

International Primatological Society

IPS Bulletin



WINTER 2018

Volume 44 Number 1

President's Corner

kbstrier@wisc.edu

It is a great pleasure to write with so many positive memories from the 27th IPS Congress still strong. The Congress, held in Nairobi, Kenya, was a resounding success, thanks in equal parts to the incredible skills of Johannes Refish and his organizing committee of GRASP-UN, Vice President Janette Wallis and her program committee, and the inimitable Vice President and Treasurer Steve Schapiro, who pulled all the pieces together both before and during the conference. Thanks are also due to the more than 800 participants who came to share their scientific findings about primates and their efforts on behalf of primate conservation and well-being.

Several historical events occurred at these meetings. In addition to the iconic "Top 25 Most Endangered Species" session, the IPS Congress welcomed the newly inaugurated African Primatological Society to its Council, co-hosted the release of the Red Colobus Action Plan, and held its first-ever "#MeToo and Primatology" roundtable.

It also provided an opportunity to celebrate the outstanding service of four outgoing IPS officers with standing ovations at the General Assembly. Three officers (Nancy Caine, Janette Wallis, and Steve Schapiro) were completing extended terms in office and were recognized with Special Presidential Service Awards supplemented with gift certificates generously donated by Jack Galante (of the Galante Family Winery Conservation Scholarship). The fourth outgoing officer, Jo Setchell, continues her extraordinary service to IPS as Editor-in-Chief of the *International Journal of Primatology* and we look forward to recognizing all aspects of her distinguished service contributions in the future.

I would like to express my deep personal gratitude to all four of these outgoing officers, and especially Steve Schapiro, who, together with my successor and ex-officio President, Tetsuro Matsuzawa, served as my guides when I took over as President of IPS in 2016. We will continue to rely on all of them for advice as IPS moves forward. I am also grateful for the opportunity to continue to work with the fantastic officers who were elected along with me in 2016 (Cat Hobaiter, Patricia Izar, and Steve Ross), and the four incoming officers (Júlio César Bicca-Marques, Marina Cords, Tatyana Humle, and Trudy Turner) who were elected in 2018 and assumed their new positions at the post-Congress Council meeting.

IPS Officers

PRESIDENT

Karen Strier
University of Wisconsin-Madison
Dept of Anthropology
Madison, WI, 53706, USA
kbstrier@wisc.edu

SECRETARY GENERAL

Júlio César Bicca-Marques
Pontifícia Universidade Católica do
Rio Grande do Sul
Escola de Ciências
Porto Alegre, RS 90619-900, BRAZIL
jcbicca@pucrs.br

TREASURER, VP FOR MEMBERSHIP

Trudy Turner
Department of Anthropology
PO Box 413 UW-Milwaukee
Milwaukee, WI 53201 USA
trudy@uwm.edu

VP FOR COMMUNICATIONS

Cat Hobaiter
School of Psychology
University of St Andrews
St Mary's College, South Street
St Andrews, KY16 9JP, SCOTLAND
clh42@st-andrews.ac.uk

VP FOR CONSERVATION

Tatyana Humle
School of Anthropology &
Conservation
University of Kent, UK
T.Humle@kent.ac.uk

VP FOR CAPTIVE CARE

Stephen Ross
Lester E. Fisher Centre
Lincoln Park Zoo
Chicago, IL 60614, USA
sross@lpzoo.org

VP FOR EDUCATION

Patricia Izar
University of São Paulo
Dept of Experimental Psychology
Av. Prof. Mello Moraes 1721
C. São Paulo, SP, CEP 05508-030,
BRAZIL
patrizar@usp.br

VP FOR RESEARCH

Marina Cords
Columbia University
Department of Ecology, Evolution,
and Environmental Biology
1200 Amsterdam Avenue
New York NY 10027, USA
marina.cords@columbia.edu

IPS Website: www.internationalprimatologicalsociety.org

Cat Hobaiter, Editor



There, it was a pleasure to welcome both returning and new Council members. This year's post-Congress Council meeting was exceptionally lively and productive, with animated discussions and approval of plans for developing and launching new initiatives that have the potential to positively impact many features of IPS and the primates we study and work to protect. The minutes of this and other meetings can be accessed at the Congress page of the IPS website. As you can see there, much of the discussion and many new initiatives revolve around increasing diversity and equity at all levels of IPS. We look forward to increased participation from Council members and our affiliate societies, and we encourage all IPS members to consider nominating their colleagues for committees and awards when the calls for these openings are made.

Vice President for Communication, Cat Hobaiter, has been exceptionally active in posting information on the News and Meetings Page of the IPS Website and the IPS Facebook Page, so please be sure to check these out. For non-Facebook members, remember you can still read the posts without signing up.

We encourage all IPS members to send news and announcements that you would like us to post. In addition, following up on Roundtables, the General Assembly and the post-congress Council meeting discussions, there is an expanding number of links to resources on the Education and Research pages of our IPS website. We are also in the process of expanding links for other pages as well, including ones relevant to

discussions of diversity, equity, and codes of conduct. If you have links or material that you would like to share, please let us know. We are striving to increase the value of the IPS to our membership, and sharing information is one way we can do this.

Our next IPS meeting will be held jointly with the Latin American Primatological Society in Quito, Ecuador, in August 2020. Although that is still more than a year into the future, the local organizing committee, led by Stella de la Torre, is already hard at work. The same is true for IPS officers. In addition to the usual upcoming grant-related activities of our various committees, we are also developing proposals for additional IPS awards and possibly a new Vice President position. Once these have been vetted by the officers and Council, we will be calling for a membership-wide vote to consider making these proposed revisions in the IPS By-Laws. Please look for an email message about this vote, which we expect will occur sometime between March and May 2019.

Related to this upcoming vote, please be sure to remember to renew your IPS membership. It is easy to let annual memberships slip in the off-years between meetings, but it is also the case that being a member is the only way that you can have a voice and vote about IPS policies and decisions. The IPS is Our society, and we need every one of our voices to keep it strong. The primates of the world have never needed us more.

With best wishes,
Karen B. Strier

VP for Communication

clh42@st-andrews.ac.uk

Hello Primate folk,

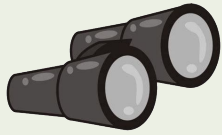
Thank you to everyone who has submitted reports and information for inclusion in this edition. As well as updates from our Officers and grantees, we have our first 'Getting To Know your IPS Officers' section. Steve Ross, our VP for Captive Care, kicks us off with a look at where he started out and what he's currently excited to be exploring.

It was fantastic to see everyone at the conference and around the world following along with all of your tweeting and sharing from our 27th

Congress in Nairobi. By the last day #IPSNairobi tweets had been seen over 27,000 times, try fitting that many people into a conference room!

For up-to-date happenings stay tuned to our online media for primate news, meetings, the IPS elections, advocacy, and other activities! And please do get in touch with feedback or ideas for what you would like to see IPS do for our fellow primates and primatologists.

Pant hoots! Cat Hobaiter
[@IPS_PrimateNews](https://twitter.com/IPS_PrimateNews)



Getting to Know Your: VP for Captive Care

sross@lpzoo.org

What is your scientific background?

I received my Bachelors of Science in Zoology from the University of Guelph in Canada and shortly thereafter took a research assistant position studying the welfare of domestic pigs under the guidance of David Fraser. Several years later, knowing my interests were in primatology, I took a volunteer researcher role at Cayo Santiago working under Carol Berman of the University of Buffalo to get my first exposure to primates. In 1996, I worked as a research assistant under Mollie Bloomsom first at M.D. Anderson Cancer Center in Texas and later at Yerkes National Primate Center in Georgia and have not stopped working with chimpanzees since that time. Since 2000, I have been at Lincoln Park Zoo's Lester Fisher Center for the Study and Conservation of Apes, working with Kristen Lukas and later, Elizabeth Lonsdorf. I received a Master's degree at University of Chicago and then a PhD from University of Copenhagen working with Jann Hau and Steve Schapiro, and I help administer a field conservation program in the Republic of Congo's Goulougo Triangle with Dave Morgan.

How did you choose your field of study?

I was motivated from a very young age to work with chimpanzees, but it wasn't until my exposure to the science of animal welfare with my work with domestic pigs, that I began to develop clear ideas about my career and how I could put that passion in context to my interests in science. Knowing that welfare was something that we could attempt to measure and assess and hopefully improve in a systematic way, was very

appealing to me.

What are you working on at the moment that you're really excited about?

In addition to my work at Lincoln Park Zoo, I am also Chair of the Board of Directors at Chim Haven, the National Chimpanzee Sanctuary in Louisiana, which is home to over 250 chimpanzees retired from research centers. Several years ago, we formed a unique partnership between the zoo and the sanctuary that aims to leverage each institution's expertise to grow the programmatic and scientific initiatives to advance chimpanzee care and welfare. It's such a privilege to work with two strong organizations that prioritize science and welfare and I am really looking forward to continuing that work with my collaborators Lydia Hopper and Amy Fultz.

What motivated you to join the IPS Council?

Since my first IPS congress in Madison in 1996, I have considered IPS to be my "home society" and I was honored when IPS Past President, Professor Tetsuro Matsuzawa suggested to me to run for Vice-President of Captive Care and Breeding. I sought to continue to past work highlighting the importance of welfare-related science and the care of the primates we all work with every day.

Steve Ross is the Director for the Lester E. Fisher Center for the Study and Conservation of Apes, at the Lincoln Park Zoo in Chicago. He has worked all over the world and published on species as diverse as primates and polar bears. He served as Chair of the Chimpanzee Species Survival Plan from 2002-2017, and has over 20 years experience

Secretary General

jbicca@pucrs.br

I am an active member of the society since 1995 and I have attended 10 of the last 12 IPS meetings. I have studied the ecology, behavior, cognition and conservation biology of wild and captive primates in Brazil for almost three decades and I have published on all major New World monkey radiations.

I took over the position of Secretary General in the post-congress meeting of the IPS council in Nairobi last August. My goals as Secretary General include stimulating a stronger

participation of range country primatological societies, promoting a higher involvement of range country scientists in the peer-review system and publication in international primate journals, and helping to strengthen the society's role in conservation.

I look forward to working with the other IPS officers and every primatologist in the next four years to help IPS to fulfill its objectives.

Júlio César Bicca-Marques, Secretary General

VP for Research

marina.cords@columbia.edu

I am pleased to serve IPS as Vice President for Research, taking over from Joanna Setchell, and thanking her for her hard work over the last 8 years.

The Research Committee is gearing up for the 2019 Research Grant competition, with deadline March 1. Remember that these grants (up to \$1500) support primate-oriented research projects with a strong theoretical component, distinct from the Conservation and Captive Care grants. Lots of helpful information for applicants is available on the IPS website: www.internationalprimatologicalsociety.org/research.cfm

and I encourage potential applicants to consult this webpage *early* in the process of preparing proposals.

I also welcome any IPS members to contact me if you would like to nominate a fellow member to join the committee, or are interested in joining yourself. Committee members review proposals submitted by the March 1 deadline, and some also provide pre-submission feedback (in early February) to applicants from range countries.

Marina Cords
VP for Research

Trea\$ury Note\$

Trudy@uwm.edu

I will be taking over from Steve Schapiro as the new Treasurer and Vice President for Membership of the IPS. We are all extremely grateful to Steve for his stewardship of the IPS treasury for many years. Much of where we are today is the result of his careful attention to all detail IPS and to his determination that this organization be successful.

Steve has provided a report on the finances of the wonderful meeting in Nairobi. There were more than 850 registrants and the conference generated over \$400,000 in revenues. Additional revenues during the year were brought in from the Silent Auction and the Photo Contest and grants. To date, about \$163,000 was distributed in research grants, conservation funds, and Project Monkey Island.

Over 80 people participated in the FIPA (Primate World Cup Football Tournament) in Nairobi.

Those who study apes defeated those who study prosimians 3-1 in the Championship game. Steve assures us that plans are underway for the 2020 FIPA Tournament in Quito, although the high altitude may require some game modifications.

I would like to encourage you to renew your membership for 2019. The officers and committee members of the IPS work every year to ensure that the organization continues and that important matters to primatologists and primates are attended to and considered. We need your support for this work to continue. Membership renewal notifications will come out shortly.

I very much look forward to working with you all. There is a lot to learn. I count on the help of the former Treasurer and all the IPS officers. Please feel free to contact me with any questions.

Trudy Turner

This was a busy year for the Education Committee. We were pleased to conduct the review of more than a hundred abstracts for the IPS student competition, besides the annual evaluation of proposals for the education grants and awards.

Lawrence Jacobsen Education Development Grants:

This year we had only 9 applications from 7 countries across Africa, South and North America, and Asia, (Brazil, Cameroon [2 applications], Canada, India, Mexico, Paraguay, and USA [2 applications]). We awarded US\$ 6,825 in four grants (two included Community Conservation Initiatives in their applications):

Karina Atkinson

Training Paraguayan "Parabiologists" and future "Eco-Leaders" to save Paraguay's Primates

Sonya Kahlenberg

Using public pledges to motivate conservation action around Grauer's gorilla habitat in Eastern Democratic Republic of Congo

Emmanuel Liyong

Production of an informative poster for awareness raising and conservation education on newly created Kimbi-Fungom National Park.

Tatiane Valença

Protecting monkeys as a way of combating Yellow Fever

I am very grateful to the dedicated IPS members who assisted with the review and judging for the 2018 Lawrence Jacobsen Education Development grants and the Charles Southwick Conservation Education Commitment Award. Acknowledgements are due to: Carlos Ruiz-Miranda, Francine Dolins, Inza Kone, Marc Myers, Renata G. Ferreira, Simplicious Gessa, Thomas Breuer, Susana Carvalho, Tatyana Humle, Zhang Peng, and Zarin Machanda.

Charles Southwick Conservation Education Commitment Award:

In 2018 we received three nominations and awarded US\$ 2,000 in one award to Liyong Emmanuel Sama, Coordinator of Centre for

Indigenous Resources Management and Development (CIRMAD), Cameroon. I am grateful for the Education Committee members that helped evaluating the nominations: Inza Kone, Marc Myers, Tatyana Humle, and Zhang Peng.

IPS 2018 Student competition

Before the meeting in Nairobi, we reviewed 161 abstracts and selected 15 finalists that were each evaluated by three judges during their presentations. We were pleased to award the three best oral presentations and one best poster during the general assembly:

First oral presentation:

Kotrina Kajokaite,
TESTING OBSERVATIONAL DATA:
COALITIONS IN WHITE-FACED
CAPUCHIN MONKEYS

Honorable mentions:

Felipe Silva
A FIRST APPRAISAL OF THE
BIOGEOGRAPHY AND EVOLUTIONARY
HISTORY OF UAKARIS, GENUS CACAJO
LESSON, 1840

Leslie Wilmett

ASSESSING THE RISK FACED BY A
THREATENED SPORTIVE LEMUR, L.
MITTERMEIERI, ENDEMIC TO THE
FRAGMENTED LANDSCAPE OF THE
AMPASINDAVA PENINSULA IN
NORTHWEST MADAGASCAR

Best Poster:

Holly Fuong,
DO RELATED WILD BLUE MONKEYS
(CERCOPITHECUS MITIS) HAVE SIMILAR
SOCIAL NETWORK POSITIONS?

If any IPS members are interested in serving on the Education Committee, or have specific issues they would like addressed, please contact me at patrizar@usp.br.

Patrícia Izar
VP for Education

VP for Conservation

T.Humle@kent.ac.uk

Dear all,

I am thrilled to act as the new VP for Conservation and I look forward to working with the Conservation Committee and representing the membership when it comes to issues related to primate conservation. I would like to take this opportunity to flag the wonderful funding opportunities we offer:

❖ 2019 IPS Conservation Grant Competition

The Conservation Committee of IPS is once again soliciting applications for the IPS Primate Conservation Grant competition for 2019. We will award several grants of up to \$1,500 to support primate conservation programs in the field and are anticipating some great applications.

The deadline for submitting your application is March 1st, 2019. Please make sure to use the 2019 form. Applications must be submitted in English and we offer special advice and mentoring for those seeking English support for their application. Such applications have an earlier deadline (February 15th, 2019). For guidelines about the application process, please see the IPS website (<http://internationalprimatologicalsociety.org/conservation.cfm>) or contact Dr. Tatyana Humle (T.Humle@kent.ac.uk).

❖ The Galante Family Scholarship

In addition to the Conservation Grants, we are also accepting applications for the 2019 Galante Family Winery Primate Conservation Scholarship. Formerly known as the Martha J. Galante Award, this fund was set up to support primate conservation and the continuing education of primatologists. More details about this scholarship can be found on the IPS web site. Applications are solicited from primatologists of primate habitat countries. Up to \$2,500 will be awarded and is to be used for obtaining further conservation training. The deadline for applications is March 1st, 2019. (See: <http://internationalprimatologicalsociety.org/conservation.cfm>)

People interested in competing for this award should:

- be officially affiliated with an academic institution or a similar organization (either taking or giving courses or doing research or conservation work)
- provide information about the program of interest (courses, congresses, symposia, field work, etc.)
- include a letter of acceptance for the respective course
- send a letter explaining his/her interest in participating in the course or event (in English)
- send a C.V. in English
- provide two recommendation letters (including information about the referee).

Send all the above by email to Dr. Tatyana Humle (T.Humle@kent.ac.uk).

If you have any suggestions for the IPS Conservation Committee – including new ways to raise money for the Conservation Funds, please do not hesitate in contacting me!

Ad hoc committee to promote sharing of experience and good practice to continue to make capture safer for non-human primates

The ad hoc committee to promote sharing of experience and good practice to continue to make capture safer for non-human primates held a successful and productive workshop at IPS 2018. This committee will now be led by myself and co-chaired with Elena Cunningham and Steve Unwin. If you are interested in this topic, please do consult <http://www.internationalprimatologicalsociety.org/policy.cfm> or email me T.Humle@kent.ac.uk

Tatyana Humle, Ph.D.,

Vice President for Conservation,
T.Humle@kent.ac.uk

Report from Conservation Grant Recipient

Elena Bersacola

Seeking people-primate coexistence: primate community response to anthropogenic activities and land transformation in Guinea-Bissau, West Africa

Elena Bersacola

Human Interactions with and Constructions of the Environment, Oxford Brookes University, Oxford, UK

Email: hellenbers@gmail.com

Awarded an IPS Conservation Grant in 2015

Project summary

The natural landscape in Guinea-Bissau, West Africa, is characterised by a mosaic of forest fragments, mangroves, savannah, human settlements and agriculture. The south of Guinea-Bissau represents the country's most biologically diverse region, the westernmost limit of the geographical range of Critically Endangered West African chimpanzees (*Pan troglodytes verus*), and a key refuge for a significant population of Endangered Temminck's red colobus (*Piliocolobus temminckii*).

In collaboration with IBAP, the national institute in charge of protected areas, our project took place in a human-dominated protected area, namely Cantanhez National Park (NP). We aimed to 1) assess the effects of anthropogenic activities and land alteration on the distribution of primates, 2) find ways to enhance human-nonhuman primate coexistence in a shared landscape, and 3) help increasing local conservation management capacity.

Covering 1067 km², Cantanhez NP includes the country's remaining coastal sub-humid forests, as well as mangroves, savannah grassland and woodland. Approximately 30,000 people inhabit the park. The main causes of deforestation is the high demand of land for shifting agriculture and the increase in cash crop cashew plantations.

Plate 1

Research assistants Braima Vieira and Iaia Tawél Camará setting up arboreal camera traps



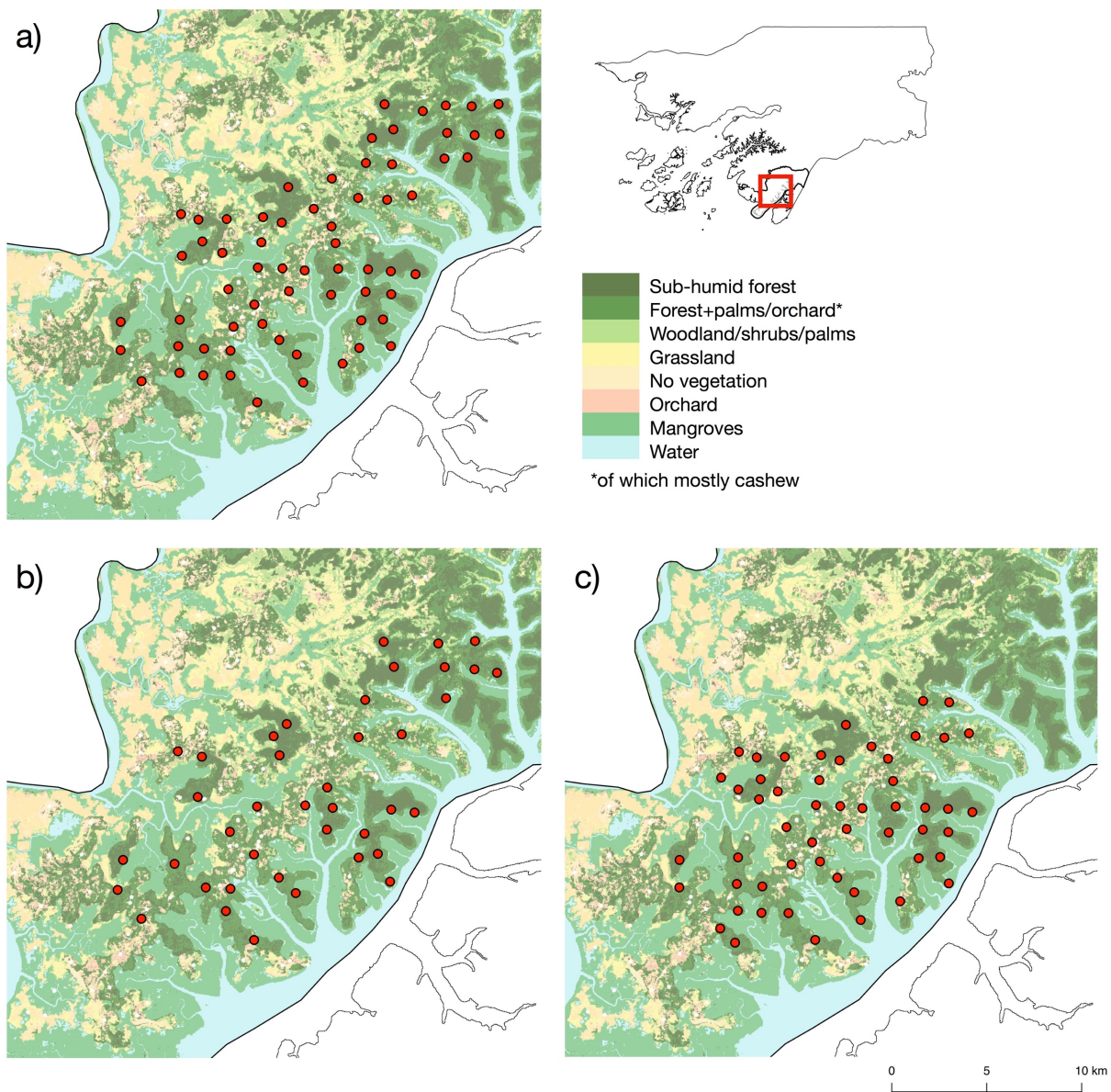
To model primate distributions, we deployed terrestrial and arboreal camera traps systematically across a 180 km² area (Figure 1, N camera trap sites = 65_{terrestrial}, 40_{arboreal}). We set up cameras in forest, savannah, mangrove and agricultural habitats, and used environmental and anthropogenic covariates as potential factors affecting primate occupancy and detection probabilities.

To set up arboreal cameras, one to two research assistants climbed using a doubled rope technique (DRT, Plate 1, above) or free climbed using the help of lianas and branches.

We also employed camera traps to explore chimpanzee perception of risk, monitoring one chimpanzee community living in a highly fragmented area for 12 months. We used participatory mapping and semi-structured interviews with local people to examine people's use of land and interactions with primates.

Figure 1

Sites of terrestrial (a) and arboreal (b) camera traps in the dry season (Nov – March), and terrestrial camera traps in the wet season (c, July – Oct) in Cantanhez National Park.



Preliminary results from the camera trap sampling period in the dry season (November 2016 – February 2017) showed that Campbell's monkeys were the most detected primate overall (N of independent events = 598_{terrestrial}, 267_{arboreal}), followed by chimpanzees (N = 221_{terrestrial}). In contrast, red colobus and king colobus' detection frequencies were low (N = 14_{arboreal} and 19_{arboreal}, respectively).

Occupancy models showed that during the dry season, chimpanzees were significantly more likely to occur near villages, therefore close to people. Baboons were considerably more likely to occupy sites in forest-dominated landscapes and closer to mangroves. Green monkeys and king colobus were also more likely to occupy sites closer to the mangroves. Occupancy of red colobus was affected by local vegetation structure (i.e. positively associated with tree density, species diversity and canopy cover).

The high occupancy of chimpanzees closer to villages was likely due to availability of orange and papaya fruit, which are typically grown in/around villages. Local people reported that during the survey period, chimpanzees were often seen in orchards feeding on oranges, as well as entering villages to take papaya fruit.

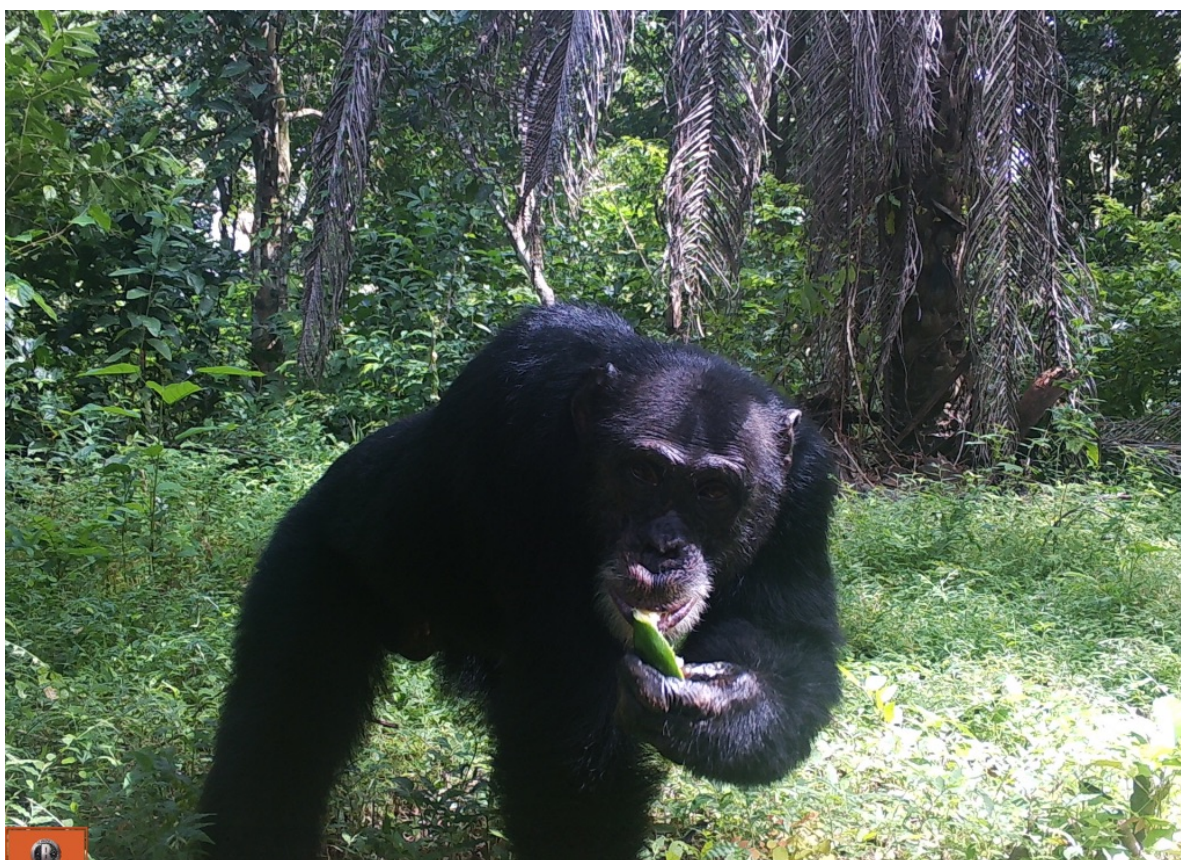


Plate 2

Chimpanzee feeding on orange in Caiquene village

Dry season primate occupancy patterns will be compared to the rainy season. Additionally, using one chimpanzee community as case study, we will explore the relationship between wild and cultivated food availability with intensity of patch use by chimpanzees at sites characterised by different levels of risk, including forest rarely used by people, forest frequently used by people, cultivated areas and villages.

Throughout the fieldwork period (October 2016 – July 2018), a total of 16 guides and guards were trained and gained first-hand experience in camera trap deployment and maintenance, as well as in conducting a habitat survey using vegetation plots. As requested by IBAP, we are currently in the process of finalising the methodology for a wildlife monitoring program to be implemented within the next two years. They

monitoring program will include systematic data collection carried out by the park guards using camera traps and vegetation plots. Therefore this project directly contributed to increasing conservation management capacity in Cantanhez NP. Data from this project will be used to develop conflict mitigation strategies, particularly during periods of high chimpanzee-human spatial overlap (e.g. orange season). Our occupancy data will be used to identify key primate areas, including forest corridors, to inform an updated land use plan which will be developed for Cantanhez NP within the next five years.

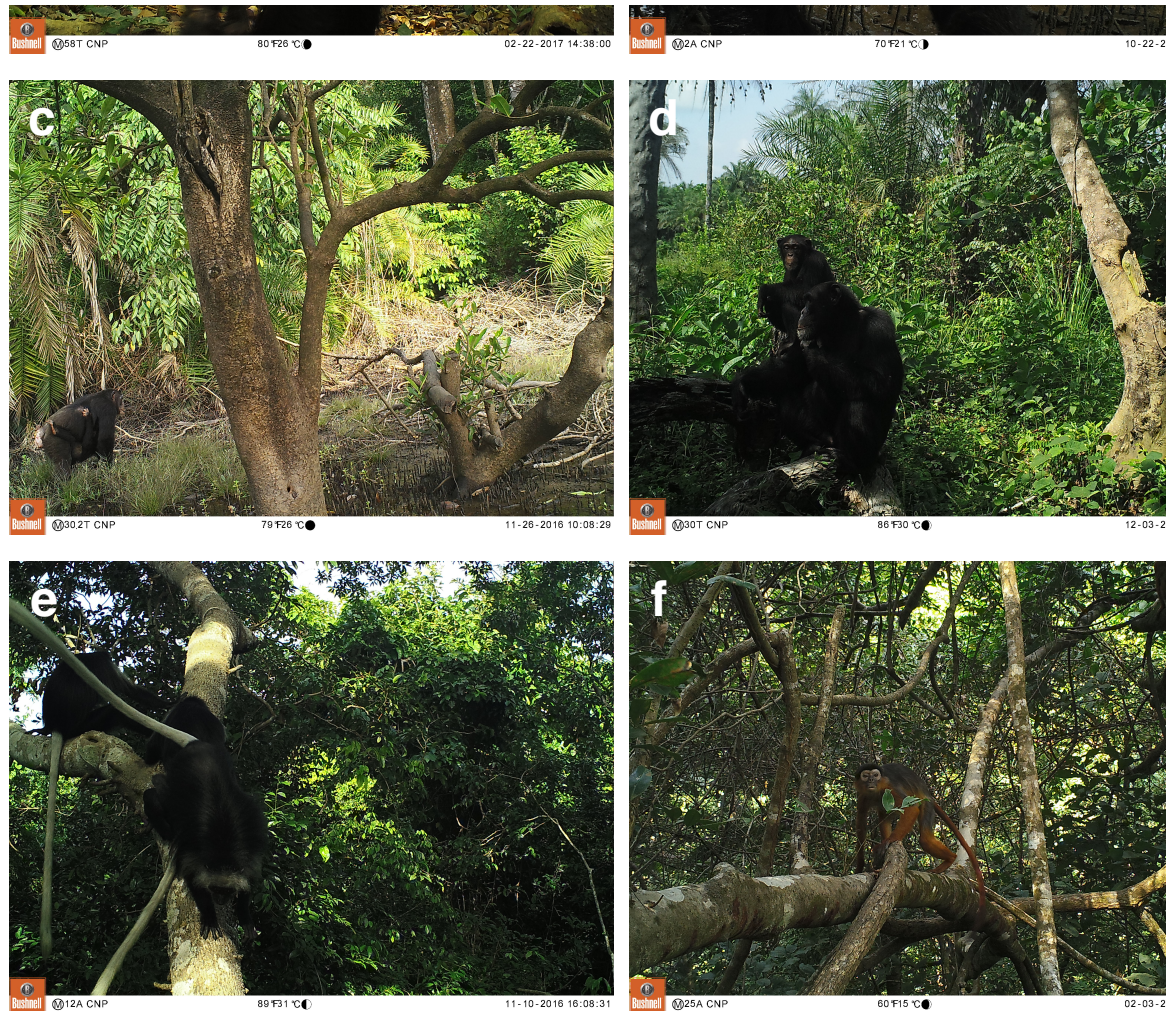


Plate 1 Selection of camera trap images from Cantanhez NP. Chimpanzees in forest (a), mangrove forest edge (b, c) and orchard (d). King colobus (e) and Temminck's red colobus (f) were detected in forest locations by arboreal camera traps.

Plate 3

Selection of camera trap images from terrestrial (a – d) and arboreal (e – f) camera traps showing chimpanzee in forest (a), mangrove (b – c) and orchard (d), king colobus (e) and Temminck's red colobus (f) in forest.

Report from Research Grant Recipient

Kelly van Leeuwen

Landscape-scale habitat use of chimpanzees at Issa Valley, Tanzania

Principal investigator: Kelly L. van Leeuwen^{1,2,3,4}
Supervisors: Amanda H. Korstjens^{1,2,3}, Ross A. Hill^{1,2}
Collaborators: Alex K. Piel^{4,5}, Fiona A. Stewart^{4,5,6}

¹*Department of Life and Environmental Sciences, Bournemouth University, Poole, UK;* ²*Landscape Ecology and Primatology (LEAP), Bournemouth University, Poole, UK;* ³*Institute for Studies on Landscape and Human Evolution (ISLHE), Bournemouth University, Poole, UK;* ⁴*Greater Mahale Ecosystem Research and Conservation, Box 108, Uvinza, Tanzania;* ⁵*School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK;* ⁶*Department of Archaeology and Anthropology, University of Cambridge, UK*

Introduction

Due to continued deforestation and climate change, primate habitat worldwide is changing rapidly, leading to increased fragmentation and altered climatic conditions of primate landscapes [e.g. Arroyo-Rodríguez and Mandujano 2009; Estrada et al. 2017]. It is therefore important to study primate habitat use at large spatial scales (i.e. primate “landscape use”, or “landscape-scale habitat use”) to determine primate responses to habitat alterations [e.g. Arroyo-Rodríguez and Fahrig 2014]. How an animal uses its landscape to forage most efficiently for food and water, and to find safe sleeping sites, determines how likely it is able to survive at any particular location [e.g. Deppe and Rotenberry 2008; Dunbar et al. 2009]. An animal’s landscape use is a hierarchical process where behavior is guided by internal physiological states; suitable habitats at a landscape scale are located accordingly for each behavior based on required and preferred micro-habitat characteristics [e.g. Deppe and Rotenberry 2008; Sutton et al. 2017]. This will vary by species, and for individuals within each species. Micro-habitat characteristics include a location’s micro-climate (e.g. temperature, luminosity) and structural vegetation features (e.g. tree height, tree and food tree density, canopy cover and connectivity, availability of food and water) [e.g. Deppe and Rotenberry 2008; Sutton et al. 2017]. Generally, landscapes are composed of different types of habitat, such as forest, woodland, savanna grassland, and swamp, and each of these vegetation types is expected to possess a distinct set of vegetation features and micro-climates [e.g. White 1983]. Theoretical understanding of a species’ habitat use at a landscape scale is required to predict how species will cope with future changes in their environments. Still, few studies use a landscape-wide approach to determine how small-scale variations in climate and vegetation affect the overall survival and distribution of species across a wider range of different landscapes [Arroyo-Rodríguez and Fahrig 2014]. It remains to be understood which vegetation features and micro-climates are most critical for primate survival and how flexibly primates may be able to adapt to various landscape conditions and different environmental change scenarios. Chimpanzees (*Pan troglodytes*) are often regarded as an adaptable primate species, as they have been shown to inhabit a wide range of different habitats across equatorial Africa: from closed-canopy, wet and evergreen rainforests (i.e. “forest chimpanzees”) to open, dry and mosaic savanna-woodland environments (i.e. “savanna chimpanzees”) [Hunt and McGrew 2002; Inskipp, 2005].

Within their environment, chimpanzees select specific types of vegetation for different behavioral activities and at different times of day based on micro-climate and vegetation characteristics. For example, they prefer specific nest locations based on tree species, tree height, and canopy cover [Koops et al. 2012], they sometimes rest in caves to find shelter from heat [Pruetz 2007], and they are more likely to find fruit in more densely forested patches [Hernandez-Aguilar 2009; Potts et al. 2016]. Hypotheses as to why chimpanzees prefer specific sites for their behavioral activities have mostly been studied with regards to nest building and include the thermoregulation hypothesis (i.e. the avoidance of overheating and/or undercooling) [e.g. Fruth and Hohmann 1996; Koops et al. 2012], the antipredation hypothesis (i.e. the protection from or avoidance

of predators) [e.g. Koops et al. 2012; Stewart and Pruetz 2013], the antivector hypothesis (i.e. the avoidance of disease vectors) [e.g. Koops et al. 2012; Samson et al. 2013], and the optimal foraging theory (i.e. the maximizing of energetic intake) [e.g. Pyke et al. 1977; Potts et al. 2016]. However, details on the micro-habitat characteristics of preferred vegetation types for chimpanzee activities are scarce and often descriptive. Considering that vegetation features and micro-climates are likely to be the first things to change due to anthropogenic influences [Arroyo-Rodríguez and Mandujano 2006; Riitters et al. 2016], it is important that more information is collected on the role these variables play in chimpanzee-habitat interactions.

Because studying the landscape-scale habitat use of primates is a multi-scaled and time-consuming process [Arroyo-Rodríguez et al. 2013], predictive modeling, such as individual-based modeling, provides an effective approach. Within individual-based models, individuals virtually interact with different environments based on rules from published literature on primate-habitat relationships [e.g. Dunbar 2002; Sellers et al. 2007]. Individual-based models on primate landscape use can, therefore, present a platform for examining current primate habitat use patterns across realistic, present-day environments, for exploring the extent of primate behavioral flexibility across different landscapes and key areas for primate conservation, and for predicting the effects of past and future landscape change scenarios and changes in overall resource abundance and distribution on primate behavior and survival [e.g. Jepsen et al. 2005; Ramos-Fernandez et al. 2006]. These findings could aid in planning effective mitigation strategies (e.g. reforestation) most efficiently to safeguard primate survival.

To date, relatively little is known about the behavior and ecology of chimpanzees living at the edge of their ecological niche in challenging savanna landscapes [e.g. Hunt and McGrew 2002; Russak 2014; Pruetz and Herzog 2017], even though they may form the key to understanding how chimpanzees will cope with increasing habitat fragmentation and climate change throughout their range [Hunt and McGrew 2002; Pruetz and Bertolani 2009]. As chimpanzee savanna landscapes are scarce and seasonal in their resource availability [McGrew et al. 1981; Moore 1996; Hunt and McGrew 2002] and are quantified to have only a minimal amount of forest cover and large, mosaic areas of more open woodland and savanna grassland [K.L. van Leeuwen, *unpublished data*], savanna chimpanzees in these already marginal habitats also deserve attention because they may be especially susceptible to further degradation of their environments. Therefore, this study explores savanna chimpanzee landscape use in Issa Valley, Tanzania (or Issa, for short) using an individual-based modeling approach based on literature and field-collected data. Specifically, it investigates **1)** the current landscape composition at Issa, **2)** the vegetation types, vegetation features, and micro-climates most important for Issa chimpanzees, and **3)** Issa chimpanzee activity budgets and daily path lengths for comparisons with forest chimpanzees elsewhere. It is hypothesized that **i)** savanna chimpanzees select sites with specific vegetation features and micro-climates for specific activities to optimize their predator avoidance, thermoregulation, and foraging efficiency (see Table 1 for predicted preferred locations); **ii)** although savanna chimpanzees are adapted to a mosaic environment, the presence of preferred vegetation features and micro-climates makes forest vegetation types most ideal for savanna chimpanzees, whereas more open woodland and savanna grassland are increasingly less ideal; **iii)** there is a wider range of structural vegetation features and micro-climates in woodland and savanna grassland vegetation types compared to forest vegetation types, and savanna chimpanzees limit their use of suboptimal woodland and savanna grassland in such a way so they do not experience conditions (e.g. temperature, canopy cover, luminosity, tree density) beyond those encountered in forests; and **iv)** in comparison to the landscape use of forest chimpanzees, during active daytime hours savanna chimpanzees spend more time traveling, feeding, and drinking, and travel longer daily distances due to the abundance and distribution of resources in savanna landscapes, and spend less time resting due to the differences in the amount of time available after performing their other daily activities.

Study site and species

The Issa study area is located in western Tanzania and lies approximately 81km east of Lake Tanganyika [Stewart 2011]. The vegetation of the 85km² core study area is mainly characterized by woodland and

other open vegetation types (i.e. swamp, savanna grassland, and rocky outcrops), and only ~7% of the area is classified as forest [Stewart 2011; *pers. comm.* A.K. Piel 13/6/2018]. Daily temperatures range between 11°C and 36°C [Russak 2014], and annual rainfall is ~1244mm [*pers. comm.* A.K. Piel 13/6/2018]. There is one dry season that lasts from May to October. Issa is inhabited by a community of semi-habituated chimpanzees of the eastern chimpanzee subspecies, *Pan troglodytes schweinfurthii* [Stewart 2011]. Based on genetic analyses from fecal samples, community size is estimated to be at least 67 individuals [Rudicell et al. 2011]. The exact home-range size of the community remains unknown but following unpublished data of the Greater Mahale Ecosystem Research and Conservation (GMERC) project, the study area for this research was set at 110 km²

Based on published Issa literature, with regards to *where* chimpanzees perform their daily activities, it is specified that most permanent water sources needed for drinking can be found in forest [Russak 2014]. Feeding, resting, travel and nesting activities are observed in forest and woodland [Hernandez-Aguilar 2009, Stewart 2011, Stewart and Pruetz 2013, Russak 2014], but forest is preferred for nesting [Stewart 2011, Stewart and Pruetz 2013]. Issa chimpanzees use specific tree species for feeding and nesting, and nest in trees with a height between 2 – 53m, a DBH between 3.0 – 199.5cm, an LBH between 0 – 20m, a crown width between 2 – 30m, a crown height between 1 – 37m, a leaf cover between 20 – 95%, a canopy cover between 5 – 100%, and a canopy connectivity between 0 – 100% [Stewart 2011, Hernandez-Aguilar et al. 2013, Russak 2013]. Nesting locations are preferably in close proximity to food sources and are more likely to be found on slopes as compared to flat terrain [Hernandez-Aguilar 2009, Stewart 2011].

Table 1. Predicted vegetation features and micro-climate characteristics of preferred locations for chimpanzee behaviors for hypothesis i.

Activity	Predicted vegetation features and micro-climates of preferred locations
<i>Hypothesis ia)</i> Nesting	Tall trees, closed canopies, high tree densities, high canopy connectivity, and high availability of food and water.
<i>Hypothesis ib)</i> Feeding	High amounts of food present, high tree densities, lower mean daily temperatures, and lower luminosity.
<i>Hypothesis ic)</i> Resting	Lower mean daily temperatures, lower luminosity, tall trees, closed canopies, high tree densities, high canopy connectivity, and high availability of food and water.
<i>Hypothesis id)</i> Drinking	High amounts of water present, lower mean daily temperatures, and lower luminosity.
<i>Hypothesis ie)</i> Travel	Tall trees, closed canopies, high tree densities, high canopy connectivity, lower mean daily temperatures, lower luminosity, and low understory densities.

Pre-existing GMERC data

GMERC has long-term data on Issa chimpanzee behavior and landscapes gathered through chimpanzee follows, reconnaissance walks, and fauna transects [*pers. comm.* A.K. Piel 24/02/17]. GMERC furthermore created a Geographical Information System (GIS) database of the Issa study area and its surroundings which comprises information on all long-term data, land cover (created by C. Johnson and referred to as the GMERC GIS vegetation map), and regional landmarks [*pers. comm.* A.K. Piel 13/6/2018], and has access to a HOBO weather station for climatic measurements. *Chimpanzee follows (2014 – 2016)*: Chimpanzee follows were conducted 15-20 days/month with the goal of fully habituating Issa chimpanzees. Research teams collected various data on chimpanzee behavioral ecology, including behavior and habitat. *Fauna transects (2014 – 2016)*: Data from seven fauna transects were used to evaluate the presence and distribution of mammals across the Issa landscape. Fauna transects traversed the study area across different vegetation types and were monitored every two months. Whenever direct or indirect evidence of chimpanzees was observed (e.g. encounters, nests, feces, footprints, feeding remains), various details were noted, including behavior¹³

and habitat. *Reconnaissance walks (2014 – 2016)*: Evidence on the presence of chimpanzees and other mammals was additionally collected during reconnaissance walks. Reconnaissance walks were conducted on a regular basis and spanned the entire GMERC study area. For all direct and indirect evidence of chimpanzees encountered, a variety of data were recorded, including habitat and behavior. *HOBOWEATHER station (May – July 2017)*: The HOBOWEATHER station, located 1.5km from the Issa camp, measured temperature (°C) and rainfall (mm) at one-hour intervals.

Methods

Field data collection and analyses

This study collected data on the structural vegetation and micro-climatic aspects of the Issa landscape using vegetation plots and micro-climate data loggers (May – July 2017). *Vegetation plots*: Twenty-four 25m x 25m plots were set up in a stratified random way throughout the Issa study area for the assessment of the vegetation structure of different vegetation types (i.e. forest, woodland, swamp, and savanna grassland). In total, 6 plots were set up in each vegetation type. For each plot, measurements were taken on total number of trees (DBH > 10cm), total number of (chimpanzee) feeding trees (DBH > 10cm), altitude, slope, canopy cover (%), canopy connectivity (%), presence of understory species (%), presence of bare land (%), presence of grass (%), presence of (chimpanzee) food. For each tree (DBH > 10cm) within a plot, measurements were taken on tree species, height (m), DBH (cm), LBH (m), crown width (m), crown height (m), crown connectivity (%), crown cover (%), and amount of (chimpanzee) foods present (%). *Micro-climate data loggers*: Thirty-six micro-climate data loggers were set up within the vegetation plots to investigate the differences in micro-climates between different vegetation types. Data loggers were set up in trees in the center of three randomly selected vegetation plots per vegetation type. Three data loggers were installed per tree at various heights. All data loggers collected data for 50 subsequent days. Data loggers were equipped with HOBOWEATHER software and measured the local temperature (°C) and luminosity (Lux) at every hour. For analyses, measurements of the structural aspects of different vegetation types were taken together to produce an overview of the ranges of vegetation features present in each type of land cover. Micro-climate data logger data were used to highlight the range of average daily and nightly temperatures (°C) and light intensities (Lux) within each vegetation type.

GMERC data analyses

Data from chimpanzee follows, fauna transects and reconnaissance walks were taken together to present the frequency of chimpanzee encounters and observed behaviors in each vegetation type. Overall and behavioral preferences for specific vegetation types were assessed using chi-square goodness of fit tests with the significance level α set at 0.05 (IBM SPSS Statistics, version 22). As chi-square tests cannot be performed when the observed frequency of a specified category equals 0, observed frequencies for all categories (i.e. vegetation types) were rounded up to a minimal frequency of 1 to produce reliable output. Data from the HOBOWEATHER station were summarized to present average daily and nightly temperatures (°C) and rainfall (mm). With respect to chimpanzee nesting times [e.g. Matsumoto-Oda 2002], daytime hours were considered between 8am – 7pm and nighttime hours between 8pm – 7am. The GMERC GIS vegetation map was converted to a grid with 50m x 50m cells adopting the majority vegetation type in each cell. For the individual-based model, this grid map was imported as a layer of 50m x 50m patches within NetLogo (version 5.2.1; Willensky 1999) to determine the percentage of cover for each vegetation type.

Model building

Findings on Issa chimpanzee behavior and habitat were used to set out specific ‘rules’ for the individual-based model on savanna chimpanzee landscape use in Issa. The individual-based model (referred to as the Issa model) was developed with NetLogo. Based on the GMERC GIS vegetation map and the HOBOWEATHER station climate data, the simulated model environment mirrors the present-day conditions on vegetation cover, spatial vegetation arrangement, home-range size, and climate at Issa. Five types of land cover are simulated: forest, woodland, savanna grassland, swamp and rocky outcrop. Based on data from vegetation plots and micro-climate data loggers, each vegetation type is assigned a specific set of features: tree height, tree density, food tree density, canopy cover, canopy connectivity, understory density, food availability,¹⁴

water availability, local temperature day, local temperature night, local luminosity day, and local luminosity night. Within the virtual Issa environment, a population of 67 chimpanzees is parameterized to perform five key daily activities: feeding, drinking, nesting, resting (incl. social time) and travel. Based on literature and GMERC data, behavioral rules highlight that these activities can only be performed at suitable times of day and at locations with suitable vegetation features and micro-climates. With the model's basic assumption being that chimpanzee activity selection is driven by the primary goal of maintaining homeostasis, simulated individuals gain and lose energy (kCal), hydration (unitless measure) and fatigue (unitless measure) throughout the model run by performing different behaviors and simply by existing. The Issa model runs over the course of 24 hours, i.e. from 7am to 7am, and produces collective output on the activity budgets, energy budgets, daily path lengths, food intake, water intake, hydration budgets, fatigue budgets, vegetation type usage, and site selection for chimpanzees at Issa.

Model output and analyses

The Issa model was run 30 times to present reliable output on Issa chimpanzee landscape use [e.g. Crawley 2011], with each run differing slightly in the initial geographical placement of individuals and the random allocation of micro-habitat characteristics of each patch with respect to the assigned vegetation type. Model output on Issa chimpanzees' time spent on different activities and in different vegetation types, energy, hydration, fatigue, food intake, water intake, site selection and daily path length was averaged across 30 runs and histograms were produced for visual assessments. Values are presented as mean \pm standard deviation. Range tables with minima, maxima and means were presented to assess site selection. Model output was tested for vegetation type preferences using chi-square goodness of fit tests ($\alpha = 0.05$). As explained above, observed frequencies had to be rounded up to a minimal frequency of 1 for each category (i.e. vegetation types) to produce reliable output. Additionally, if expected values for a category fell below 5, observed frequencies for each category were multiplied by 100, 1000, or 10000, as appropriate, to not violate this chi-square test assumption.

Results

Field-collected data

Averages and ranges for the vegetation features and micro-climates of forest, swamp, grassland and woodland measured through vegetation plots and micro-climate data loggers are outlined in Table 2.

GMERC data

A total of 8686 behaviors were observed in the Issa core study area (85km²) during 2320 direct and 2815 indirect chimpanzee encounters (2014 – 2016). Of these, 3766 were observed in forest, 4724 in woodland, 9 in swamp, and 0 in grassland. For 187 behaviors, no vegetation type was recorded. Of the behaviors, 1014 were attributed to feeding, 3806 to resting, 2651 to nesting, and 1028 to travel. Without controlling for survey effort, relative to vegetation type presence at Issa, forest is preferred overall ($\chi^2 = 105652.0$, $df = 2$, $p < 0.001$), and for each behavior separately (feeding: $\chi^2 = 17965.3$, $df = 2$, $p < 0.001$; resting: $\chi^2 = 59762.1$, $df = 2$, $p < 0.001$; nesting: $\chi^2 = 18597.2$, $df = 2$, $p < 0.001$; travel: $\chi^2 = 12575.5$, $df = 2$, $p < 0.001$). HOBO weather station climate data showed that Issa daytime temperatures had a mean of $23.3 \pm 2.3^\circ\text{C}$, and nighttime temperatures averaged $18.4 \pm 1.2^\circ\text{C}$ between May and July 2017. There was no rainfall for this period. The Issa study area (110km²) contained 2.8% forest, 87.6% woodland, 0.1% savanna grassland, 5.4% swamp, and 4.1% rocky outcrops.

Table 2. Averages and ranges of vegetation features and micro-climates measured through vegetation plots (25m x 25m) and micro-climate data loggers in forest, woodland, swamp, and savanna grassland.

	Forest			Woodland			Swamp			Savanna Grassland		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Plot data												
# trees (>10cm DHH)	32	18	43	15.2	12	19	6.2	0	25	7.8	1	21
# feeding trees (>10cm DBH)	11.5	1	21	7.2	5	11	3.8	0	20	0.5	0	2
% feeding trees (>10cm DBH)	36	5.6	75	47	35.7	69.2	62	0	100	6	0	40
% feeding trees (>10cm DBH) bearing fruit	4.0	0	23.8	27.9	0	54.5	4.2	0	25	8.3	0	50
Altitude (m)	1516	1364	1619	1488	1249	1635	1641	1603	1690	1216	1150	1255
Slope*	-	-	-	-	-	-	-	-	-	-	-	-
Canopy cover (%)**	-	51	100	-	1	75	-	0	50	-	1	50
Canopy connectivity (%)**	-	26	100	-	1	75	-	0	50	-	0	25
Understory (%)**	-	51	100	-	1	75	-	0	50	-	1	25
Grass (%)**	-	0	0	-	26	75	-	26	100	-	75	100
Bare land (%)**	-	76	100	-	26	50	-	0	50	-	0	25
THV (%)**	-	0	0	-	0	0	-	0	25	-	0	0
Water (%)	2.5	0	5	0	0	0	0	0	0	0	0	0
Ant nests (#)	0.5	0	2	0	0	0	0	0	0	0	0	0
Termite mounts (#)	0	0	0	0.5	0	3	0	0	0	0		0
Chimp evidence (#)	0	0	0	0	0	0	0	0	0	0	0	0
Plot tree data (trees > 10cm DBH)												
Species***	-	-	-	-	-	-	-	-	-	-	-	-
Tree DBH (cm)	21.5	10	81	21.2	10.1	69.7	23.1	10.5	71.9	28.1	10	163.3
Tree LBH (m)	4.2	0	18.5	2.8	0	8.3	1.3	0	3.2	1.4	0	5.8
Tree height (m)	11.8	1.5	29.5	8.8	2.6	18.5	5.8	2.3	11.6	7.5	1.7	24.6
Crown width N (m)	2.2	0	13.6	2.2	0	7.9	1.9	0	5.3	2.9	0	12.4
Crown width S (m)	2.8	0	13.5	2.1	0	7	1.9	0	5.5	3.2	0	9.8
Crown width E (m)	2.1	0	7.7	1.7	0	7.2	1.9	0	5.5	2.7	0	8.5
Crown width W (m)	2.5	0	16.9	2.2	0	12.6	1.8	0	6.2	2.8	0	10.2
Crown height (m)	7.6	0.5	22.7	5.9	0	14.5	4.5	1.3	9.3	6.2	0.9	19.3
Crown connectivity (%)**	-	0	100	-	0	100	-	0	100	-	0	75
Crown cover (%)**	-	0	100	-	0	100	-	1	100	-	0	100
Tree ripe chimp food coverage (%)**	-	0	25	-	0	50	-	0	25	-	0	25
Micro-climates												
Temperature day (average, °C)	23.3	22.3	24.4	26.6	23.9	29	25.8	23.8	28.9	29.8	28.5	31.7

Temperature night (average, °C)	18.5	16/8	20.1	18.6	16.7	20.4	15.7	14.8	16.2	21.1	20.7	21.8
Luminosity day (average, Lux)	3767	1012	8113	14440	6854	39578	19454	13059	29192	21968	10092	44272
Luminosity night (average, Lux)	3	0	9	8	3	18	30	11	76	23	10	50

*For forest, slopes were either flat or steep, for woodland slopes ranged from flat to steep, for swamp slopes were flat, and for grassland slopes ranged from flat to mild; **For canopy cover, canopy connectivity, understory, grass, bare land, THV, crown connectivity, crown cover, and tree ripe chimp food coverage, no average can be presented as these variables were measured in categories (0 = 0%, 1: 1 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, 4 = 76 – 100%); ***Various tree species are observed, for forest, woodland, swamp, and savanna grassland.

Model rules based on results from literature, GMERC and field-collected data

Literature and field-collected data were used to set out specific rules for the Issa model on savanna chimpanzee landscape use. For modeling purposes, based on reviews from chimpanzee experts [Koops 2017, Pascual-Garrido 2017, Reynolds 2017] and landscape-scale studies [e.g. Isabirye-Basuta and Lwanga 2008, Arroyo-Rodríguez and Mandujano 2009], important landscape-scale features for each chimpanzee activity are outlined in Table 3. The Issa environment was simulated to represent the exact vegetation cover, spatial vegetation arrangement and climate of the Issa landscape as highlighted by the GMERC GIS vegetation map and the HOBO weather station data. Values for vegetation features and micro-climates per model patch (50m x 50m) were selected randomly within the specified range of Table 2 with regards to the respective vegetation type and patch size. No field measurements were taken to assess the vegetation features and micro-climates of rocky outcrops, but this land cover type is included within the Issa model. Based on personal observations [K.L. van Leeuwen, May – July 2017], however, rocky outcrops were assumed to contain no vegetation and to have similar micro-climates to savanna grassland. Model rules for *where* Issa chimpanzees should perform their daily feeding, drinking, nesting, and resting activities were specified as follows: Issa chimpanzees select nesting and resting locations with tree heights between 2 – 29.5m, with a canopy cover between 5 – 100%, and a canopy connectivity between 0 – 100%. Feeding, resting and nesting locations should contain enough food to feed, and drinking locations should have enough water to drink. As no empirical data is available on the ranges of the other important micro-habitat characteristics used by Issa chimpanzees, the finding that forest is the preferred vegetation type provided a solution: ranges for each of the important vegetation features and micro-climates should fall within the ranges found in forest. Although this initially seems to restrict individuals to only use forest vegetation types, the selected ranges of vegetation features and micro-climates also exist in other vegetation types such as woodland (Table 2). As travel is directed towards a suitable location for the selected activity, no restrictions were set as to where Issa chimpanzees can travel. With regards to *when* chimpanzees perform their daily activities, and *how much* energy, hydration and fatigue is gained and lost, no data is available for Issa. For the Issa model, therefore, these data had to be estimated based on findings from other studies or general knowledge-based assumptions [K.L. van Leeuwen, *unpublished data*].

Table 3. Important landscape-scale vegetation features and micro-climates for chimpanzee activities used for the Issa model, based on findings from expert-based reviews [e.g. Koops 2017] and landscape-scale studies [e.g. Isabirye-Basuta and Lwanga 2008].

	Feeding	Drinking	Nesting	Resting
Important, landscape-scale vegetation features and micro-climate characteristics for chimpanzee activities for the Issa model.	Food availability Food tree density Tree height Tree density Local temperature Local	Water availability Local temperature Local luminosity	Tree height Canopy cover Canopy connectivity Tree density Food availability Understory density Food tree density	Local temperature Local luminosity Tree height Canopy cover Canopy connectivity Understory density Tree density Food tree density

	luminosity		Water availability Local temperature Local luminosity	Food availability Water availability
--	------------	--	---	---

Model output

Over the course of 24 hours, modeled Issa chimpanzees spent, on average, $12.8 \pm 9.3\%$ of their time feeding, $1.2 \pm 1.0\%$ drinking, $11.2 \pm 8.9\%$ resting, $48.9 \pm 2.1\%$ nesting, and $25.9 \pm 15.1\%$ traveling (Figure 1). Simulated Issa chimpanzees traveled $7.1 \pm 5.6\text{km}$ per day, had a daily food intake of 64.6 ± 46.7 food items, a daily water intake of 87.6 ± 72.5 hydrations, an energy budget of $-577.0 \pm 516.4\text{kCal}$, a hydration budget of -155.2 ± 152.1 hydrations, and a fatigue budget of 79.9 ± 110.6 fatigues (Figure 2 and 3). On average, modeled Issa chimpanzees spent $59.0 \pm 37.8\%$ of their 24-hour time in forest, $39.2 \pm 36.8\%$ in woodland, $0.0 \pm 0.2\%$ in savanna grassland, $1.0 \pm 2.6\%$ in swamp, and $0.8 \pm 2.6\%$ in rocky outcrops (Figure 4). When controlling for vegetation type availability, forest was the preferred vegetation type for Issa chimpanzees ($\chi^2 = 167354.3$, $df = 4$, $p < 0.001$).

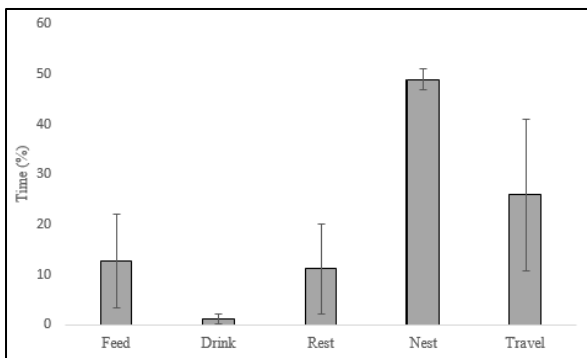


Figure 1. Model output for Issa chimpanzee activity budgets.

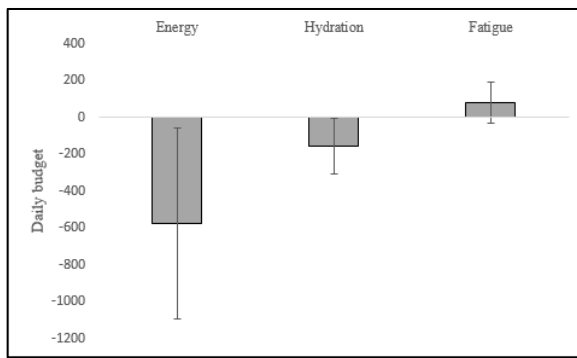


Figure 2. Model output for Issa chimpanzee energy, hydration, fatigue.

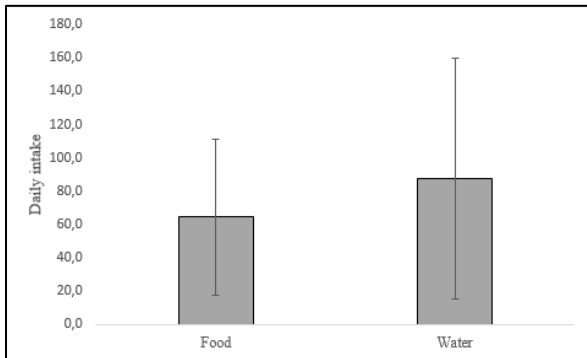


Figure 3. Model output for Issa chimpanzee food and water intake.

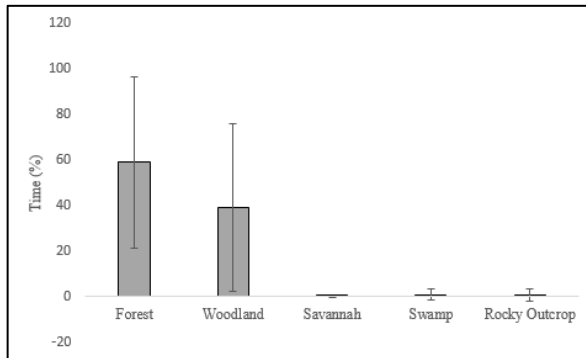


Figure 4. Model output for Issa chimpanzee vegetation type usage.

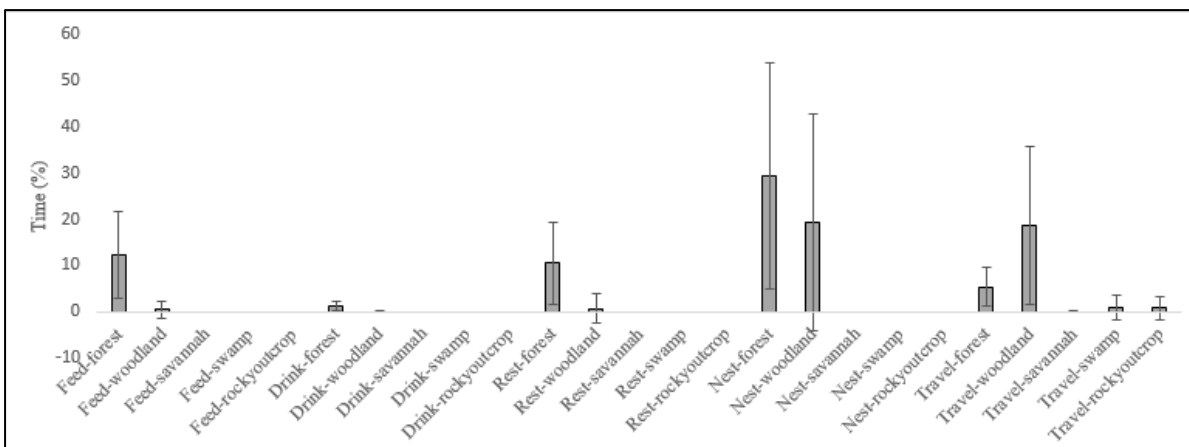


Figure 5. Model output for Issa chimpanzee behavioral vegetation type usage.

When breaking down their total time to time spent on different activities in different vegetation types, modeled Issa chimpanzees spent $12.3 \pm 9.5\%$ feeding in forest and $0.5 \pm 1.9\%$ feeding in woodland, $1.2 \pm 1.0\%$ drinking in forest, $0.0 \pm 0.1\%$ drinking in woodland, $10.5 \pm 8.9\%$ resting in forest, $0.7 \pm 3.1\%$ resting in woodland, $29.5 \pm 24.4\%$ nesting in forest, and $19.4 \pm 23.4\%$ nesting in woodland (Figure 5). Chimpanzees in the Issa model never used swamp, savanna grassland, and rocky outcrops for nesting, resting, feeding and drinking (Figure 5). Simulated Issa chimpanzees spent $5.4 \pm 4.2\%$ of their total time traveling in forest, $18.7 \pm 17.0\%$ traveling in woodland, $0.0 \pm 0.2\%$ traveling in grassland, $1.0 \pm 2.6\%$ traveling in swamp, and $0.8 \pm 2.6\%$ traveling in rocky outcrops (Figure 5). Relative to vegetation type presence, modeled Issa chimpanzees preferred forest vegetation types for all behaviors, whereas woodland, savanna grassland, swamp and rocky outcrops were avoided (feeding: $\chi^2 = 589622.3$, $df = 4$, $p < 0.001$; drinking: $\chi^2 = 589996.1$, $df = 4$, $p < 0.001$; resting: $\chi^2 = 496370.1$, $df = 4$, $p < 0.001$; nesting: $\chi^2 = 858499.5$, $df = 4$, $p < 0.001$; travel: $\chi^2 = 45181.3$, $df = 4$, $p < 0.001$).

Following Issa model rules, it was shown that modeled Issa chimpanzees used the total range of micro-habitats available to them for traveling but were more selective in their site selection for feeding, drinking, nesting and resting, and predominantly used locations where the vegetation features and micro-climates were similar to those found in forest (Table 2). This, however, did not restrict them to use only forest vegetation types, and woodland was also exploited. Overall, modeled Issa chimpanzees selected locations (i.e. patches) with tree heights between 0 – 29.5m, canopy covers, canopy connectivities and understory densities between 0 – 100%, tree densities between 0 – 172 trees, food tree densities between 0 – 62 food trees, food availabilities between 0 – 69.8 fruits, water availabilities between 0 – 100 hydrations, temperatures at night between 14.8 – 21.8°C, temperatures during daytime between 22.3 – 31.7°C, luminosities at night between 0 – 76 Lux, and luminosities at daytime between 1012 – 44272 Lux for their daily activities (Table 4). Further analyses will explore whether behavioral site selection is mainly restricted to certain conditions within this range.

Table 4. Model output on the range of vegetation features and micro-climates used by Issa chimpanzees for performing their daily activities: **a.** ranges for tree height, canopy cover, canopy connectivity and understory

a.		Tree height (m)			Canopy cover (%)			Canopy connectivity (%)			Understory density (%)		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Issa	Feeding	1.5	15.4	29.5	1	74.1	100	1	62	100	0	49.5	100
	Drinking	1.5	15.4	29.5	1	74.8	100	1	62.2	100	0	50.6	100
	Nesting	2	13.8	29.5	5	61.6	100	1	52.9	100	0	45	100
	Resting	2	15.4	29.5	5	73.6	100	1	61.8	100	0	49	100
	Travel	0	11.1	29.5	0	44.3	100	0	41.7	100	0	39.8	100

density, **b.** ranges for tree density, food tree density, food availability and water availability, and **c.** ranges for temperature and luminosity at nighttime and daytime.

b.		Tree density (#)			Food tree density (#)			Number fruit (#)			Amount water (#)		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Issa	Feeding	72	126.4	172	25.9	45.8	61.9	3.5	10.8	69.8	0	48.8	100
	Drinking	48	123.8	172	22.6	44.7	61.9	0	8.6	69.8	50	74.2	100
	Nesting	72	105.1	172	25.9	41.1	61.9	3.5	33.1	69.8	50	69.5	100
	Resting	72	124.3	172	25.9	45.2	61.9	3.5	13.3	69.8	50	74	100
	Travel	0	72.4	172	0	31.5	62	0	42	69.8	0	38	100

c.		Temperature night (°C)			Temperature day (°C)			Luminosity night (Lux)			Luminosity day (Lux)		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Issa	Feeding	16.7	18.5	20.3	22.3	23.4	24.4	0	4.7	18	1012	4732	8113
	Drinking	16.8	18.5	20.3	22.3	23.4	24.4	0	4.6	18	1014	4682	8113
	Nesting	16.8	18.4	20.1	22.3	24.5	29	0	5.1	9	1014	11942	39520
	Resting	16.8	18.5	20.2	22.3	23.4	24.4	0	4.8	18	1012	4673	8110
	Travel	14.8	18.5	21.8	22.3	25.9	31.7	0	11	76	1012	19345	44272

Discussion

This study aimed to explore the landscape-scale patterns of savanna chimpanzee habitat use in Issa Valley, Tanzania, in order to present a realistic picture of the behavior and ecology of chimpanzees living at the edge of their ecological niche in challenging savanna landscapes, and to assess how flexibly chimpanzees are able to cope with increasing habitat fragmentation and climate change throughout their range. As relatively little is still known about savanna chimpanzees, this study provided a first attempt to characterize savanna chimpanzee daily landscape use using an individual-based modeling approach based on literature review and field-collected data from Issa. Specifically, it investigated **1)** the current landscape composition at Issa, **2)** the vegetation types and micro-habitats most important for Issa chimpanzees in performing their daily activities, and **3)** Issa chimpanzee activity budgets and daily path lengths for comparisons with forest chimpanzees elsewhere. Within marginal savanna landscapes, following hypothesis ii, model output showed that forest is the preferred vegetation type for simulated Issa chimpanzees and that woodland and other more open vegetation types are increasingly less ideal due to the micro-habitats present. Additionally, hypothesis iii that savanna chimpanzees at Issa would limit their usage of woodland and other open vegetation types to locations with vegetation features and micro-climates similar to those encountered in forests, was supported by the Issa model. As model output showed that simulated Issa chimpanzees selected locations for different behavioral activities with a wide range of vegetation features and micro-climates which partly follow from Issa model rules, it is difficult to currently identify exact behavioral preferences and support hypothesis i. Following Stewart [2011], however, preferred vegetation features for nest building behavior at Issa can, in part, be attributed to the thermoregulation hypothesis, the anti-predation hypothesis and anti-vector hypothesis.

When comparing the findings of the Issa model to published data on savanna chimpanzees at other sites, it can be shown that the Issa model correctly predicts patterns of savanna chimpanzee landscape use. Findings from the Issa model are largely in agreement with current literature. For example, time spend feeding for modeled Issa chimpanzees is similar to observed patterns of feeding time for chimpanzees at Fongoli, a

savanna chimpanzee site in Senegal [Pruetz and Bertolani 2009; Pruetz and Herzog 2017]. Similarly, Wessling et al. [2018a; 2018b] showed that Fongoli chimpanzees experienced extensive periods of dehydration stress, which supports the negative hydration budgets presented for Issa chimpanzees. Savanna chimpanzee literature also highlights that forest, woodland, and to some extent, more open vegetation types were used for feeding [e.g. Schoeninger et al. 1999] and nesting [e.g. Baldwin et al. 1981; Stewart 2011], and that forest vegetation types are preferred for nesting [e.g. Stewart 2011]. The Issa model is the first to quantify savanna chimpanzee food and water intake, fatigue budgets and daily path lengths. It is generally assumed that chimpanzees in savanna environments travel further to acquire their necessary resources due to the great resource seasonality and distribution in savannas [e.g. Moore 1996; Hunt and McGrew 2002]. Therefore, the long daily path lengths reported by the Issa model support this assumption.

Some incongruences between Issa model output and published savanna chimpanzee literature are, however, also observed. Fongoli chimpanzees, for example, spend more time resting, less time traveling and have more neutral energy budgets than simulated Issa chimpanzees [Pruetz and Bertolani 2009; Pruetz and Herzog 2017; Wessling et al. 2018a; Wessling et al. 2018b]. These divergences may be attributable to current model limitations or more extreme climatic conditions at Fongoli [Pruetz and Bertolani 2009], forcing the chimpanzees to rest more and travel less, but are equally likely to result from additional behaviors observed at savanna sites. For instance, chimpanzees at Fongoli uniquely hunt with spears to gain access to prey [Pruetz and Bertolani 2007], use caves or soak in pools of water at the hottest times of day for thermoregulation [Pruetz 2007; Pruetz and Bertolani 2009], and include novel items into their diet such as unripe fruit [Wessling et al. 2018a]. Chimpanzees at Semliki, a savanna environment in Uganda, dig wells for drinking water [Hunt and McGrew 2002]. For Issa, Hernandez-Aguilar [2009] noted that chimpanzees include underground storage organs in their diet. As quantitative data remains limited, these behaviors are not currently included within the Issa model. For future purposes, however, these unique behaviors should be kept in mind, as these could alter the internal states, and, therefore, the decision-making process, of modeled individuals.

Findings from the Issa model can additionally be compared to published data on the activity budgets and daily path lengths of forest chimpanzees. This information can be used to assess how behavioral patterns respond to landscapes. Across study sites, forest chimpanzees spent, on average, 37.3% (range: 22 – 54%) of their active day on feeding, 44.6% (range: 22 – 70%) on resting, and 18.5% (range: 8 – 32%) on travel, and travel about 3.0km (range: 1.2 – 6.2km) per day [Bates and Byrne 2009; Doran 1997; Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2004; N'guessan et al. 2009; Pontzer and Wrangham 2004; Potts et al. 2011; Matsumoto-Oda 2002; Goodall 1986; Matsuzawa et al. 2011; Yamanashi and Hayashi 2011]. Time spent nesting and drinking is not outlined for forest chimpanzees. When including only the active day range (i.e. 12 hours), simulated Issa chimpanzees spent 25.6% of time feeding, 22.4% resting, and 51.8% traveling, and move 7.1km per day. These findings support, in part, hypothesis iv that, in comparison to forest chimpanzees, during active daytime hours savanna chimpanzees spend more time traveling, feeding, and drinking, and travel longer daily distances due to the abundance and distribution of resources in savanna landscapes, and spend less time resting due to the differences in the amount of time available after performing their other daily activities. Whereas the daily path lengths and time spent traveling and resting for Issa chimpanzees are thus in agreement with this hypothesis, the decreased feeding time of simulated Issa chimpanzees may be due to the large time investment necessary for travel (i.e. for finding the required resources) and the consequent 'enforced' resting time [e.g. Korstjens et al. 2010]. Even though energy budgets, fatigue budgets, hydration budgets, food intake and water intake are not generally specified for chimpanzees in forested environments, some studies specify that periods of nutritional and dehydration stress are common [N'guessan et al. 2009; Wessling et al. 2018b], which supports the findings of the Issa model. For forest chimpanzees, literature has furthermore outlined that they use all vegetation types available to them, but prefer forest [e.g. Morgan et al. 2006, Carvalho et al. 2015], which supports the forest preference found for modeled Issa chimpanzees.

All in all, when combining the Issa model output with evidence from savanna chimpanzee field sites and comparing these pooled savanna data to chimpanzees in forest environments, it can be concluded that, when environments differ along an environmental gradient from forests to more open and mosaic savannas, chimpanzees spend increasingly less time feeding and resting, spend increasingly more time traveling,²¹

travel further, have low energy budgets, hydration budgets, food intake and water intake, have high levels of fatigue, and rely on forest vegetation. This argues in favor of remarkable chimpanzee behavioral adaptability. Chimpanzees are able to adapt their activity budgets, daily path lengths and preferred vegetation to suit their current landscape, with energy, hydration and fatigue budgets, and food and water intake following accordingly, even when their new environments are marginal savannas. Patterns of adaptation shown by savanna chimpanzees are largely similar to other primates' responses to habitat fragmentation, which include increases in travel time and distance, decreases in resting time, and increases in feeding time [e.g. Clarke et al. 2002; Asensio et al. 2007]. Regardless of the extent of chimpanzee behavioral adaptability, however, with rapidly declining primate habitat worldwide, chimpanzees continue to face critical survival challenges, and savanna chimpanzees may be especially susceptible as they already inhabit challenging landscapes. Appropriate mitigation plans should therefore be developed to safeguard savanna chimpanzees. As the Issa model showed that savanna chimpanzees are reliant on forest vegetation types, forest can be regarded as their critical habitat. Protecting forest vegetation types within savanna chimpanzee habitats should therefore present a priority area for chimpanzee conservation. However, as the availability of forest vegetation types within savanna landscapes is already limited, conservation efforts should also include a focus on protecting those parts of the environment with micro-habitats comparable to forest, and thus those with optimal resource availability.

The Issa chimpanzee landscape use model provides important implications for future research and conservation efforts. The Issa model, for instance, can facilitate predictions on the effects of future landscape change scenarios on chimpanzee behavior and survival. Through scenario testing, chimpanzees' current adaptations to a wide variety of present-day environments can be extrapolated to provide insights into how chimpanzees would cope with, for example, increasing loss or fragmentation of habitat (e.g. forest, woodland) due to deforestation practices [e.g. Arroyo-Rodriguez and Mandujano 2009; Arroyo-Rodriguez and Fahrig 2014]. It can also facilitate predictions on the relative importance of various environmental changes, e.g. whether habitat loss per se is more damaging than pure fragmentation [e.g. Fahrig 2003; Arroyo-Rodriguez et al. 2013], as well as chimpanzees' tipping points for coping versus non-coping with environmental change. In scenario testing, small modifications to the current model code enable the setup of slightly different environments (e.g. less forest, increased fragmentation), which can be used to assess the difference in chimpanzee landscape use patterns in comparison to the 'original' (i.e. non-modified) situation. Exploring these prominent questions would be of great benefit to chimpanzee conservation, and would aid the development of appropriate mitigation strategies, either focused on the entire range of chimpanzee distribution throughout equatorial Africa or centered at a particular chimpanzee study site of interest.

Additionally, the Issa model can be used as a referential model for the landscape use of early hominins and as framework for understanding the underlying reasons of behavioral innovation and adaptation to specific landscapes in hominin evolution. One of the most daunting challenges in the study of human origins is the reconstruction of early hominin behavior, as, unlike skeletal remains, behavior does not fossilize [e.g. Mitani 2013; Plavcan 2013; Carlson and Kingston 2014]. Chimpanzees provide one of the best extant models for behavioral reconstructions, not only due to their close phylogenetic relatedness to hominins, but also due to their many morphological similarities and the finding that (savanna) chimpanzees inhabit similarly challenging savanna-woodland environments [e.g. Moore 1996; Jolly 2013; Mitani 2013; Plavcan 2013]. Hominins adapted to various environmental changes during the Plio-Pleistocene, with landscapes generally becoming gradually more open [e.g. Bobe et al. 2002; Potts 2007]. Using a referential modeling approach based on chimpanzee landscape use and adapting the Issa model to suit the characteristics of early hominins based on available fossil evidence will highlight new insights into how early hominins may have used their landscapes differently or similarly to extant chimpanzees, how they may have responded to environmental changes in their habitats, and when novel behaviors (such as dietary and locomotor adaptations; Doran 1996; Ungar and Daegling 2013; Ward 2013; Carlson and Kingston 2014) may have become advantageous. As such, the Issa model can shed a new light on early human origins.

It should be noted that, as models are always simplified representations of reality [e.g. van der Vaart et al. 2016], the Issa model is subject to certain limitations. Potential model improvements include updating movement and chimpanzee foresight codes, adding model codes on grouping and varying food quality, temperature and micro-climate changes, energy additions, behavioral *where* and *when* additions, and the

inclusion of novel behaviors. These improvements might make the current model predictions more accurate and should be considered for future purposes. Additionally, increased resolution of model output would also follow from complete Issa chimpanzee habituation, which would lead to more fine-grained and detailed behavioral data for Issa model rule development.

Budget

The three-month visit of Kelly L. van Leeuwen to the chimpanzee field study site at Issa Valley, Tanzania, was funded by Bournemouth University in combination with grants from the International Primatological Society (IPS) and the Primate Society of Great Britain (PSGB). The IPS grant was used to cover a part of the costs of field data collection.

Item	Requested (\$)	Final cost (\$)
Transport (Kigoma – Issa)	\$250	\$250
Accommodation at Issa (\$29/day, 36.2 days)	\$1050	\$1050
Field assistant (\$200/month, 1 month)	\$200	\$200
Total	\$1500	\$1500

Acknowledgements

We thank the Tanzanian authorities TAWIRI and COSTECH. We are grateful to field assistants Jonas Bukende and Shedrack Lucas, student assistants Bethan Harries and Arron Mallory, and additionally to Mlela Juma, Patrick Hassan, Arcado Hussein and Emma Hankinson for help with field data collection. We thank K. Koops, A. Pascual-Garrido and V. Reynolds for filling out the questionnaire on the environmental determinants of chimpanzee site selection for specific activities; responses were used to set out model rules. Research was supported by grants from the IPS and the PSBG to Kelly L. van Leeuwen.

References

- Arroyo-Rodriguez et al., *Primates in fragments: complexity and resilience*, 13-28 (2013); Arroyo-Rodriguez and Fahrig, *Am. J. Primatol.*, **76**, 901-909 (2014); Arroyo-Rodriguez and Mandujano, *Int. J. Primatol.*, **27**, 1079-1096 (2006); Arroyo-Rodriguez and Mandujano, *Int. J. Primatol.*, **30**, 497-514 (2009); Asensio et al., *Folia Primatol.*, **78**, 141-153 (2007); Baldwin et al., *Primates*, **22**(4), 474-486 (1981); Bates and Byrne, *Behav Ecol Sociobiol.*, **64**, 247-255 (2009); Bobe et al., *J. Hum. Evol.*, **42**, 475-497 (2002); Boesch and Boesch-Achermann, *The chimpanzees of the Tai Forest: behavioural ecology and evolution* (2000); Carlon and Kingston, *J. Hum. Evol.*, **76**, 107-115 (2014); Clarke et al., *Int. J. Primatol.*, **23**(2), 365-381 (2002); Crawley, *Statistics: an introduction using R* (2011); Deppe and Rotenberry, *Ecol. Monogr.*, **78**(3), 461-487 (2008); Doran, *Great ape societies*, 213-224 (1996); Doran, *Int. J. Primatol.*, **18**(2), 183-206 (1997); Dunbar, *Int. J. Primatol.*, **23**(4), 785-818 (2002); Dunbar et al., *Biol. Rev.*, **84**, 413-429 (2009); Estrada et al., *Sci. Adv.*, **3**, 1-16 [online] (2017); Fahrig, *Annu. Rev. Ecol. Evol. Syst.*, **34**, 487-515 (2003); Fruth and Hohmann, *Great ape societies*, 225-240 (1996); Goodall, *The Chimpanzees of Gombe: Patterns of Behavior* (1986); Hernandez-Aguilar, PhD thesis (2006); Hernandez-Aguilar, *J. Hum. Evol.*, **57**, 350-364 (2009); Hernandez-Aguilar et al., *Am. J. Primatol.*, **75**, 979-994 (2013); Hunt and McGrew, *Behavioural diversity in chimpanzees and bonobos*, 35-51 (2002); Inskipp, *Chapter 4 Chimpanzee (Pan troglodytes)*, 53-81 (2005); Isabirye-Basuta and Lwanga, *Int. J. Primatol.*, **29**, 35-48 (2008); Jepsen et al., *Agr. Ecosyst. Environ.*, **105**, 581-594 (2005); Jolly, *Early hominin paleoecology*, 437-455 (2013); Koops, *PhD thesis* (2011); Koops, *Expert-based review: ecological determinants of chimpanzee site selection* (2017); Koops et al., *Int. J. Primatol.*, **33**(2), 356-380 (2012); Korstjens et al., *Anim. Behav.*, **79**, 361-374 (2010); Lehmann and Boesch, *Behav Ecol Sociobiol.*, **56**, 207-216 (2004); Matsumoto-Oda, *Primates*, **43**(2), 103-117 (2002); Matsuzawa et al., *The chimpanzees of Bossou & Nimba* (2011); McGrew et al., *J. Hum. Evol.*, **10**, 227-244 (1981); Mitani, *Early23*

hominin paleoecology, 397-435 (2013); Moore *Great ape societies*, 275-292 (1996); N'guessan et al., *Int. J. Primatol.*, **30**, 481-496 (2009); Pascual-Garrido, *Expert-based review: ecological determinants of chimpanzee site selection* (2017); Plavcan, *A companion to paleoanthropology*, 226-243 (2013); Pontzer and Wrangham, *J. Hum. Evol.*, **46**, 317-335 (2004); Potts, *Hominin environments in the east African Pliocene*, 25-49 (2007); Potts et al., *Int. J. Primatol.*, **32**, 669-690 (2011); Potts et al., *Am. J. Primatol.*, **78**, 432-440 (2016); Pruetz, *Primates*, **48**, 316-319 (2007); Pruetz and Herzog, *Curr. Anthropol.*, **58**(16), S337-S350 (2017); Pruetz and Bertolani, *Curr. Biol.*, **17**, 412-417 (2007); Pruetz and Bertolani, *PaleoAnthropology*, 252-262 (2009); Pyke et al., *Q. Rev. Biol.*, **52**(2), 137-154 (1977); Ramos-Fernandez et al., *Behav. Ecol. Sociobiol.*, **60**, 536-549 (2006); Reed, *J. Hum. Evol.*, **32**, 289-322 (1997); Reynolds, *Expert-based review: ecological determinants of chimpanzee site selection* (2017); Riitters et al., *Landscape Ecol.*, **31**, 137-148 (2016); Rudicell et al., *J. Virol.*, **85**(19), 9918-9928 (2011); Russak, *PhD thesis* (2013); Russak, *Int. J. Primatol.*, **35**, 1202-1221 (2014); Samson et al., *Primates*, **54**, 73-80 (2013); Schoeninger et al., *Am. J. Primatol.*, **49**, 297-314 (1999); Sellers et al., *Phil. Trans. R. Soc. B*, **362**, 1699-1710 (2007); Stewart, *PhD thesis* (2011); Stewart and Piel, *Primates*, **55**, 35-40 (2014); Stewart and Pruetz, *Am. J. Primatol.*, **75**, 593-604 (2013); Sutton et al., *Forest. Ecol. Manag.*, **391**, 469-481 (2017); Ungar and Daegling, *Early hominin paleoecology*, 203-250 (2013); van der Vaart et al., *Ecol. Modell.*, **326**, 113-123 (2016); Ward, *Early hominin paleoecology*, 163-201 (2013); Wessling et al., *J. Hum. Evol.*, 1-11 [in press] (2018a); Wessling et al., *Front. Ecol. Evol.*, [online] (2018b); White, *The vegetation of Africa: A descriptive memoir to accompany the Unesco/ AETFAT/ UNSO vegetation map of Africa* [online] (1983); White et al., *Science*, **326**, 75-86 (2009); Willensky, *NetLogo* [online] (1999); Wondra et al., *African Primates*, **11**(1), 1-18 (2016); Yamanashi and Hayashi, *Am. J. Primatol.*, **73**, 1231-1238 (2011).



Principal investigator Kelly van Leeuwen during one of her vegetation plots.
Issa chimpanzee female and offspring. © K.L.vanLeeuwen

Report from Lawrence Jacobsen Education Development Grant Recipient LWT Primate Conservation Learning Facility

“LWT Primate Conservation Learning Facility” By Genevieve Crisford

IPS – Lawrence Jacobsen Education Development Grant report

“LWT Primate Conservation Learning Facility”

By Genevieve Crisford



Following a generous contribution from the IPS Lawrence Jacobsen Education Development Grant, great strides have been made to implement our “Primate Conservation Learning Facility” project at the LWT Wildlife Centre (LWC) in Malawi. This report aims to summarize our project activities and evaluate the impact of this project.

Project activities

It has been the aim of this project to build an education facility at the LWT Wildlife Centre filled with different interactive learning tools, focusing on primates and the issues which affect them in Malawi. There have been several aspects to the completion of this project:

1. Building a structure to house our new education facility:

The structure required to house this new facility was a major part of this project, both financially and logistically. The proposed site was mapped and approved by our board of trustees, under the provision of size and use of natural materials. As a result, we have proceeded with an open-walled rondavel structure, with natural flooring and a thatched roof. Local labour was commissioned to construct the structure.



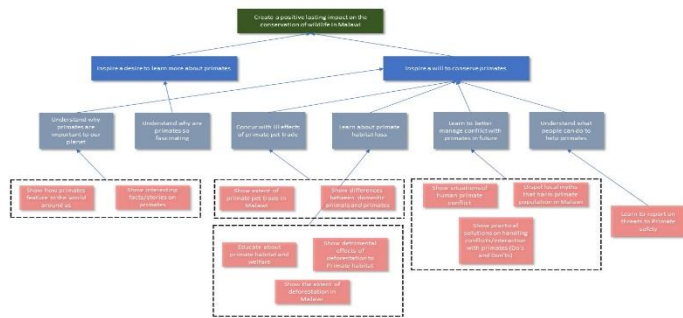
A few challenges were experienced along the way. Malawi has a very unstable economy and many prices of materials had risen between the grant proposal budget and the time of construction. LWT worked closely with local thatcher's to achieve the most competitive prices but was unable to achieve the projected cost. LWT supplemented the cost of this aspect of the project to ensure that enough budget remained for the displays.

2. Displays covering issues faced by primates in Malawi today:

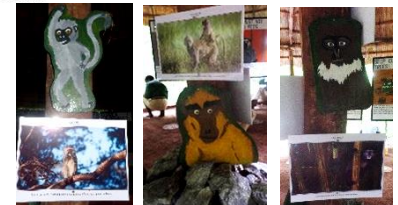
This aspect of the project was taken on largely by LWT's volunteers under supervision by LWT management. Research and planning was completed first to ensure well thought out messaging for our facility.

It was decided to produce six main topic displays covering the following issues:

- Benefits of conserving primates
- The threat of deforestation
- The threat of bushmeat trade
- The threat of the pet trade
- Human wildlife Conflict
- How you can help



The three species of primate commonly found in Malawi were also introduced – the Vervet monkey, Yellow baboon and Blue monkey. The displays were stencilled, and hand painted using basic materials, but the results were very effective:



In addition to information display boards we had a strong desire to incorporate interactive activities into the facility. Three further boards were produced with the following topics:

- A game matching the five freedoms of a human to that of a Vervet monkey
- Images depicting facial expressions of a Yellow baboon with mirrors to try yourself
- A crossword puzzle to test what you have learnt



Finally, as an extension to the information provided on deforestation, we have produced a display of alternatives to burning firewood. Here, a selection of fuel efficient stoves are displayed, in addition to a variety of alternative fuel “briquettes”. Visitors can request a demonstration of this equipment and even a practical lesson in briquette making, which we hope will inspire a reduction of firewood use and resulting deforestation.

Efforts have been made to decorate the facility in an attractive manner to entice visitors and school groups to take an interest in primate conservation. Ten mosaics were produced by LWT volunteers using broken tiles and handmade paving slabs.



The Primate Conservation Learning Facility can be found at the entrance to our Wildlife Centre sanctuary tours and is available for visitors to self-guide in their own time. School groups can be guided through to ensure a good understanding, and this can be offered in conjunction with one of our education modules or an educational film. We are fortunate to have received educational films from PASA which cover relevant topics such as habitat loss, snaring and bush meat.

3. Community engagement programme:

Despite planning to undertake this community project in the Kasungu district, a greater need was established by our outreach team in the Salima district, bordering Kuti Wildlife Reserve.

It was noted that there is an increased rate in human- primate conflict in some of the communities surrounding the reserve. This was so because the communities were lacking knowledge on how best they can protect themselves and their crops from wild animals. In order to fill the gap which was there among the communities in terms of conserving primates, a training was conducted at Yonamu Village. This training accommodated 8 VNRC's, from different communities which are working hand in hand with Lilongwe Wildlife Trust.



Educational guides containing the information from LWC's new primate conservation facility were developed and translated into Chichewa, the local tribal language used in the Salima district. These were distributed to the VNRC's during the training, for further dissemination within the surrounding communities.

The training was hugely successful in that resulting action occurred immediately. A number of the communities involved requested for tree seedlings as a way of conserving their local forest and 1,100 tree seedlings were delivered to the different villages.

On March 7th 2018, 200 tree seedlings were planting with the LWT team and one community planted Kankhande trees which is used as a fence in order to protect their crops from primates. The remaining seedlings comprising of cassia species were later planted by the community groups. The education visit was a great success as communities showed much interest in conserving both the wild animals and natural resources in general. Feedback suggested community members were happy to attend because the training created a platform where they were able to raise their concerns in conserving their natural resources and in human-wildlife conflict, especially those involving primates.



Impact/evaluation

The education objectives of this project are as follows:

- To inspire children and adults to learn about the threats affecting different primate species in Malawi and encourage the conservation of these species
- To provide a platform to educate the Malawian population on environmental issues such as deforestation, wildlife conflict & illegal trade in wildlife such as pets and bush meat
- To develop knowledge through interactive learning and fun activities
- To incorporate practical solutions to environmental issues
- To have a positive lasting impact on the conservation of wildlife and habitats in Malawi, with a particular focus on primates.

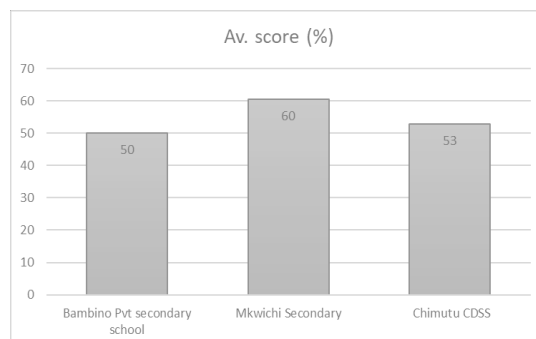
Evaluation of these aims was conducted through means of visitor data collection and pre/post-delivery questionnaires for selected schools. Four schools (Lilongwe Pvt, Chimutu, Mkwichi and Bambino Pvt) were targeted for assessment and each provided with 20 questionnaires at their school. Students were not given any assistance or training for the assessments, to accurately evaluate their current levels of knowledge on the following topics:

- Knowledge of Malawian wildlife including threats to primates
- Conservation of wildlife and primates
- Sustainable energy sources as a practical solution to deforestation

Finally, 15 questionnaires were evaluated from each school due to some challenges in collecting all the forms back from the schools. Lilongwe Private also absconded from the process due to examination commitments. Results of the pre-assessment were hence as follows:

Name of school	Marks/47	Rate (%)
Bambino Pvt secondary school	23.5	50
Mkwichi Secondary	28.4	60
Chimutu CDSS	24.8	53

Table 1: Pre-assessment questionnaire data

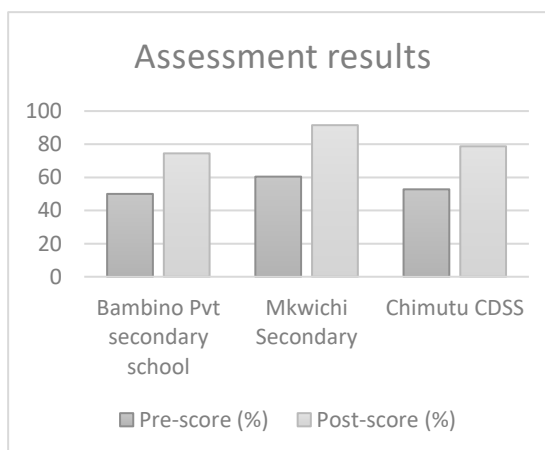


Following completion of the project components, the schools were invited to visit the Lilongwe Wildlife Centre for a taster session of the new facilities.

On completion of their experience, students were asked to repeat the same questionnaire, with the following results:

Name of school	Marks/47	Rate (%)	% difference
Bambino Pvt secondary school	35	74	49
Mkwichi Secondary	43	91	51
Chimutu CDSS	37	79	49

Table 2: Post-assessment questionnaire data



All schools evaluated saw a distinct improvement in performance, with an average difference of 49.8%. Specific primate conservation questions saw an even bigger improvement with an average of 59%.

Name of school	Pre-test	Post-test	% diff
Bambino pvt	55	80	45
Mkwichi	57	95	67
Chimutu	48.5	80	65
Average improvement			59

Table 3: Primate conservation questionnaire data

This is a very positive indication of the potential for this project to raise awareness of wildlife and environmental conservation within Malawi.

Since the launch of this programme in February 2018, the LWT Wildlife Centre has received a total of 9708 visitors with the following breakdown:

	February	March	April	May	Total
No of school children	709	2122	710	1320	4861
School children receiving educational lessons	146	892	176	299	1513
Other visitors	862	1216	1734	1035	4847
Total no of visitors	1571	3338	2444	2355	9708

Table 4: Visitor statistics Feb 2018 – May 2018

Visitors come from a wide range of society in Malawi, all of whom will benefit from the displayed information. Feedback suggests that our visitors are greatly enjoying the new facilities, especially as increasing welfare standards makes wildlife viewing less common.

“Much improved lessons and extra activities” Christian Heritage

“Teach more schools these good developments, really good to the nation” Marantha Secondary

“Good signage and improved delivery” Bishop Mackenzie

“Good initiative to train more learners on briquettes at our school” Chisomo Private Secondary

“Happy for a place to raise concerns in conserving resources” Katchenembwe Village VNRC

Challenges:

Several challenges have been faced throughout the execution of this project, despite a thoroughly positive final result.

- As mentioned, difficulties were had throughout the budgeting and construction of the new facility structure. Ongoing inflation and national rising of material/labour costs makes it challenging to accurately project the cost of a building project ahead of time. To counter this problem, it may be necessary to add allowances for an increase in prices.
- Developing and implementing new educational displays took more time than initially allocated due to the involvement of volunteers, who have been slightly lower in numbers this year than in past years. Our sincerest apologies to IPS for the delay in reporting on this much appreciated project opportunity.
- Involving local schools in pre/post evaluations posed various challenges. Teachers required much chasing for the processing of questionnaires. Several visits were made to each school to

complete this process and not all questionnaires were received back, lowering our quantity of usable data. In addition, one pre-assessed school was unable to attend the taster day throughout the assessment period due to exams and holiday commitments. Additional surveys can be added to allow for incomplete responses in such assessment strategies.

- Further to the above point, certain costs of the evaluation process were not considered when budgeting for this project. Local schools were unable to provide their own transport and so LWT paid for a bus to collect and return the students to their schools. In addition, it is customary in Malawi to pay allowances to teachers for supervising such occasions. In future these costs should be included from the beginning, but some re-distribution from the community budget allowed for the assessment to go ahead.

Financial report:

	Spent (MWK)	Spent (US\$)
Thatched rondavel	1,093,330	1,508
Display materials	99,845	138
Community engagement	265,385	366
TOTAL	1,458,560	2,012

Table 5: Project expense summary

Full records of expenses have been made in detail throughout the project and are available on request should you require further information.

Conclusion:

The project fulfils set objectives to raise awareness of issues/threats affecting primates and to incorporate practical solutions to human-primate conflict. Assessment results have shown a huge improvement in knowledge gaps in these areas, in addition to general topics of wildlife and environmental conservation in Malawi. 9708 visitors have had access to facilities since the project was completed. This number will increase exponentially into the future.

As a country struggling with economic issues and population growth, it is more important than ever to inspire an importance for primate conservation in Malawians, and especially in the youth. In sponsoring this project, IPS has helped us to greatly improve facilities at Malawi's number one conservation education facility. We hope that by demonstrating practical solutions and by getting communities directly involved, they will take home these concepts into their everyday lives.

Sustainability of the project has been ensured through the involvement of key local staff members at the LWT Wildlife Centre, as well as the LWT outreach team, who are responsible for disseminating information to the wider LWT staff, visitors and community groups. LWT would like to expand upon these facilities further in the future, covering other wildlife species and environmental issues as needed.

LWT would like to thank IPS for the financial support of this grant, without which this project wouldn't have been possible. Many thanks also to contributions from LWT volunteers and local schools (Lilongwe Pvt, Chimutu, Mkwichi and Bambino Pvt), for their commitment during this exercise.

Report from Research Grant Recipient

Elizabeth Mallott

Project report: Do white-faced capuchins use preferred partners to mitigate foraging costs associated with color vision phenotypes?

Elizabeth Mallott, Postdoctoral Fellow, Department of Anthropology, Northwestern University

Introduction

Most taxa of New World monkeys, including white-faced capuchins (*Cebus capucinus*) exhibit a X-linked color vision polymorphism (Bunce, Isbell, Neitz, et al., 2011; Dominy, Lucas, Osorio, & Yamashita, 2001; Hiramatsu et al., 2005; Smith, Buchanan-Smith, Surridge, Osorio, & Mundy, 2003; Surridge, Smith, Buchanan-Smith, & Mundy, 2002). Therefore, females with two different M/LWS opsin alleles on their X chromosomes have trichromatic vision, while females with two identical M/LWS opsin alleles and all males have dichromatic vision. Previous research in spider monkeys (*Ateles geoffroyi*) and white-faced capuchins showed a strong signal of balancing selection for the M/LWS opsin gene (Hiwatashi et al., 2010); however, the specific selective process by which both the trichromatic and dichromatic phenotypes are being maintained in populations is unclear (Hiwatashi et al., 2010; Melin, Fedigan, Hiramatsu, & Kawamura, 2007; Surridge, Osorio, & Mundy, 2003).

Several selective processes have been proposed to explain the maintenance of both trichromacy and dichromacy in New World monkeys – negative frequency-dependent selection, niche divergence, heterozygote advantage, and the mutual benefit of association hypothesis (Bunce, Isbell, Grote, & Jacobs, 2011; N G Caine & Mundy, 2000; Nancy G Caine, Osorio, & Mundy, 2010; Green, 2014; Hiwatashi et al., 2010; Melin et al., 2009; Melin, Fedigan, Hiramatsu, Sendall, et al., 2007; Melin, Fedigan, Hiramatsu, & Kawamura, 2007; Saito et al., 2005; Smith et al., 2003; Surridge et al., 2005). Current evidence does not support the first two hypotheses, and evidence that a heterozygote advantage exists is mixed. Some studies indicate that trichromat individuals have increased foraging efficiency, particularly in fruit foraging or low light contexts (Bunce, Isbell, Grote, et al., 2011; Green, 2014; Melin, Fedigan, Hiramatsu, Sendall, et al., 2007; Melin et al., 2009; Smith et al., 2003), and that trichromat individuals have higher body mass, reproductive rates, and survival than dichromats (Green, 2014; Surridge et al., 2005). Conversely, other studies indicate that color vision phenotype does not influence foraging behavior (Hiramatsu et al., 2008; Melin, Fedigan, Hiramatsu, & Kawamura, 2007; Vogel, Neitz, & Dominy, 2007), or that dichromats have increased invertebrate capture success in some foraging contexts (N G Caine & Mundy, 2000; Nancy G Caine et al., 2010; Melin, Fedigan, Hiramatsu, Sendall, et al., 2007; Saito et al., 2005).

A fourth hypothesis, the mutual benefit of association hypothesis (where having a mix of phenotypes in the population confers advantage on all individuals), is consistent with the current evidence that trichromats and dichromats each have foraging advantages in different foraging contexts (Hiwatashi et al., 2010; Melin, Fedigan, Hiramatsu, Sendall, et al., 2007; Melin, Fedigan, Hiramatsu, & Kawamura, 2007). The costs of having the trichromat phenotype in invertebrate foraging contexts may be mitigated by foraging near individuals with the dichromat phenotype, and vice versa for fruit foraging contexts. However, to date, no studies have tested this hypothesis (Hiwatashi et al., 2010).

This project combined genetic evidence with an observational dataset to examine whether 1) individuals with trichromatic vision had a nearest neighbor that is a dichromat more frequently than expected by chance while foraging for invertebrates; 2) individuals with dichromatic vision had a nearest neighbor that is a trichromat more frequently than expected by chance while foraging for fruit; 3) nearest neighbor distances between trichromat-dichromat pairs were smaller than that of trichromat-trichromat pairs and dichromat-dichromat pairs in fruit and invertebrate foraging contexts; and 4) trichromat-dichromat pairs had increased foraging efficiency.

Methods



The observational dataset this project used was collected from a group of 22 individually recognizable white-faced capuchins (9 female and 13 male) at La Suerte Biological Field Station, Costa Rica from January 2013 to January 2014. Focal animal sampling was used to collect data on activity budget (feeding, foraging, resting, traveling, social), diet (ripe fruit, unripe fruit, invertebrates, flowers, vertebrates, other), and nearest neighbor distance and identity. In the study population, 48% of foraging time is spent on ripe fruit and 46% on invertebrate prey (Mallott, Garber, & Malhi, 2017).

Fecal samples were collected from all individuals throughout the study period ($n=225$) and stored in 90% ethanol at -20°C . Data collection and export permits were obtained from MINAET, CONAGEBIO, and SINAC in Costa Rica. The University of Illinois at Champaign-Urbana IACUC approved all data collection methods.

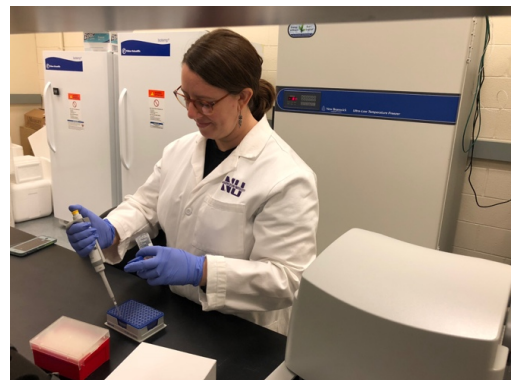
DNA was extracted from all fecal samples using a QIAamp DNA Stool Mini Kit using established protocols (Mallott et al., 2017).

The L/MWS opsin gene was amplified from 3 high-concentration samples from each of 22 individuals in the study group (Hiramatsu et al., 2005; Hiwatashi et al., 2010). Molecular work was carried out in the Amato Laboratory at Northwestern University. Sanger sequencing was performed for all samples at the NUSeq Core at Northwestern University. 4Peaks (Nucleobytes) was used to identify and visually verify base calls.

Results

I was able to unequivocally determine color vision phenotype for 20 of 22 individuals in the group. Four of the five adult females were trichromats, and all of the juvenile females from whom we had three fecal samples were trichromats.

Foraging partner preference was influenced by color vision phenotype. In this group, on average a dichromat is slightly more likely to forage near a trichromat during fruit foraging bouts than we expect by chance (40.1% observed vs. 36.8% expected). Trichromats, however, were not more likely to forage for invertebrates near dichromats than we expected by chance (64.9% observed vs. 68.4% expected). Nearest neighbor distances were also influenced by color vision phenotype during fruit foraging contexts, but not in the expected direction. When foraging for fruit, nearest neighbor distances were smaller when both the focal individual and the nearest neighbor had the same color vision phenotype. There was no effect of color vision phenotype on nearest neighbor distances during invertebrate foraging bouts. Foraging efficiency, assessed using feeding rates, did not differ between trichromats and dichromats.



Conclusions and future directions

While our results do not indicate that trichromats are mitigating their decreased invertebrate foraging efficiency by foraging near dichromats, dichromats may be mitigating their decreased fruit foraging efficiency by foraging near trichromats. The remaining hypotheses were not supported with the current dataset. However, these results are not conclusive, as seven of the group's eight females were trichromats, potentially biasing the analyses. I will be combining my data with a larger dataset from another white-faced capuchin site in Costa Rica to expand this analysis. Additionally, the larger dataset will allow me to examine more robustly the effect of color vision phenotype on foraging partner networks across multiple groups.

Budget Report

Date	Item	Vendor	Cost
5/31/17	PCR cleanup kits	Qiagen	381.49
5/31/17	Primers	IDT	37.45
10/6/17	Primers	IDT	37.45
4/9/18	Sanger round 1	ACGT	640
4/26/18	Sanger round 2	ACGT	96
		Total	1192.39

**References**

- Bunce, J. A., Isbell, L. A., Grote, M. N., & Jacobs, G. H. (2011). Color Vision Variation and Foraging Behavior in Wild Neotropical Titi Monkeys (*Callicebus brunneus*): Possible Mediating Roles for Spatial Memory and Reproductive Status. *International Journal of Primatology*. <https://doi.org/10.1007/s10764-011-9522-y>
- Bunce, J. A., Isbell, L. A., Neitz, M., Bonci, D., Surridge, A. K., Jacobs, G. H., & Smith, D. G. (2011). Characterization of opsin gene alleles affecting color vision in a wild population of titi monkeys (*Callicebus brunneus*). *American Journal of Primatology*, 73(2), 189–196. <https://doi.org/10.1002/ajp.20890>
- Caine, N. G., & Mundy, N. I. (2000). Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*) dependent on food colour. *Proceedings. Biological Sciences / The Royal Society*, 267(1442), 439–44. <https://doi.org/10.1098/rspb.2000.1019>
- Caine, N. G., Osorio, D., & Mundy, N. I. (2010). A foraging advantage for dichromatic marmosets (*Callithrix geoffroyi*) at low light intensity. *Biology Letters*, 6(September 2009), 36–38. <https://doi.org/10.1098/rsbl.2009.0591>
- Dominy, N. J., Lucas, P. W., Osorio, D., & Yamashita, N. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology*, 10(5), 171–186. <https://doi.org/10.1002/evan.1031>
- Green, A. T. (2014). *Consequences of color vision variation on performance and fitness in capuchin monkeys*. University of Montana.
- Hiramatsu, C., Melin, A. D., Aureli, F., Schaffner, C. M., Vorobyev, M., Matsumoto, Y., & Kawamura, S. (2008). Importance of achromatic contrast in short-range fruit foraging of primates. *PLoS ONE*, 3(10), e3356. <https://doi.org/10.1371/journal.pone.0003356>
- Hiramatsu, C., Tsutsui, T., Matsumoto, Y., Aureli, F., Fedigan, L. M., & Kawamura, S. (2005). Color vision polymorphism in wild capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi*) in Costa Rica. *American Journal of Primatology*, 67, 447–461. <https://doi.org/10.1002/ajp>
- Hiwatashi, T., Okabe, Y., Tsutsui, T., Hiramatsu, C., Melin, A. D., Oota, H., ... Kawamura, S. (2010). An explicit signature of balancing selection for color-vision variation in new world monkeys. *Molecular Biology and Evolution*, 27(2), 453–64. <https://doi.org/10.1093/molbev/msp262>
- Mallott, E. K., Garber, P. A., & Malhi, R. S. (2017). Integrating feeding behavior, ecological data, and DNA barcoding to identify developmental differences in invertebrate foraging strategies in wild white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 162(2), 241–254. <https://doi.org/10.1002/ajpa.23113>
- Melin, A. D., Fedigan, L., Hiramatsu, C., Sendall, C., Kawamura, S., & Biosciences, I. (2007). Effects of colour vision phenotype on insect capture by a free-ranging population of white-faced capuchins, *Cebus capucinus*. *Animal Behaviour*, 73(1), 205–214. <https://doi.org/10.1016/j.anbehav.2006.07.003>
- Melin, A. D., Fedigan, L. M., Hiramatsu, C., Hiwatashi, T., Parr, N., & Kawamura, S. (2009). Fig foraging by dichromatic and trichromatic *Cebus capucinus* in a tropical dry forest. *International Journal of Primatology*, 30(6), 753–775. <https://doi.org/10.1007/s10764-009-9383-9>

- Melin, A. D., Fedigan, L. M., Hiramatsu, C., & Kawamura, S. (2007). Polymorphic color vision in white-faced capuchins (*Cebus capucinus*): Is there foraging niche divergence among phenotypes? *Behavioral Ecology and Sociobiology*, 62(5), 659–670. <https://doi.org/10.1007/s00265-007-0490-3>
- Saito, A., Mikami, A., Kawamura, S., Ueno, Y., Hiramatsu, C., Widayati, K. A., ... Hasegawa, T. (2005). Advantage of dichromats over trichromats in discrimination of color-camouflaged stimuli in nonhuman primates. *American Journal of Primatology*, 67(4), 425–36. <https://doi.org/10.1002/ajp.20197>
- Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., Osorio, D., & Mundy, N. I. (2003). The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). *The Journal of Experimental Biology*, 206(Pt 18), 3159–3165. <https://doi.org/10.1242/jeb.00536>
- Surridge, A. K., Osorio, D., & Mundy, N. I. (2003). Evolution and selection of trichromatic vision in primates. *Trends in Ecology and Evolution*, 18(4), 198–205. [https://doi.org/10.1016/S0169-5347\(03\)00012-0](https://doi.org/10.1016/S0169-5347(03)00012-0)
- Surridge, A. K., Smith, A. C., Buchanan-Smith, H. M., & Mundy, N. I. (2002). Single-copy nuclear DNA sequences obtained from noninvasively collected primate feces. *American Journal of Primatology*, 56(3), 185–90. <https://doi.org/10.1002/ajp.1073>
- Surridge, A. K., Suárez, S. S., Buchanan-Smith, H. M., Mundy, N. I., Caine, N. G., Mundy, N. I., ... Mollon, J. D. (2005). Non-random association of opsin alleles in wild groups of red-bellied tamarins (*Saguinus labiatus*) and maintenance of the colour vision polymorphism. *Biology Letters*, 1(4), 465–8. <https://doi.org/10.1098/rsbl.2005.0367>
- Vogel, E. R., Neitz, M., & Dominy, N. J. (2007). Effect of color vision phenotype on the foraging of wild white-faced capuchins, *Cebus capucinus*. *Behavioral Ecology*, 18(2), 292–297. <https://doi.org/10.1093/beheco/arl082>