sites de camera pièges; 2) l'occupation et la détection des primates (le chimpanzé, le babouin cynocéphale et le cercopithèque ascagne) a été influencée principalement ou - dans le cercopithèque ascagne - même limité par des types d'habitat, qui peut être le résultat des adaptations de l'espèce au risque de prédation (ou de prédation perçu); 3) les babouins peuvent éviter les zones de hautes occupation du léopard, pendant que l'occupation des cercopithèque ascagne ne semble pas être influencée par l'occupation du léopard. Cependant, les méthodes de sélection des données ont conduit à un ensemble de données qui limitait les conclusions sur les interactions entre deux espèces à ces deux interactions mentionnées. Malgré ces limites, la méthode d'analyse des données est trouvée d'être appropriée pour atteindre l'objectif de cette étude. C'est pour cette raison que ces méthodes sont recommandées pour être utilisées dans d'autres études sur les modèles de cooccurrence, si les recommandations de cette étude sont considérées. Plus important – pour éviter de rencontrer les mêmes limitations que cette étude – les études futures sont recommandées de 1) sélectionner les sites de camera piège systématiquement pour représenter tout la zone d'étude et prévenir les préjudices causés par les préférences d'autres études pour certain sites (p. Ex. l'emplacement de camera pièges chez termitières pour les études de chimpanzés), et 2) analyser les interactions des espèces en utilisant la probabilité de détection ainsi que la probabilité d'occupation pour intégrer (modèles dans) la fréquence avec laquelle les espèces visitent les emplacements.

1.   Introduction

Most – if not all – primate species in the world face some risk of predation (Bidner, 2014). This risk is likely to have contributed to shaping primate ecology, such as (social-) behaviour (*e.g.* Anderson, 1986; Stanford, 1998; 2002; Colquhoun, 2006; Zuberbühler, 2007; Coleman & Hill, 2014), population dynamics and group size (*e.g.* Anderson, 1986; Hill & Dunbar, 1998; Hill & Lee, 1998; Irwin, Raharison & Wright, 2009), and spatial distribution (*e.g.* Irwin et al., 2009; Lwanga, Struhsaker, Struhsaker, Butynski, & Mitani, 2011; Coleman & Hill, 2014). Nonetheless, studies of predator-primate dynamics are scarce and often face difficulties when it comes to data collection (Stanford, 2002; Klailova et al., 2012; Bidner, 2014; Farris, Karpanty, Ratelolahy, & Kelly, 2014). For this reason, the effects of predation on primate ecology are still partially unknown (Bidner, 2014). Some studies on the subject have revealed that anthropogenic factors such as habitat destruction (*e.g.* loss, fragmentation or degradation), hunting or encroachment can alter the species composition of an area and thereby influence species interactions such as predator-primate dynamics (Klailova et al., 2012; Farris et al., 2014; Bidner, 2014). Previous studies have therefore stressed the need for a better understanding of predator-primate dynamics to enable more effective protection of species against an expected increase in anthropogenic threats, for instance by the use of novel approaches to study these relationships (Farris et al., 2014).

Primates serve important ecological functions in their natural habitats, such as pollination and seed dispersal (Gross-Camp, Mulindahabi, & Kaplin, 2009; Heymann, 2011; Lambert, 2011; Wich & Marshall, 2016). They also benefit human communities as a source of food to local people, by attracting tourists or by providing researchers with insights into early human evolution (*e.g.* Nishida, 1989; Moore, 1996; Wich & Marshall, 2016; Estrada et al., 2017). In addition, conservation efforts can benefit from using primates as flagship species that stimulate support for the protection of their habitat, or as an umbrella species whose protection indirectly protects other species in the habitat (Lambert, 2011; Supriatna & Ario, 2015; Wich & Marshall, 2016). Nonetheless, an estimated 60% of the 504 extant primate species are classified as threatened, and populations of an estimated 75% are declining (Estrada et al., 2017). Fortunately, only a single primate species is thought to have gone extinct since modern times: the Miss Waldron's red colobus (*Procolobus badius waldroni*) (Oates, Abedi-Lartey, McGraw, Struhsaker, & Whitesides, 2000; McGraw, 2005; Oates, Struhsaker & McGraw 2016). Anthropogenic factors are the main threat to these primates, of which habitat destruction and hunting are thought to be most pressing (Cowlishaw & Dunbar, 2000; Harcourt & Doherty, 2005; Mittermeier, 2013; Estrada et al., 2017). A third major threat – especially to African great apes – are human diseases (*e.g.* common cold, influenza, tuberculosis and Ebola fever) that can be transferred by contact with humans as a result of hunting, human encroachment, research or eco-tourism (Woodford, Butynski, & Karesh, 2002; Köndgen et al., 2008; Mittermeier, 2013; Wolf, Sreevatsan, Travis, Mugisha, & Singer, 2014; Wich & Marshall, 2016; Estrada et al., 2017). These threats can affect primate communities in countless ways, of which only a few are well understood.

Many previous studies have stressed the need for a better understanding of the effects of anthropogenic factors on primate communities (*e.g.* Anderson, 1986; Stanford, 2002; Colquhoun, 2006; Wasserman, Chapman, Milton, Goldberg, & Ziegler, 2013; Bidner, 2014; Farris et al., 2014). These factors can directly affect a primate species (*e.g.* hunting), its natural habitat (*e.g.* habitat loss) or its food sources (*e.g.* logging). However, these factors can also influence a primate species in indirect ways, for instance by altering species composition in its habitat and thereby disturbing species interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008; Valiente-Baunet et al., 2015). Disturbances in these interactions are considered an often missed but major component of biodiversity loss or ecosystem health that can go along with or even cause species extinction (McCann, 2007; Tylianakis et al., 2008; Aizen, Sabatino, & Tylianakis, 2012). Conservation and research efforts often assess biodiversity loss or ecosystem health on a species or community level but do not consider species interactions (McCann, 2007; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010; Valiente-Baunet et al., 2015). However, it is the network of species interactions – and not only the species – which ensures that the ecosystem functions (McCann, 2007). Therefore, a better examination of these interactions is needed to prioritise the conservation of species interaction networks instead of particular species or diversity (McCann, 2007; Tylianakis et al., 2008). A failure to consider these networks may lead to counterproductive conservation methods (Tylianakis et al., 2010). For instance, the absence of grey wolves (*Canis lupus*) in North America and Eurasia was found to result in a nearly six times higher cervid density (Ripple & Beschta, 2012). As a result, the increased grazing pressure on vegetation led to an alteration in plant communities and tree recruitment, which may eventually even lead to a shift in ecosystem state (Beschta & Ripple, 2009). As a result, time, resources and labour will be negated and the targeted species may still become extinct.

Predator-primate dynamics are such an interaction that can be affected by anthropogenic factors (*e.g.* Klailova et al., 2012; Farris et al., 2014; Bidner, 2014). There are numerous examples of how disturbances in these interactions can influence primate populations. For instance, habitat fragmentation can force predator and primate populations into forest remnants. Populations in these remnants are often not representative of the original population (Fahrig, 2003; Gibbons & Harcourt, 2009), which might express itself in an increased predator density. In addition to the factors of habitat fragmentation that already limit a species (*e.g.* human encroachment, declining habitat quality), this increased predator density can result in an increased predation risk (Irwin et al., 2009; Farris et al., 2014). Anthropogenic factors can also influence primate populations by causing the decline or extinction of predator populations. As a result, primate populations once limited by predation can increase, which may lead to competition between species that rely on the same limited resources (Walsh, 2013). When species rely on the same resource but with different competitive strength, predation may limit population growth of the stronger species. Predation thereby allowed the weaker species to obtain the necessary resources to sustain their population (Walsh, 2013). The decline or absence of the predator can cause the stronger species to outcompete the weaker, resulting in the decline and possible extinction of the weaker species (Holt, 1984; Walsh, 2013; Bidner, 2014; McPeek, 2014). The difficulties involved in studying these indirect effects of predation has led to a lack of knowledge on some components of predator-primate dynamics that – if known – may be beneficial to primate conservation.

Previous studies of predator-primate dynamics often focussed on the direct effects of predation (*e.g.* lethal predation events) and relied on indirect observations (*e.g.* chance sightings, scat studies) (Anderson, 1986; Isbell, 1994; Farris et al., 2014). These observations are difficult to obtain and are rarely collected systematically (Stanford, 2002; Klailova et al., 2012; Farris et al., 2014). Methods to study predator-primate dynamics were therefore time-consuming and labour-intensive. In addition, human presence in these studies (*e.g.* in studies of habituated populations) affected the dynamics of the studied species (Tutin, McGrew, & Baldwin, 1981; Klailova et al., 2012; McGrew, Baldwin, Marchant, Pruetz, & Tutin, 2014). Most current knowledge of predator-primate dynamics is derived from the aforementioned studies. However, alternative approaches that are less time-consuming, less labour-intensive and non-invasive are needed to study some of the components of predator-primate dynamics that are more complicated to apply, such as spatial dynamics (Farris et al., 2014) and the 'landscape of fear' concept (patterns in species spatial variation as a result of their perceived predation risk; Laundré, Hernández & Altendorf, 2001; Willems & Hill, 2009; Coleman & Hill, 2014). Camera traps offer an alternative approach to collect accurate data on species presence and dynamics in a non-invasive way (Klailova et al., 2012; Farris et al., 2014), especially at times and locations otherwise prohibited for researchers. Although camera traps hardly ever capture direct predation events, they offer accurate data on species presence. These data allow for the analysis and comparison of patterns in species spatial distribution, which may – for example – provide insight in the trade-offs that species make between resource acquisition and perceived predation risk.

To investigate these spatial patterns of predator-primate dynamics, a study site was sought where primates live in sympatry with their terrestrial mammalian predators. As little is known of predation on great apes and a better understanding of this subject is called for (*e.g.* D'Amour, Hohman, & Fruth, 2006; Klailova et al., 2013; Stewart & Pruetz, 2013), the presence of a great ape species in the study site was a plus. A suitable site was found in the Issa Valley in the Katavi Region of western Tanzania. This valley hosts seven primate species (including one great ape: eastern chimpanzee *Pan troglodytes schweinfurthii*) that live in sympatry with four large, mammalian predators (all species listed in *2.1 Study area and period*) (Stewart & Pruetz, 2013; Hernandez-Aguilar, Moore, & Stanford, 2013; Russak, 2014; McLester, Stewart, & Piel, 2016). However, the number of species included in this study may vary as a result of the available data (see *2.2.2 Detection history and species selection*). The Issa Valley is dominated by Miombo woodland habitat (Hernandez-Aquilar, 2009; Piel, Cohen, Kamenya, Ndimuligo, Pintea, & Stewart, 2015a; Piel, Lenoel, Johnson, & Stewart, 2015b; Johnson, Piel, Forman, Stewart, & King, 2015) and might serve as a mainly undisturbed representative of sub-Saharan Africa's largest ecosystem: the Miombo Woodlands (est. 2.4 to 2.7 million km^2) (Frost, 1996; Dewees et al., 2011). This ecosystem is threatened by anthropogenic factors (Prins & Kikula, 1996; Kutsch et al., 2011; Romijn, 2011; Ryan & Williams, 2011; Jew, Dougill, Sallu, O'Connell, & Benton, 2016) that are likely to increase with the prospect of population growth in the countries it covers (UN, 2015). The data used in this study were previously collected by the Ugalla Primate Project (hereafter 'UPP'), a research project that has permanently studied the valley since 2008. As researcher presence is increasingly seen as protecting wildlife (Campbell, Kuehl, Diarrassouba, N'Goran, & Boesch, 2011; Laurance, 2013; Piel et al., 2015b), UPP researchers will also be included in this interaction study in an attempt to uncover how researcher presence influences Issa primates and predators.

1.1   Problem statement

Ideally, conservationists consider species interactions such as predator-primate dynamics while assessing ecosystem health or planning primate conservation measures. However, a lack of knowledge about these dynamics currently prevents their inclusion in conservation policy development. This lack of knowledge can result in counterproductive conservation methods in which time, resources and labour are negated by unpredictable circumstances. To support future primate conservation, research is needed to uncover these dynamics, especially in areas threatened by an increase in anthropogenic factors. In the Miombo Woodlands ecosystem – one such area under threat – no previous study of predator-primate dynamics has been performed (see *Appendix I* for keywords and search engines used in search of previous studies), and therefore a knowledge gap prevents the inclusion of data on this subject in the planning of primate conservation measures. A study of predator-primate dynamics in the Miombo Woodland habitat is therefore expected to be beneficial to the future conservation of Miombo primates and can also provide a basis for future research on the subject.

1.2   Aim, objective and hypothesis

This study aims to assess the co-occurrence of primates and their likely predators in the Issa Valley. To achieve this aim, camera trap data collected in a long-term study of the Issa Valley were used to quantify the occupation probability of primates and their likely predators, as well as to discover signs of possible spatial interactions between predator-primate, researcher-primate and researcher-predator. In this report, the results are used to describe and discuss possible patterns in species co-occurrence and to inform future studies on both findings and methods.

The aim of this study was accomplished by fulfilling the following research objectives: 1) calculate trap success per species to provide a preliminary measure of species activity that was consequently used to compare species activity between seasons and score the otherwise nominal covariates; 2) estimate the probability that a location is occupied by each species whilst taking into account the probability that a species is encountered; and 3) calculate a measure of co-occurrence between primates and their likely predators. Fulfilling these objectives will answer the following research questions:

- o   What is the occupation probability of primates and their predators in the Issa Valley, and how does predator presence influence the occupation of primates?
    - -   Does the trap success of species differ between the dry and the wet season?
    - -   How do key variables habitat type, location type and distance to the researcher basecamp influence species occupation?
    - -   What relationships are there between predator and primate occupation?
    - -   What relationships are there between researcher and primate occupation?
    - -   What relationships are there between researcher and predator occupation?

Hypotheses that were tested are: 1) the probability of occupation for all species was expected to be high (more than half of the included locations) – despite the fact that some species are known to occur in low densities – for there are no known limiting factors to their occupation amongst camera locations; 2) it was believed to be unlikely that 14 cameras randomly distributed in an 85km^2 area would uncover seasonal patterns in species activity in the current dataset, despite previous studies reporting seasonality in species encounters in the Issa Valley (*e.g.* Russak, 2014; Piel et al. 2015b); 3) covariate habitat type was expected to be main variable influencing species' occupation and detection probability, as this variable was believed to be the best delineated (*e.g.* in covariate location type, location types may overlap, as a location labelled as termite mound may also be a termite mound passed by a wildlife path); 4) the interaction model was expected to show primate to co-occur less frequently than would be expected when co-occurring independently with predators and researcher; and 5) the interaction model will show predators to co-occur less frequently than would be expected when co-occurring independently with researcher.

2. Methodology

2.1 Study area and period

The Issa Valley is an 85km[2] area (Stewart & Piel, 2013) in the Katavi Region of western Tanzania. This valley is described as a primate-rich, dry, open and seasonal habitat (Kalousová et al., 2014; Piel et al., 2015a; Johnson et al., 2015) and has no formal protective status (Piel et al., 2015b). It is characterised by broad valleys, steep mountains and flat plateaus ranging between 900 and 1800 meters above sea-level (Piel et al., 2015b). The different habitat types of the valley can be classified as forest (hill forest, thicket forest, gallery forest), open (Miombo) woodland and wooded grassland (Hernandez-Aguilar, 2009; Stewart, 2011), of which Miombo woodland is the dominant habitat type (Hernandez-Aquilar, 2009; Piel et al., 2015a; Piel et al., 2015b; Johnson et al., 2015). Miombo woodland is a type of dry and nutrient-poor savannah woodland dominated mainly by trees of the *Brachystegia*, *Julbernardia* and *Isoberlinia* genera (Frost, 1996; Dewees et al., 2011; Ryan & Williams, 2011). In this study, a distinction is made between two of these habitat types: forest and woodland. On average the study area receives a yearly rainfall ranging from 900 to 1400mm (Piel et al., 2015b) and temperatures range from 11 to 35°C (Stewart, Piel, & McGrew, 2011). Seasons can be divided into a wet season (>100mm rain/month; Oct.-Apr.) and a dry season (<100mm rain/month; May-Sept.) (Hernandez-Aguilar, 2009; Stewart, 2011).

Data for the current study come from a long-term study using camera traps in the study area. From this dataset, a one-year period was selected to be used in this study: from 15 September 2013 (00:00:00hr) to 14 September 2014 (23:59:59hr). The study area and camera placement are displayed in *Map 1*.
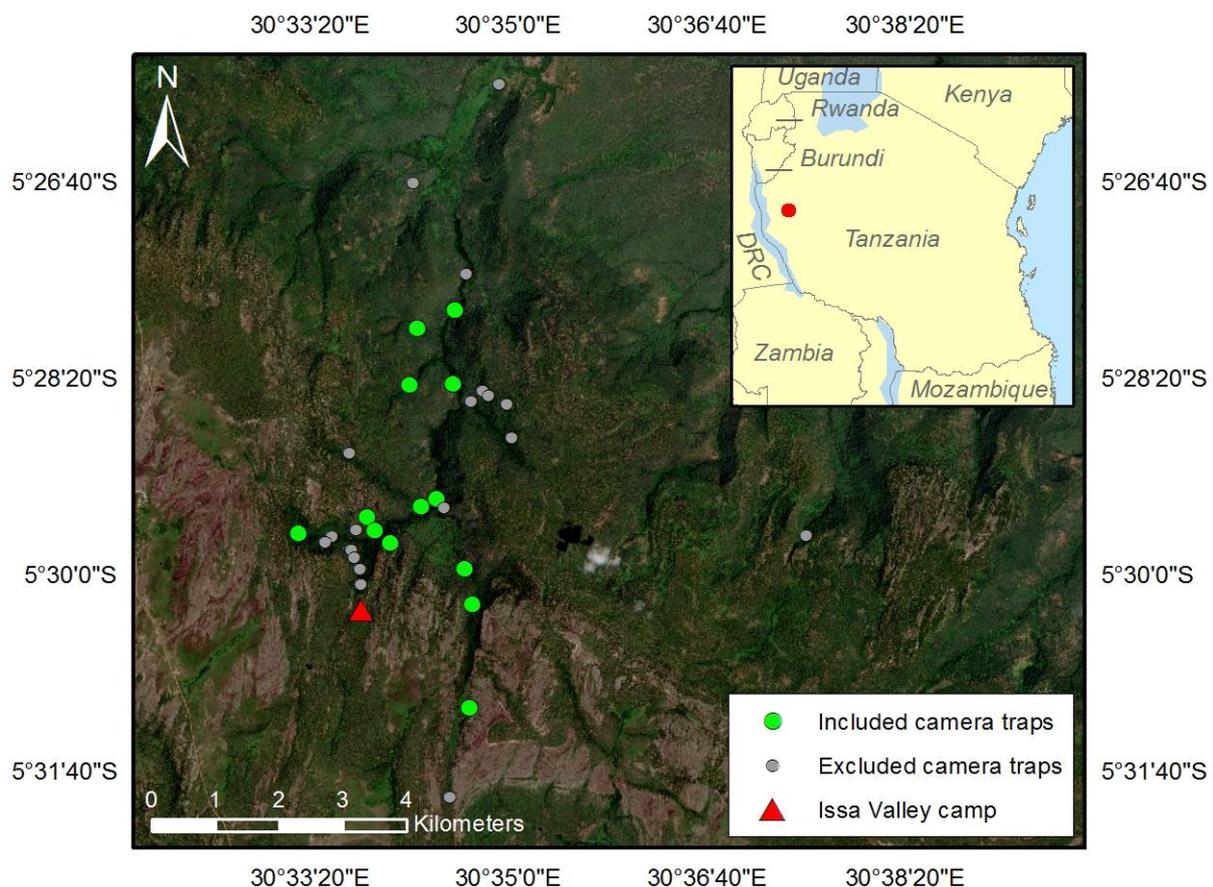
Map 1 – Issa Valley study area and camera trap placement
*Satellite map layer derived from the Copernicus Sentinel free scientific data hub (*Copernicus Sentinel data, 2017*).*
See 2.2.1 Camera traps *for further information on camera selection.*

Seven primate species are present in the Issa Valley: eastern chimpanzee (*Pan troglodytes schweinfurthii*), yellow baboon (*Papio cynocephalus*), red-tailed monkey (*Cercopithecus ascanius*), blue monkey (*Cercopithecus mitis*), vervet monkey (*Chlorocebus aethiops*), red colobus (*Procolobus tephrosceles*), and greater galago (*Otolemur crassicaudatus*) (Russak, 2014). These primates exhibit unique adaptations to the predominantly open and marginal habitat of the Issa Valley. In eastern

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chimpanzee, for instance, so-called "savanna adaptations" (Moore 1992; 1996) include animals living at extremely low population densities and simultaneously exhibiting large group ranges (Moore, 1992; Piel & Stewart, 2014; Kalousová et al., 2014). The Issa primates live in sympatry with four large mammalian predators: lion (*Panthera leo*), leopard (*P. pardus*), spotted hyena (*Crocuta crocuta*) and African wild dog (*Lycaon pictus*) (Stewart & Pruetz, 2013; Hernandez-Aguilar et al., 2013; Russak, 2014; McLester et al., 2016). Other possible primate predators such as raptors and snakes are not included in this study, as camera traps do not allow for the collection of reliable data on these species. Although the valley is described as mainly undisturbed, humans are present in the area: UPP researchers that study the area and local residents who illegally exploit forest resources (*e.g.* timber, wildlife, etc.) (Piel et al., 2015b). These humans will also be included in this study, as human presence may influence species distribution. All abovementioned species will hereafter be referred to by their common name.

2.2 Data selection and preparation

2.2.1 Camera traps

The UPP deployed cameras at 37 locations for varying time periods during the abovementioned study period. As these camera traps were deployed with various objectives, not all camera data fitted the objective of this study. Some cameras did not cover a location throughout the entire study period or contained lengthy gaps in the data, which could either be periods of which data had not been analysed or result from malfunctions (*e.g.* broken camera, battery failure, misdirected or blocked camera/sensor). To filter out cameras with lengthy malfunction periods, the term 'malfunction' had to be quantified. First, all camera traps that had been active during the entire study period were selected. Datasets of these cameras had to meet the requirement that it contained data at the start and the end of the study period. Periods of non-footage during the study period did not influence camera selection at this point, as malfunctions and non-footage periods could not yet be distinguished. Of these selected camera traps, the mean continuous period of non-footage (5.6 days) and its standard deviation (9.4 days) were calculated. All continuous non-footage periods that last longer than the sum of this average and standard deviation (15 days) were considered malfunction periods. All camera traps of which the sum of the malfunctions exceeded 60 days were then excluded from further analysis. As a result, 14 of the 37 camera traps were included in further analysis (see *Map 1* for camera trap locations and *Appendix II* for camera coverage periods).

2.2.2 Detection history and species selection

Data from the 14 selected camera traps was divided into sampling occasions: 24hr periods (00:00:00-23:59:59) during which a species is either detected (1) or not detected (0). This detection/non-detection data will hereafter be referred to as 'detection history', sampling occasion during which a species is detected will be referred to as a 'positive sampling occasion', and a sampling occasion during which a species is not detected will be referred to as a 'negative sampling occasion'. As a result of the division into 24hr sampling occasions, the detection history of a species contains 365 sampling occasions per camera. If a species detection history contained less than 10 positive sampling occasions in the total detection history the species was excluded from further analysis, for this may show a distorted image of a species distribution (Martin, Ndibalema, & Rovero, 2016).

This selection process has led to the exclusion of seven of the 12 targeted species, as they did not meet the required number of positive sampling occasions ($n≥10$). As a result, this study includes five species and the two species groups, *i.e.* researchers, leopard, eastern chimpanzee, yellow baboon, red-tailed monkey and the predator and primate species groups (*Table 2*). Excluded were three predator species: lion ($n = 0$), spotted hyena (0) and African wild dog (0); and four primate species: blue monkey (0), vervet monkey (0), red colobus (0) and greater galago (5). Even though most of these species were not recorded by the selected camera traps during this study, these species have previously been recorded in the Issa Valley. Spotted hyena and African wild dog have both been recorded by UPP camera traps (spotted hyena, UPP, 2015a; UPP, 2017; African wild dog, UPP, 2015b; McLester et al., 2016), and signs of lion presence have been recorded by UPP researchers in the valley (*e.g.* Russak, 2014). The exclusion of the four primate species (previously reported present by among others Russak, 2014) may have been caused by the disadvantage of using terrestrially located camera traps in monitoring arboreal primates, as these species may have been present in the canopy, thereby remaining out of reach of the camera trap.

Table 2 – Species and species groups as included in further analyses

Species	n	Category	Description
Researcher (*Homo sapiens*)	343	Researcher	UPP researchers and local residents, though mainly (*n* = 341) consisting of UPP researchers.
Leopard (*Panthera pardus*)	18	Predator	
Eastern chimpanzee (*Pan troglodytes schweinfurthii*)	271	Predator, prey	Chimpanzee is included both as a predator and a prey species, as it may predate on other (primate) species while it may be predated on by larger predators.
Yellow baboon (*Papio cynocephalus*)	24	Prey	
Red-tailed monkey (*Cercopithecus ascanius*)	12	Prey	
Species group predator *	608	Predator	Species group composed of the combined detection histories of all above-mentioned predators, including chimpanzee.
Species group primate *	306	Prey	Species group composed of the combined detection histories of all abovementioned non-human primates.

*   *Detection histories of species groups may contain fewer positive sampling occasions (n) than the sum of the positive sampling occasions of all species included in the group, as multiple species could have been recorded at the same location in the same sampling occasion. Combining two positive sampling occasions from two different species led to a single positive sampling occasion for the species group.*

2.2.3   Trap success

Trap success (hereafter 'TS') is the probability a species is recorded by a camera trap, which provided a first measure of activity for each of the targeted species in the study area. Although TS is a rudimentary measure of species activity that does not incorporate the probability a species is present if it is not detected, it could be used to prepare some of the data before further analysis of species occupancy and interactions. TS was used to 1) compare species activity between seasons by calculating TS per species per season (see *2.2.4 Seasonal sub-division and seasonality*), and to 2) provide a measure to the otherwise nominal covariates (habitat type and location type) by calculating TS per species per habitat or location type (see *2.2.5 Covariates and standardisation*).

TS was calculated by dividing the number of positive sampling occasions by the total number of sampling occasions. Because malfunction periods do not represent positive or negative sampling occasions, they are no part of the total sampling occasions and were therefore subtracted from the total sampling occasions (Farris et al., 2011). This calculation made use of the 24hr sampling occasions of the detection history per species (see *2.2.2 Detection history and species selection*), and was performed with Microsoft Excel software.

$$TS = \frac{positive\ sampling\ occasions}{total\ sampling\ occasions - malfunctions}$$

2.2.4   Season sub-division and seasonality

A Wilcoxon signed rank test for paired samples was performed to test whether species activity displayed signs of seasonality (Martin et al., 2016). To perform this test, the detection histories of all included species was divided into two seasons: wet season (15 September 2013 to 14 April 2014) and dry season (15 April 2014 to 14 September 2014). This division is based on average annual start and end of rains in the period 2009-2014 (Piel et al., 2015b). For each species, the trap success (see *2.2.3 Trap success*) was calculated per season. The Wilcoxon test then compared (per species) the medians of two matched samples (wet and dry season) to test for significant differences in species trap success between the seasons. If this test found no significant difference in trap success of a species between the seasons (*p-value* > 0.05; H$_0$), further analysis was performed with the species' detection histories of the entire study period. If this test did find a significant difference in the trap success of a species between the seasons (*p-value* < 0.05; H$_1$), further analysis would be performed with separate wet and dry season detection histories per species. The Wilcoxon test was performed using R software (R Foundation, 2016).

2.2.5   Covariates and standardisation

Certain habitat variables in the study area that were expected to influence species occupancy have been included in the occupation model (see *2.3.1 Single-season, single-species occupancy model*) as standardised covariates. The included variables are: 1) habitat type (forest or woodland), as some species may prefer one habitat type over another; 2) location types (human path, wildlife path or termite mound), as factors present at one location may cause a species to frequent that location more often; and 3) distance to the UPP basecamp, as researcher presence may be seen as a threat by wildlife while

permanent research stations may also serve as a deterrent of poaching, possibly causing an increased encounter probability for some species (Campbell et al., 2011; Piel et al., 2015b). Because data for this study was provided by the UPP and the camera traps were not specifically placed for this study, the degree of detail in which the covariates were specified was determined by the way they were recorded by UPP field staff.

Because the occupation model only allows for numerical covariates, the nominal covariates (habitat type and location type) had to be quantified before inclusion. These covariates were therefore given a value by use of the average trap success of a species (see *2.2.3 Trap success*) in a certain habitat or location type. When these nominal covariates were quantified, all three covariates still consisted of random variables measured on different scales (*e.g.* habitat and location type as trap success, and distance to UPP basecamp as kilometres). To improve the maximum likelihood of convergence between covariates – and because the modelling software works best with covariate values close to 0 – the random covariate variables had to be Z-scored to create a standardised covariate value (Farris et al., 2014). Z-scores were calculated per species, per covariate by subtracting the covariates' mean (μ) from the covariate variable at a camera location (x), which was then divided by the covariates' standard deviation (σ). Standardised covariates per species are listed in *Appendix III*.

$$Z = \frac{x - \mu}{\sigma}$$

To prevent over-parametrisation, models were fitted with covariates according to the '*n*/10' rule of thumb (Anderson, 2008; also used in Pamplin, 2013). This rule states that for every species, the maximum number of covariates to be fitted in the model should not exceed the number of positive sampling occasions divided by ten: *n*/10, in which *n* = no. positive sampling occasions. For instance, for red-tailed monkey (*n* = 12) the number of covariates included should not exceed 12/10 = 1.2, which is rounded down to 1 covariate. As a result, red-tailed monkey models could only be fitted with one covariate at a time.

2.3 Analysis

2.3.1 Single-season, single-species occupancy

A single-season, single-species occupancy model (hereafter 'SS-SSO') was used to quantify species occupation. By estimating two population parameters (occupation and detection probability) SS-SSO provided an estimate of the proportion of the area that is occupied by a species while accounting for the probability a species is detected (MacKenzie et al., 2006; Farris et al., 2014). This model also accounted for some of the covariates that may influence species occupancy (see *2.2.5 Covariates and standardisation*).

The detection histories and (standardised) covariates of a species were uploaded to the program PRESENCE (Hines, 2006), which then performed multiple types of SS-SSO models. First, a pre-defined '1 group-constant P' model was performed, which estimated species occurrence and detection probability for a single population without including covariates. Then, multiple custom models were performed in which the covariates were included as influencing either the occurrence or detection probability. These custom models were meant to uncover whether and how species are influenced by the different covariates. The relative quality of each model was measured by use of Akaike Information Criterion (hereafter 'AIC'; a measure of the relative quality of a model) (Akaike, 1973), which was calculated by the program PRESENCE. The models with the best (lowest) AIC score and those with ΔAIC ≤2 (difference in AIC from the best ranking model) were recorded, as models with ΔAIC ≤2 are thought to have substantial empirical support and are therefore of the same relative quality as the top ranking model (Burnham & Anderson, 2002). The fitness of these models was assessed with a Pearson's goodness of fit test of the 'global model', which is the model with most covariates included. This goodness of fit test (performed by program PRESENCE when selecting the 'assess model fit' option) provided a value for over-dispersion ($\hat{c}$) in the output, which could then be fitted into PRESENCE to account for possible overdispersion. Overdispersion is classified as a $\hat{c} > 1$. If $\hat{c} > 1$, AIC was re-calculated as Quasi-AIC by program PRESENCE, and standard errors in the output had to be multiplied by the square root of $\hat{c}$. If $\hat{c} \leq 1$, the modelled $\hat{c}$ was left 1. This analysis method was performed per species.

After performing this SS-SSO, the programs' output presented a set of data of which the following values were used in analysis: 'AIC', Akaike Information Criterion; 'ΔAIC', difference in AIC from the highest ranking model; 'Naïve occupation estimate', percentage of locations where the species was recorded at least once; 'Ψ', occupation probability, and 'p', detection probability.

2.3.2   Two-species interaction

A two-species interaction model (hereafter 'TSI') was used to test for patterns in species co-occurrence. A TSI model accounts for four possible states of occupation for a location: 1) occupied by both species A and B, 2) occupied by species A only, 3) occupied by species B only, or 4) occupied by neither species (MacKenzie, Bailey, & Nichols, 2004). In this analysis, the covariates proven by the SS-SSO model to influence a species occupation or detection were included to find out if and how these covariates may have influenced the patterns of co-occurrence. The species and species groups that were plotted against each other in this part of the analysis are presented in *Table 3.*

Table 3 – TSI model species combinations
Species combinations that were plotted in TSI models

	Eastern chimpanzee	Yellow baboon	Red-tailed monkey	Primate species group	* Leopard
Researcher	X	X	X	X	X
Leopard *	X	X	X	X	
Eastern chimpanzee		X	X		
Predator species group		X	X		

* Leopard was listed twice in this table to enable a TSI model to assess effect of human presence on leopard distribution.

Detection histories of two species were uploaded to the program PRESENCE as a single dataset of which the first rows are the detection history of species A, followed by the detection history of species B. The program will then perform a 'psiBa/r Ba parametrization' model. This model uses 8 parameters (listed below) to calculate an occupation Species Interaction Factor (φ, occupation SIF):

ψA   Occupation probability of species A.
ψBA   Occupation probability of species B, when species A is present.
ψBa   Occupation probability of species B, when species A is not present.
pA   Detection probability of species A, when species B is not present.
pB   Detection probability of species B, when species A is not present.
rA   Detection probability of species A, when both are present.
rBA   Detection probability of species B, when both are present, and – during this sampling occasion – species A was detected.
rBa   Detection probability of species B, when both are present, and – during this sampling occasion – species A was not detected.

The occupation SIF shows species to occur independently ($\varphi = 1$), to co-occur less frequently than expected when distributed independently (*e.g.* exclude or avoid each other) ($\varphi < 1$), or to co-occur more frequently than expected if they were independent (*e.g.* attraction) ($\varphi > 1$) (MacKenzie et al., 2004; 2006; Farris et al., 2014). If TSI models resulted in species occurring independently, a formal comparison was needed to evaluate whether species co-occur truly independently. To do so, two models were created: a full model in which occupancy of both species and SIF are estimated, and a reduced model in which occupancy of both species is estimated, and SIF is fixed to 1 (independence). Species were said to be independent If the difference in AIC (ΔAIC) between the full and reduced model was ≥ 2.00. If ΔAIC < 2.00, results were not reported as species were not formally proven to occur independently (MacKenzie et al., 2006; Farris et al., 2011).

3.   Results

The dataset selected by use of the selection methods described in the above methods (*2.2.1 Camera traps* and *2.2.2 Detection history and species selection*), consisted of 4678 sampling occasions distributed over 14 camera locations. Of these, the targeted species were recorded during 648 occasions. As these positive sampling occasions were used to select the targeted species, positive sampling occasions per species are already given in *Table 2* in *2.2.2 Detection history and species selection*, and the number of covariates modelled per species in the occupation models have been adjusted accordingly. In total, 432 sampling occasions were lost to malfunctions, which was 8.5% of sampling occasions. Camera coverage periods and malfunctions are visualised per camera in *Appendix II*. Trap success data (used to test for seasonality) were found to be distributed non-normally.

3.1   Seasonality

With the exception of researchers, none of the species or species groups demonstrated signs of seasonality in trap success (Wilcoxon signed rank test for paired samples; researchers, *p-value* = 0.0383; other, *p-value* > 0.05) (*Table 5*). However, this apparent researcher seasonality was not believed to be of interest to the objective of this study, as variation in researcher activity was not believed to represent yearly recurrent patterns. As a result, seasonal sub-division was not included in further analysis. Trap success and test results are listed in *Table 5*.

Table 5 – Trap success and results of the Wilcoxon signed rank test for paired samples per species
Tests were performed with location-specific trap-success values per species. Species trap success was demonstrates seasonality when p-value < 0.05.

Species	Trap success			Seasonality test results	
	Wet	Dry	Total	W*	p-value
Researcher	0.0818	0.0407	0.1225	68	0.0383
Leopard	0.0039	0.0025	0.0064	14	0.3428
Eastern chimpanzee	0.0686	0.0282	0.0968	38	0.3795
Yellow baboon	0.0054	0.0032	0.0086	7	0.1410
Red-tailed monkey	0.0029	0.0014	0.0043	0	0.0579
Species group predator	0.1543	0.0714	0.2257	75	0.1673
Species group primate	0.0771	0.0332	0.1104	52	1.0000

* W = sum of the ranks

3.2   Single-season, single-species occupancy

Two species (researcher and chimpanzee) and the two species groups were estimated to occur at all 14 locations without error (Ψ = 1.0000, SE 0.0000), due to the fact that these species were recorded at least once at all locations (NE = 1.0000). Leopard was also estimated to occupy all locations (Ψ = 0.9719, SE±0.1502) despite the fact that the species was only detected at 9 out of 14 locations (NE = 0.6429). This high occupation probability was the result of the species' low detection probability (p = 0.0184, SE±0.0080), as the model will have accounted for the chance that the species may occupy a location while it was not detected. Baboon and red-tailed monkey were estimated to occupy 10 and 6 of 14 locations (Ψ = 0.7450, SE±0.2339 and Ψ = 0.4146, SE±0.2160 resp.). As with leopard, these species were estimated to occupy more locations than recorded (8 and 5 locations resp.). *Table 6* gives species averaged SS-SSO model results, and *Figure 7* plots naïve estimates next to estimated occupation probability. *Table 8* lists all top-ranking models (models that scored ΔAIC ≤ 2.00) per species. These top-ranking models give an impression of which covariates are most likely to influence a species' occupation and detection probability. The influence of covariates on the species is further described per species in *3.2.1 Researcher* to *3.2.7 Primate*.

Table 6 - Species averaged SS-SSO results

Species	NE	Ψ (SE)	p (SE)
Researcher	1.0000	1.0000 (0.0000)	0.2778 (0.0270)
Leopard	0.6429	0.9719 (0.1502)	0.0184 (0.0080)
Eastern chimpanzee	1.0000	1.0000 (0.0000)	0.2108 (0.0399)
Yellow baboon	0.5714	0.7450 (0.2339)	0.0314 (0.0134)
Red-tailed monkey	0.3571	0.4146 (0.2160)	0.0298 (0.0628)
Predator	1.0000	1.0000 (0.0000)	0.4440 (0.0353)
Primate	1.0000	1.0000 (0.0000)	0.2372 (0.0291)

Proportion of locations where a species was recorded (NE) and their average occupation (Ψ) and detection (p) probability. Location-specific occupation probability and detection probability are listed in Appendix IV *and* V *resp..*
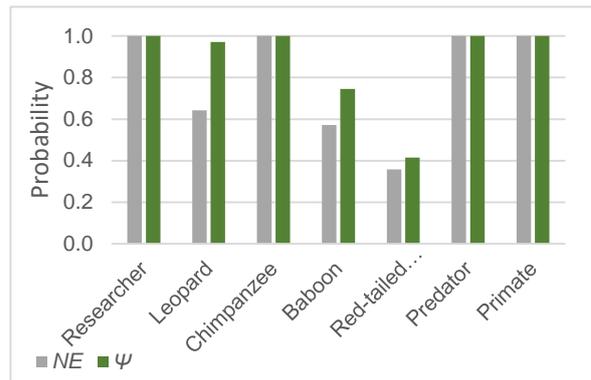
Figure 7 – Naïve estimate and species averaged occupation probability

Plotting the proportion of sites at which a species was recorded (NE) next to the estimated occupation probability (Ψ) shows that species that were not recorded at all locations (leopard, baboon and red-tailed monkey) were estimated to occur at more sites than where they were recorded as a result of their low detection probabilities. The species that were recorded at all locations were also estimated to occur at all locations.

Table 8 – Top-ranking Single-season, single-species Occupancy models
*Modelled covariates describe which parameters are modelled to either influence occupation (Ψ) or detection probability (p). Parameters modelled: **.** = no covariates included; HT = habitat type; LT = location type: DH = distance from the nearest human habitation. The '1 group, constant p' model reported in* 2.3.1 single-season, single-species occupancy model *is modelled with no covariates included for both occupation and detection probability. (Q)AIC = Akaike information criterion, measure of ranking models; Δ(Q)AIC = difference in AIC between listed and top ranking model; NE = Naïve Estimate, the proportion of locations where a species is recorded at least once; Ψ (SE) = estimated occupation probability with standard error; and p (SE) = estimated detection probability with standard error. A complete version of this table is given in* Appendix VI.

| | Modelled covariates | | (Q)AIC* | | | |
	Ψ	**p**	**(Δ(Q)AIC)**	**NE**	**Ψ (SE)**	**p (SE)**
Researcher	.	LT	1125.95 (0.00)	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	.	HT, LT	1126.61 (0.66)	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	.	.	1127.24 (1.29)	1.0000	1.0000 (0.0000)	0.2776 (0.0145)
	LT	LT	1127.95 (2.00)	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	HT	LT	1127.95 (2.00)	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
Leopard	.	LT	168.66 (0.00)	0.6429	1.0000 (0.0000)	0.0178 (0.0058)
	.	HT, LT	170.15 (1.49)	0.6429	1.0000 (0.0000)	0.0177 (0.0073)
	HT	LT	170.66 (2.00)	0.6429	1.0000 (0.0000)	0.0178 (0.0058)
Eastern chimpanzee	.	HT, LT, DH	960.34 (0.00)	1.0000	1.0000 (0.0000)	0.2110 (0.0258)
	HT, LT, DH	.	960.34 (0.00)	1.0000	1.0000 (0.0000)	0.2103 (0.0132)
	HT	HT, LT, DH	962.34 (2.00)	1.0000	1.0000 (0.0000)	0.2110 (0.0258)
Yellow baboon	.	LT	204.36 (0.00)	0.5714	0.7583 (0.1978)	0.0296 (0.0108)
	HT	LT	205.24 (0.88)	0.5714	0.7579 (0.1862)	0.0297 (0.0103)
	DH	LT	205.58 (1.22)	0.5714	0.7583 (0.2294)	0.0297 (0.0109)
	.	HT, LT	206.12 (1.76)	0.5714	0.7566 (0.1934)	0.0303 (0.0136)
Red-tailed monkey	HT	LT	123.03 (0.49)	0.3571	0.4094 (0.1616)	0.0303 (0.0103)
Predator	.	HT, LT	1301.30 (0.00)	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	.	HT, LT, DH	1302.24 (0.94)	1.0000	1.0000 (0.0000)	0.4442 (0.0320)
	HT	HT, LT	1303.30 (2.00)	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	LT	HT, LT	1303.30 (2.00)	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	DH	HT, LT	1303.30 (2.00)	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
Primate	.	HT, LT, DH	1018.08 (0.00)	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	.	HT, LT	1019.64 (1.56)	1.0000	1.0000 (0.0000)	0.2372 (0.0235)
	LT	HT, LT, DH	1020.08 (2.00)	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	DH	HT, LT, DH	1020.08 (2.00)	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	HT	HT, LT, DH	1020.08 (2.00)	1.0000	1.0000 (0.0000)	0.2374 (0.0270)

* AIC in all species except researcher and primate, where ĉ was altered to account for over-parametrisation (ĉ = 1.0002 and 1.0021 resp.). Because estimated ĉ values were small, only AIC changed when fitting the factor and standard errors did not.

3.2.1 Researcher

As the SS-SSO models resulted in a 100% occupation estimate for researchers at all locations (*Table 6* and *8*), no influence of any of the covariates on the occupation probability of researchers could be found. Researcher detection probability, however, did vary per location. This detection probability seems to be related to the covariate location type, as four of the five top ranking models displayed this correlation (*Table 8*). The species' weighted location-specific detection probabilities (*Appendix V*) confirm this correlation and indicate that detection probability for researchers is highest at termite mound locations ($p = 0.3071$, SE±0.0351), followed by wildlife paths ($p = 0.2679$, SE±0.0221) and then human paths ($p = 0.2585$ SE±0.0259).

3.2.2 Leopard

The SS-SSO models estimated a near 100% occupation for leopard ($\Psi = 0.9719$, SE±0.1502) that did not seem to be influenced by the covariates (*Table 6* and *8*). Leopard detection probability was found to be influenced by the covariate location type, as all top-ranking models displayed this correlation (*Table 8*). The species' weighted location-specific detection probabilities (*Appendix V*) confirm this correlation and indicate that detection probability for leopard is highest at wildlife path locations ($p = 0.0269$, SE±0.0081), followed by human paths ($p = 0.0088$, SE±0.0077) and then termite mounds ($p = 0.0074$, SE±0.0078).

3.2.3 Eastern chimpanzee

As the SS-SSO models resulted in a 100% occupation estimate for chimpanzee at all locations (*Table 8*), no influence of any of the covariates on the occupation probability of chimpanzee could be found. Chimpanzee detection probability, however, did vary per location. This detection probability may be related to a combination of all three included covariates, as two of the three top-ranking models displayed this correlation (*Table 8*). The species' weighted location-specific detection probabilities (*Appendix V*) confirm this correlation and indicate that 1) chimpanzee is more likely to be detected in forest habitat ($p = 0.2279$, SE±0.0384) than in woodlands ($p = 0.1681$, SE±0.0433); 2) chimpanzee is more likely to be detected at human path and termite mound locations ($p = 0.2570$, SE±0.0516 and $p = 0.2397$, SE±0.0411 resp.) than at wildlife paths ($p = 0.1848$, SE±0.0356); and 3) chimpanzee is more likely to be detected at locations near the UPP basecamp than further away from the camp (Pearson's product-moment correlation test: p-value 0.002 $\rho = -0.76$).

3.2.4 Yellow baboon

The SS-SSO models estimated baboon to occupy 10 of the 14 locations included in this study ($\Psi = 0.7450$, SE±0.2339; *Table 6*). Baboon occupation probability may be related to the covariates habitat type and distance to the UPP basecamp, as all top-ranking models displayed this correlation (*Table 8*). The species' weighted location-specific occupation probabilities (*Appendix IV*) confirm the correlation with covariate habitat type and indicate that occupation probability for baboon is higher at woodland locations ($\Psi = 0.8039$, SE±0.2315) than at forested locations ($\Psi = 0.7214$, SE±0.2348). The weighted location-specific averages did not confirm that a correlation existed between baboon occupation and distance to the UPP basecamp (Pearson product-moment correlation test: *p-value* = 0.2123). Baboon detection probability may be related to the covariate location type, as all four top ranking models displayed this correlation (*Table 8*). The species' weighted location-specific occupation probabilities confirm the correlation and indicate that baboon is more likely to be detected at termite mound locations ($p = 0.0516$, SE±0.0161), followed by human paths ($p = 0.0363$, SE±0.0106) and then wildlife paths ($p = 0.0200$, SE±0.0125).

3.2.5 Red-tailed monkey

The SS-SSO models estimated red-tailed monkey to occupy 6 of the 14 locations included in this study ($\Psi = 0.4146$, SE±0.2160; *Table 6*). Red-tailed monkey detection probability was found to be influenced by the covariate habitat type, as its single top-ranking models displayed this correlation (*Table 8*). The species' weighted location-specific occupation probabilities (*Appendix IV*) confirm this correlation and indicate that occupation probability is higher in forest habitat ($\Psi = 0.5000$, SE±0.0.2036) than in woodland habitats ($\Psi = 0.2011$, SE±0.2444). However, as the small weighted species average occupation estimate of the species in woodland is believed to have been biased by the inclusion of models that estimated equal occupation probabilities for all locations in averaging, the top ranking model is believed to be a better representation of red-tailed monkey occupation. This model reported the species to only occupy forest locations ($\Psi = 0.1000$, SE±0.0000), and no woodland locations ($\Psi = 0.0000$, SE±0.0000). Such a strong correlation that may be the result of the species only being recorded in forested habitat. Red-tailed monkey detection probability seems to be unrelated to any of the covariates.

3.2.6 Predator

As the SS-SSO models resulted in a 100% occupation estimate for predators at all locations (*Table 6* and *8*), no influence of any of the covariates on the occupation probability of this species group could be found. Predator detection probability, however, did vary per location. This detection probability may be related to the covariates habitat type and location type and possibly also to the covariate distance to the UPP basecamp, as four of the five top-ranking models display a correlation with habitat type and location type, and the fifth also includes the covariate distance to the UPP basecamp (*Table 8*). The species' weighted location-specific detection probabilities (*Appendix V*) confirm these correlations and indicate that 1) predators are more likely to be detected in forest habitats (p = 0.4614, SE±0.0335) than in woodland habitats (p = 0.4007, SE±0.0396), 2) predators are more likely to be detected at termite mound locations (p = 0.4953, SE±0.0408), than at human paths (p = 0.4583, SE±0.0312) or wildlife paths (p = 0.4148, SE±0.0333), and 3) predators are more likely to be detected near the UPP basecamp than further away (Pearson's product-moment test: *p-value* = 0.002, ρ = -0.74).

3.2.7 Primate

As the SS-SSO models resulted in a 100% occupation estimate for primates at all locations (*Table 6* and *8*), no influence of any of the covariates on the occupation probability of this species group could be found. Primates' detection probability, however, did vary per location. This detection probability may be related to the covariates habitat and location type and possibly to the covariate distance to the UPP basecamp, as four of the five top-ranking models display this correlation (*Table 8*). The species' weighted location-specific detection probabilities (*Appendix V*) confirm these correlations and indicate that 1) primates are more likely to be detected in forest habitat (p = 0.2640, SE±0.0296) than in woodlands (p = 0.1701, SE±0.0277); 2) primates are more likely to be detected at human path locations (p = 0.3275 SE±0.0401) than at termite mounds (p = 0.2858, SE±0.0307) or wildlife paths (p = 0.1903, SE±0.0246); and 3) primates are more likely to be detected near the UPP basecamp than further from the camp (Pearson's product-moment correlation test: *p-value* = 0.016, ρ = -0.63).

3.3   Two-species interaction

Of the 14 species combinations that were tested, 13 combinations were found to co-occur independently (φ = 1.0000) and one combination was found to co-occur less frequently than would be expected when co-occurring fully independently (leopard-baboon; φ = 0.9448, SE±0.8047). These results are listed in *Table 9* and displayed in *Figure 10*, and the top-ranking models per species are listed in *Table 11*.

In most species combinations, including covariates resulted in signs of over-parametrisation in the model output. This may have been caused by the inclusion of too many covariates in some species combinations, as including all covariates influencing species A resulted in too large a number of parameters for species B (according to the *n*/10 rule described in *2.2.5 Covariates and standardisation*). For instance, the *n*/10 rule allowed the inclusion of all (three) covariates in modelling chimpanzee, while it allowed for only one covariate to be included when modelling red-tailed monkey. When these two species are combined in a TSI model, modelling all covariates (as allowed for chimpanzee) is no longer possible since the number of covariates will exceed the maximum number allowed for red-tailed monkey. The models in which the maximum number of covariates for one of the species was exceeded were therefore excluded. However, in most cases those models that included covariates were excluded, as they did not reach the top-ranking models.

Table 9 – Occupation Species Interaction Factor (φ) per species combination

| Species combination	φ (SE)
Researcher - leopard	1.0000 (0.3570)
Researcher – chimpanzee	1.0000 (1.3622)
Researcher – baboon	1.0000 (0.1638)
Researcher – red-tailed monkey	1.0000 (0.4874)
Researcher – primate	1.0000 (0.2585)
Leopard – chimpanzee	1.0000 (0.0642)
Leopard - baboon	0.9448 (0.8047)
Leopard – red-tailed monkey	1.0000 (0.0002)
Leopard – primate	1.0000 (0.1142)
Chimpanzee – Baboon	1.0000 (0.2835)
Chimpanzee – red-tailed monkey	1.0000 (0.0000)
Predator – baboon	1.0000 (0.2325)
Predator – red-tailed monkey	1.0000 (0.0259)
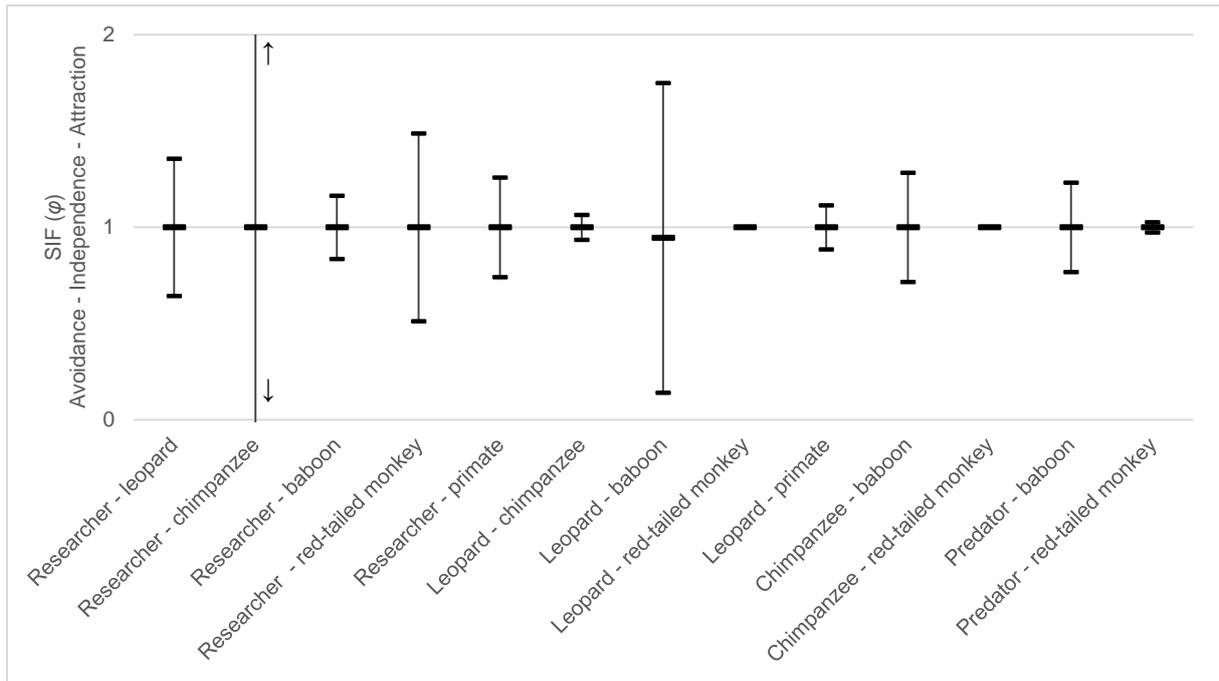
Figure 10 – Weighted average occupation SIF (*φ*) per species combination
Per species combination listed on the x-axis, the primary tick mark displays the occupation SIF and the vertical lines and secondary tick marks display range of the standard error.

Table 11 – Top-ranking Two-species interaction models
*Modelled covariates describe which parameters are modelled to either influence occupation (Ψ) or detection probability (p, r). Parameters modelled: **.** = no covariates included; S = species-specific parameters estimated; HT = habitat type. (Q)AIC = Akaike information criterion, measure of ranking models; Δ(Q)AIC = difference in AIC between listed and top ranking model; φ (SE) = estimated interaction factor, which shows species to occur independently (φ = 1), to co-occur less frequently than expected when distributed independently (e.g. exclude or avoid each other) (φ < 1), or to co-occur more frequently than expected if they were independent (e.g. attraction) (φ > 1). A complete version of this table is given in* Appendix VII.

	Modelled covariates			(Q)AIC* (Δ(Q)AIC)	φ (SE)
	ψ	**p**	**r**		
Researcher – Leopard	.	S	.	1305.98 (0.00)	1.0000 (-)
	.	S	S	1307.82 (1.84)	1.0000 (-)
	S	S	.	1307.98 (2.00)	1.0000 (0.8132)
Researcher – Chimpanzee	.	S	.	2113.78 (0.00)	1.0000 (-)
	.	S	S	2115.57 (1.79)	1.0000 (-)
	S	S	.	2115.78 (2.00)	1.0000 (2.9120)
Researcher – Baboon	.	S	S	1334.15 (0.00)	1.0000 (-)
	S	S	S	1336.15 (2.00)	1.0000 (0.2479)
Researcher – Red-tailed monkey	.	S	S	1261.29 (0.00)	1.0000 (-)
	S	S	S	1263.29 (2.00)	1.0000 (0.9795)
Researcher – Primate	.	S	.	2176.09 (0.00)	1.0000 (-)
	.	S	S	2178.02 (1.93)	1.0000 (-)
	S	S	.	2178.09 (2.00)	1.0000 (0.4981)
Leopard – Chimpanzee	.	S	.	1160.83 (0.00)	1.0000 (-)
	.	S	S	1162.71 (1.88)	1.0000 (-)
	S	S	.	1162.83 (2.00)	1.0000 (-)
Leopard - Baboon	S	S	.	383.41 (0.00)	0.9428 (0.6442)
	S	S	S	384.80 (1.39)	0.9471 (0.3397)
Leopard – Red-tailed monkey	HT	S	.S	303.55 (0.00)	1.0000 (-)
	.	S	.	303.92 (0.37)	1.0000 (-)
	HT	S	S	305.20 (1.65)	1.0000 (-)
	.	S	S	305.50 (1.95)	1.0000 (-)
Leopard – Primate	.	S	.	1199.51 (0.00)	1.0000 (0.0003)
	.	S	S	1201.49 (1.98)	1.0000 (0.1391)
	S	S	.	1201.51 (2.00)	1.0000 (0.1098)
Chimpanzee – Baboon	.	S	.	1182.75 (0.00)	1.0000 (-)
	.	S	S	1183.91 (1.16)	1.0000 (-)
	S	S	.	1184.75 (2.00)	1.0000 (0.6504)
Chimpanzee – Red-tailed monkey	.	S	S	1120.96 (0.00)	1.0000 (-)
	S	S	S	1122.96 (2.00)	1.0000 (-)
Predator – Baboon	.	S	.	1495.75 (0.00)	1.0000 (-)
	S	S	.	1497.75 (2.00)	1.0000 (0.4827)
Predator – Red-tailed monkey	.	S	.	1416.75 (0.00)	1.0000 (-)
	.	S	S	1417.41 (0.66)	1.0000 (-)
	S	S	.	1418.75 (2.00)	1.0000 (0.0375)

* AIC in all species except researcher and primate, where ĉ was altered to account for over-parametrisation (ĉ = 1.0002 and 1.0021 resp.). Because estimated ĉ values were small, only AIC changed when fitting the factor and standard errors did not.

4.   Discussion

4.1   Species trap success and seasonality
This study used species trap success as a measure of relative activity which could be used to test for patterns of seasonality in species' activity in the selected dataset and to score the nominal habitat variables habitat type and location type. Though previous studies have reported seasonality in species encounters in the Issa Valley (*e.g.* Russak, 2014; Piel et al. 2015b), it was believed to be unlikely that 14 cameras randomly distributed in an 85km^2 area would uncover seasonal patterns in species activity in the current dataset. To test this expectation and to assess whether seasonal patterns should be incorporated in further analysis by dividing data into a wet and a dry season dataset, a Wilcoxon signed rank test was used to test for seasonality.

The Wilcoxon signed rank test found that none of the included species – except researchers – displayed signs of seasonality in their relative activity. However, this apparent researcher seasonality was believed to have been caused by factors that had nothing to do with seasonal changes (*e.g.* the number of researchers present). Therefore, researcher seasonality was ignored and it was concluded that none of the included species displayed signs of seasonality. This confirmed the expectation that the current dataset would not contain signs of seasonality in species activity, but contradicts previous studies in Issa which have reported seasonality to be the best predictor of mammal encounters (Piel et al. 2015b) and reported seasonal patterns of habitat use for most species in Issa (Russak, 2014). The current study, however, attempted to find out whether the current dataset was influenced by species seasonality, whereas the previous studies provide an insight in species seasonality that is representative for the Issa Valley. Therefore, the current test was less extensive and focussed solely on the current dataset. As a result, the current test did not incorporate as many factors as the previous studies (*e.g.* group sizes, behavioural variation or habitat preferences) and contained only one wet and one dry season sample for each of the 14 camera traps in the 85km^2 study area. To put this in perspective: the research period of Piel et al. (2015b) lasted four years, during which seven transects (4.8 to 6.1km each) and one 3-day recce walk were sampled at least monthly, and a large number of samples were collected during work on other projects. Therefore, these previous studies are regarded as representative of species seasonality in the Issa Valley, while the current test results only indicate whether the currently used dataset was influenced by species seasonality. As no such seasonal patterns were discovered in the current dataset, further analysis was performed using a single year-long dataset.

4.2   Single-season, single-species occupancy
In the Issa Valley, no previous studies of species occupancy and the effects of habitat variables on occupancy have so far been performed. Therefore, this study modelled species occupancy (accounting for the probability that a species was detected) while allowing habitat variables to influence estimates. Modelling species occupation was expected to find that: 1) all included species occupy at least half of the included locations, despite an expected low detection probability; and that 2) covariate habitat type would be the main variable influencing species' occupation and detection probability, as this variable was believed to be the best delineated (*e.g.* in covariate location type, location types may overlap, as a location labelled as termite mound may also be a termite mound passed by a wildlife path).

4.2.1   Species occupation
Modelling species occupation has confirmed the first occupation hypothesis for all species except red-tailed monkey. Three species (researcher, leopard and chimpanzee) and both species groups (predator and primate) were estimated to occupy all 14 included locations, whereas baboon was estimated to occupy 10 of 14 locations, and red-tailed monkey 6 of 14 locations. This low occupation estimate for red-tailed monkey is expected to have been caused by the species' strong habitat preference, as its mainly arboreal ecology (Butynski, 2002; McGraw, 2002; Sargis, Terranova, & Gebo, 2002; Nilsson, 2010) is believed to limit it to occur only in forested areas (further discussed in *4.2.2 Covariates*). Apart from this habitat preference, the arboreal ecology of red-tailed monkey is also expected to have influenced its occupation estimate in another way. McGraw (2002) reported the species to spend only 10% of its time terrestrially. In theory, this could suggest that terrestrially placed camera traps only record 10% of the species' presence, missing the remaining 90% of time that it spends in the canopy. The terrestrial placement of camera traps is therefore also expected to have led to the exclusion of the remaining arboreal primates from this study (*e.g.* red colobus).

Two of the species that were estimated to occupy all locations (researcher and chimpanzee) were estimated to occupy all locations with a 100% certainty without error. For researchers, this estimate is not surprising. As all researcher detections – including detections of researchers during camera trap

deployment and maintenance – were included in the researcher detection history, the deployment of a camera trap caused that the location was occupied by researchers. In chimpanzee, however, this estimate was more surprising. Before selecting locations to be included in this study (*2.2.1 Camera traps*), the dataset included some locations where no chimpanzees were recorded (5 of 37 locations). However, as only a few locations contained no chimpanzee footage, the 100% occupation estimate may not be far from actual chimpanzee occupation. As both species groups (predators and primates) contain chimpanzee detection history and species group predator also contains researcher detection history, the 100% occupation estimates of chimpanzee and researcher consequently led to the 100% occupation estimates of the two species groups. In both species and the species groups, these occupation estimates have constrained the assessment of the correlation between habitat variables and species occupation, as there was no variation in species occupation between locations. As a result, variation could not be compared with habitat variables and influences of habitat variables on species occupation could not be assessed.

4.2.2   *Effects of habitat variables on species occupation*
The second occupation hypothesis could only be confirmed for the included primate species, as modelling species occupation found covariate habitat type to be the key driver behind variation in primate occupation and detection probability. Results indicate that chimpanzee detection probability was higher in forested habitat than in woodlands, baboon occupation probability was higher in woodland and red-tailed monkey occupation probability was higher in – and possibly even limited to – forests. In predatory species, covariate location type was found most likely to influence detection probability.
In chimpanzee, the higher detection probability in forests corresponds with larger encounter and density estimates in Issa forests than in woodlands reported by previous studies (*e.g.* Russak, 2014; Piel et al., 2015a; 2015b). Generally, such habitat preferences are attributed to a higher food availability in forests (*e.g.* Hunt & McGrew, 2002; Hernandez-Aguilar, 2009). However, previous studies report that Issa woodlands are more productive in chimpanzee foods than its forests, which are reported to be unusually poor providers of chimpanzee foods compared to other savannah sites (Hernandez-Aguilar, 2009; Russak, 2013). This general explanation is therefore believed to be unlikely in Issa chimpanzees. An alternative driver behind this apparent habitat preference may be the availability of water and shade (especially in the dry season), as seasonal rivers and streams that run in these forests during the wet season may still contain pools of water into the late dry season and the closed canopy provides shading from the sun (Russak, 2014). However, as no seasonal differences in chimpanzees' relative activity were found in the current dataset, such seasonal habitat preferences could not be further assessed. A final alternative explanation for this habitat preference might be that it is driven by the species' perceived predation risk, as forests may provide chimpanzee with cover from potential predators roaming Issa woodlands (*e.g.* lion or hyena). As a result, chimpanzee spatial distribution may be the result of a trade-off between resource availability and a higher (perceived) predation risk, supporting the theory that Issa chimpanzees live in a landscape of fear.
The landscape of fear concept is also believed to be the driver behind variation in baboon and red-tailed monkey occupation probability. In baboon, variation in occupation may be the result of a preference for open habitats (previously reported in Issa/Ugalla baboons by Iida, Idani, & Ogawa, 2012; Russak, 2014) that can be attributed to baboons' perceived predation risk, as baboons are known to shun high-risk areas such as areas of dense vegetation that can conceal the approach of a predator (*e.g.* Cowlishaw, 1997). Woodlands may therefore be perceived safe, as there is less vegetation and predators are more likely to be detected by a member of the group. In red-tailed monkey, variation in occupation is most definitely the result of a strong preference for forested habitat over woodland (previously reported in Issa/Ugalla red-tailed monkeys by Iida et al., 2012; Russak, 2014). Such a strong preference for forests is believed to be related to the species' mainly arboreal ecology, which is seen as a response to (perceived) predation risk (Butynski, 2002; Nilsson, 2010) as it minimizes the risk of predation by providing (among others) shelter and dimensional escape routes (Garber et al., 2008; Nilsson, 2010). Woodlands are believed to be less suitable for such an ecology as canopies don not intertwine, forcing the species to spend more time terrestrially or in exposed parts of the canopy, which drastically minimises the number of possible escape routes.

Against the expectations, predator detection probability was found to be influenced by covariate location type. This variable was believed to be insufficiently defined, as each location was labelled with only one location type while – in reality – a location might have been a combination of two or more types (*e.g.* termite mound passed by a wildlife path). Nevertheless, modelling species occupation found that researchers were most likely to be detected at termite mound locations, leopard at wildlife path locations and chimpanzee at human path and termite mound locations. However, after further analysis, it is unclear whether these results portray true location preferences or apparent preferences that were

actually caused by other variables. For instance, chimpanzees' apparent preference for human paths may have been caused by the fact that all human path locations included in this study are located in forests, and chimpanzees are more likely to be detected at forested locations than woodland. Also, leopard apparent preference for wildlife paths over human paths may indicate human avoidance. However, as researchers were more likely to be detected at wildlife paths than human paths, and locations labelled as human paths were actually wildlife paths that are used by researchers, this suggestion was eliminated. The only apparent location type preference that could not be defeated by alternative explanations was chimpanzee preference for termite mound locations. This preference may be explained by chimpanzee termite fishing, as the availability of termites as a protein rich resource draws chimpanzees to the location resulting in more chimpanzee detections and a higher detection probability.

A second unanticipated finding of this occupancy model was the relation between chimpanzee detection probability and the distance to the UPP basecamp, in which chimpanzee was more likely to be detected near the UPP basecamp than further from the camp. This finding corresponds with a previous study by Piel et al. (2015b), who report an increasing encounter probability for chimpanzee near the UPP basecamp. This previous study explains this correlation by a significant increase in snare encounter probability further from the basecamp, which is possibly the result of researcher avoidance by poachers. The current study found no supporting or alternative explanation for this correlation, and could therefore neither confirm nor deny this explanation.

4.3 Species interactions

In the Issa Valley (and other comparable areas), patterns of predator-primate co-occurrence were previously unreported. Therefore, this study used a two-species interaction model to calculate a measure of co-occurrence, which was expected to show primates and their potential predators to co-occur less frequently than expected when co-occurring independently (a possible sign of predator avoidance by primates). The same pattern was expected in primates and researchers and in predators and researchers, as researchers (and humans in general) were expected to be seen as a potential threat by wildlife in general.

The findings of this study, however, suggest that all except one species combination – leopard-baboon – co-occur independently. Whether these independent co-occurrence estimates for most species combinations are representative for the species in Issa is difficult to assess, as some combinations have been influenced by the 100% occupation estimates of one or both of the modelled species. The co-occurrence model compares variation in species occupation to uncover patterns in species co-occurrence. However, as species with 100% occupation estimates have no variation in their occupation estimates, the model will be unable to uncover possible co-occurrence patterns, resulting in an independent co-occurrence estimate. Only two of the 13 modelled species combinations were not influenced by this limitation as these did not include species with 100% occupation estimates: leopard-baboon and leopard-red-tailed monkey. As these were the only combinations for which conclusions on species co-occurrence could be drawn, these two combinations will be discussed below.

4.3.1 Leopard-baboon

Modelling leopard-baboon co-occurrence found the species to co-occur less frequently than expected when co-occurring independently, which may indicate avoidance of one species by the other. Logically, the prey would then be expected to avoid the predator, i.e. baboons avoid areas of high leopard occupation. Such a pattern would support the landscape of fear theory mentioned above as a possible driver behind baboon habitat preference. As past experiences or instinct may cause baboon to make a trade-off between resource availability and predation risk, baboon may shun certain high-risk areas (*e.g.* Cowlishaw, 1997; Russell & Hill, 2014). As leopards are considered baboons' primary predator (Cowlishaw, 1994; Jooste, Pitman, Hoven, & Swanepoel, 2012), an area of high leopard occupation could be considered a high-risk area by baboon and may therefore be avoided. Such a possible avoidance may have resulted in possible avoidance measured by the interaction model.

However, two alternative explanations for this finding could be that 1) leopard avoids areas of high baboon occupation, or that 2) other factors influence the species occupation probabilities in different ways and thereby cause species to have varying patterns of habitat use. Leopards have been found to avoid predating on baboon if possible (Hayward et al., 2006), and are reported to only predate on primate when larger prey are scarce (Seidensticker, 1983; Hayward et al., 2006). Hunting baboon – as well as other primates – may have smaller chances of success, as primates can utilise arboreal refuges. In addition to this, hunting baboon may bring extra risks such as extreme aggressiveness, group vigilance and mobbing which can lead to injury or death of the leopard (Cowlishaw, 1994; Bailey, 2005; Hayward et al., 2006). However, avoidance of predation on baboon does not necessarily influence leopard

occupation in such a way that leopard would avoid areas of high baboon occupation. Also, as both species' occupation estimates were not influenced by the same covariates, this study could not support the second alternative explanation. However, as there are more possible variables influencing these species' occupation than were included in this study, it is acknowledged that the second alternative explanation cannot be entirely excluded.

4.3.2   Leopard-red-tailed monkey

Modelling leopard-red-tailed monkey co-occurrence found no recognisable patterns in species spatial overlap and found the species to co-occur independently. Despite a possible predatory interaction (Hayward et al., 2006), the species seem uninfluenced by the others' occupation. Avoiding high-risk areas may not be necessary, as red-tailed monkey deals with its perceived predation risk by living mainly arboreally. On the other hand, the species does avoid a high-risk area (the forest floor) by living arboreally, which may be seen as a form of vertical spatial variation in response to perceived predation risk. Because of the terrestrial placement of camera traps, such a vertical pattern could not be investigated further in this study. However, the terrestrial placement of cameras may provide another suggestion about these species' interaction. As all red-tailed monkey detections were of monkeys foraging or travelling terrestrially or in the lower levels of the forest, and species were found to co-occur independently, red-tailed monkeys descending into these lower levels do not seem to account for high leopard occupation. The forest and all of its refuges and escape routes may – even in the lower levels – provide a sense of safety to the monkey as it ascertains a quick retreat to the safety of the canopy when danger is spotted.

Large standard errors with some of the co-occurrence estimates may place a possible limitation on the adoption of the interaction model findings. Given these large error margins, the range in which the true value lies is broad and often overlaps the ranges of independent co-occurrence, 'avoidance' or 'attraction'. As a result, some of the co-occurrence estimates reported in this study may be flawed, and follow-up studies are recommended to come to final conclusions.

5.   Conclusion

This study was designed to answer the question: 'What is the occupation probability of primates and their predators in the Issa Valley, and how does predator presence influence the occupation of primates?'. To answer this question, camera trap data collected in a year-long period were used to model single-species occupancy and two-species interaction models using PRESENCE software.

Results of these models have shown that most included species are estimated to occupy over half of the 14 included locations of the Issa Valley. Only one species – red-tailed monkey – was estimated to occupy less than half (6) of the included locations, as this species' arboreal ecology is believed to limit it to only occur in forested habitat. Also, primate occupation and detection probabilities were found to be mostly influenced or even limited by the covariate habitat type, which may be the result of the species' adaptations to (perceived) predation risk. Chimpanzees were found to be more likely to be detected at forested locations (despite occupying all locations), baboons were more likely to occupy woodland locations, and red-tailed monkeys were found to only occupy forested habitat. Lastly, two-species interaction models have indicated all species combinations to co-occur independently, except leopard-baboon. However, most of these species combinations are believed to have been caused by a lack of variation in the occupation estimates because of a 100% occupation estimate at all locations for some of the species. As a result, conclusions could only be drawn on the two species combinations that remained uninfluenced by this limitation: leopard-baboon and leopard-red-tailed monkey. These two species combinations indicated that baboons may shun areas of high leopard occupation, whereas red-tailed monkey occupation does not seem to be influenced by leopard occupation.

Based on these principal findings it may be concluded that occupation of the included primates and their predators is high in the Issa Valley, as all except one – red-tailed monkey – were found to occupy over half of the included locations and three were estimated to occupy all 14 locations included in this study. Also, variation in primate occupation and detection probabilities was found to be mainly caused by variation in habitat types. Such variations may be the result of the species' perceived predation risk, as forests may provide shelter to chimpanzee and red-tailed monkey, whereas baboon may prefer woodlands as open habitat structures prevent predators from concealing their approach. Also, from species interaction models it was concluded that baboon may shun areas of high leopard occupation, whereas red-tailed monkey occupation does not seem to be influenced by variations in leopard occupation. However, red-tailed monkey distribution does seem to be influenced by the presence of terrestrial predators (such as leopard), as its arboreal ecology and consequently its limitation to forests are believed to be a vertical adaption to perceived predation risk.

This study can be seen as a first step in solving the problem stated in the introduction (*1.1 Problem statement*), as it has successfully investigated one of the possible methods of gathering information on the subject, paving the way for future studies of the subject. Findings of this study may aid future conservation planning in the Issa Valley and other Miombo woodland areas by informing on species habitat use and interactions among species. Most importantly, the current study may aid future studies on the subject by informing on both current findings and on ways to apply and improve the method used here.

6.   Recommendations

During this study, certain factors were encountered that led to the formulation of recommendations for future studies (either to prevent limitations or to enable a more in-depth assessment of the subject). First, these recommendations for future studies will be discussed, followed by the possible implications of the current study.

The first recommendation for future studies on the subject is to select more (representative) locations and mitigate the effect of possible biases. The currently used camera selection method (*2.2.1 Camera traps*) has led to a selection of locations that did not represent the Issa Valley as a whole and may have formed a biased occupation estimate of at least one species, as some cameras used in this study were placed for the purpose of chimpanzee studies (*e.g.* at termite mound locations). Ideally, such a limitation is prevented by placing camera traps for the purpose of the study (possibly systematically placed in a grid, as previously used in comparable studies by among others Farris et al., 2011). However, as the placement of cameras for the purpose of a co-occurrence study may not always be possible, camera selection should include only truly randomly placed cameras and prevent the inclusion of locations that are biased in favour of certain species such as termite mounds, den entrances or bait stations.

Secondly, to provide a more thorough analysis of species interactions, species interactions may be analysed based on a detection probability interaction factor in addition to the currently used occupation probability interaction factor. This detection probability interaction factor can provide a more thorough understanding of species interactions as it may discover patterns in the frequency with which species are present at a location. This factor can therefore uncover new (otherwise missed) patterns in species co-occurrence and may also be able to uncover patterns in species co-occurrence when species occupation seems to be uninfluenced by the other species. This factor was not included in the current study as this study was set up to be a first of its kind that – with limited time available – attempted to provide a first insight in species interaction. However, over the course of this study it has become clear that modelling a detection interaction factor will be a valuable addition to species interaction studies using this method, hence this recommendation.

The findings of this study may have several implications. Findings on species occupation may support future conservation measures of endangered species (*e.g.* eastern chimpanzee) – both in Issa as well as in other parts of the miombo woodlands ecosystem – as it may provide an indication of the distribution and priority areas of species. By incorporating such findings in conservation measures, new protection areas can be appointed and the effect of large-scale interventions in the habitat (*e.g.* mining, logging or agriculture) can be assessed. Consequently, threats to these species may be either prevented or mitigated, and human-wildlife conflicts can be prevented. With this information, time, resources and labour can be directly appointed to those areas where it is most needed, leading to more successful conservation measures and a better protection of species.

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Appendixes

I. Keyword combinations used in the search for previous studies of the subject

This appendix lists the search engines and keyword combinations used in search of previous studies of predator-primate dynamics in Miombo woodland areas. The assumption that (to date) there has been no previous research on predator-primate dynamics in the Miombo Woodland ecosystem was based on this search. Although this search was performed thoroughly, the possibility always exists that it may have missed some previous studies that could have been found using other search engines or keyword combinations.

Search engines:
-   Wageningen University library's global search
-   ScienceDirect
-   Wiley online library
-   Google scholar

Keyword combinations:
-   Predator; prey; miombo
-   Predator; prey; dynamics; Miombo
-   Predator; prey; interaction; Miombo
-   Predator; prey; relation; Miombo
-   Predator; prey; co-occurrence; Miombo
-   Predator; prey; distribution; Miombo
-   Primate; prey; Miombo
-   Predator; primate; Miombo
-   Predator; primate; dynamics; Miombo
-   Predator; primate; interaction; Miombo
-   Predator; primate; relation; Miombo
-   Predator; primate; co-occurrence; Miombo
-   Predator; primate; distribution; Miombo
-   Primate; predation; Miombo
-   Predator; prey; woodland
-   Predator; primate; dynamics; woodland
-   Predator; primate; interaction; woodland
-   Predator; primate; relation; woodland
-   Predator; primate; co-occurrence; woodland
-   Predator; primate; distribution; woodland
-   Primate; predation; woodland

II. Camera coverage and malfunction periods
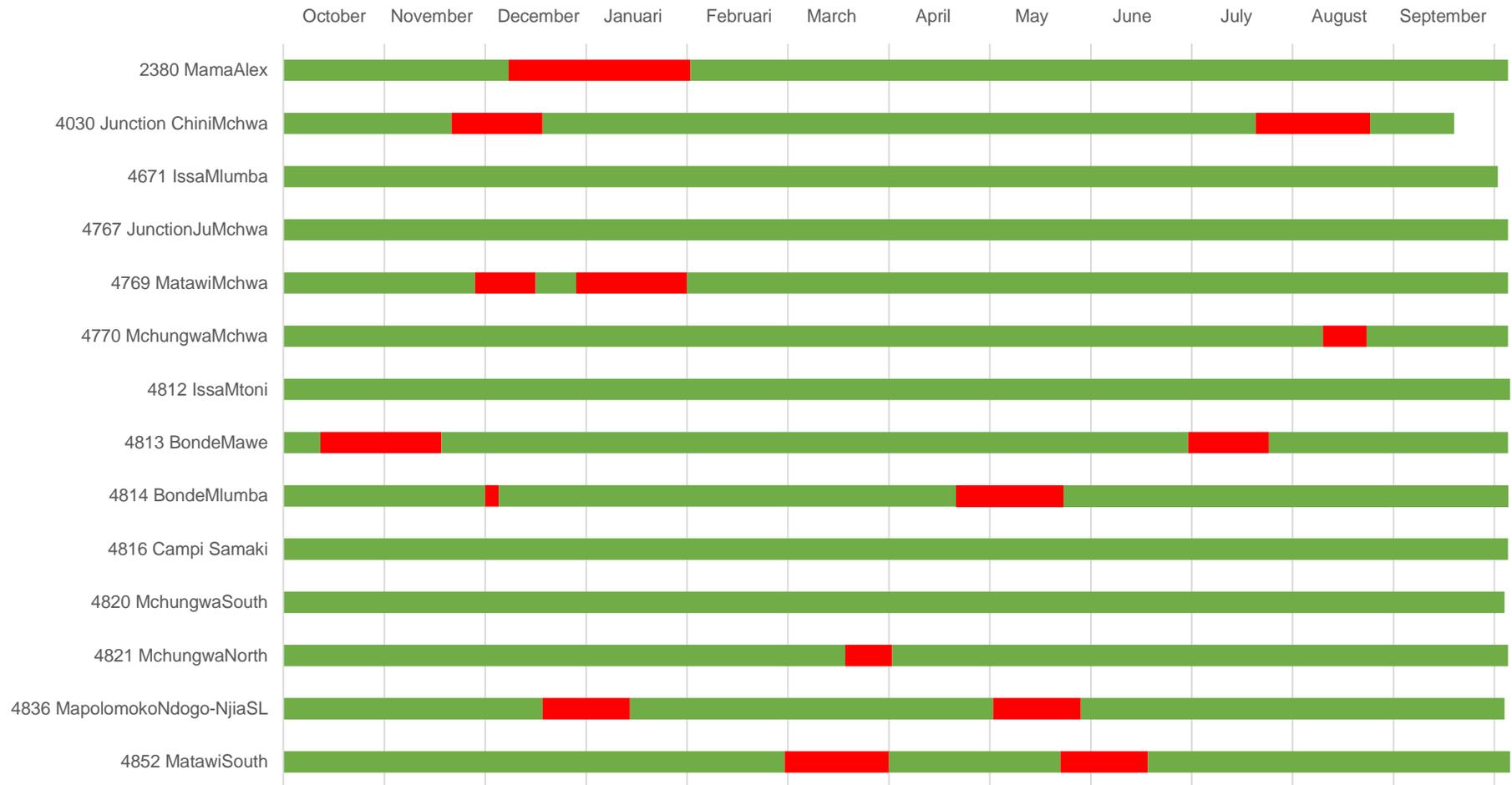
III. Standardised covariates per species per location

Camera	Habitat type	Location type	Dist. UPP	DH All	HT Researcher	HT Leopard	HT Chimpanzee	HT Baboon	HT Red-tail	HT Predator	HT Primate	LT Researcher	LT Leopard	LT Chimpanzee	LT Baboon	LT Red-tail	LT Predator	LT Primate
2380	F	P	1,2	-0,6296	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,8034	-0,4480	0,6970	0,2125	0,7546	-0,3146	0,6223
4030	F	T	1,25	-0,5796	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	1,1110	-0,6977	0,4488	0,8767	0,3797	1,1195	0,5312
4671	F	P	3,9	2,0704	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,8034	-0,4480	0,6970	0,2125	0,7546	-0,3146	0,6223
4767	W	T	1,45	-0,3796	0,7071	-0,7071	-0,7071	0,7071	-0,7071	-0,7071	-0,7071	1,1110	-0,6977	0,4488	0,8767	0,3797	1,1195	0,5312
4769	F	T	1,35	-0,4796	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	1,1110	-0,6977	0,4488	0,8767	0,3797	1,1195	0,5312
4770	W	T	1,8	-0,0296	0,7071	-0,7071	-0,7071	0,7071	-0,7071	-0,7071	-0,7071	1,1110	-0,6977	0,4488	0,8767	0,3797	1,1195	0,5312
4812	F	W	5,3	3,4704	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4813	W	W	4,5	2,6704	0,7071	-0,7071	-0,7071	0,7071	-0,7071	-0,7071	-0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4814	W	W	3,6	1,7704	0,7071	-0,7071	-0,7071	0,7071	-0,7071	-0,7071	-0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4816	F	W	2,15	0,3204	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4820	F	W	2,25	0,4204	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4821	F	W	1,75	-0,0796	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4836	F	W	1,95	0,1204	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535
4852	F	W	1,6	-0,2296	-0,7071	0,7071	0,7071	-0,7071	0,7071	0,7071	0,7071	-0,3166	1,1457	-1,1458	-1,0892	-1,1342	-0,8049	-1,1535

Habitat type: F = forest, W = woodland
Location type: P = human path, T = termite mound, W = wildlife path
Distance to the UPP basecamp is given in kilometres, other factors are given as standardised (Z-scored; 2.2.5 Covariates and standardisation) trap success.

IV. Location-specific average occupation probabilities per species
Species weighted location-specific average occupation probability estimate with standard errors given in brackets

Species	2380	4030	4671	4767	4769	4770	4812	4813	4814	4816	4820	4821	4836	4852	Total
Researcher	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998
	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)
Leopard	0.9707	0.9373	0.9707	0.8956	0.9373	0.8956	1.0001	0.9994	0.9994	1.0001	1.0001	1.0001	1.0001	1.0001	0.9719
	(0.1509)	(0.2165)	(0.1509)	(0.2966)	(0.2165)	(0.2966)	(0.0004)	(0.0180)	(0.0180)	(0.0004)	(0.0004)	(0.0004)	(0.0004)	(0.0004)	(0.1502)
Chimpanzee	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001	1.0001
	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)
Baboon	0.7414	0.7237	0.7795	0.8025	0.7257	0.8091	0.7342	0.8054	0.7987	0.7057	0.7073	0.6988	0.7024	0.6961	0.745
	(0.2343)	(0.2295)	(0.2271)	(0.2229)	(0.2273)	(0.2169)	(0.2447)	(0.2420)	(0.2430)	(0.2368)	(0.2372)	(0.2368)	(0.2364)	(0.2376)	(0.2339)
Red-tailed monkey	0.5271	0.5206	0.5071	0.2232	0.5198	0.2204	0.4694	0.1777	0.1831	0.4896	0.4888	0.4927	0.4911	0.4939	0.4146
	(0.2039)	(0.1968)	(0.2147)	(0.2635)	(0.1962)	(0.2594)	(0.2232)	(0.2265)	(0.2256)	(0.1995)	(0.1996)	(0.2000)	(0.1995)	(0.2006)	(0.2160)
Predator	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998	0.9998
	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)	(0.0002)
Primate	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995	0.9995
	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)	(0.0005)

V. Location-specific average detection probabilities per species

Species weighted location-specific average detection probability estimate with standard errors given in brackets

Species	2380	4030	4671	4767	4769	4770	4812	4813	4814	4816	4820	4821	4836	4852	Total
Human	0.2595 (0.0276)	0.3157 (0.0374)	0.2575 (0.0240)	0.2988 (0.0327)	0.3156 (0.0375)	0.2985 (0.0327)	0.27 (0.0262)	0.2557 (0.0287)	0.2563 (0.0279)	0.2721 (0.0176)	0.2720 (0.0175)	0.2724 (0.0184)	0.2722 (0.0180)	0.2725 (0.0188)	0.2778 (0.0260)
Leopard	0.0088 (0.0077)	0.0078 (0.0080)	0.0089 (0.0078)	0.0071 (0.0077)	0.0078 (0.0079)	0.0071 (0.0077)	0.0271 (0.0081)	0.0245 (0.0091)	0.0245 (0.009)	0.0269 (0.0076)	0.0269 (0.0076)	0.0269 (0.0077)	0.0269 (0.0076)	0.0269 (0.0077)	0.0184 (0.0077)
Chimpanzee	0.2885 (0.0588)	0.2781 (0.0510)	0.2254 (0.0432)	0.2059 (0.0299)	0.2756 (0.0494)	0.1992 (0.0284)	0.1555 (0.0461)	0.1287 (0.0566)	0.1384 (0.0509)	0.2069 (0.0195)	0.2049 (0.0192)	0.2149 (0.0223)	0.2108 (0.0205)	0.2180 (0.0240)	0.2108 (0.0366)
Baboon	0.0382 (0.0112)	0.0526 (0.0166)	0.0345 (0.0098)	0.0509 (0.0155)	0.0525 (0.0166)	0.0504 (0.0155)	0.0174 (0.0100)	0.0178 (0.0103)	0.0187 (0.0108)	0.0210 (0.013)	0.0208 (0.0128)	0.0216 (0.0141)	0.0213 (0.0135)	0.0218 (0.0146)	0.0314 (0.0130)
Red-tailed monkey	0.0315 (0.1253)	0.0309 (0.0756)	0.0310 (0.1254)	0.0309 (0.0756)	0.0309 (0.0756)	0.0308 (0.0756)	0.0285 (0.0119)	0.0286 (0.0113)	0.0288 (0.0106)	0.0290 (0.0100)	0.0290 (0.0100)	0.0291 (0.0100)	0.0291 (0.0100)	0.0292 (0.0100)	0.0298 (0.0531)
Predator	0.4741 (0.0256)	0.5365 (0.0426)	0.4426 (0.0361)	0.4568 (0.039)	0.5353 (0.0432)	0.4527 (0.0379)	0.4057 (0.0476)	0.3417 (0.0398)	0.3515 (0.0416)	0.4415 (0.0237)	0.4403 (0.0230)	0.4462 (0.0272)	0.4438 (0.0252)	0.4479 (0.0288)	0.4440 (0.0347)
Primate	0.3564 (0.0311)	0.3485 (0.0295)	0.2986 (0.0474)	0.2272 (0.0331)	0.3463 (0.0288)	0.2211 (0.0311)	0.1723 (0.0362)	0.1116 (0.0231)	0.1205 (0.0217)	0.22 (0.0208)	0.2183 (0.0203)	0.227 (0.0238)	0.2234 (0.0221)	0.2296 (0.0252)	0.2372 (0.0278)

VI. Top-ranking single-season, single-species occupancy models

Model names describe which parameters are modelled to either influence occupation (Ψ) or detection probability (p). Parameters modelled: habitat type (HT), location type (LT), distance from the nearest human habitation (DH) and no covariates included (.). The '1 group, constant p' model reported in 2.3.1 single-season, single-species occupancy model is named Ψ(.),p(.) in this table. (Q)AIC = Akaike information criterion, measure of ranking models; Δ(Q)AIC = difference in AIC between listed and top ranking model; (Q)AIC wgt. = estimated weight of the model, used in calculation weighted averages; k = number of included parameters; NE = Naïve Estimate, the proportion of locations where a species is recorded at least once; Ψ (SE) = estimated occupation probability and p (SE) = estimated detection probability.

	Model name	(Q)AIC* (Δ(Q)AIC)	(Q)AIC wgt.	k	NE**	Ψ (SE)	p (SE)
Researcher	Ψ(.), p(LT)	1125.95 (0.00)	0.2349	3	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	Ψ(.),p(HT,LT)	1126.61 (0.66)	0.0830	4	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	Ψ(.),p(.)	1127.24 (1.29)	0.1232	2	1.0000	1.0000 (0.0000)	0.2776 (0.0145)
	Ψ(LT),p(LT)	1127.95 (2.00)	0.0864	4	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
	Ψ(HT),p(LT)	1127.95 (2.00)	0.0864	4	1.0000	1.0000 (0.0000)	0.2779 (0.0208)
Leopard	Ψ(.),p(LT)	168.66 (0.00)	0.3032	3	0.6429	1.0000 (0.0000)	0.0178 (0.0058)
	Ψ(.),p(HT,LT)	170.15 (1.49)	0.1439	4	0.6429	1.0000 (0.0000)	0.0177 (0.0073)
	Ψ(HT),p(LT)	170.66 (2.00)	0.1115	4	0.6429	1.0000 (0.0000)	0.0178 (0.0058)
Chimpanzee	Ψ(.),p(HT,LT,DH)	960.34 (0.00)	0.2331	5	1.0000	1.0000 (0.0000)	0.2110 (0.0258)
	Ψ(HT,LT,DH),p(.)	960.34 (0.00)	0.2331	5	1.0000	1.0000 (0.0000)	0.2103 (0.0132)
	Ψ(HT),p(HT,LT,DH)	962.34 (2.00)	0.0857	6	1.0000	1.0000 (0.0000)	0.2110 (0.0258)
Baboon	Ψ(.),p(LT)	204.36 (0.00)	0.2624	3	0.5714	0.7583 (0.1978)	0.0296 (0.0108)
	Ψ(HT),p(LT)	205.24 (0.88)	0.1690	4	0.5714	0.7579 (0.1862)	0.0297 (0.0103)
	Ψ(DH),p(LT)	205.58 (1.22)	0.1426	4	0.5714	0.7583 (0.2294)	0.0297 (0.0109)
	Ψ(.),p(HT,LT)	206.12 (1.76)	0.1088	4	0.5714	0.7566 (0.1934)	0.0303 (0.0136)
Red-tailed monkey	Ψ(HT),p(.)	123.03 (0.49)	0.3404	3	0.3571	0.4094 (0.1616)	0.0303 (0.0103)
Predator	Ψ(.),p(HT,LT)	1301.30 (0.00)	0.1680	4	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	Ψ(.),p(HT,LT,DH)	1302.24 (0.94)	0.1050	5	1.0000	1.0000 (0.0000)	0.4442 (0.0320)
	Ψ(HT),p(HT,LT)	1303.30 (2.00)	0.0618	5	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	Ψ(LT),p(HT,LT)	1303.30 (2.00)	0.0618	5	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
	Ψ(DH),p(HT,LT)	1303.30 (2.00)	0.0618	5	1.0000	1.0000 (0.0000)	0.4442 (0.0277)
Primate	Ψ(.),p(HT,LT,DH)	1018.08 (0.00)	0.2618	5	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	Ψ(.),p(HT,LT)	1019.64 (1.56)	0.1200	4	1.0000	1.0000 (0.0000)	0.2372 (0.0235)
	Ψ(LT),p(HT,LT,DH)	1020.08 (2.00)	0.0963	6	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	Ψ(DH),p(HT,LT,DH)	1020.08 (2.00)	0.0963	6	1.0000	1.0000 (0.0000)	0.2374 (0.0270)
	Ψ(HT),p(HT,LT,DH)	1020.08 (2.00)	0.0963	6	1.0000	1.0000 (0.0000)	0.2374 (0.0270)

* AIC in all species except researcher and primate, where ĉ was altered to account for over-parametrisation (ĉ = 1.0002 and 1.0021 resp.). Because estimated ĉ values were small, only AIC changed when fitting the factor and standard errors did not.

VII. Top-ranking two-species interaction models

Model names describe which parameters are modelled to either influence occupation (Ψ) or detection probability (p, r). Parameters modelled: (.) = no covariates included; (S) = species-specific parameters estimated; (HT) = habitat type. (Q)AIC = Akaike information criterion, measure of ranking model; Δ(Q)AIC = difference in AIC between listed and top ranking model; (Q)AIC wgt. = estimated weight of the model, used in calculation weighted averages; k = number of included parameters; φ (SE) = estimated interaction factor, which shows species to occur independently (φ = 1), to co-occur less frequently than expected when distributed independently (e.g. exclude or avoid each other) (φ < 1), or to co-occur more frequently than expected if they were independent (e.g. attraction) (φ > 1).

	Model name	(Q)AIC[*1] (Δ(Q)AIC)	(Q)AIC[*1] wgt.	k	φ (SE)
Researcher – Leopard	$\psi(.),p(S),r(.)$	1305.98 (0.00)	0.5227	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	1307.82 (1.84)	0.2083	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	1307.98 (2.00)	0.1923	7	1.0000 (0.8132)
Researcher – Chimpanzee	$\psi(.),p(S),r(.)$	2113.78 (0.00)	0.5090	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	2115.57 (1.79)	0.2080	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	2115.78 (2.00)	0.1872	7	1.0000 (2.9120)
Researcher – Baboon	$\psi(.),p(S),r(S)$	1334.15 (0.00)	0.6463	7	1.0000 (-)
	$\psi(S),p(S),r(S)$	1336.15 (2.00)	0.2378	8	1.0000 (0.2479)
Researcher – Red-tailed monkey	$\psi(.),p(S),r(S)$	1261.29 (0.00)	0.5261	7	1.0000 (-)
	$\psi(S),p(S),r(S)$	1263.29 (2.00)	0.1935	8	1.0000 (0.9795)
Researcher – Primate	$\psi(.),p(S),r(.)$	2176.09 (0.00)	0.4928	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	2178.02 (1.93)	0.1878	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	2178.09 (2.00)	0.1813	7	1.0000 (0.4981)
Leopard – chimpanzee	$\psi(.),p(S),r(.)$	1160.83 (0.00)	0.5257	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	1162.71 (1.88)	0.2054	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	1162.83 (2.00)	0.1934	7	1.0000 (-)
Leopard - baboon	$\psi(S),p(S),r(.)$	383.41 (0.00)	0.6405	7	0.9428 (0.6442)
	$\psi(S),p(S),r(S)$	384.80 (1.39)	0.3197	8	0.9471 (0.3397)
Leopard – Red-tailed monkey	$\psi(HT),p(S),r(.)$	303.55 (0.00)	0.3041	8	1.0000 (-)
	$\psi(.),p(S),r(.)$	303.92 (0.37)	0.2527	6	1.0000 (-)
	$\psi(HT),p(S),r(S)$	305.20 (1.65)	0.1333	9	1.0000 (-)
	$\psi(.),p(S),r(S)$	305.50 (1.95)	0.1147	7	1.0000 (-)
Leopard – Primate	$\psi(.),p(S),r(.)$	1199.51 (0.00)	0.5330	6	1.0000 (0.0003)
	$\psi(.),p(S),r(S)$	1201.49 (1.98)	0.1981	7	1.0000 (0.1391)
	$\psi(S),p(S),r(.)$	1201.51 (2.00)	0.1961	7	1.0000 (0.1098)
Chimpanzee – Baboon	$\psi(.),p(S),r(.)$	1182.75 (0.00)	0.4649	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	1183.91 (1.16)	0.2603	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	1184.75 (2.00)	0.1710	7	1.0000 (0.6504)
Chimpanzee – Red-tailed monkey	$\psi(.),p(S),r(S)$	1120.96 (0.00)	0.5691	7	1.0000 (-)
	$\psi(S),p(S),r(S)$	1122.96 (2.00)	0.2093	8	1.0000 (-)
Predator – Baboon	$\psi(.),p(S),r(.)$	1495.75 (0.00)	0.6305	6	1.0000 (-)
	$\psi(S),\varphi,p(S),r(.)$	1497.75 (2.00)	0.2320	7	1.0000 (0.4827)
Predator – Red-tailed monkey	$\psi(.),p(S),r(.)$	1416.75 (0.00)	0.3890	6	1.0000 (-)
	$\psi(.),p(S),r(S)$	1417.41 (0.66)	0.2797	7	1.0000 (-)
	$\psi(S),p(S),r(.)$	1418.75 (2.00)	0.1431	7	1.0000 (0.0375)

* AIC in all species except researcher and primate, where ĉ was altered to account for over-parametrisation (ĉ = 1.0002 and 1.0021 resp.). Because estimated ĉ values were small, only AIC changed when fitting the factor and standard errors did not.