Volume 4 Number 2 2014
ISSN 1979-1631

Asian Primates Journal

A Journal of the Southeast Asia, South Asia and China Sections of the IUCN SSC Primate Specialist Group

CONSERVATION INTERNATIONAL
SSC Species Survival Commission
MARGOT MARSH BIODIVERSITY FOUNDATION
IUCN SSC PRIMATE Specialist Group
SeAPA Southeast Asian Primatological Association

Asian Primates Journal

A Journal of the Southeast Asia, South Asia and China Sections of the IUCN SSC Primate Specialist Group

EDITORS

Ramesh Boonratana
IUCN SSC PSG SE Asia (Regional Vice-Chair) / Mahidol University International College, Thailand

John R. Fellowes
Kadoorie Farm & Botanic Garden, China / UK

Christian Roos
IUCN SSC PSG SE Asia (Regional Vice-Chair) / German Primate Center, Germany

Jatna Supriatna
IUCN SSC PSG SE Asia (Regional Vice-Chair) / University of Indonesia, Indonesia

EDITORIAL ASSISTANTS

Nurhafizie binti Mohamad Hapiszudin
Bukit Merah Orang Utan Island Foundation, Malaysia

Rosimah binti Roslan
Bukit Merah Orang Utan Island Foundation, Malaysia

EDITORIAL BOARD

Noviar Andayani
Wildlife Conservation Society, Indonesia / University of Indonesia, Indonesia

Warren Y. Brockelman
Mahidol University, Thailand

Colin Groves
Australian National University, Australia

Michael A. Huffman
Primate Research Institute, Japan

Ajith Kumar
National Centre of Biological Sciences, India

Le Xuan Canh
Institute of Ecology and Biological Resources, Vietnam

Long Yongcheng
IUCN SSC PSG China (Regional Vice-Chair) / The Nature Conservancy, China

Russell A. Mittermeier
IUCN SSC PSG (Chairman) / Conservation International, USA

Anna Nekaris
Oxford Brookes University, UK

Anthony B. Rylands
IUCN SSC PSG (Deputy Chairman) / Conservation International, USA

Myron Shekelle
Ewha Womans University, Republic of Korea

Ian Singleton
Sumatran Orangutan Conservation Program, Indonesia

Barth Wright
Kansas City University of Medicine and Biosciences, USA

LAYOUT

Pratchaya Leelapratchayanont
Mahidol University International College, Thailand

COVER PAGE

Southern Pig-tailed Macaque *Macaca nemestrina* with infant. Photo by Sandra Schweiger.

ASIAN PRIMATES JOURNAL is produced in collaboration with Conservation International, IUCN Species Survival Commission and SeAPA (Southeast Asian Primatological Association)

The Asian Primates Journal wishes to acknowledge the following persons and agencies/institutions for disseminating or covering the costs of dissemination of the journal in the following countries:

China	Bosco Chan & Kadoorie Conservation China, Kadoorie Farm & Botanic Garden
India	Ajith Kumar
Japan	Michael Huffmann
Indonesia	Jatna Supriatna
Lao PDR	Wildlife Conservation Society Lao PDR
Malaysia	Sabapathy Dharmalingam & The Bukit Merah Orang Utan Island Foundation
Sri Lanka	Charmalie Nahallage
Vietnam	Le Xuan Canh & Institute of Ecology and Biological Resources

The IUCN SSC Primate Specialist Group

The Primate Specialist Group is a network of scientists and conservationists who stand against the tide of extinction which threatens humanity's closest kin.

Active throughout the tropical world, working in dozens of nations in Africa, Asia and Latin America, the PSG promotes research on the ecology and conservation of hundreds of primate species — monkeys, apes, lemurs and their many nocturnal relatives. Now more than ever they need our intervention: one in every four primate species is threatened or endangered, and the double hammer of overhunting and forest devastation has brought some species to within a few dozen heads of final extinction.

The PSG works on behalf of these and all other primates by supporting field research, conservation measures and educational programs in those regions where primates still occur. The PSG's primary responsibility is to evaluate the conservation status of all primate species and subspecies, working with current information from experts in the field. These assessments contribute to the IUCN Red List, a comprehensive summary of threats to the world's biodiversity. In addition, the PSG produces Action Plans targeted to particular species or groups of species. Much larger and more detailed than the general assessments, these Action Plans serve to summarize the available knowledge on a particular species group and to lay out a program for their conservation.

Beyond these core functions, the PSG provides a unique forum for scientific publications through the newsletters and journals it sponsors, which are widely read by primatologists and often contain the only information available on rare and poorly-studied species. The PSG produces a journal or newsletter for each of the four global primate regions — Africa, Asia, Madagascar and the Neotropics — as well as an overarching journal, Primate Conservation, which publishes research on threatened primates from around the world.

The PSG is just one of over one hundred and thirty Specialist Groups organized within the framework of the IUCN Species Survival Commission, an international alliance of conservationists that produces the IUCN Red List and is involved in a range of other conservation initiatives. The IUCN Species Survival Commission is a science-based network of more than 9,000 volunteer experts from almost every country of the world, all working together towards achieving the vision of, *"A just world that values and conserves nature through positive action to reduce the loss of diversity of life on earth"*.

The PSG's current incarnation was organized in 1977 by Dr. Russell Mittermeier, a primatologist, herpetologist, prominent conservationist and Executive Vice Chair of Conservation International, USA, who has now led the PSG as Chairman for more than 30 years. His Deputy Chair is Dr. Anthony Rylands, also at Conservation International. The PSG includes a group which specifically deals with conservation issues for the great apes, coordinated by Liz Williamson of Stirling University, UK and a number of world-renowned experts who act as regional coordinators for the major regions where primates occur (see the current team) besides a further 450 or so members organized by interests and geography.

Last, but by no means least, the PSG has for many years relied on the expert abilities of Stephen D. Nash, Scientific Illustrator for Conservation International. His artwork has become an international standard for the illustration of the world's primate taxa, and we are glad to be able to include some of it on our website (www.primate-sg.org), including the PSG's logo on the preceding page.

EDITORIAL: GIBBON TALES

2015 has been proclaimed as the Year of the Gibbon by the IUCN Species Survival Commission Primate Specialist Group Section on Small Apes (SSA) and this is resulting in a flurry of activity, helping raise the profile of gibbon conservation around the world. Here we report news of four species.

Several releases of Javan Gibbon (*Hylobates moloch*) have been conducted over the last 12 months. In April alone, gibbons from both the Javan Gibbon Center and Aspinall Foundation were released in West Javan forests. These are part of longer-term projects, to reintroduce gibbons to locations where they have been extirpated in the past, or to reinforce existing wild populations, respectively. SSC considers such translocations will be increasingly needed where gibbon populations are depressed and fragmented. Compared with those gibbons lost to deforestation and hunting, this small number of reintroduced gibbons may seem insignificant, but they have great symbolic value in our changing attitudes to the species: reinforced, at the latest release, by the involvement of the Indonesian President. The process has also been used to test new IUCN Best Practice Guidelines for Rehabilitation and Translocation of Gibbons (Campbell et al., 2015), launched in June 2015 and available from the SSA website at http://www.gibbons.asia.

A contrasting story comes from eastern Cambodia, where the spectre of PADDD (Protected Area downgrading, downsizing and degazettement) has reared its head. For some years conservationists have worked to safeguard the Seima Protection Forest (Evans et al., 2013), with some success: securing a home for some one thousand Yellow-cheeked Crested Gibbons (*Nomascus gabriellae*) and over 20,000 Black-shanked Douc Langurs (*Pygathrix nigripes*) (Nuttall et al., 2013; Wildlife Conservation Society, unpublished), making it a global stronghold for these species. But from early on they had to do some hard thinking, about which forests could realistically be saved with limited resources, and which were impossible. Sadly the adjoining Snuol Wildlife Sanctuary, home to some 850 gibbon groups (Geissmann et al., 2008), with its ready accessibility to loggers, was one of the latter. Accelerated by a road built through the sanctuary in about 2000 (Clements et al., 2014) and a raft of Economic Land Concessions in recent years (Matthew Nuttall, in litt.), most of the mature forest in the Sanctuary has now been lost – along with most of its gibbons. This must be one of the most dramatic declines in a “protected” ape population.

The world’s rarest ape is the Hainan Gibbon (*Nomascus hainanus*). The report from the second international Hainan Gibbon conservation workshop in March 2014 was recently published (Turvey et al., 2015). Since the first international workshop in 2003 the population has doubled (Fellowes et al., 2008; Turvey et al., 2015); this progress has even been cited, on a highly selective sifting of the evidence, to claim that continued economic growth is good for conservation (Anon., 2013; cf. Czech, 2008; Monbiot, 2014; Miller, 2015). The new report, however, gives a gloomy outlook for the species based on a population viability assessment. Still, it’s hoped more people will belatedly join in the conservation effort, and various actions have been proposed to improve the chances of success. Its sister taxon, the Cao Vit Gibbon (*N. nasutus*), found on the Sino-Vietnamese border, also shows some signs of recovery, with the population increasing between 2007 and 2012 and now around 130 individuals (Fauna & Flora International, unpublished). Transboundary action planning has recently concluded and will hopefully lead to ongoing status improvements.

Both poverty and affluence have been blamed for the ongoing biodiversity crisis. The truth is more complicated and yet more simple; nature declines wherever it is not valued by society, and where human demands on nature are not balanced by responsible care. How can the resulting loss of our common wealth be depicted as “economic growth”? The language is perverse (Daly, 2015).

So could primatologists be more effective in conserving their study animals? They certainly can’t do it alone. We salute all who are fighting their corner, whether to seek best conservation and welfare outcomes for the primates in their care, to fend off the direct threats to primate survival, or to engage wider society in this struggle.

John Fellowes and Ben Rawson

References

Anon., 2013. More growth, not less, is the best hope for averting a sixth great extinction. *The Economist* 14 September 2013.

Campbell, C.O., Cheyne, S.M. and Rawson, B.M., 2015. *Best Practice Guidelines for the Rehabilitation and Translocation of Gibbons*. IUCN SSC Primate Specialist Group, Gland, Switzerland, 56 pp. http://www.gibbons.asia/wp-content/uploads/2015/05/Best-Practice-Guidelines_Gibbons_LR.pdf

Clements, G.R., Lynam, A.J., Gaveau, D., Yap, W.L., Lhota, S., Goosem, M., Laurance, S. and Laurance, W.F., 2014. Where and how are roads endangering mammals in Southeast Asia's Forests? *PLoS ONE* 9(12): e115376. doi:10.1371/journal.pone.0115376

Czech, B. 2008. Prospects for reconciling the conflict between economic growth and biodiversity conservation with technological progress. *Conservation Biology* **22**: 1389-1398.

Daly, H. 2015. Economics for a full world. http://www.greattransition.org/publication/economics-for-a-full-world, downloaded 27 June 2015.

Evans, T.D., O'Kelly, H.J., Men Soriyun, Nut Meng Hor, Pet Phaktra, Sorn Pheakdey and Pollard, E.H.B., 2013. Seima Protection Forest. Pp. 157-186 in Sunderland TCH, Sayer J and Hoang M-H (eds), *Evidence-based Conservation: Lessons from the Lower Mekong*. CIFOR, Bogor, Indonesia.

Fellowes, J.R., Chan, B.P.L. Zhou J., Chen S., Yang S. and Ng S.C., 2008. Current status of the Hainan Gibbon (*Nomascus hainanus*): progress of population monitoring and other priority actions. *Asian Primates Journal* **1**(1): 2-8.

Geissmann, T., Manh Ha, N., Rawson, B., Timmins, R., Traeholt, C. and Walston, J. 2008. *Nomascus gabriellae*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 May 2015.

Miller, L., 2015. The Limits of Growth revisited. http://www.synchronicityearth.org/blog/2015/03/the-limits-of-growth-revisited/

Monbiot, G., 2014. It's simple. If we can't change our economic system, our number's up. *The Guardian* 24 May 2014.

Nuttall, M., Menghor, N. and O'Kelly, H., 2013. *Monitoring of Key Species in the Seima Protected Forest*. Wildlife Conservation Society Cambodia Program and the Forestry Administration, Cambodia, 29 pp.

Turvey, S.T., Traylor-Holzer, K., Wong, M.H.G., Bryant, J.V., Zeng X.Y., Hong X.J. and Long Y.C. (eds.), 2015. *International Conservation Planning Workshop for the Hainan Gibbon: Final Report*. ZSL, London/ IUCN SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA.

Asian Primates Journal 4(2), 2014

PRELIMINARY EVIDENCE FOR THE HIRED GUNS HYPOTHESIS AND INDIRECT MATE DEFENCE IN A WILD GROUP OF MAROON LANGURS *Presbytis rubicunda* (Müller, 1838) IN SABANGAU TROPICAL PEAT-SWAMP FOREST, CENTRAL KALIMANTAN, INDONESIAN BORNEO

David A. Ehlers Smith

[1] Orangutan Tropical Peatland Project, Centre for the International Cooperation in Sustainable Management of Tropical Peatlands, Universitas Palangka Raya, Palangka Raya 73112, Central Kalimantan, Indonesia. E-mail: DEhlersSmith@outrop.com
[2] Oxford Brookes University, Gipsy Lane, Headington, Oxford OX3 0BP, UK.

ABSTRACT

Group-living primates enjoy numerous benefits, including effective resource defence from conspecifics in other groups. Resource contest often results in intergroup aggression, for which several hypotheses exist to explain its function: direct mate defence; direct food-resource defence; indirect food defence via 'hired guns'; mate attraction via infanticide, and indirect mate defence via male resource defence. I studied a focal group of Maroon Langurs *Presbytis rubicunda* in Sabangau tropical peat-swamp forest and examined the nature of intergroup aggression. Evidence supported direct mate defence in the majority of intergroup encounters. However, given that the resources in this frugivorous population may be defensible, and that most intergroup encounters occurred within their 'core range' of valuable resources, it is likely that the females in the group benefited from indirect resource defence as a result of aggression by the male as a 'hired gun'. The focal group was the subject of a takeover by an invading male. The post-takeover home range and core range overlapped pre-takeover ranges by 75% and 43% respectively and post-takeover, the group reused 47% of sleeping trees (N=14), suggesting that the invading male established himself in the territory of the resident females, who then continued to use the resources therein. The focal group also fulfilled three criteria proposed to predict indirect mate defence via male resource defence in colobine monkeys. Thus, it appears that indirect mate defence may have been employed by the invading male to obtain reproductive access to females. This study represents the first preliminary evidence for both indirect-resource-defence-via-hired-guns and indirect-mate-defence-via-resource-defence hypotheses in the genus *Presbytis*.

Keywords: aggression, colobinae, hired guns, intergroup encounters, mate defence, resource defence

INTRODUCTION

Living in groups requires gregarious animals to coordinate their movements and make daily decisions regarding where, when and how to perform specific activities, incorporating the varying nutritional requirements and social and reproductive strategies of group members (Erhart & Overdorff, 1999; Conradt & Roper, 2005; Petit & Bon, 2010; Van Belle et al., 2013). Whatever differences in physiological and social needs, group-living primates receive numerous benefits, including increased vigilance and protection from predators, opportunities for social learning, and effective resource defence from conspecifics (Conradt & Roper, 2003; 2007).

Indeed, competition for resources can occur between individuals of different groups, and intergroup competition often results in aggression, which can influence both the behaviour and the social structure of primate groups (van Schaik & Janson, 2000), and have long-term consequences for individual fitness (Williams et al., 2004; Harris, 2010). However, resource competition does not adequately describe all aggressive intergroup encounters (IGEs); indeed, several hypotheses exist to explain the function of intergroup aggression by examining their nature and participants. The 'direct food-resource defence' hypothesis predicts that predominantly females cooperatively engage in the aggressive defence of food resources within their territory (Wrangham, 1980), as female reproductive fitness is limited by access to food (Trivers, 1972). Alternatively, males can engage in 'direct mate defence', as male reproductive fitness is determined by access to females (Trivers, 1972; Wrangham, 1980). In this scenario, resident males aggressively repel invading males' attempts at mating, or 'herd' females away from invading males, forcing them to stay in the center of the group and preventing them from transferring to other groups (Davies, 1987; Stanford, 1991; Steenbeck, 1999). Direct mate defence potentially serves a second function of 'indirect food resource defence' for adult females and their offspring, as by repelling extra-group individuals, males are acting as 'hired guns' and securing food resources for other members of their group and themselves (Rubenstein, 1986; Wrangham & Rubenstein, 1986). In an additional strategy, an invading male may attempt "mate attraction via infanticide" by killing the offspring of female(s) he is trying to attract, to show the weakness of the father in his inability to protect his young, and also to rapidly gain reproductive access to females by terminating lactational amenorrhea (Hrdy, 1977; van Schaik, 1996; Steenbeck, 1999). Finally, males can also engage in 'indirect mate defence via male resource defence', by defending resources for a group of females in return for reproductive access, either by taking over a group of adult females and defending the resources from extra-group individuals within their range, or by defending a resource patch and attempting to attract females (resource defence polygyny; Emlen & Oring, 1977; Fashing, 2001).

Evaluating the validity of these explanations is problematic, however, as each hypothesis is not necessarily mutually exclusive (Rubenstein, 1986; Fashing, 2001). Male participation in aggressive IGEs has been traditionally viewed as evidence for the mate defence hypothesis, and female participation as evidence for resource defence. More recently, however, studies have begun empirically testing patterns of male and female participation in IGEs, and the results suggest that the strategies adopted are highly complex (Fashing, 2001; Harris, 2010; Fashing, 2011). Intergroup aggression and group takeovers have been particularly well-documented in African colobine monkeys (e.g. Onderdonk, 2000; Fashing, 2001; Harris & Montfort, 2003; Sicotte & MacIntosh, 2004; Saj & Sicotte, 2005; Sicotte et al., 2007), and males appear to play an important role in food-resource defence, both directly (Fashing, 2001; Sicotte & MacIntosh, 2004), and indirectly, as hired guns, during direct mate defence (Fashing, 2001).

Aggression is particularly evident during group takeover, when a resident male is replaced by an invading male. Group takeover is one strategy used by adult male colobines to gain reproductive access to females (e.g. Rudran, 1973; Saj & Sicotte, 2005; Sicotte et al., 2007), as many colobine societies are structured into single-male multi-female groups (Fashing, 2011; Kirkpatrick, 2011). Takeovers regularly involve aggression between the invading and resident adult male (e.g. Davies, 1987; Saj & Sicotte, 2005), and infanticide of resident infants by the invading male can occur (Curtin & Dolhinow, 1979; Sterck, 1995; Borries, 1997; Borries et al., 1999; Onderdonk, 2000; Sicotte et al., 2007). In Asian colobine monkeys, typically only males interact and show aggression during IGEs (Steenbeck et al., 1999), often with threatening displays, chases and "loud calls" (Steenbeck et al., 1999; Wich & Sterck, 2010). Such behaviours are not dependent on the proximity of food resources (Steenbeck, 1999), and this is often viewed as evidence for the mate defence hypothesis rather than resource defence hypothesis (van Schaik et al., 1992; Reichard & Sommer, 1997). Indeed, being folivores, colobine food resources tend to be more abundant and evenly distributed than those of frugivorous primates, although there is evidence to suggest that not all folivores' food resources are abundant, evenly spread and of low quality (Koenig et al., 1998; Koenig, 2000; Grueter et al., 2009). However, the socioecological model generally assumes frugivores' food resources to be scarcer, more patchily distributed, and therefore more defensible than those of folivores, meaning that for colobine monkeys, resource defence may not play such a crucial role in intergroup aggression (Mitani & Rodman, 1979). They may instead defend 'core ranges' of frequent use that contain particularly valuable resources within their larger home range (Oates, 1977). Within Asian colobine socioecology, however, the application of both indirect mate defence, and indirect resource defence through the use of hired guns, remains largely untested.

A population of Maroon Langur *Presbytis rubicunda* (Müller, 1838) in Sabangau tropical peat-swamp forest, Central Kalimantan is extremely frugivorous, with >83% of its annual diet comprising fruit parts (>75% comprises seeds, thus making it granivorous) (Ehlers Smith et al., 2013). It has the longest day-ranges recorded in any "folivorous" primate in their pursuit of these fruits (mean 1,645 m/day; Ehlers Smith et al., 2013b). This offers the potential for investigating the effect on intergroup encounter strategy of a preference for a more nutritiously valuable (Harrison, 2009 at this site), scarce (Ehlers Smith et al., 2013b), and therefore potentially defensible dietary resource (Wrangham, 1980) than is typical in colobine ecology. Despite their heavy reliance on seeds, however, this group is apparently non-female bonded, as social interactions between individuals are virtually absent (Ehlers Smith et al., 2013b).

Presbytis rubicunda is an Asian colobine endemic to Borneo (Medway, 1970) and is socially organized into single adult male multi-female groups ranging from three to ten individuals (Supriatna et al., 1986; Ehlers Smith & Ehlers Smith, 2013). Extra-group males form all-male bands or range alone (Supriatna et al., 1986; Davies, 1987; Ehlers Smith & Ehlers Smith, 2013). Group takeover in *Presbytis rubicunda* has been previously described from Sepilok, Sabah. In this case, an invading male aggressively formed a new group with the two nulliparous females of an original group and used some 20% of the original group's territory, while the parous female and a small juvenile male stayed with the deposed adult male (Davies, 1987).

Here, I describe the nature of IGEs between a mixed-sex focal group of *P. rubicunda* and its neighbouring groups, and its subsequent takeover, in Sabangau tropical peat-swamp forest, Central Kalimantan. I aimed to examine the nature of the aggressive encounters and group takeover and the behaviour of both the new and remaining group members post-takeover, by testing the evidence for: direct mate defence; direct food-resource defence; indirect food resource defence via 'hired guns'; mate attraction via infanticide and indirect mate defence via male resource defence (Table 1). I predicted that:

1) If only direct mate defence occurred, only males should participate in intergroup aggression; male-male aggression should most likely be between a resident male and all-male bands/single male or incumbent males seeking to force females to transfer from one group to another, and the resident male should seek to protect the resident females and engage in herding behaviour to separate females and invading males; aggressive encounters would be just as likely to occur outside the 'core range' as inside (the core range is defined as the area in which the group spends >50% of its time (Ehlers Smith et al., 2013b), and is characterized by a high density of feeding trees (Ehlers Smith et al., 2013a) and sleeping trees).

2) If direct food-resource defence prevailed females should be more likely to participate in intergroup aggression; resident females should direct aggression to all invading group members, and aggressive encounters should be more likely to occur inside the core range.

3) If indirect resource defence via the 'hired guns' strategy occurred, resident males should participate in intergroup aggression toward extra-group males; females should avoid participation in the encounter; aggressive encounters should be more likely to occur within the core range.

4) If mate attraction via infanticide occurred, invading males should act aggressively toward resident females and attempt to kill their offspring; females with infants should attempt to avoid IGEs and behave defensively, and females would transfer to invading males that successfully achieved infanticide.

5) If indirect mate defence via male resource defence occurred, resident males should participate in intergroup aggression toward extra-group members; the male should defend resources within the territory for the benefit of the females to use.

METHODS

Study site and study subjects

The study was conducted as part of the Orangutan Tropical Peatland Project (OuTrop) – Center for the International Cooperation in Sustainable Management of Tropical Peatlands (CIMTROP) multi-disciplinary research project in the Natural Laboratory for the Study of Peat-swamp Forest. This is a 500 km^2 area within the Sabangau tropical peat-swamp forest, located between the Sabangau and Katingan rivers in Central Kalimantan, Indonesia (2°19′S and 113°54′E), and is contiguous with a larger landscape covering 8,750 km^2 of ombrogenous tropical peat-swamp forest between two major rivers. Detailed descriptions of the study site are published in Ehlers Smith & Ehlers Smith (2013).

The study subjects were a single, mixed-sex focal group of *P. rubicunda*, first identified in May 2010. Prior to October 2010, the group consisted of 8 individuals: 1 adult male, 3 adult females, 1 sub-adult male, and 3 very young infant males. In October 2010, the sub-adult male emigrated from the group. In July 2011, one of the adult females died and her juvenile offspring disappeared less than a month later. Thus, from July 2011 until the group was taken over by an invading male in May 2012, the group consisted of 5 individuals: the adult male, 2 adult females, and 2 juvenile males. Post-takeover, the group consisted of 3 individuals: the new invading male, and the 2 remaining adult females.

Data collection

We habituated the focal study group, Group KB, between May and December 2010, to the stage where reliable feeding (Ehlers Smith et al., 2013a), ranging and behavioural data (Ehlers Smith et al., 2013b) could be recorded. From January 2011, we recorded instantaneous focal behavioural data every 5 minutes on a single adult female of the group (Altmann, 1974). We selected an adult female as the focal target before the beginning of the follow on the basis of ensuring an even balance between focal individuals and minimizing observer bias (Ehlers Smith et al., 2013a, b). This individual was then closely followed for the rest of the day. Focal females were readily identifiable by individual distinguishing characteristics of overall body sizes, nipple lengths and shape of tails (Ehlers Smith et al., 2013a). Using a team of two researchers, we recorded behavioural and ranging data including 1) primary behaviours (feeding, resting, traveling, social behaviours); 2) secondary behaviours (how the primary behaviour was achieved); 3) vocalizations including the loud call (a series of "kekekekeke" notes emitted by the adult male), alarm calls (a shorter burst of "keke-keke-keke" notes, emitted by the adult and sub-adult males, alarm "hiccups" (emitted by all members of the group, and "purr" (a contact call by the mother to her offspring); 4) height of focal animal in tree/bush by 5 m categories (1-5 m, 6-10 m etc.); 5) height of tree/bush by the same 5 m categories, and 6) a GPS location for each instantaneous behavioural sample, enumerated uniquely for each follow. We recorded continuous feeding data on the focal animal (Ehlers Smith et al., 2013a), for which we documented the species, food type and food item during all feeding bouts ≥ 30 seconds, and tagged, enumerated and obtained GPS locations of all feeding stems. We similarly tagged, enumerated and obtained GPS locations of all morning and evening sleeping-tree sites. Data collection was divided between the two researchers, with instantaneous behavioural and continuous feeding data recorded by the first researcher, and GPS locations and tree enumeration recorded by the second researcher.

Pre-takeover, we followed the group from morning sleeping-tree to evening sleeping-tree for 2-11 days each month from January 2011 until May 2012 with the exception of January and February 2012 when no data were collected (N=96 sleeping trees; mean=6.6 sleeping trees/month), for a total of 1070.9 hours (N=15 months; mean=71.4±SD 26.6 hour/month). Post-takeover, data collection occurred in all months between May 2012 and July 2013 with the exception of January, February and May 2013. We followed the group from morning sleeping-tree to evening sleeping-tree for 1-11 days of those months (N=41 sleeping trees; mean=4.9 sleeping trees/month of data collection), for a total of 441.4 hours (N=11 months; mean=29.4±SD 30.5 hour/month of data collection).

Data analysis

Intergroup encounter locations within home range and core range of Group KB

I defined an intergroup encounter as an occurrence of 2 groups within 50 m of each other (Oates, 1977; Stanford, 1991). We obtained a GPS location at the onset of each intergroup encounter, and then at subsequent locations on the 5 minute instantaneous sample during encounters that lasted for longer than 5 minutes. I then converted these locations into ArcGIS shapefiles and overlaid them with the home range and core range of Group KB (90% and 50% volume contours, respectively, as determined using the Smooth Cross-Validation bandwidth estimator in kernel density estimates; Ehlers Smith et al., 2013b), to examine any patterns of interactions within these localities. Finally, I separated the locations involving encounters with known mixed-sex groups and all-male groups.

Post-takeover reuse of resources

I calculated the home-range and core-range use by Group BD post-takeover using the Geospatial Modeling Environment suite v.0.7.1.0 and the Smooth-Cross Validation bandwidth (Beyer, 2012) to create a kernel density estimate of range utilization distribution, and selected 50% and 90% volume contours to represent the core range and home range, respectively (Ehlers Smith et al., 2013b). I then calculated the degree of overlap between the range-use by Group BD as a percentage of that used previously by Group KB (Ehlers Smith et al., 2013b).

To test for the defence of resources post-takeover, the home-range and core-range area, and suitable sleeping tree resources therein, should be reused. Sleeping-tree sites can be considered a defensible resource, as the abundance and selection of suitable sites can impact individuals' survival chances (Lutermann et al., 2010; Phoonjampa et al., 2010). Primates are often highly selective in their choices of sleeping-tree sites, as their locations and distributions can influence ranging patterns and foraging decisions (Spironello, 2001), and also offer protection against predators (Chapman, 1989). Individual trees are often reused if characteristics such as predator protection, structural safety and proximity to food resources are desirable (Heymann, 1995; Reichard, 1998; Di Bitetti et al., 2000; Radespiel et al., 2003). To investigate sleeping site reuse post-takeover, I compiled a list of all sleeping tree tag numbers representing usage by both groups, and calculated the percentage of reuse by Group BD.

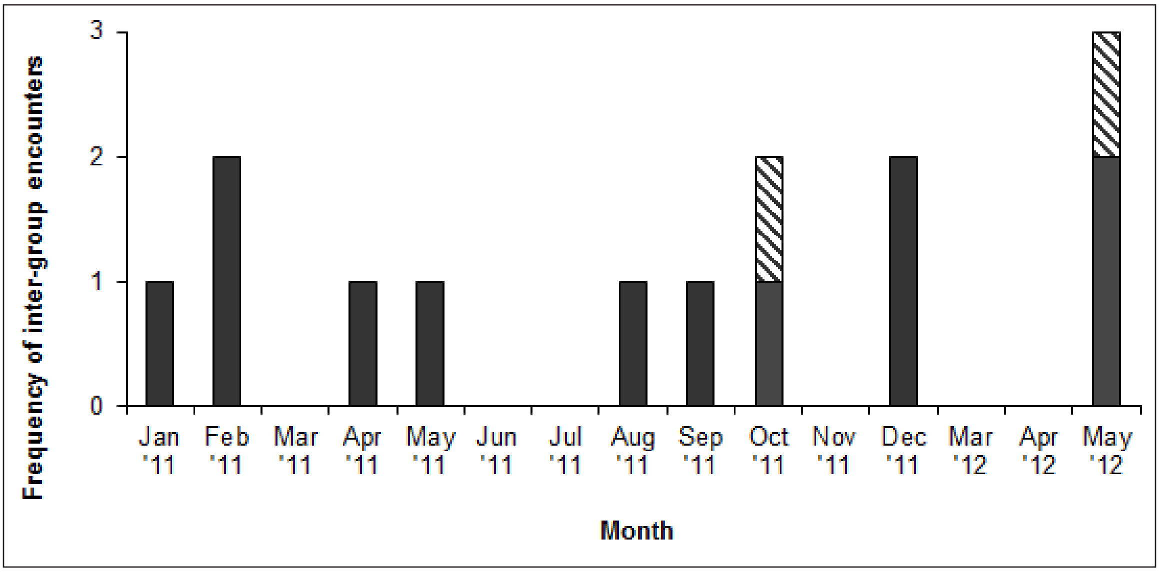
Location of feeding and sleeping tree sites

To analyze the locations of feeding and sleeping trees, I converted all GPS points of feeding and sleeping tree locations for Group KB into GIS shapefiles using the DNR GPS program v.6.0.0.11 (DNR, 2011) and projected all shapefiles into the UTM WGS_1984 49S coordinate projection. I used the Geospatial Modeling Environment suite v.0.7.1.0 and the Smooth-Cross Validation bandwidth (Beyer, 2012) to create a kernel density estimate of the feeding tree utilization distribution, and selected a 50% volume contour to represent the feeding tree core-range. I then overlaid this core range with the focal group's total home- and core-range area, as determined previously through 90% and 50% volume contours (Ehlers Smith et al., 2013b), and calculated the percentage of overlap of these respective ranges. I also overlaid the sleeping tree sites with the core home- and feeding-ranges to calculate percentage of sleeping trees located within these localities.

RESULTS

Intergroup encounters between Group KB and other groups prior to takeover

A total of 13 IGEs were recorded between Group KB and other groups across 9 of the 15 months at a rate of 1 encounter per 82.4 observation hours Fig. 1 and Fig. 2a. Of these, 85% (N=11) were with neighbouring mixed-sex groups: 46% of encounters (N=5) occurred with Group GC to the east of Group KB's home range; 27% (N=3) occurred with Group GN to the west; 18% (N=2) occurred with Group TD to the south, and a single encounter occurred with Group TN, also to the south. Two encounters occurred with an all-male group consisting of two unknown adult males, deep within the western portion of the Group KB's core range Fig. 2a. In the first case, on 11 October 2011, Group KB had climbed into an evening sleeping tree and two unknown males approached from the west loud calling. No individuals of Group KB offered response and the two males retreated in the direction they had come. In the second case, on 10 May 2012, an adult male approached as Group KB were entering their evening sleeping tree in a similar location to the first case. The invading male was aggressively chased off by the resident male of Group KB, and no other member of the group responded.



Key: Solid=encounter with a mixed-sex group; Cross-hatch=encounter with an all-male group

Fig. 1. Frequency of intergroup encounters between Group KB and other groups of *Presbytis rubicunda* across the study period in Sabangau Tropical Peat-swamp Forest between January 2011 and May 2012.

Aggression, herding and protective behaviours during IGEs

A total of 69% of encounters (N=9) involved aggressive chases by the adult males, and 85% of all encounters (N=11) involved loud calls. Only the adult males vocalized during IGEs. Two of these encounters lasted longer than 5 minutes across multiple locations: >20 minutes with Group GN and >15 minutes with Group TN (Fig. 2a). Both of these prolonged IGEs were aggressive, resulted in the retreat of the invading group, and occurred outside the core range.

Adult females were not recorded to instigate any aggressive chases, but were the recipients of aggressive chases from extra-group males in 23% (N=3) of encounters. 69% of all encounters occurred within the core range (N=9), and of these, 78% involved aggressive chases (N=7), and the invading groups retreated. 78% of encounters in the core-range were with mixed-sex groups (N=7), and of the two encounters with all-male groups within the core-range, one was aggressive (Fig. 2a).

Herding behaviour was not recorded during any intergroup encounter; however on 10 May 2012, herding behaviour was recorded prior to, but not during, an encounter with an unknown male. On 14 May 2012, the adult male was once again recorded herding Adult Female 1 and loud calling, but no physical contact was observed. No IGEs or other groups were recorded in proximity to the focal group on this day.

Occurrence of adult male takeover

On 10 May 2012, we recorded the adult male of Group KB multiple times throughout the day approaching and running in a circular direction around both adult females of the group whilst loud calling. We recorded no physical contact but the females were positioned increasingly close to each other as the male ran around them, indicating a herding behaviour. Later that day, an unknown adult male approached Group KB, but was aggressively chased away by the resident adult male. After an encounter with Group TD on 15 May 2012, Group KB was no longer seen as a complete unit and the group was not encountered for the next four days. However, the composition of Group TD remained unchanged.

On 20 May 2012, we encountered and followed the two adult females travelling alone. Upon the next encounter with the adult females on 6 June 2012, a new, unhabituated adult male was seen travelling with the group. This new male was reluctant to approach the research team but maintained proximity to the two adult females for most of the day. We subsequently followed this new group (named Group BD) over the following days, during which many loud calls were heard by both the new male and other males across the original territory of Group KB. Group BD now occupied the original territory and was using 8 of the established sleeping trees originally used by Group KB.

Between 27 and 29 May 2012, we encountered and followed the original adult male travelling with the two juvenile males of Group KB in the extreme south-east of their original territory and recorded a wound on the adult male’s right leg. On 9 June 2012, we recorded new wounds across the lower right abdomen and right leg. By 14 June 2012, the youngest juvenile was no longer recorded with the adult male and elder juvenile. The deposed males were using only the south-eastern portion of their original home-range.

Sleeping site selection

Group KB regularly revisited sleeping sites. We recorded 47 different individual trees used as sleeping sites over 96 follows that resulted in a sleeping tree. Nineteen sleeping trees were reused (40% reuse, range 2-9 revisits per tree). Group KB were highly selective in their choice of sleeping tree, using only 11 species of a total 200 that are available (~5%; S. Husson, unpublished data) (*Aglaia rubiginosa* [Hiern] Pannell, *Calophyllum sclerophyllum* Vesque, *Combretocarpus rotundatus* [Miq.] Danser, *Dactylocladus stenostachys* Oliv., *Dipterocarpus borneensis* Slooten, *Dyera polyphylla* [Miq.] Steenis, *Koompassia malaccensis* Benth., *Nephelium lappaceum* L., *Palaquium leiocarpum* Boerl., *Shorea teysmanniana* Dyer ex Brandis, *Xylopia fusca* Maingay ex Hook.f. & Thomson; N=47 trees, mean height 21-25 m, range 16-30 m; mean DBH=56.6±SD 21.8 cm, range 27-96 cm).

Group BD similarly revisited their sleeping sites. We recorded 30 different individual trees used as sleeping sites over 41 follows that resulted in a sleeping tree. Seven sleeping trees were reused (23.3% reuse, range 2-6 revisits per tree). They selected 8 species for use as sleeping trees (some ~4% of those available; S Husson et al., unpublished data), including *Calophyllum sclerophyllum*, *Combretocarpus rotundatus*, *Dactylocladus stenostachys*, *Dipterocarpus borneensis*, *Koompassia malaccensis*, *Mezzettia parviflora* Becc, *Shorea teysmanniana*, and *Tetramerista glabra* Miq. (N=41 trees, mean height 21-25 m, range 21-30 m; mean DBH=54.1±SD 20.1 cm, range 28-83 cm).

As the focal individuals were solely adult females the sleeping tree reuse is reflected as such, with all adult females and their offspring using the same sleeping site. It is worth noting, however, that the adult male consistently slept separately, in trees located within 10 m of the group's sleeping site.

Resource use, reuse and overlap

The total home range and core range of Group BD was 85.0 ha and 32.7 ha, respectively, and the total home range and core range of Group KB was 108 ha and 47 ha, respectively. The home range and core range of Group BD overlapped with that of Group KB by 75% and 43%, respectively (Fig. 2b). The core feeding-range used by Group KB constituted 36.6 ha, and overlapped with their core home-range by 79% (Fig. 3a). Of the 47 sleeping trees recorded in use by Group KB, 77% (N=36) were located within the core home-range, and 71% (N=32) occurred within the core feeding-range (Fig. 3b). Of 30 sleeping trees recorded in use by Group BD, 14 of them were also those of Group KB (47%).

DISCUSSION

Resource use

Post-takeover, Group BD maintained ~75% of Group KB's original home range and ~45% of their original core range (Fig. 2b); 47% of the sleeping tree resources were reused by Group BD. Sleeping site choice appeared to be highly selective in both groups, ith only ~4-5% of species used as sleeping trees in comparison to the total species available (E. Husson et al., unpublished data). This is the first detailed description of sleeping site selection by *P. rubicunda*. Sleeping tree sites were selected within both the core feeding- and core home-range area in >70% of cases (Fig. 3b). Both their locations and percentage of reuse support the theory that sleeping sites are defensible resources that play an important role in primate ecology, by facilitating predator avoidance (Reichard, 1998; Radespiel et al., 2003) and maintaining proximity to food resources (Chapman, 1989; Li et al., 2013). It is also worth noting that no other groups were ever recorded using a sleeping tree established by the focal group.

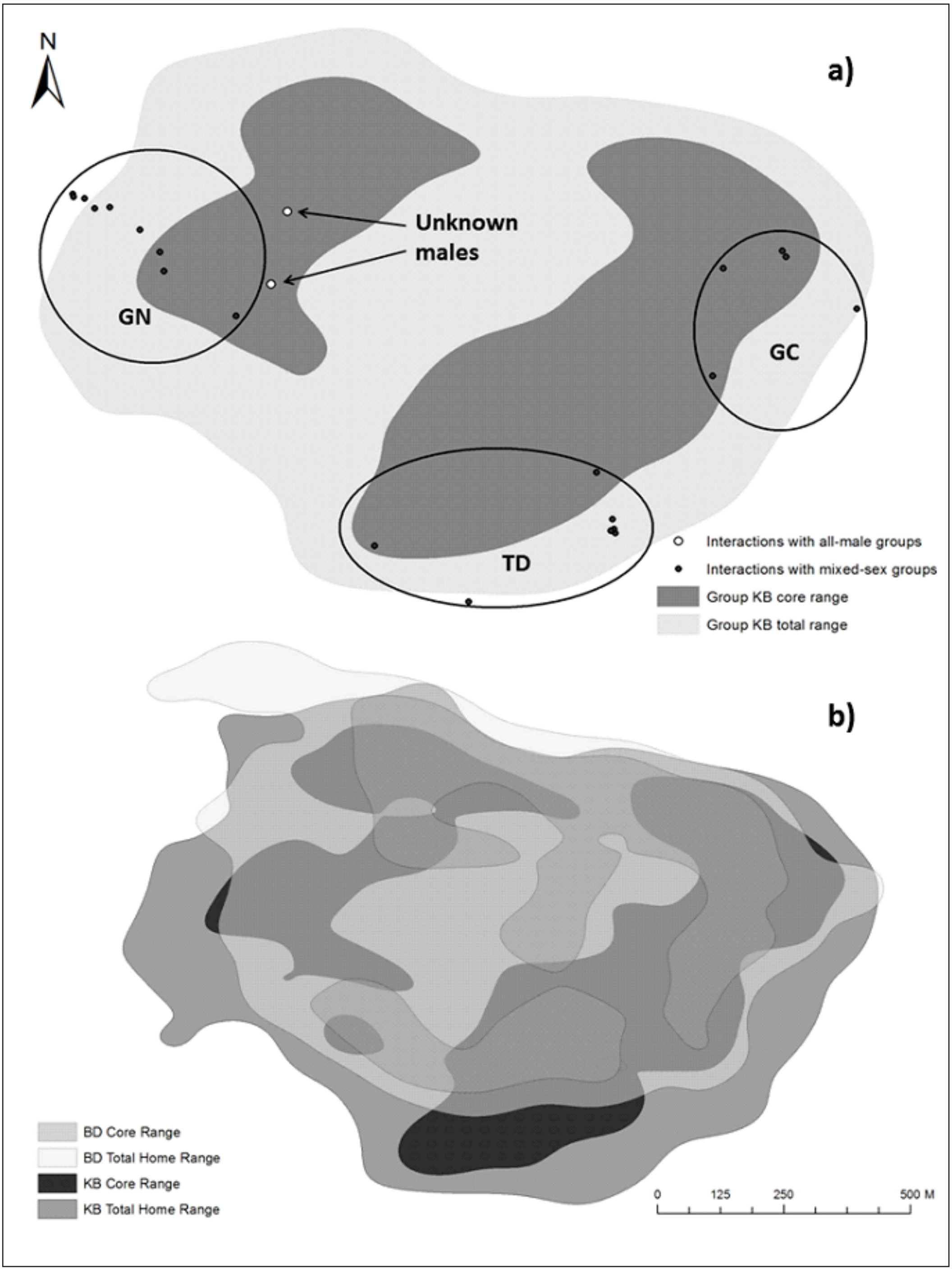
All sleeping trees were representative of the tallest genera found in this habitat sub-class of Sabangau (Page et al., 1999; Morrogh-Bernard et al., 2003). Sabangau was subject to legal logging concession until the early 2000s (Page et al., 1999; Husson et al., 2002; Page et al., 2009), which targeted the largest and most economically valuable genera (e.g. *Shorea* spp., *Dipterocarpus* spp., Husson et al., 2002). Since legal concession ended, illegal loggers took over and were less discriminate in the species extracted, instead targeting all large trees regardless of genus (Page & Reiley, 2005). Consequently, suitable sleeping sites are less available, and therefore represent important resources to be defended at this site. This, in turn, has long-term conservation implications since the selection of sleeping sites can impact each individual's chances of survival and reproductive success (Lutermann et al., 2010; Phoonjampa et al., 2010).

Intergroup encounters

Intergroup encounters were fairly evenly spread across the study period and involved mixed-sex groups in the majority of cases (Fig. 1). Adult males were the only aggressors, although adult females were occasionally the recipients of invading male aggression. The male-initiated aggression appears to affirm the first prediction that resident males would respond aggressively to invading males in the pursuit of direct mate defence. In the cases of invasions by single males or all-male bands, this prediction is particularly supported. Resident females were chased by invading males in several of the aggressive encounters, and in each case sought to avoid and flee the aggression. In most cases, the aggressive invading male held tenure of a mixed-sex group, which may have indicated an attempt to force the resident females to transfer groups. In each case, the resident male intervened to chase away the aggressor, and in at least one case, he appeared to herd his females before an aggressive encounter occurred. This provides further evidence for the first prediction that direct mate defence was the motivation behind the aggression.

Hired guns, resource reuse and indirect mate defence

One must be cautious when inferring evidence for hypotheses based on small sample sizes, such as those in this study. There is, however, the possibility for further explanation of the strategies employed, given that a) the main aggressors were males holding tenure over a mixed-sex group, and b) ~70% of aggressive encounters occurred in the core range of the focal group (Fig. 2a). Fruit is generally assumed to be more defensible than other food resources (Wrangham, 1980), and in the pursuit of fruit, which is rarer,



Note: the IGEs in the extreme top left (GN circle) and bottom right (TD circle) were respectively 20 minutes and 15 minutes in duration; thus multiple localities were recorded.

Fig. 2. Location of a) intergroup encounters between Group KB and surrounding groups of *Presbytis rubicunda* within the home range (90% density contour volumes) and core range (50% density contour volumes; Ehlers Smith 2013b) of Group KB between January 2011 and July 2012; and b) overlap of the core and total home-ranges of Group BD (light grey) and Group KB (dark grey) post-takeover between June 2012 and September 2013.

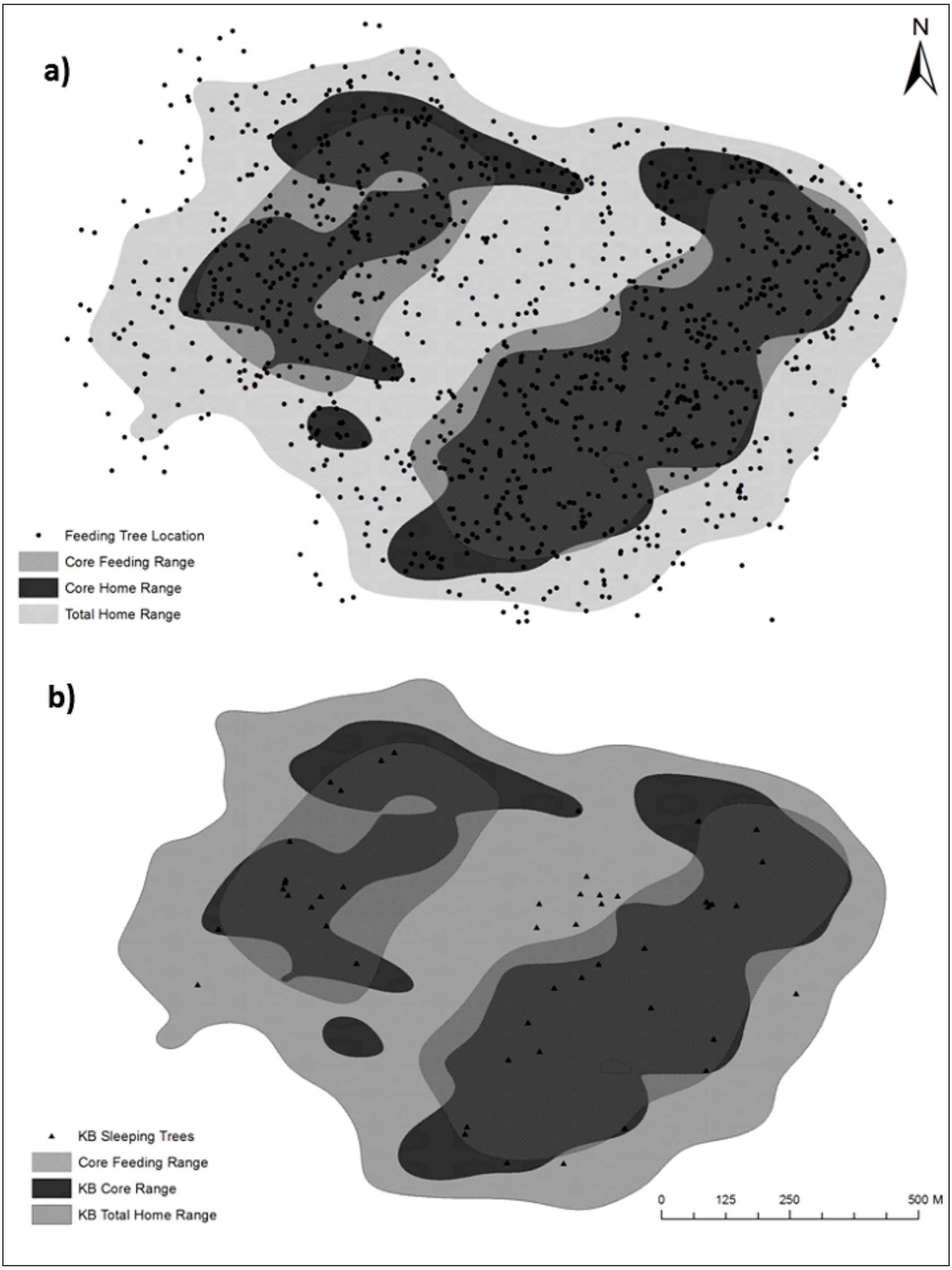


Fig. 3. Location of a) all feeding trees used by Group KB, core feeding-range (50% density contour volume) and overlap with core home-range; and b) all sleeping trees used by Group KB and overlap with core feeding- and home-ranges between January 2011 and May 2012 in Sabangau Tropical Peat-swamp Forest.

more patchily distributed and of high nutritional value, this population has the highest day-range length recorded in any folivorous primate (I refer here to the morphological adaptations of *P. rubicunda*, rather than the clearly granivorous nature of the study population; Ehlers Smith et al., 2013b). Evidence suggests that adult females lead group movements in their pursuit of nutrition (Salafsky, 1988; Stanford, 1990). Thus, females may have led their groups into the core range of Group KB to obtain high quality food resources, and incited aggressive IGEs between the resident and invading males. However, the second prediction that resource defence was the motivation behind aggression is not supported, as no females from either the resident or the invading groups participated in the aggression at any time. Instead, there is support for the third prediction that females may have benefitted from indirect resource defence, as males aggressively defended the females in their territory, and in turn, acted as hired guns in the defence of food resources in the core areas (Rubenstein, 1986). To the best of my knowledge, this represents the first preliminary evidence for this strategy in the genus *Presbytis*. Home-range data from the neighbouring groups, including the location and nature of IGEs, are unfortunately lacking here, but may further elucidate the context of encounter strategies and should be considered a priority for further research.

Again, with respect to caution when inferring support for a hypothesis based on a small sample size, there may also be preliminary evidence for the fifth prediction of indirect mate defence via male resource defence, as provided by the tenure change. After the successful deposal of the resident male of Group KB, the females transferred to the invading male, who then established tenure in the deposed male's territory and proceeded to defend ~75% of the original area and ~50% of the sleeping tree resources therein for the females to continue to reuse. Male-male aggression appeared to continue between the deposed and the invading adult male post-tenure change as new wounds were recorded in conjunction with a high frequency of loud calling for several days, indicating that tenure and territory had been aggressively established, and providing evidence for resource defence polygyny (Emlen & Oring, 1977). This formation of a group that contained the adult and juvenile males post-tenure-change is consistent with that reported in Sepilok, Sabah (Davies, 1987) where the deposed male maintained tenure of his parous females and his juvenile male offspring, and is likely a result of the independent status of the juveniles from their mothers.

Fashing (2001) presents a hypothesis to predict when male primates living in single-male multi-female groups are expected to employ the indirect mate defence strategy that describes 3 criteria: 1) "food must be limited and distributed in defensible patches (Wrangham, 1980; van Schaik, 1989); 2) groups must include relatively small numbers of females and/or females exhibiting oestrous asynchrony so that the females are virtually reproductively monopolizable; 3) females are expected to choose to mate with males that defend resources, and to transfer to other groups once the male in their group begins to defend resources poorly" (Fashing, 2001, 227-228). In the Sabangau population of *P. rubicunda*, each of these criteria are fulfilled, which strengthens the evidence found in the small sample size provided, and further supports the fifth hypothesis. Criterion 1 is fulfilled given that seeds and fruit parts constitute >80% of the annual diet (Ehlers Smith et al., 2013a) and that the focal group has the largest day range recorded in any 'folivorous' primate (mean 1,645 m per day; max 2,041 m per day), apparently in the pursuit of fruits (Ehlers Smith et al., 2013b). Criterion 2 is also fulfilled given females do not exceed 3 individuals per group (Ehlers Smith & Ehlers Smith, 2013) and females do not exhibit oestrous synchrony (DA Ehlers Smith, unpublished data). Evidence for criterion 3 is provided in the group takeover and transfer of the females to the invading male. Thus, this study also represents the first preliminary evidence of indirect mate defence via male resource defence in the genus *Presbytis* to the best of my knowledge.

Conclusions

The evidence for direct mate defence as the motivation for aggressive IGEs was supported in the majority of cases. However, given that resources in this population may be defensible, and that most of the aggressive encounters occurred within the core range of the focal group, it is likely that the females of the group further benefited from indirect resource defence as a result of the aggressive protection provided by the resident male as a hired gun. Post-takeover, the invading male established himself in the territory of the resident females, who then continued to use the resources therein. The study group fulfills the 3 criteria proposed by Fashing (2001) to predict indirect mate defence; thus, there is also preliminary evidence for indirect mate defence by the invading male in his pursuit of reproductive access to females. The findings of this study are consistent with the assertion that the hypotheses seeking to explain the nature of intergroup aggression in primates are not mutually exclusive.

Table 1. Overview of hypotheses to explain the nature of intergroup encounters, and evidence for the predictions in this study.

Hypothesis	Prediction	Evidence
1: Direct mate defence	Only males should participate in intergroup aggression; male-male aggression should most likely be between a resident male and all-male bands/single males; resident male should seek to protect the resident females, engage in herding behaviour; aggressive encounters just as likely to occur outside core range as inside	Yes - adult males were the only aggressors; aggression occurred between the resident group and all-male bands; apparent herding of females before aggressive encounter occurred but majority (~70%) of aggressive encounters occurred inside core range
2: Direct food defence	Females should be more likely to participate in intergroup aggression; resident females should direct aggression to all invading group members, and aggressive encounters should be more likely to occur inside the 'core range'	No
3: Indirect food defence via hired guns	Resident males should participate in intergroup aggression toward extra-group males; aggressive encounters should occur within the core range; no female participation	Yes - main aggressors were males holding tenure over a mixed-sex group; majority of the aggressive encounters occurred in core range of the focal group; no female participation in aggressive encounters
4: Mate attraction via infanticide	Invading males should act aggressively toward resident females and attempt to kill their offspring; females with infants should attempt to avoid IGEs and behave defensively, and females would transfer to invading males that successfully achieved infanticide	No
5: Indirect mate defence via male resource defence	Resident males should participate in intergroup aggression toward extra-group members; the male should defend resources within the territory for the benefit of the females to use	Yes - after deposal of the resident male, transference of females to invading male who established tenure in the deposed male's territory where reuse of resources occurred

ACKNOWLEDGEMENTS

I thank the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA) and the Center for the International Cooperation in Sustainable Use of Tropical Peatlands (CIMTROP) for research permissions. Funding was provided by Chester Zoo and the North of England Zoological Society, Columbus Zoo and Aquariums, Primate Conservation, Inc. and the Orangutan Tropical Peatland Project (OuTrop). CIMTROP provided essential logistical support. I would like to thank all field researchers who assisted in data collection: Supian Sabangau; Abdul Azis; Yvette Ehlers Smith; Karen Jeffers; Camille Hill; Helen Thompson; Claire Neale; Emma Jackson; Nick Marchant; Bernat Ripoll; Luke Ward, and Ben Buckley. Thanks also to Dr Suwido H. Limin; Dr Susan M. Cheyne, and Professor Vincent Nijman, and to three anonymous reviewers for their helpful comments that greatly improved the manuscript.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**: 227-267.

Beyer, H.L. 2012. Geospatial modeling environment (Version 0.7.1.0). <http://www.spatialecology.com/gme>. Downloaded on 24 May 2012.

Borries, C.B. 1997. Infanticide in seasonally breeding multi-male groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (south Nepal). *Behavioral Ecology and Sociobiology* **41**: 139-150.

Borries, C.B, Launhardt, K., Epplen, C., Epplen, J.T. and Winkler, P. 1999. DNA analyses support the hypotheses that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society B* **266**: 901-904.

Chapman, C.A. 1989. Spider monkey sleeping sites: use and availability. *American Journal of Primatology* **18**: 53-60.

Conradt, L. and Roper, T.J. 2003. Group decision-making in animals. *Nature* **421**: 155-158.

Conradt, L. and Roper, T.J. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution* **20**: 449-456.

Conradt, L. and Roper, T.J. 2007. Democracy in animals: the evolution of shared group decisions. *Proceedings of the Royal Society B* **274**: 2317-2326.

Curtin, S.H. and Dolhinow, P.J. 1979. Infanticide among langurs: a solution to overcrowding. *Science Today* **13**: 35-41.

Davies, A.G. 1987 Adult male replacement and group formation in *Presbytis rubicunda*. *Folia Primatologica* **49**: 111-114.

Di Bitetti, M.S., Vidal, E.M.L., Baldovino, M.C. and Benesovsky, V. 2000. Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology* **50**: 257–274.

Ehlers Smith, D.A. and Ehlers Smith, Y.C. 2013. Population density of red langurs in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesia. *American Journal of Primatology* **75**: 837-847.

Ehlers Smith, D.A., Husson, S.J., Ehlers Smith, Y.C. and Harrison, M.E. 2013a Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *American Journal of Primatology* **75**: 848-859.

Ehlers Smith, D.A., Ehlers Smith, Y.C. and Cheyne, S.M. 2013b. Home-range use and activity patterns of *Presbytis rubicunda* in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesian Borneo. *International Journal of Primatology* **34**: 957-972.

Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215-223.

Erhart, E.M. and Overdorff, D.J. 1999. Female coordination of group travel in wild *Propithecus* and *Eulemur. International Journal of Primatology* **20**: 927-940.

Fashing, P.J. 2001. Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology* **50**: 219-230.

Fashing, P.J. 2011. African colobine monkeys: patterns of between-group interaction. **In**: *Primates in Perspective 2nd* Edition, C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger and S.K. Bearder, (eds.), pp. 203-229. Oxford University Press, Oxford, UK.

Grueter, C.C., Li, D., Ren, B., Wei., F. and van Schaik, C.P. 2009. Dietary profile of *Rhinopithecus bieti* and its socioecological implications. *International Journal of Primatology* **30**: 601-624.

Harris, T.R. and Monfort, S.L. 2003. Behavioral and endocrine dynamics associated with infanticide in a black and white colobus monkey (*Colobus guereza*). *American Journal of Primatology* **61**: 135-142.

Harris, T.R. 2010. Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). *Animal Behaviour* **79**: 89-98.

Heymann, E.W. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia, Primates, Callitrichidae), in north-eastern *Peru. Journal of Zoology* (*London*) **237**: 211-226.

Hrdy, S.B. 1977. *The Langurs of Abu*. Harvard University Press, Cambridge, UK.

Husson, S.J., Morrogh-Bernard, H., McLardy, C., Driscoll, R., Fear, N.F. and Page, S.E. 2002. The effects of illegal logging on the population of orangutan in the Sebangau tropical peat swamp forest, Central Kalimantan. **In**: *Peatlands for People: Natural Resource Functions and Sustainable Management.* J.O. Rieley and S.E. Page (eds.). Proceedings of the international symposium on tropical peatland, 22-23 August 2001, Jakarta, Indonesia, BPPT and Indonesian Peat Association, Jakarta.

Kirkpatrick, R.C. 2011. The Asian colobines: diversity among leaf-eating monkeys. **In**: *Primates in Perspective 2nd* Edition, C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger and S.K. Bearder (eds.), pp. 189-202. Oxford University Press, Oxford, UK.

Li, D., Grueter, C.C., Ren, B., Li, M., Peng, Z. and Wei, F. 2013. Distribution of sleeping sites of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) in the Samage Forest, China. *Integrative Zoology* **8**: 327-334.

Lutermann, H., Verburgt, L. and Rendigs, A. 2010. Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour* **79**: 1211-1219.

Medway, L. 1970. The monkeys of Sundaland. **In**: *Old World Monkeys*, J.R. Napier and P.H. Napier (eds.), pp. 513-554. Academic Press, New York.

Mitani, J.C. and Rodman, P.S. 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology* **5**: 241-251.

Oates, J.F. 1977. The social life of a black-and-white colobus monkey, *Colobus guereza. Zeitschrift fur Tierpsychologie* **45**: 1-60.

Onderdonk, D.A. 2000. Infanticide of a newborn black-and-white colobus monkey (*Colobus guereza*) in Kibale National Park, Uganda. *Primates* **41**: 209-212.

Page, S.E. and Rieley, J.O. 2005. *Wise Use Guidelines of Tropical Peatlands: Focus on Southeast Asia*. Alterra Publishers, Wageningen, Netherlands.

Page, S.E., Rieley, J.O., Shotyk, Ø.W. and Weiss, D. 1999. Interdependence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society B* **354**: 1885-1897.

Page, S.E., Hoscilo, A., Wosten, H., Jauhiainen, J., Ritzema, H., Tansey, K., Silvius, M., Graham, L., Vasander, H., Rieley, J. and Limin, S. 2009. Ecological restoration of lowland tropical peatlands in Southeast Asia – current knowledge and future research directions. *Ecosystems* **12**: 888-905.

Petit, O. and Bon R. 2010. Decision-making processes: the case of collective movements. *Behavioural Processes* **84**: 635-647.

Phoonjampa, R., Koenig, A., Borries, C., Gale, G.A. and Savini, T. 2010. Selection of sleeping trees in pileated gibbons (*Hylobates pileatus*). *American Journal of Primatology* **72**: 617-625.

Radespiel, U., Ehresmann, P. and Zimmermann, E. 2003. Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus and M. ravelobensis*) in northwestern Madagascar. *American Journal of Primatology* **59**: 139–151.

Reichard, U. and Sommer, V. 1997. Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation, and the concept of infanticide. *Behaviour* **134**: 1135-1174.

Reichard, U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbon (*Hylobates lar*). *American Journal of Primatology* **46**: 35-62.

Rubenstein, D.I. 1986. Ecology and sociality in horses and zebras. **In**: *Ecology and Social Evolution: Birds and Mammals*, D.I. Rubenstein and R.W. Wrangham (eds.), pp. 282-302. Princeton University Press, Princeton, USA.

Rudran, R. 1973. Adult male replacement in one-male troops of purple faced langurs (*Presbytis senex*) and its effect on population structure. *Folia Primatologica* **19**: 166-192.

Saj, T.L. and Sicotte, P. 2005. Male takeover of a bisexual group in *Colobus vellerosus* at Boabeng Fiema MS, Central Ghana. *Primates* **46**: 211–214.

Salafsky, N.N. 1988. *The foraging patterns and socioecology of the kelasi* (*Presbytis rubicunda*). MSc dissertation, Harvard, Cambridge, MA, USA.

Sicotte, P. and MacIntosh, A.J. 2004. Intergroup encounters and male incursions in *Colobus vellerosus* in central Ghana. *Behaviour* **141**: 533-553.

Sicotte, P., Teichroeb, J.A. and Saj, T.L. 2007. Aspects of male competition in *Colobus vellerosus*: preliminary data on male and female loud calling, and infant deaths after a takeover. *International Journal of Primatology* **28**: 627–636.

Spironello, W.R. 2001. The brown capuchin monkey (*Cebus apella*): ecology and home range requirements in Central Amazonia. **In**: *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, R.O. Bierregaard, C. Gascon, T.E. Lovejoy and R. Mesquita (eds.), pp. 271-283. Yale University Press, New Haven, USA.

Stanford, C.B. 1991. The capped langur in Bangladesh: behavioral ecology and reproductive tactics. *Contributions to Primatology* **26**: 1-179.

Steenbeck, R. 1999. Tenure related changes in wild Thomas's langurs I: between-group interactions. *Behaviour* **136**: 595-625.

Steenbeck, R., Assink, P. and Wich, S.A. 1999. Tenure related changes in wild Thomas' langurs II: loud calls. *Behaviour* **136**: 626-665.

Sterck, E.H.M. 1995. *Females, foods and fights*. PhD dissertation, University of Utrecht, Utrecht, Netherlands.

Supriatna, J., Manullang, B.O. and Soekara, E. 1986. Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates* **27**: 185-190.

Trivers, R.L. 1972. Parental investment and sexual selection. **In**: *Sexual Selection and the Descent of Man*, B. Campbell (ed.), pp. 136-179. Adeline Press, Chicago, USA.

Van Belle, S., Estrada, A. and Garber, P.A. 2013. Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology* **67**: 31-41.

van Schaik, C.P. 1989. The ecology of social relationships amongst female primates. **In**: *Comparative socioecology: The Behavioral Ecology of Humans and Other Mammals*, V. Standen and R.A. Foley (eds.), pp. 195-218. Blackwell Publishers, Oxford.

van Schaik, C.P. 1996. Social evolution in primates: the role of ecological factors and male behaviour. *Proceedings of the British Academy* **88**: 9-31.

van Schaik, C.P., Assink, P.R. and Salafsky, N. 1992. Territorial behaviour in Southeast Asian langurs: resource defence or mate defence? *American Journal of Primatology* **26**: 233-242.

van Schaik, C.P. and Janson, C.H. 2000. *Infanticide by Males and its Implications*. Cambridge University Press, Cambridge, UK.

Wich, S.A. and Sterk, E.H.M. 2010. Thomas langurs: ecology, sexual conflict and social dynamics. **In**: *Indonesian Primates. Developments in Primatology: Progress and Prospects*, J. Supriatna and S. Gursky-Doyen (eds.), pp. 285-309. Springer Science, Chicago, USA.

Williams, J., Oehlert, G.W., Carlis, J.V. and Pusey, A. 2004. Why do male chimpanzees defend a group range? *Animal Behaviour* **68**: 523-532.

Wrangham, R.W. 1980. An ecological model of female-bonded primate groups. *Behaviour* **75**: 262-300.

Wrangham, R.W. and Rubenstein, D.I. 1986. Social evolution in birds and mammals. **In**: *Ecology and Social Evolution: Birds and Mammals*, D.I. Rubenstein and R.W. Wrangham (eds.), pp. 452-470. Princeton University Press, Princeton, USA.

Asian Primates Journal 4(2), 2014

POPULATION DENSITY OF *Presbytis rubicunda* IN A SMALL PRIMARY DIPTEROCARP FOREST IN EAST KALIMANTAN, INDONESIAN BORNEO

Elena Bersacola[1*], David A. Ehlers Smith[1,2], Wiwit J. Sastramidjaja[3], Yaya Rayadin[4] and Susan M. Cheyne[2,5]

[1] Faculty of Humanities and Social Sciences, Oxford Brookes University, Headington Campus, Gipsy Lane, Oxford, OX3 0BP, UK. E-mail: hellenbers@gmail.com

[2] Orangutan Tropical Peatland Project, Jl. Semeru 91, Palangka Raya, 73112, Central Kalimantan, Indonesia. E-mail: dehlers-smith@outrop.com

[3] E-mail: wiwitjuwita@gmail.com

[4] Pusat Studi Reboisasi Hutan Tropis Lembab, Universitas Mulawarman, Jl. Kihajar Dewantara Kampus Gunung Kelua Samarinda, Samarinda, 75123, East Kalimantan, Indonesia. E-mail: yrayadin@yahoo.com

[5] Wildlife Conservation Research Unit (WildCRU), Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon, OX13 5QL, UK. E-mail: susan.cheyne@zoo.ox.ac.uk

[*] Corresponding author

ABSTRACT

Tropical rainforests on Borneo are rapidly shrinking due to human activities and related fires. Monitoring wildlife populations in their remaining habitats is crucial for developing effective conservation strategies. In 2012, we conducted surveys in Balikpapan Bay within the Sungai Wain forest, Indonesia, to estimate the population density of Maroon Langur *Presbytis rubicunda* (Müller, 1838). We surveyed Sungai Wain's primary core area using distance sampling of line transects, and assessed the vegetation structure using 100 m^2 square plots. We calculated density of *P. rubicunda* at 5.35 groups/km^2 (95% CI=3.4-8.43). Cluster size ranged between two and eight individuals and group size averaged 5.2 individuals (SE=1.4). The habitat within the core area of Sungai Wain appears suitable to support a high density of this colobine. Anthropogenic activities in the surrounding areas, as well as encroachment and illegal logging within the regenerating habitat, could become threats for *P. rubicunda* in Sungai Wain. This forest represents an important refuge for this primate in Balikpapan Bay. We recommend further surveys in degraded and regenerating forests to quantify the remaining suitable habitat for *P. rubicunda* in East Kalimantan.

Keywords: Colobinae, conservation, distance sampling, habitat, langur, refuge

INTRODUCTION

Tropical rainforests in Southeast Asia have decreased massively since 1990 (Stibig et al., 2014). For example, between 2000 and 2010 the total forested area on Borneo decreased by 12% with a mean annual forest cover loss of 1.3% (Miettinen et al., 2011). Human activities such as logging, mining, habitat conversion for oil palm plantations, as well as an increase in magnitude of *El Niño* droughts and fires, are the driving causes of deforestation (Curran et al., 1999; Sodhi et al., 2004). Except for the Maroon Langur *Presbytis rubicunda* (Müller, 1838), all endemic primates of Borneo are considered threatened, and are classified as either Vulnerable, Endangered or Critically Endangered by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2013). *Presbytis rubicunda* is believed to be widespread and may persist in degraded habitats; however, the population is decreasing due to habitat loss and hunting for medicine (Nijman & Meijaard, 2008). Densities of *P. rubicunda* in Kalimantan differ across habitats and study sites (Davies, 1984; McConkey & Chivers, 2004; Marshall, 2010; Nijman & Nekaris, 2012; Ehlers Smith & Ehlers Smith, 2013), but in disturbed habitats or at high elevations (>750 m) group densities of this species generally decrease and populations may not be viable (Blouch, 1997; Marshall, 2010).

In 2012, we conducted a survey in the Sungai Wain Protection Forest (SWPF), Indonesia. The SWPF is located within Balikpapan Bay, a large lowland ecosystem that extends to the Mahakam River, about 70 km north of Sungai Wain (Wilson & Wilson, 1975; Stark et al., 2012). Part of the forest outside the SWPF was already selectively logged and encroached upon by humans in the 1970s (Wilson & Wilson, 1975), and was later affected by the *El Niño* fires in 1982-83 (Cleary & Genner, 2004). In 1998, subsequent fires were started at a nearby logging concession and quickly spread inside the SWPF (Fredriksson, 2002). The 1998 fires caused further change in the forest structure, reducing the primary habitat to a 40 km^2 core area. Most of the core area's surrounding habitat consisted of burned forest, with intact fragments along rivers (Fredriksson, 2002). It is likely that during and after the fires, primates and other animals relied on these intact fragments and the core area for refuge, thus altering their density and ranging patterns (S. Lhota, pers. comm.). Over the subsequent seven years following the 1998 fires, the vegetation structure and species composition of burned areas changed substantially (Fredriksson et al., 2006; Slik et al., 2011). Pioneer species such as *Macaranga gigantea* (Rchb.f. & Zoll.) Müll.Arg. dominated the landscape (Slik et al., 2008). Canopy cover and tree diversity began to increase in more recent years, and in 2010 there were indications that Malayan Sun Bears *Helarctos malayanus* (Raffles, 1821) were gradually moving back to the regenerating forest (Fredriksson et al., 2012).

According to the IUCN Red List of Threatened Species, the average density of *P. rubicunda* across Borneo is estimated to be 2.6 (SD ± 1.4) groups/km^2 (Nijman & Meijaard, 2008). No density estimate is available for *P. rubicunda* in the SWPF prior the 1998 fires; but surveys conducted there in 1999-2005 indicated a high density of this primate, with 3.3 groups/km^2 (Nijman & Nekaris, 2012). The aim of our study was to obtain a new population density estimate of *P. rubicunda* in the SWPF and identify possible conservation threats to the population present in the area. We also hope that our data help encourage local and national authorities to increase their efforts to protect the remaining forests of this region.

METHODS

We acquired all the relevant permits and visas for the research from the Indonesian State Ministry of Research and Technology (RISTEK), adhering to Indonesian legislation. Our research was purely observational in nature. We collected data between May and July 2012.

Study area

The SWPF (S1°16', E 116°54') occupies an area of approximately 100 km^2 (Fig. 1), and is located within the administrative area of Balikpapan, Kalimantan's second largest city and the second major oil production and commerce centre in Indonesia. The SWPF is categorised as *Hutan Lindung*, meaning that it does not have official protection but was established to be managed as a water catchment area for the oil company 'Pertamina' in Balikpapan. The SWPF is part of the Balikpapan Bay ecosystem, which consists of a network of freshwater rivers, marine waters, mangroves, dipterocarp as well as other non-mangrove forests (Stark et al., 2012). It is characterised by high biological diversity, and taxa present in Balikpapan Bay include Sunda Clouded Leopard *Neofelis diardi* (G. Cuvier, 1823), Proboscis Monkey *Nasalis larvatus* (Wurmb, 1787) and the Critically Endangered Mahakam River subpopulation of Irrawaddy Dolphin *Orcaella brevirostris* (Owen in Gray, 1866). Road construction, logging and the increase in magnitude of fires due to deforestation are major conservation threats in Balikpapan Bay, as animal populations and habitats are becoming increasingly fragmented. At present, the SWPF's core area is the largest lowland primary forest left in the south-eastern part of East Kalimantan (Fredriksson, 2002).

The study site (20 km^2) lies within the northern part of the primary forest within the 40 km^2 core area. We used a system of thirteen parallel-line transects, which were already established prior to our study. The transects were set 70-600 m apart (average=286.8 m, SD=121.1) and were 1.70-2.06 km in length (Average=1.99 km, SD=0.11). The forest within the transect system was a mixture of humid and dry hilly dipterocarp forest, with occasional small swamp forest patches. The average annual rainfall in the SWPF is 2790 mm (Simbolon et al., 2012).

Study species

Presbytis rubicunda is a medium-bodied, gracile arboreal colobine (males 6.3 kg, females 6.0 kg; Davies & Payne, 1982) endemic to the island of Borneo and the adjacent Karimata Island (Nijman & Meijaard, 2008). They live in single-male, multi-female groups ranging from 3 to 12 individuals (Supriatna et al., 1986; Davies, 1987; Ehlers Smith & Ehlers Smith, 2013), and extra-group males typically form all-male bands or travel alone (Davies, 1987; Ehlers Smith & Ehlers Smith, 2013). *Presbytis rubicunda* has been observed mainly feeding on fruits, seeds and young leaves, with the proportions of consumption of these items vary-

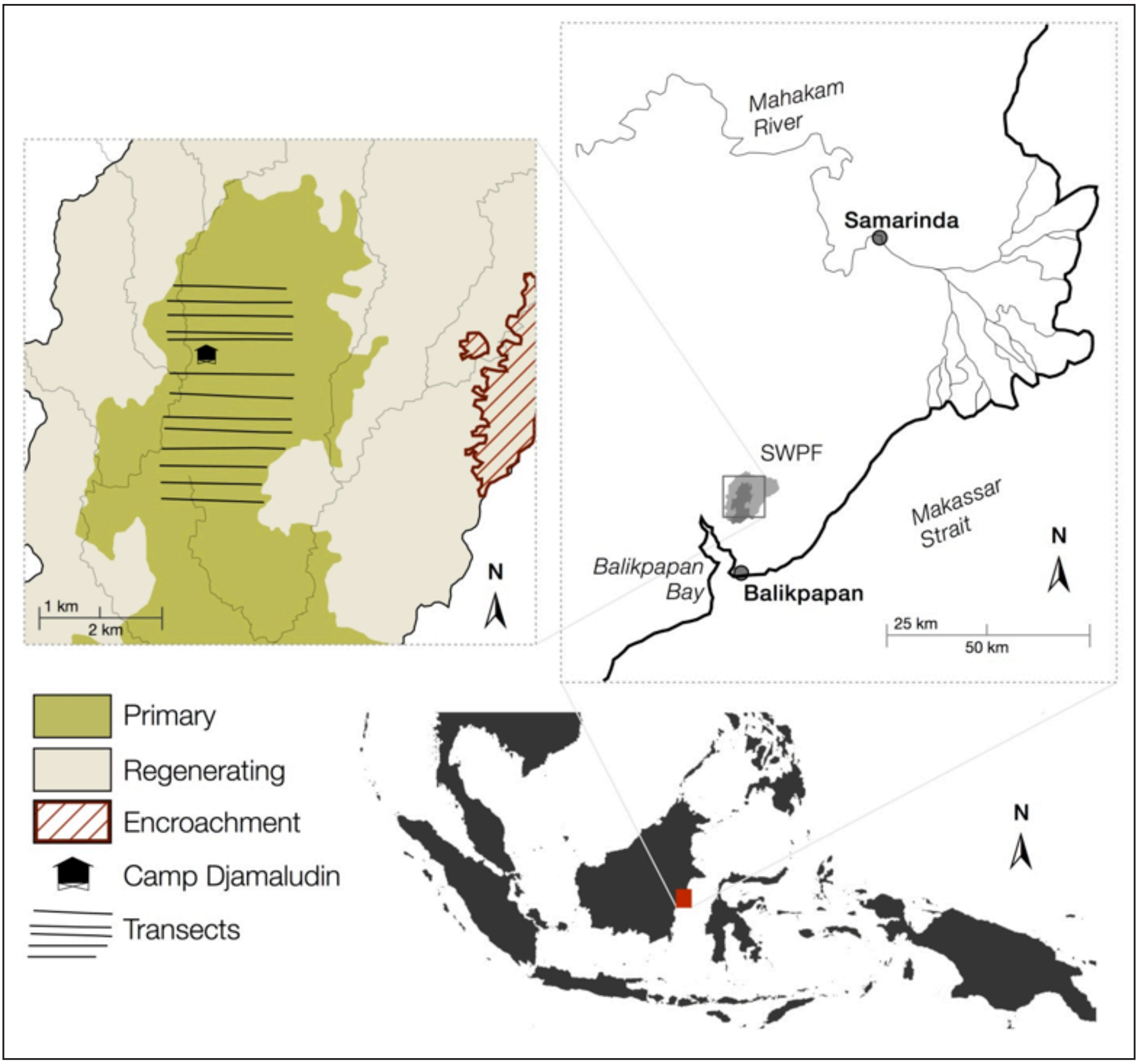


Fig. 1. Map and location of study site.

ing across sites (Supriatna et al., 1986; Davies et al., 1988; Davies, 1991; Marshall, 2004; Hanya & Bernard, 2012; Ehlers Smith et al., 2013b). Home ranges of this species were reported at a number of sites, ranging from 0.33 ha in Tanjung Puting (Supriatna et al., 1986) to 108.3 ha in Sabangau Forest (Ehlers Smith et al., 2013a)

Transect surveys

To monitor wild population trends over time and understand changes in ecological patterns, repeated surveys must be conducted using standardised methods. The importance of repetitive surveys using identical methods to identify a population trend is highlighted by previous studies (Mitani et al., 2000; Mbora & Meikle, 2004). Distance sampling is based on the detection function *g(y)*, i.e., the statistical probability of seeing an object at a ≥0 m distance from the transect line (Buckland et al., 2001), and is considered an effective method for estimating and monitoring densities of various taxa, such as deer (Focardi et al., 2005), birds (Marques et al., 2007) and primates (Johnson et al., 2005; Ehlers Smith & Ehlers Smith, 2013). Analysis with the program DISTANCE (Thomas et al., 2010) enables users to choose different parameters to obtain a fit between the statistical model and the survey data.

We estimated population density of *P. rubicunda* using distance sampling on line transects (Buckland et al., 2001; Thomas et al., 2010). We walked thirteen parallel transects in two or three teams simultaneously, maintaining >750 m distance between teams during all surveys. All team members conducted prior practice surveys and one week of training on data collection with an established survey protocol. During surveys we measured distances visually, as the use of laser range finders could not provide us with true distances because of the dense structure of the forest. To ensure that distances were recorded precisely and to reduce researcher bias, we carried out distance training with the aid of a measuring tape and laser range finder every 4-5 days throughout the study period.

At each detection of *P. rubicunda* we collected the following data: group size, group spread, distance between the observer and the centre of the group, compass bearing of the centre of the group and the transect (later calculated to angle and then perpendicular distance), height above ground of observed animals, group composition and response behaviour to our presence. We recorded all data at the animals' initial location. As *P. rubicunda* is known to split into subgroups for foraging during the day (Supriatna et al., 1986), we considered all animals encountered within 100 m of the first detection as the same group, thus as a single sighting event. We walked two transects per team; one in the morning between 06:30 and 11:00 h and one in the afternoon between 13:30 and 18:00 h, at an average walking speed of ~1 km/h. We did not conduct surveys during midday hours, rainy days or strong wind as *P. rubicunda* becomes less active during these periods, thus reducing detectability (DA Ehlers Smith, pers. obs.). Where possible, we followed and observed the langurs until we could obtain full group counts. On 17 of such encounters we were able to observe groups gathering and remaining on emergent trees for approximately 20 minutes; thus were confident that all animals in the group were counted.

Vegetation sampling

To measure habitat characteristics we established 73 plots, a sample size considered large enough to obtain a good representation of the habitat within the study site (Ganzhorn, 2003). Plots measured 10 m x 10 m, and were systematically located on both sides of transect lines at a minimum distance of 30 m from each other to ensure sampling independence. To assess vegetation structure we recorded the following data: diameter at breast height (DBH) of all the ≥10 cm DBH trees, height of all ≥10 DBH trees (measured on an ordinal scale: 1-5 m, 6-10 m, etc.) and total number of trees (Ganzhorn, 2003; Hamard et al., 2010).

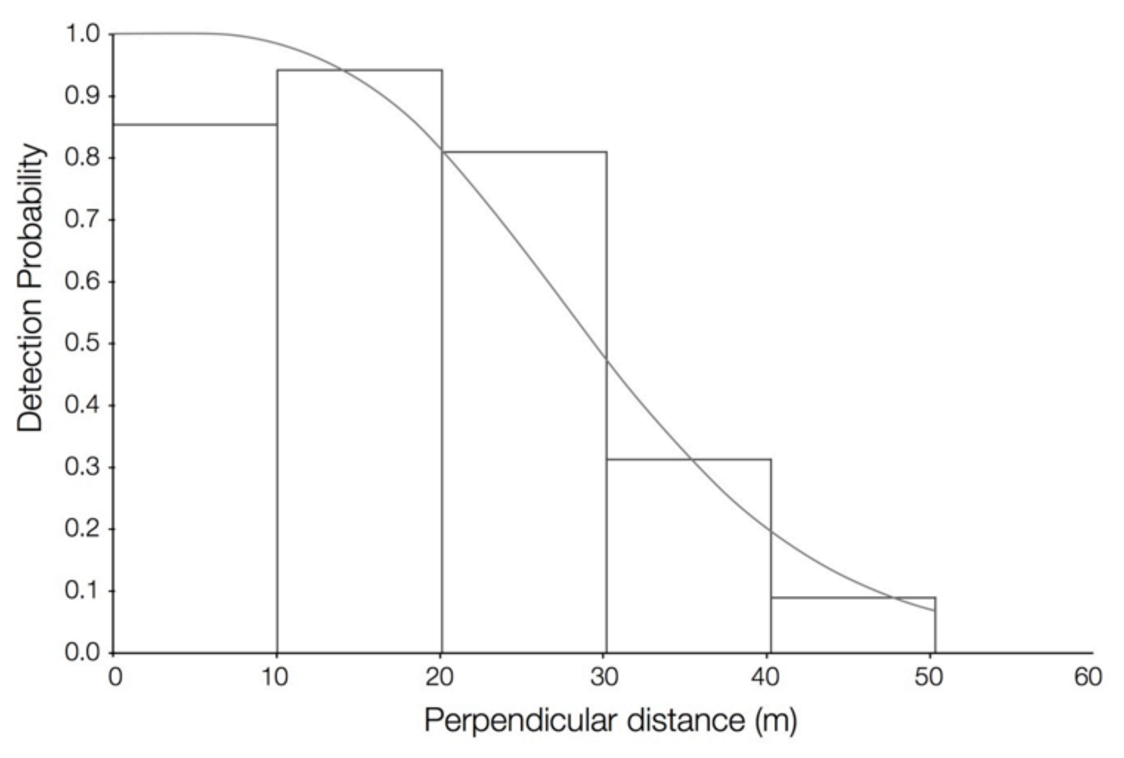


Fig. 2. Estimated detection function for *P. rubicunda* based on the best model computed in DISTANCE.

Data analysis

We entered survey data into DISTANCE v. 6.0 (Thomas et al., 2010), and evaluated a number of models for selecting the one with the best fit. We analysed the survey data using three detection probability functions: uniform, half-normal and hazard rate, with and without cosine and simple polynomial adjustments. Upon a visual inspection of the sighting distances histograms (Fig. 2), we discarded the outermost observations by selecting a right truncation (32-50.4 m) to eliminate obvious outliers (Buckland et al., 2001). Cut points were maintained at equal sighting distance intervals. We used the Akaike's Information Criterion (AIC) and assessed the delta AIC as an indicator for selecting the model (Buckland et al., 2001; Burnham & Anderson, 2002).

To estimate the mean cluster size we used the size-bias regression computed by the software DISTANCE, which tests the observed cluster size against the estimated detection probability (Buckland et al., 2001). In addition, we considered that mean cluster size was likely to be underestimated due to the difficulty in detecting all animals in the group during census in a dense forest (Hassel-Finnegan et al., 2008). Therefore we calculated the average number of individuals/km^2 and abundance both with the mean cluster size (3.88, SE±0.25) as well as from the mean group size calculated from observations where full group counts were obtained.

RESULTS

There was no significant difference in the number of observations of *P. rubicunda* (N_1=26, N_2=26, N_3=17; chi-square: $\chi^2(2)=2.348$, p=0.309), and in the means of estimated perpendicular distances (ANOVA: F(2, 66)=0.211, p=0.810) across the three survey teams. The estimated cluster size did not differ across the three survey teams (Kruskal-Wallis: H(2)=0.884, p=0.643), as well as across transect lines (Kruskal-Wallis: H(12)=19.701, p=0.073). We also found no correlation between estimated perpendicular distances and cluster sizes (N=69) (Spearman's: r_s=0.007, p=0.956), thus we concluded there was no inter-observer bias in the sighting data.

Population density

We surveyed 13 line transects for a total effort of 207.12 km. During the surveys we observed 69 groups of *P. rubicunda*, with a mean encounter rate of 0.32 groups/km surveyed (95% CI=0.26-0.40). Observed mean cluster size was estimated to be 3.76 individuals (SE=0.20). Based on the size-bias regression computed by DISTANCE, the expected cluster size was estimated at 3.88 individuals (SE=0.25). All six models selected as the potential best ones displayed a delta AIC <2 (Burnham & Anderson, 2002). Differences between Akaike weights were minimal (<0.01). The half-normal key with cosine adjustments had the lowest AIC (195.13) and was thus chosen as the most suit-

Table 1. Density estimates obtained from various models as computed by DISTANCE v. 6.0

Model (adj., RT)	AIC	ESW	Density (groups/km^2)	N	GOF K-S p	GOF Chi-sq p	Detection Probability
Half-normal (C, >50.4 m)	195.13	30.26	5.35 (3.4-8.43,0.23)	415	-	0.461	0.6 (0.4-0.91, 0.21)
Half-normal (>32 m)	424.62	30.04	4.90 (3.43-7.01, 0.18)	370	0.913	0.477	0.94 (0.70-1.00, 0.15)
Half-normal (SP, 9%)	447.38	30.89	4.92 (3.74-6.47, 0.13)	374	0.916	0.873	0.91 (0.78-1.00, 0.07)
Half-normal (10%)	437.54	29.33	5.10 (3.57-7.29, 0.18)	386	0.838	0.366	0.87 (0.65-1.00, 0.14)
Hazard-rate (10%)	437.35	30.56	4.90 (3.77-6.37, 0.13)	381	0.911	0.491	0.9 (0.79-1.00, 0.07)
Uniform (10%)	436.61	33.82	4.43 (3.5-5.58, 0.11)	335	0.361	0.438	1.00 (1.00-1.00, 0.0)

Note: Densities are provided with the 95% confidence interval and the coefficient of variation.
RT=right truncation; AIC=Akaike's Information Criterion; ESW=effective strip width; N=abundance; GOF K-S p=goodness of fit Kolmogorov-Smirnov test; GOF Chi-sq p=goodness of fit Chi-square test; Cos=cosine adjustment; SP=simple polynomial adjustment

able model. It also showed a high goodness of fit value (0.461 chi-square tests of probability), with a detection probability of 0.6 (95% CI=0.4-0.91, Table 1). Density of *P. rubicunda* in the 20 km^2 pristine dipterocarp forest was estimated to be 5.35 groups/km^2 (95% CI=3.4-8.43) and 20.76 individuals/km^2 (95% CI=12.97-33.24) based on the half-normal/cosine.

We were able to obtain full group counts on 17 occasions, from which we calculated the mean group size to be 5.2 individuals, and the population density to be 27.82 individuals/km^2.

Other primates recorded

In addition to *P. rubicunda* within the study area we observed six individuals (two groups) of Bornean Orangutan *Pongo pygmaeus* (Linnaeus, 1760), 14 individuals (six groups) of Müller's Gibbon *Hylobates muelleri* Martin, 1841, ≥8 individuals (two groups) of Pig-tailed Macaque *Macaca nemestrina* (Linnaeus, 1766), ≥4 individuals (two groups) of Long-tailed Macaque *M. fascicularis* (Raffles, 1821) and four individuals (one group) of White-fronted Langur *Presbytis frontata* (Müller, 1838).

Vegetation sampling

We recorded 653 trees in the primary forest in a total sampling area of 0.73 ha and computed vegetation variables (Table 2).

Of the total trees recorded, most trees (85%) were <20 m tall, a few (15%) were 20-40 m tall and a very few (0.2%) exceeded 40 m. The height of *P. rubicunda* above the ground (16-20 m) was significantly higher than the median vegetation height (11-15 m) (Mann-Whitney U=5369.5, p<0.001).

Table 2. Vegetation characteristics within the primary forest in SWPF.

Vegetation attributes	SWPF primary forest*
Mean DBH (cm)	23.8 (± 0.8)
Density (stems/ha)	894.5 (± 27.5)
Proportion of ≥20 cm DBH trees (%)	38.4
Basal area (m^2/ha)	59.7 (± 4.6)
Median tree height (m)	11-15
Canopy cover (%)	84.5 (± 1.90)

* Values are given with standard errors.

DISCUSSION

Density of *P. rubicunda* within the 20 km^2 primary dipterocarp forest in Sungai Wain was relatively high within genus *Presbytis* (Kirkpatrick, 2012). Densities of Hose's Langurs *P. hosei* (Thomas, 1889) are reported to range from 5.5 individuals/km^2 in a young secondary forest to 18.9 individuals/km^2 in primary hill forest (Nijman, 2004). A density of 7.8 individuals/km^2 was estimated for Natuna Island Langur *P. natunae* (Thomas & Hartet, 1894) on Bunguran Island (Lammertink et al., 2003), and 13.5 individuals/km^2 were reported for Mentawai Langur *P. potenziani* (Bonaparte, 1856) on Siberut Island (Watanabe, 1981).

Compared with previous distance sampling density estimates of *P. rubicunda* (Blouch 1997; Marshall, 2010; Ehlers Smith & Ehlers Smith, 2013), this study showed the highest group density to date. Our mean group size and group density differ from those reported by Nijman & Nekaris (2012), most likely due to differences in methods of survey design and data analysis (Table 3). Our population density estimate, however, is comparable to that from the 1999-2005 surveys in the SWPF (Nijman & Nekaris, 2012). Thus at present, the Sungai Wain population of *P. rubicunda* appears to be stable within the primary forest. In Sarawak, similar population densities of *P. rubicunda* were found in the primary dipterocarp forests, where sympatric primate species assemblages coincided with those living in the SWPF (Blouch, 1997). These data suggest that undisturbed dipterocarp forests can support relatively high densities of *P. rubicunda*.

Between 2001 and 2012 it appears that there was an increase in tree density within the SWPF's primary habitat, with a slight bias towards larger trees. Our overall tree density (≥10 cm DBH) was double that found by Slik & Eichhorn (2003) in the same habitat in 2001. The proportion of ≥20 cm^2 DBH trees that we found in 2012 was 2.6 % higher than that reported by Slik & Eichhorn (2003). These are promising results for the conservation of *P. rubicunda* in the SWPF, as large trees represent a significant source of food for this colobine (Ehlers Smith et al., 2013b; Ehlers Smith & Ehlers Smith, 2013). A relatively high availability of large, preferred-food-bearing stems appears to play a crucial role for determining the presence of *P. rubicunda* (Ehlers Smith & Ehlers Smith, 2013). Within the mixed-swamp forest in Sabangau, Ehlers Smith et al. (2013b) found a positive correlation between fruiting tree DBH and the length of time that *P. rubicunda* spent feeding.

In the SWPF the majority of trees were well below 15 m high. In Barito Ulu vegetation height was found to be higher relative to the SWPF, with the mean height

Table 3. Comparison of density estimate of *P. rubicunda* across Borneo.

Study site	Forest type	Pop. density (ind/km²)	Group size	Survey method	Group size estimation method	Source
Sungai Wain Protection Forest, East Kalimantan, Indonesia	Primary dipterocarp forest	27.1	8.2	Line transect (4)	Complete counts from 54 groups observed during surveys	Nijman & Nekaris, 2012
Sungai Wain Protection Forest, East Kalimantan, Indonesia	Primary dipterocarp forest	27.8	5.2	Line transect (13), DISTANCE	Complete counts from 17 group encounters during survey	This study
Sabangau, Central Kalimantan, Indonesia	Peat swamp forest	17.5	7	Line transect (12), DISTANCE	Observation and complete counts of 7 groups	Ehlers Smith & Ehlers Smith, 2013
Gunung Palung NP, West Kalimantan, Indonesia	Alluvial bench	10.5	4.5	Line transect (2), DISTANCE	Observation during surveys	Marshall 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Lowland sandstone	5.9	2.9	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Freshwater swamp	7.8	5	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Peat swamp	2.5	3.8	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Lowland granite forest	7.3	3.8	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Upland granite forest	6.9	3.3	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Gunung Palung NP, West Kalimantan, Indonesia	Montane forest	1.24	3.2	Line transect (2), DISTANCE	Observation during surveys	Marshall, 2004; 2010
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary dipterocarp forest	21.5	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary and secondary dipterocarp forest	20.8	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia	Primary and secondary heavily disturbed forest	5.4	4.4	Line transect, TRANSECT	Estimation from counts and sound movements during survey	Blouch, 1997
Barito Ulu, Central Kalimantan, Indonesia	Mixed lowland dipterocarp forest	8.4	4.3	Regular monitoring	Regular monitoring	McConkey & Chivers, 2004

Study site	Forest type	Pop. density (ind/km2)	Group size	Survey method	Group size estimation method	Source
Sepilok, Sabah, Malaysia	Lowland dipterocarp forest	18.9	7	Line transect	Observations during surveys across different sites in Sabah	Davies, 1984
Tanjung Putting Reserve, Central Kalimantan, Indonesia	Mixed lowland forest	9.8	6.1	Total group counts within study area	Observation and complete counts of 9 groups	Supriatna et al., 1986

Note: Where known, survey methods, number of transect lines in parentheses and software for analysis are indicated.

of trees ranging from 19 m in old secondary forest to 22.1 m in primary forest (Brearley et al., 2004). From the observations made during our survey, *P. rubicunda* appeared to prefer exploiting the canopy above the median vegetation height. In Sabangau Forest, *P. rubicunda* exclusively selected large, tall trees as sleeping sites (≥27 cm DBH and ≥16 m tall trees [Ehlers Smith, 2014a]). In addition, Nijman & Nekaris (2012) found that as a response to human presence, *P. rubicunda* fled upwards more often and would only use the ground or under-storey as a fleeing route on rare occasions. This species is therefore likely to rely on taller emergent trees to avoid predators and use the relatively high canopy to travel and feed. These findings might have important conservation implications, as selective logging causes a decrease in abundance of large trees and mean vegetation height (White et al., 1995; Okuda et al., 2003). To date, virtually no evidence is available on the effect of negative changes in habitat structure for *P. rubicunda*. In the SWPF, human encroachment and illegal logging are gradually increasing within the regenerating habitat. Meijaard et al. (2008) proposed that *P. rubicunda* is likely to be negatively affected by logging due to their diet consisting of mainly fruit and seeds. While *P. rubicunda* is able to increase leaf consumption when necessary, in logged areas and closer proximities to humans, colobines are also exposed to risks of disease (Gillespie & Chapman, 2008) and hunting (Nijman, 2005; Marchal & Hill, 2009).

Between 2000 and 2010 nearly 10% of the habitat occupied by *P. rubicunda* was lost due to habitat conversion (Ehlers Smith, 2014b). In 2012, logging concessions within the range of the subspecies present in the SWPF, *P. r. rubicunda* (Müller, 1838), accounted for 40.8% of the total remaining area (Ehlers Smith, 2014b). The relatively high abundance of *P. rubicunda* within the SWPF's primary habitat makes this forest an important conservation area for this species in East Kalimantan. At present, the SWPF is still connected to the ecosystem of Balikpapan Bay. Populations of *P. rubicunda* are present in Bukit Bangkirai Forest, a 15 km^2 rainforest approximately 6 km north of the SWPF, as well as along the coast of Balikpapan Bay. While the SWPF is becoming increasingly encircled by human activities, it remains unknown to what extent *P. rubicunda* is able to move between these areas.

We recommend further density assessments of *P. rubicunda* in regenerating and disturbed habitats across East Kalimantan. A focus on determining the primate carrying capacity of both primary and regenerating forests should also be considered. These investigations will provide us with the required information to quantify the remaining suitable habitat and develop further status assessments and conservation plans.

ACKNOWLEDGEMENTS

We would like to thank *Le Conservatoire pour la Protection des Primates* and AZA Ape Tag Conservation Initiative for kindly funding our research. We thank the Indonesian State Ministry of Research and Technology for their permission to conduct our study. We also thank Pak Agus, Professor Vincent Nijman, Dr Stanislav Lhota, and the Universitas Mulawarman, Samarinda for their support. For the fieldwork we thank the survey team: Sabri, Misran, Joely, Arye, Aidil and the logistic team at Camp Djamaludin, Sungai Wain. We are also grateful to the anonymous reviewers for their useful comments on previous versions of this manuscript.

REFERENCES

Blouch, R.A. 1997. Distribution and abundance of orang-utans (*Pongo pygmaeus*) and other primates in the Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia. *Tropical Biodiversity* **4**: 259-274.

Brearley, F.Q., Prajadinata, S., Kidd, P.S. and Proctor, J. 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *Forest Ecology and Management* **195**: 385-397.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.

Burnham, K.P. and Anderson, D.R. 2002. *Model Selection and Multi-model Inference: a Practical Information-theoretic Approach*. Springer, New York, USA.

Cleary, D.F.R. and Genner, M.J. 2004. Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. *Global Ecology and Biogeography* **13**: 129-140.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E. and Haeruman, H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**: 2184-2188.

Davies, A. 1984. An Ecological Study of the Red Leaf Monkey (*Presbytis rubicunda*) in the Dipterocarp Forests of Sabah, Northern Borneo. PhD dissertation, University of Cambridge, UK.

Davies, G. 1987. Adult male replacement and group formation in *Presbytis rubicunda*. *Folia Primatologica* **49**: 111-114.

Davies, G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *International Journal of Primatology* **12**: 119-144.

Davies, A.G. and Payne, J. 1982. *A Faunal Survey of Sabah*. WWF Malaysia, Kuala Lumpur, Malaysia.

Davies, A.G., Bennett, E.L. and Waterman, P.G. 1988. Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda and Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **34**: 33-56.

Ehlers Smith, D.A. 2014a. Preliminary evidence for the hired guns hypothesis and indirect mate defense in a wild group of red langurs (*Presbytis rubicunda*) in Sabangau tropical peat-swamp forest, Central Kalimantan, Indonesian Borneo. *Asian Primates Journal* **4**(2): 2-15.

Ehlers Smith, D.A. 2014b. The effects of land-use policies on the conservation of Borneo's endemic *Presbytis* monkeys. *Biodiversity and conservation* **23**: 891-908.

Ehlers Smith, D.A. and Ehlers Smith, Y.C. 2013. Population density of red langurs in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesia. *American Journal of Primatology* **75**: 837-847.

Ehlers Smith, D.A., Ehlers Smith, Y.C. and Cheyne, S.M. 2013a. Home-range use and activity patterns of the Red Langur (*Presbytis rubicunda*) in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesian Borneo. *International Journal of Primatology* **34**: 957-972.

Ehlers Smith, D.A., Husson, S.J., Ehlers Smith, Y.C. and Harrison, M.E. 2013b. Feeding ecology of red langurs in Sabangau Tropical Peat-Swamp Forest, Indonesian Borneo: frugivory in a non-masting forest. *American Journal of Primatology* **75**: 848-859.

Focardi, S., Montanaro, P., Isotti, R., Ronchi, F., Scacco, M. and Calmanti, R. 2005. Distance sampling effectively monitored a declining population of Italian roe deer *Capreolus capreolus italicus. Oryx* **39**: 421-428.

Fredriksson, G.M. 2002. Extinguishing the 1998 forest fires and subsequent coal fires in the Sungai Wain Protection Forest, East Kalimantan, Indonesia. **In**: *Communities in Flames*, P. Moore, D. Ganz and L.C. Tanet (eds.), pp. 74-80. Food and Agriculture Organisation, Bangkok, Thailand.

Fredriksson, G.M., Danielsen, L.S. and Swenson, J.E. 2006. Impacts of El Nino related drought and forest fires on sun bear fruit resources in lowland dipterocarp forest of East Borneo. **In**: *Plant Conservation and Biodiversity*, D.L. Hawksworth and A.T. Bull (eds.), pp. 249-264. Springer, The Netherlands.

Fredriksson, G.M., Garshelis, D.L., Sastramidjaja, W.J. and Menken, S.B.J. 2012. Exploring the use of sign surveys for monitoring relative abundance of sun bears: a case study in burned and unburned forests in East Kalimantan, Indonesian Borneo. **In**: *Effects of El Niño and Large-Scale Forest Fires on the Ecology and Conservation of Malayan Sun Bears* (Helarctos malayanus) *in East Kalimantan, Indonesian Borneo*, G.M. Fredriksson (ed.), pp. 131-160. PhD dissertation, University of Amsterdam, The Netherlands.

Ganzhorn, J. 2003. Habitat description and phenology. **In**: *Field and Laboratory Methods in Primatology*, J.M. Setchell and D.J. Curtis (eds.), pp. 40-56. Cambridge University Press, Cambridge, UK.

Gillespie, T.R. and Chapman, C.A. 2008. Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. *American Journal of Primatology* **70**: 222-230.

Hamard, M., Cheyne, S.M. and Nijman, V. 2010. Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. *American Journal of Primatology* **72**: 607-616.

Hanya, G. and Bernard, H. 2012. Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley, Borneo. *International Journal of Primatology* **33**: 322-337.

Hassel-Finnegan, H.M., Borries, C., Larney, E., Umponjan, M. and Koenig, A. 2008. How reliable are density estimates for diurnal primates? *International Journal of Primatology* **29**: 1175-1187.

IUCN. 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 07 January 2014.

Johnson, A.E., Knott, C.D., Pamungkas, B., Pasaribu, M. and Marshall, A.J. 2005. A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. *Biological Conservation*, **121**: 495-507.

Kirkpatrick, R.C. 2011. The Asian colobines: diversity among leaf eating monkeys. **In**: *Primates in Perspective*, C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger and S.K. Bearder (eds.), pp. 189-202. Oxford University Press, Oxford, UK.

Lammertink, M., Nijman, V. and Setiorini, U. 2003. Population size, Red List status and conservation of the Natuna leaf monkey *Presbytis natunae* endemic to the island of Bunguran, Indonesia. *Oryx* **37**: 472-479.

Marchal, V. and Hill, C. 2009. Primate crop-raiding: a study of local perceptions in four villages in North Sumatra, Indonesia. *Primate Conservation* **24**: 107-116.

Marques, T.A., Thomas, L., Fancy, S.G. and Buckland, S.T. 2007. Improving estimates of bird density using multiple-covariate distance sampling. *The Auk* **124**: 1229-1243.

Marshall, A.J. 2004. Population Ecology of Gibbons and Leaf Monkeys across a Gradient of Bornean Forest Types. PhD dissertation, Harvard University, USA.

Marshall, A.J. 2010. Effect of habitat quality on primate populations in Kalimantan: gibbons and leaf monkeys as a case study. **In**: *Indonesian Primates*, S. Gursky and J. Supriatna (eds.), pp. 157-177, Springer, New York, USA.

Mbora, D.N.M. and Meikle, D.B. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus (*Procolobus rufomitratus*). *Biological Conservation* **118**: 67-77.

McConkey, K.R. and Chivers, D.J. 2004. Low mammal and hornbill abundance in the forests of Barito Ulu, Central Kalimantan, Indonesia. *Oryx* **38**: 439-447.

Meijaard, E., Sheil, D., Marshall, A.J. and Nasi, R. 2008. Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica* **40**: 76-85.

Miettinen, J., Shi, C. and Liew, S.C. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology* **17**: 2261-2270.

Mitani, J.C., Struhsaker, T.T. and Lwanga, J.S. 2000. Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *International Journal of Primatology* **21**: 269-286.

Nijman, V. 2004. Effects of habitat disturbance and hunting on the density and the biomass of the endemic Hose's leaf monkey *Presbytis hosei* (Thomas, 1889) (Mammalia: Primates: Cercopithecidae) in east Borneo. *Contributions to Zoology* **73**: 283-291.

Nijman, V. 2005. Decline of the endemic Hose's langur *Presbytis hosei* in Kayan Mentarang National Park, east Borneo. *Oryx* **39**: 223-226.

Nijman, V. and Meijaard, E. 2008. *Presbytis rubicunda*. **In**: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 07 January 2014

Nijman, V. and Nekaris, K.A.I. 2012. Loud calls, startle behaviour, social organization and predator avoidance in arboreal langurs (Cercopithecidae: *Presbytis*). *Folia Primatologica* **83**: 274-287.

Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N.A., Manokaran, N. 2003. Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. *Forest Ecology and Management* **175**: 297-320.

Simbolon, H., Suzuki, E. and Susanti, R. 2012. Some vegetation types studied with the same methodology in Indonesia. **In**: *The Biodiversity Observation Network in the Asia-Pacific Region*, S. Nakano, T. Yahara and T. Nakashizuka (eds), pp. 71-92. Springer, Japan.

Slik, J.W.F. and Eichhorn, K.A.O. 2003. Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologia* **137**: 446-455.

Slik, J.W.F., Bernard, C.S., Van Beek, M., Breman, F.C. and Eichhorn, K.A. 2008. Tree diversity, composition, forest structure and aboveground biomass dynamics after single and repeated fire in a Bornean rain forest. *Oecologia* **158**: 579-588.

Slik, J.W.F., van Beek, M., Bernard, C., Bongers, F., Breman, F.C., Cannon, C.H. and Sidiyasa, K. 2011. Limited edge effects along a burned-unburned Bornean forest boundary seven years after disturbance. *Biotropica* **43**: 288-298.

Sodhi, N.S., Koh, L.P., Brook, B.W. and Ng, P.K.L. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution* **19**: 654-660.

Stark, D.J., Nijman, V., Lhota, S., Robins, J.G. and Goossens, B. 2012. Modeling population viability of local proboscis monkey *Nasalis larvatus populations*: conservation implications. *Endangered Species Research* **16**: 31-43.

Stibig, H.J., Achard, F., Carboni, S., Raši, R. and Miettinen, J. 2014. Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences* **11**: 247-258.

Supriatna, J., Manullang, B.O. and Soekara, E. 1986. Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates* **27**: 185-190.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. and Burnham, K.P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**: 5-14.

Wantanabe, K. 1981. Variation in group composition and population density of the two sympatric Mentawaian leaf-monkeys. *Primates* **22**: 145-160.

White, F.J., Overdorff, D.J., Balko, E.A. and Wright, P.C. 1995. Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. *Folia Primatologica* **64**: 124-131.

Wilson, C.C. and Wilson, W.L. 1975. The influence of selective logging on primates and some other animals in East Kalimantan. *Folia Primatologica* **23**: 245-274.

ETHOLOGY OF THE CRITICALLY ENDANGERED JAVAN SLOW LORIS *Nycticebus javanicus* É. Geoffroy Saint-Hilaire IN WEST JAVA

E. Johanna Rode-Margono[1], V. Nijman[1], Wirdateti[2], K. A. I. Nekaris[1*]

[1] Oxford Brookes University, Oxford, UK. E-mail: anekaris@brookes.ac.uk

[2] Research Center for Biology-LIPI, Jakarta-Bogor, Cibinong 16911, Indonesia. E-mail: wirdateti@lipi.go.id

[*] Corresponding author

ABSTRACT

Considered amongst the most endangered primates in the world, Javan Slow Lorises *Nycticebus javanicus* É. Geoffroy Saint-Hilaire are threatened by habitat destruction, and by the wildlife trade for pets and traditional medicines. Despite some studies of captive or rescued and released animals, little is known about the behaviour and ecology of wild animals. We present preliminary behavioural data of the first-ever study of wild *N. javanicus*. The study population, in Cipaganti, West Java, persists in a mosaic habitat including agricultural fields (*talun*) and interspersed trees and patches of bamboo, trees, bushes and abandoned fields. We directly observed animals for some 170 hours during the onset of the dry season, between April and June 2012. Animals spent 31% of their time foraging and feeding, 33% sleeping and resting, 14% traveling, 12% alert, 7% grooming and 1% socializing. They fed mainly on exudates of Green Wattle *Acacia decurrens* (Willd.) (56%) and the nectar of Red Calliandra *Calliandra calothyrsus* (Meisn.) (32%). We found the animals to be relatively gregarious, spending 13% of observations within sighting distance of one another, for 37% of which they were seen in bodily contact. Animals preferred bamboo and Green Wattle over other tree species. We provide recommendations for management in captivity and reintroduction schemes, particularly urging rescue centres to provide gum and adequate social partners. Finally, we stress the importance unprotected, human-modified landscapes can have for this species and for reintroduction programmes.

Keywords: activity budget, behaviour, conservation, diet, habitat use, unprotected habitat

INTRODUCTION

South-East Asia is considered a biodiversity hotspot due to high diversity and a high percentage of endemic species, many of which are threatened by habitat loss (Sodhi et al., 2010). The human influence on nature in the region is immense, and includes deforestation and land modification for agriculture, development, large-scale palm oil plantations, pollution, and hunting of wildlife for traditional medicine or for luxury products (Sodhi et al., 2010). The Indonesian island of Java is amongst the most densely populated places on earth, with a population density averaging 1071 people per km^2. The Javan Slow Loris *Nycticebus javanicus* É. Geoffroy Saint-Hilaire is one of the species that is highly affected by habitat loss and the pet trade in South-East Asia. The species is listed as Critically Endangered on the IUCN Red List (Nekaris et al., 2013b), and on the World's 25 Most Endangered Primates 2012-2014 (Nekaris et al., 2014).

The plight of the Javan Slow Loris has long been known in Indonesia. Like other slow lorises, the Javan Slow Loris has a small bear-like appearance with big eyes, characteristics that make it very desirable in the pet trade. Indeed, it is one of the primates most commonly observed, along with other Indonesian species of Slow Loris, in the illegal trade (Shepherd et al., 2004; Nekaris et al., 2009; Shepherd, 2010). Trade in Slow Loris, and in wildlife in general, is fuelled by the extensive use of the internet, including online shops, social networks or sharing platforms (Nekaris et al., 2013a).

Some projects have attempted to reintroduce animals that were confiscated from illegal markets, but their attempts have met with limited success (Moore, 2012). Many nocturnal, solitary and arboreal primates are difficult to study (Wiens & Zitzmann, 2003) and lack long-term studies of their behavior and ecology in the wild (Nekaris & Bearder, 2011). Likewise, the Javan Slow Loris was listed as Data Deficient until 2006 (Nekaris et al., 2013b). Although we now have some information regarding wild Greater Slow Loris *N. coucang* (Boddaert) from Malaysia (Wiens et al., 2006), Pygmy Slow Loris *N. pygmaeus* Bonhote from Cambodia (Starr et al., 2013), and Bengal Slow Loris *N. bengalensis*

(Lacépède) from various parts of its range (Das et al., 2009; Pliosungnoen et al., 2010; Swapna et al., 2010; Rogers & Nekaris, 2011), it is still not clear to what extent these species differ in social organization, diet and home range size, and we cannot plan effective conservation strategies for Javan Slow Loris based on what is known about their congeners. Winarti (2011), Nekaris (2012) and Wirdateti (2012) all identified the agro-forest gardens around Cipaganti, Garut, as containing high numbers of Javan Slow Loris, and urged that long-term studies of the species be undertaken.

Here, we present the first behavioural and ecological data recorded from wild Javan Slow Loris, and compare them with information regarding other slow loris species. These data will inform captive care and release schemes of rescued slow lorises. We give a detailed description of the habitat where Javan Slow Loris are known to occur at relatively high density; report basic morphometric measurements of captured slow lorises; provide an ethogram of wild Javan Slow Loris and describe their activity budget, diet, basic social behaviour and habitat use over the first three months of a planned 1.5 year study.

METHODS

Study site

We established our field station in Cipaganti village, near the city of Garut in West Java (S7°6’6” – 7°7’ & E107°46’ – 107°46’5”, Fig. 1) in April 2012. Cipaganti lies in the foothills of Mount Puntang, which is part of the mountain range containing the active volcano Gunung Papandayan. While Gunung Papandayan is recognized as a nature reserve (*cagar alam*), the partly agricultural areas surrounding the nature reserve are not protected. The distance between the edge of the village and the boundary of the protected forest on slopes of the ridges that cannot be cultivated, is approximately 1300 m, while the first contiguous forest is about 2000 m away from the village. The land in between reaches up to 1750 m asl and is covered with a mosaic of cultivated fields (called *talun* by Sundanese people) under crops like tea, beans, chili, tomato, tobacco, potato, cabbage, onion, carrot etc., abandoned fields and shrub patches, bamboo patches, tree plantations and forest patches. Fields are often bordered by trees with a more-or-less connected canopy.

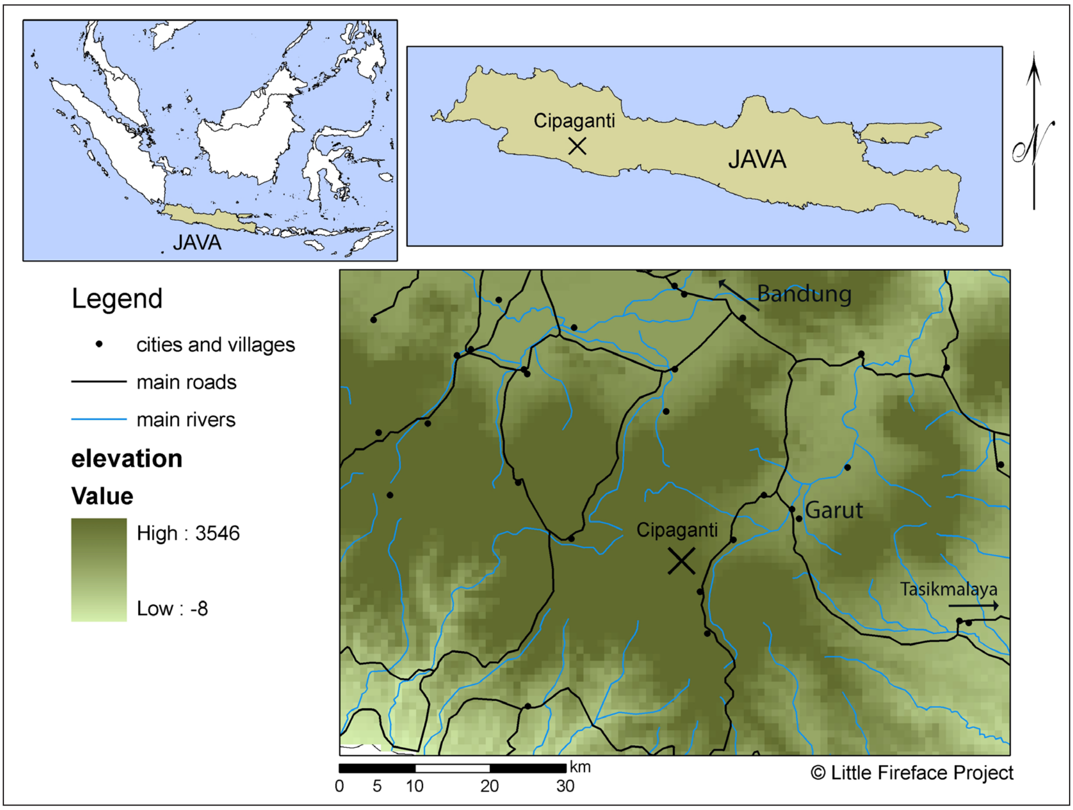


Fig. 1. Location of the field site of the Javan Slow Loris study, adjacent to Cipaganti Village, Garut District, West Java.

We conducted our study during the dry period from April to June 2012. Temperature, humidity and rainfall during the study period are presented in Table 1. The dry period corresponded with low minimum temperatures. During dry periods rivers dried out and some trees shed their leaves (e.g. Japanese Persimmon *Diospyros kaki* L.f., Indonesian Mahogany *Toona sureni* [Blume] Merr.). One of the important nectar-producing plants for slow lorises, Red Calliandra *Calliandra calothyrsus* Meisn., did not bloom during the dry period. The study site comprises about 50 ha and is located between 1300-1650 m asl, adjacent to Cipaganti village. Accordingly, the terrain is steep and difficult to traverse. Human presence and disturbance in the study site are high. Many people work in the fields every day, starting at about 05:00 h. Trees and bushes are regularly cut for wood production or clearance. Furthermore, people set traps for pigs, to protect crops, and traps for birds to sell them into the trade. Hunting or disturbance of pigs during the night has been observed. Bee hives are harvested once per year during the dry season. Landslides are common during the rainy season.

Table 1. Temperature, humidity and rainfall during April to June 2012.

Temperature day (°C) 06:00-18:00 h	
Average	22.6 ± 2.9
Minimum	12.4
Maximum	28
Temperature night (°C) 18:00-06:00 h	
Average	18.9 ± 2.2
Minimum	12.6
Maximum	26.7
Humidity (%)	
Average	74.1 ± 8.9
Minimum	33
Maximum	91
Rainfall 24 h (mm)	
Average	0.6 ± 2
Minimum	0
Maximum	11.7

Radio-tracking

As trapping success for slow lorises is low (Wiens & Zitzmann, 2003), we captured animals by hand. We did not sedate animals, but processed them immediately at the place of capture, and released them afterwards on the same tree. We used leather gloves for bite protection and rubber gloves for infection control. We determined the sex of the animals, checked for pregnancy using abdominal palpation, and assessed stage of the oestrous cycle (Manley, 1966; Izard et al., 1988). We also monitored lactation by checking for elongated nipples and milk expression (Wiens & Zitzmann, 2003). We weighed animals using spring balances (Pesola®, Canada). Age classes were determined by body mass and pelage pattern and length. Adults had body masses greater than 750 g, juveniles between 250 g and 750 g, and infants below 250 g. As body mass varied substantially, and sub-adults can reach adult size while retaining juvenile pelage coloration and length, mass was considered an inconclusive indicator of adolescence. The pelage of infants and juveniles was fluffy and contained long hairs with white tips which gave the appearance of frosting; the transition between this condition and an adult coat pattern without white tips contributed to the categorization of sub-adults (Fig. 2). We examined the general condition of captured animals. Head-body length was defined as the distance between the base of the tail and the tip of the nose, and measured using a tape measure. Animals were stretched out as far as the natural body shape allowed and the measurement tape was applied along the middle of the back and head. We attached radio collars (17 g, on average 1.9% of body weight, BioTrack, UK) to adult animals, and marked them individually by fitting one or two coloured stainless-steel bead chains (2 mm per bead) around their wrists.

We followed the radio-collared lorises in two shifts during the night, from18:00 h to 00:00 h and 00:00 h to 06:00 h (following Wiens & Zitzmann, 2003), covering one animal per shift. We tracked animals with the aid of an antenna (6 and 8 element flexible Yagi antenna, Biotrack, UK) and receiver (R1000, Communication Specialists, US). If uncollared but identifiable animals were encountered, they were observed as long as possible until they moved away. We used instantaneous behaviour sampling with 5-minute intervals and took *ad libitum* notes (Altman, 1974; Nekaris, 2001). The behavioural ethogram is included as Appendix 1. At each sample point we also recorded the tree species used by the animal, and the distance to the closest Slow Loris, if present. For the latter we used the categories “in bodily contact” or “less than a body length

Fig. 2. Javan Slow Lorises change their coat pattern, colour and fur density as they age. Shown here are a very pale infant (~4 weeks old) with fluffy fur; juvenile with characteristic pale coat with very dark markings and very long fur; and typical brown adult with shorter fur and paler markings.

away", "less than 5 m distance", and "within sighting distance". We included all vegetation of more than 1m height in our vegetation dataset, because we observed animals moving on bushes and other small plants. A tree was defined as having a minimum diameter at breast height (DBH) of 2.5 cm, and being at least 3 m high. If the animals were feeding, we noted the food type and recorded qualitative observations of the feeding method.

In order to test whether slow lorises showed a preference for certain tree species, we recorded available tree species in the study site along nine, approximately-1-km-long, parallel line transects through the home ranges of the radio-collared animals. We used point intercept transects with intercepts of 15 m (Hill et al., 2005; Rode et al., 2013). At each point we recorded the nearest tree species, and classified the vegetation type as cultivated field, abandoned field, bush, bamboo patch, tree patch or path (Rode et al., 2013). This method was deemed appropriate as we needed to minimize damage to the crops of the local farmers. We took samples of the tree species used by the animals, which were identified at the Indonesian Institute of Sciences, Research Center for Biology (LIPI).

We used descriptive statistics (means and standard deviations), and calculated differences in activity budgets between the sexes using a Pearson Chi-square test (Dytham, 2001), only including radio-collared adult animals with more than 100 observation points. We grouped feeding and foraging, sleeping and resting, alert and freezing, and social activity (aggression, playing, other social activities) for the activity budget. For the general activity budget we merged auto- and allogrooming into a single category ("grooming") such that the latter was not considered in the category "social behaviour", while for the analysis of social behaviour we also considered allogrooming. Social activity and distance between animals were recorded for all animals. We used a Pearson Chi-square test to detect if there were differences between the frequency at which the lorises used certain tree species and the frequency at which these species occurred in the dataset of available trees at the site. The null hypothesis was that there was no difference between the frequencies at which the animals used the different tree species and the frequency of available tree species, meaning that the lorises used trees at the study site randomly. A positive deviation from the null hypothesis was interpreted as a preference for the more frequently used tree species. We included only the ten most frequently used tree species in our analysis. All other trees used were added as a single category into the analysis.

RESULTS

In April and May 2012 we captured 12 *N. javanicus* (Table 2). Three of these animals were not collared because they were juveniles or because we were out of collars. On various occasions uncollared animals were sighted. The female adult individuals RO and EL were lost on 11 June and 6 July, respectively. RO was initially

Table 2. Details and basic morphometrics of twelve Javan Slow Lorises.

No.	ID	Sex	Age	Date captured	Weight (g)	Head and body length (cm)	Hand span (mm)	Foot span (mm)	Obs.	Days
1	GU	Male	Adult	17/04/2012	885	36.9	63	75	284	26
2	EN	Female	Adult	18/04/2012	740	33.6	61	75	339	22
3	YO *	Male	Sub-adult	19/04/2012	740	28.4	57	73	37	9
4	HE *	Female	Sub-adult	20/04/2012	676	31.3	57	78	4	4
5	AZ	Male	Adult	20/04/2012	855	-	70	71	121	16
6	ON	Female	Adult	20/04/2012	994	31.5	53	64	118	14
7	TE	Female	Adult	07/05/2012	765	31	51	68	247	22
8	MO	Male	Adult	08/05/2012	945	33.7	60	78	175	11
9	EL	Female	Adult	09/05/2012	935	31.2	64	82	165	8
10	RO	Female	Adult	11/05/2012	904	31.6	60	79	162	7
11	CH	Female	Adult	11/05/2012	915	31.3	57	74	205	15
12	MR *	Male	Adult	12/05/2012	904	33		64	27	7
13	TA *	Unknown	Juvenile	-	-	-	-		40	9
14	LU *	Unknown	Infant	-	-	-	-		1	1
	UN *	-	Adult	-	-	-	-		64	16
Average adult males (n = 4; 3)					897.25 ± 37.7	34.5 ± 2.1	64 ± 5	72 ± 4	1989	
Average adult females (n = 6)					875.5 ± 100.5	31.7 ± 0.1	58 ± 5	74 ± 7		

* Animals that were not radio-collared.

brought to the field station by local inhabitants and was suspected to have been in captivity. When she was released at the site where people claimed they had found her, she started to travel very long distances, and was finally lost in the nearby protected forest area. The collar of EL broke and, although there were a few sightings of her, we could not catch her again.

We followed the radio-collared animals for 327.75 hours on 70 days between 4 April and 1 August 2012. We collected 1,989 5-minute observation points, totaling 165.75 hours of direct observation. Thus, the animals were out of sight 50% of the time.

Figure 3 shows the activity budget for nine adult Javan Slow Loris. Animals spent 33±15% of the observation time sleeping and resting, 31±14% feeding and foraging, 14±7% traveling, 12±5% being alert and freezing, 7±4% grooming, 2±2% engaging in other activities, and 1±2% engaging in social activities (n=1996) Although individual variation was detected, preliminary results suggest that females spent more time foraging while males were more alert, travelled more and showed more social behavior (χ^2=70.971, df=9, p<0.001, n=1660). This result may have been influenced by one prolonged bout of aggression between the adult male GU and an uncollared individual, and the intensive relationship between GU and the juvenile male YO (including social activities like playing, allogrooming and following each other). Removing GU from the analysis resulted in a still-significant test outcome in broad behaviour type (χ^2=73.010, df=9, p<0.001, n=1396) but no significant difference between sexes in social behaviour subcategories.

Animals were seen within sighting distance of other lorises in 13% of the observations (n=258). In 57% of these cases (n=147), animals were closer than 5 m, while in 37% of cases (n=96), animals were in bodily

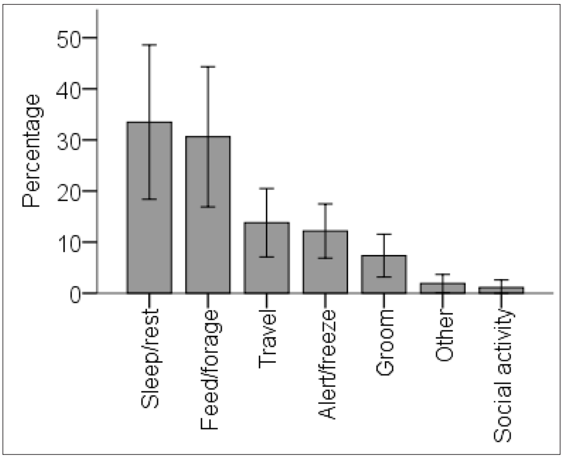


Fig. 3. Proportion of instantaneous sample points of nine radio-collared and unidentified adult Javan Slow Lorises (n=1590). Error bars denote ±1 standard deviation.

contact or less than a body length away. Social behaviours recorded (n=40) included allogrooming (38%), playing (35%), aggression (15%; only one incident, between two adult males, spanning several observations) and other social behaviours (13%). We also observed following and sleeping in contact with another animal.

We recorded animals feeding 81 times (4.7% of observations). In 68 cases we could identify the food items. Animals fed mainly on the gum of Green Wattle *Acacia decurrens* Willd. (56%), the nectar of flowers of Red Calliandra (32%), and insects (7.4%). In only two cases, animals fed on fruit (Japanese Persimmon and Jackfruit *Artocarpus heterophyllus* Lam.). Amongst the insects consumed were caterpillars (Lepidoptera), grasshoppers (Orthoptera) and cockroaches (Dictyoptera), taxa that may be perceived as pest species by local farmers. When feeding on exudates, animals climbed up and down the trunks and branches and checked existing, loris-made gouge holes, or created new holes. They then licked the leaking exudates or expanded the holes by anchoring their teeth and gouging strongly or chiseling away the bark. The nectar of Red Calliandra was eaten as described by Moore (2012), by climbing among the terminal branches of the tree or bush, stabilizing themselves in a standing or hanging position, and grabbing and bending the flower towards them using one or both hands. They then licked the nectar accumulating between the stamens without damaging the flower.

In total, 261 ‘available’ trees and 1,875 used trees of 38 species were recorded (Appendix 2). Comparing the numbers of the ten most commonly used tree species with the available trees, we found that slow lorises preferred bamboo (String Bamboo *Gigantochloa apus* [Schult.] Kurz, and Sweet Bamboo *G. atter* [Hassk.] Kurz), Green Wattle, and Red Calliandra, but used other common species less than expected (Cajeput Tree *Melaleuca leucadendra* (L.) L., Chinese Mahogany, Japanese Persimmon and other species) (χ^2=205.926, df=10, p<0.001, n=2136). On the transects we recorded 65% of the points to be in cultivated fields, 18% in abandoned fields, 8% in bush area, 5% on paths, 3% in tree patches and 2% in bamboo patches (n=354).

DISCUSSION

Our study area is situated in an area of Java where most land has been modified by humans (Smiet, 1990; Lavigne & Gunnell, 2006). Natural habitat remains only in inaccessible places such as at high altitude and on steep slopes (Smiet, 1992; Lavigne & Gunnell, 2006). At our study site, slow lorises live in agricultural areas (*talun*) where humans live and work. They are confined to habitat fragments surrounded by fields, threatened by habitat loss through the cutting of trees and bamboo, and exposed to human activities mainly during the day. Our transect data show that 83% of the land comprises cultivated and abandoned fields. The area is not protected and thus lorises rely on the good will of people for their survival. This situation is similar for other threatened primates throughout Asia, such as Purple-faced Langurs *Trachypithecus vetulus* (Erxleben) (Moore et al., 2010) and Hainan Gibbons *Nomascus hainanus* (Thomas) (Zhou et al., 2005). Effects of degraded and human-altered habitat on primates may include reduced feeding resources, fewer sleeping or hiding places, higher susceptibility to invasive or aerial predators, increased hunting pressure, disturbance and higher exposure to parasites (Wright et al., 2009; Schwitzer et al., 2010b, 2011). Slow lorises, however, apparently can sufficiently adjust to human-modified habitats like this mosaic landscape of agricultural fields, bamboo stands and forest fragments.

We determined the activity budget of adult Javan Slow Loris. In accordance with other studies (Table 3), the percentages of resting and sleeping, being alert and freezing were relatively high, in contrast to the findings of Wiens & Zitzmann (2003), who reported low frequencies of resting and sleeping in Malaysian *Nycticebus coucang*. Our study and that of Swapna et al. (2010) were conducted during the dry, cold season. A combination of season, temperature and moonlight may have affected the level of activity and alertness.

Nocturnal primates are described as lunar-phobic, lunar-philic or lunar-neutral, depending on whether they decrease, increase or do not change their level of activity during bright moonlit nights. Increased activity may be related to higher foraging efficiency (Gursky, 2003) and better detection of predators (Bearder et al., 2006; Nash, 2007). Rogers & Nekaris (2011) report that Bengal slow lorises in Cambodia become more active during the dark moon phase. Rode et al. (2014, in press) found Javan Slow Loris to be lunar-phobic but attributed this behaviour to predator-independent factors such as availability of arthropod prey. Although Pygmy Loris seemed unaffected by light on warm nights, Starr et al. (2012) found them to be lunar-phobic on cold, bright nights, probably as a result of the higher risk of detection by predators and heat loss.

Solitary mammal species usually forage alone during their active period, yet may still be in contact with conspecifics (e.g. via olfaction or vocalizations), sleep in groups or live in complex social networks (Waser & Jones, 1983). Several studies in captivity concluded that *Nycticebus* spp. are very gregarious given the opportunity. Animals spent one third of their time in proximity and shared nest boxes (Ehrlich & Musicant, 1977) and rarely engaged in agonistic behaviours (Daschbach, 1983; Ehrlich & MacBride, 1989). Although animals occasionally show aggressive behaviour in rescue centres, this might be a by-product of the trauma animals have experienced in the pet trade, and rescue centres may house up to eight animals in social groups (Moore, 2012). In wild Javan Slow Loris, we only observed one case of aggression in three months. In studies of *N. bengalensis*, *N. pygmaeus* and *N. coucang*, social activities clearly occurred outside the sample points that made up activity budgets, as the frequency of social activities recorded was relatively low (Table 3). *Nycticebus coucang* and *N. javanicus* individuals were often observed within sighting distance of one another (13% for *N. javanicus*, this study; 8% for *N. coucang*, Wiens, 2002). We have shown that the social behaviours of wild *N. javanicus* are similar to those of other species of lorises studied in the wild, including allogrooming, playing, following, and sleeping in contact with another animal (Wiens & Zitzmann, 2003). Javan Slow Loris thus do not qualify as gregarious, but they are definitely social.

Slow lorises feed on gum, invertebrates, nectar of flowers, fruit, small vertebrates, mollusks, bird eggs, leaves, bark, bamboo and fungi (Table 4) (Tan & Drake, 2001; Wiens, 2002; Wiens & Zitzmann, 2003; Winarti, 2003; Pliosungnoen & Savini, 2008; Streicher et al., 2009; Nekaris et al., 2010; Swapna et al., 2010; Rogers & Nekaris, 2011; Winarti, 2011; Starr & Nekaris, 2013; Streicher et al., 2013). Nash & Burrows (2010) reviewed several primate species that form part of a gum-feeding guild. Some species use gum opportunistically while searching for insects on tree surfaces or as a staple or fallback food in times of food shortage (Porter et al., 2009; Streicher, 2009). For other species gum is an obligatory dietary component. Only a few species are able to stimulate exudate flow actively by gouging. This behaviour is shown by the callitrichine genera *Callithrix* (Erxleben), *Callibella* (van Roosemalen & van Roosemalen), *Mico* (Lesson) and *Cebuella* (Gray), the Masoala Fork-marked Lemur *Phaner furcifer* (Blainville) and the Southern Needle-clawed Galago *Euoticus elegantulus* (Le Conte) (Vinyard et al., 2003; Schwitzer et al., 2010a). Sixty-five per cent of the diet of *Phaner* is gum, which is available all year round. *Euoticus elegantulus* (Le Conte) includes gum as 75% of its diet; the rest consists of insects and fruit (Charles Dominique, 1977). All *Nycticebus* species gouge, and spend a considerable amount of their feeding time consuming exudates (*Nycticebus pygmaeus*: Tan & Drake [2001]; Nekaris et al. [2010]; Starr & Nekaris [2013]; Streicher et al. [2013]; *N. coucang*: Barrett [1984]; Wiens et

Table 3. Activity budget of *Nycticebus* species.

	N. bengalensis[1]	*N. bengalensis*[2]	*N. coucang*[3]	*N. javanicus*[4]
Rest, sleep	40.5	41; 7	5.4	33
Travel	23.2	36 (incl. forage)	-	14
Forage, feed	5.1; 22.3	6 (only feed)	20.5 (only feed)	31
Groom	7.2	4	-	7
Alert	-	7	-	12
Social	0.4	0	3.5	1

1=Swapna *et al*., 2010; 2=Rogers & Nekaris, 2011; 3=Wiens & Zitzmann, 2003; 4=this study al. [2006]; Nekaris & Munds [2010] ; *N. bengalensis*: Pliosungnoen & Savini [2008]; Nekaris et al.[2010]; Swapna et al.[2010]; Das et al. [2014]; *N. javanicus*: Winarti [2003]; Nekaris et al. [2010]; Winarti [2011]; and Bornean Slow Loris *N. menagensis* [Trouessart]: Nekaris et al. [2010]) (see Table 4). Nekaris et al. (2010) reviewed exudate feeding in Asian lorises, and listed 12 plant families exploited by *Nycticebus* for exudates. *Nycticebus javanicus* was seen feeding on exudates of Fabaceae, Arecaceae and Moraceae (Nekaris et al., 2010; Winarti, 2011). Nectar is another important component of the diet (Table 4). Re-introduced Javan Slow Loris spent 90% of their feeding time consuming nectar (Moore, 2012). Javan Slow Loris feed on the nectar of Red Calliandra (Moore, 2012; this study) and Banana *Musa* × *paradisiaca* L., Family Musaceae (Winarti, 2011). Pliosungnoen & Savini (2008) saw *N. bengalensis* feeding on *Parkia* flowers (R.Br.), Family Fabaceae. Porter et al. (2009) observed the Goeldi's Monkey *Callimico goeldii* (Thomas) in Bolivia using pod exudates of *Parkia* flowers as a fallback food during the dry season. Our study was conducted during the onset of the dry season and dietary component proportions may differ between seasons (Charles-Dominique, 1977; Hladik et al., 1980). Considerable seasonal differences in feeding budgets were observed for *N. bengalensis* and *N. pygmaeus* (Swapna et al., 2010; Starr & Nekaris, 2013). The proportion of gum in the diet was higher in the winter, while more nectar and insects were consumed in the summer by *N. bengalensis* (Swapna et al., 2010). *Nycticebus pygmaeus* did not feed on nectar or fruits in the cold season at all, and more than doubled the proportion of insects they consumed (Starr & Nekaris, 2013). In this study, feeding on insects was likely to be underestimated as it often involved very fast movements between sampling intervals, and could easily be missed, especially when animals were in very dense habitat like bamboo or bushes. Slow lorises consume some insect taxa that are potentially harmful for crops; thus they play an important role in pest control. Even though we saw animals feeding on two different fruits (Japanese Persimmon and Jackfruit) also consumed by humans, this occurred rarely and did not qualify Javan Slow Loris as a pest species. We never observed animals feeding on vegetables planted in the fields.

Few studies have reported the tree species that *Nycticebus* uses during general activity. The amount of bamboo in a forest seems to have a positive effect on the encounter rates of *N. javanicus* (Voskamp et al., 2014). Bamboo species seem to be important as sleeping and resting sites (Winarti, 2003, 2011; Dahrudin & Wirdateti, 2008). *Nycticebus bengalensis* was found more often in plantations with high numbers of *Acacia* (Mill.) and *Leucaena* (Benth.) trees and *Bauhinia* (L.) lianas (all members of the legume family Fabaceae) as compared with primary forest (Pliosungnoen et al., 2010). Diet is also likely to influence tree species preferences. Fabaceae, for instance, are used by all *Nycticebus* species as sources of exudates (Nekaris et al., 2010). In this study, Green Wattle and Red Calliandra were preferred for their gum and nectar. As for diet, the preferences of lorises for certain tree species may change with the season. Non-preferred tree species may not play a special role in the animals' diet or sleeping-site choice, but may be used during travel. Almost all tree species recorded in this study as used by Javan Slow Loris are non-native. Nevertheless, we found a healthy population of lorises in this habitat and the animals seemed to have adapted well to the dietary options, habitat structures and relatively confined space provided by this human-modified landscape.

Adjustment to human-modified mosaic landscapes and exotic tree species bear important implications for the re-introduction of confiscated animals that might have been caught in those habitats. One of the possible reasons for failed re-introductions of Javan Slow Loris to the wild is that animals that have grown accustomed to agricultural areas and their component plant species are released into dense rainforests; newly released Javan Slow Loris often moved out of the old stage forests where they were released into agricultural areas up to a few kilometers away (Moore, 2012).

RECOMMENDATIONS

Although slow loris species differ in aspects of their ecology, we found Javan Slow Loris to have similar needs in terms of fundamental feeding and social activities to other slow loris species. Whether in zoos, rescue centres or when preparing rescued animals for release, we stress the importance of providing social partners, and including gum in the animals' diet. For the Javan Slow Loris, in particular, certain tree species are important for species conservation planning and for the specific protection of the modified habitats in our study area (String Bamboo, *Gigantochloa apus*; Sweet Bamboo, *G. atter*; Green Wattle, *Acacia decurrens*; Red Calliandra, *Calliandra calothyrsus*). Javan Slow Loris can thrive in human-altered habitat that is very different from dense rainforest and are surprisingly adaptable to exotic plant species. The provenance of confiscated animals and their behavioural and ecological adaptation to their original habitats must be con-

Table 4. Feeding budgets of *Nycticebus* species.

	N. bengalensis[1*]	*N. bengalensis*[2]	*N. coucang*[3]	*N. javanicus*[4]	*N. pygmaeus*[5]	*N. pygmaeus*[6*]
Exudates	86.5	80.9	43.3	55.9	60	50
Insects	2.9	2.3	2.5			
(Arthropods)	7.4	40	20			
Nectar	6.4	3.2	31.7	32.2		10
Fruit	0.3	4.5	22.5	2.9		18
Fungi						3
Bamboo						5
Vertebrates						1
Bark	1.9	7.3				
Bird eggs	1.2					
Tender leaves		1.8				
Bouts	329	243	139	68	27	168

1=Swapna et al., 2010; 2=Das et al., 2014; 3=Wiens et al., 2006; 4=this study; 5=Streicher et al., 2013; 6=Starr & Nekaris 2013; *=averaged between seasons

sidered in re-introduction programs. When evaluating suitable release sites, native equivalents of exotic agricultural and native rainforest species must be identified. Finally, human-modified landscapes should be included in habitat protection schemes, and community-based conservation should be emphasized.

ACKNOWLEDGMENTS

We would like to thank the authorities Riset and Teknologi (Ristek), Balai Konservasi Sumber Daya Alam Bandung (BKSDA Bandung), Research Center for Biology, Indonesian Institute of Sciences (LIPI) and Konservasi Sumber Daya Alam Garut (KSDA Garut) for their support in this project. The anonymous reviewers greatly improved the quality of this manuscript. This study was funded by the Leverhulme Trust (RPG-084), Mohamed bin Zayed Species Conservation Fund, People’s Trust for Endangered Species, Conservation International Primate Action Fund, Cleveland Zoological Society and Cleveland Metroparks Zoo, Chicago Zoological Society/ Chicago Board of Trade (CBOT) Endangered Species Fund, Primate Society of Great Britain Conservation Working Party, Columbus Zoo, Amersfoort Zoo, Primate Conservation Inc. and the International Primate Protection League. We thank M. Ward and S.R. Putri for their help in the study.

REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* **49**: 227-267.

Barrett, E.B.M. 1984. *The ecology of some nocturnal arboreal mammals in the rain forest of peninsular Malaysia*. PhD dissertation, Cambridge University, UK.

Bearder, S., Nekaris, K.A.I. and Curtis, D. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatologica* **77**: 50-71.

Charles-Dominique, P. 1977. *Ecology and behaviour of nocturnal primates: Prosimians of equatorial West Africa*. Columbia University Press, New York, USA.

Dahrudin, H. and Wirdateti. 2008. Jenis tumbuhan dan tempat bersarang kukang (*Nycticebus coucang menagensis*) di hutan lindung pegunungan Merratus, Kalimantan Selatan. *Zoo Indonesia* **17**(1): 7-14.

Das, N., Biswas, J., Das, J., Ray, P. C., Sangma, A. and Bhattacharjee, P.C. 2009. Status of Bengal Slow Loris *Nycticebus bengalensis* (Primates: Lorisidae) in Gibbon Wildlife Sanctuary, Assam, India. *Journal of Threatened Taxa* **1**: 558-561.

Das, N., Nekaris, K.A.I. and Bhattacharjee, P.C. 2014. Medicinal plant exudativory by the Bengal Slow Loris *Nycticebus bengalensis. Endangered Species Research* **23**: 149-157.

Daschbach, N.J., Schein, M.W. and Haines, D.E. 1983. Cage-size effects on locomotor, grooming and agonistic behaviours of the Slow Loris, *Nycticebus coucang* (Primates, Lorisidae). *Applied Animal Ethology* **9**: 317-330.

Dytham, C. 2007. *Choosing and using statistics: a biologist's guide*. Wiley-Blackwell, Malden, USA.

Ehrlich, A. and Macbride, L. 1989. Mother-infant interactions in captive Slow Lorises (*Nycticebus coucang*). *American Journal of Primatology* **19**: 217-228.

Ehrlich, A. and Musicant, A. 1977. Social and individual behaviors in captive Slow Lorises. *Behaviour* **60**: 195-220.

Fitch-Snyder, H., Schulze H. and Larson, L. 2001. *Management of Lorises in Captivity: A Husbandry Manual for Asian Lorisines* (*Nycticebus & Loris ssp*.). Center for Reproduction of Endangered Species, Zoological Society of San Diego, San Diego, US.

Gursky, S. 2003. Lunar philia in a nocturnal primate. *International Journal of Primatology* **24**: 351-367.

Hart, D. 2007. Predation on primates: a biogeographical analysis. **In**: *Primate anti-predator strategies*, L. Gursky and K.A.I. Nekaris (eds.), pp. 27-59. Springer, New York, USA.

Hladik, C.M., Charles-Dominique, P. and Petter, J.J. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. **In**: *Nocturnal Malagasy primates: ecology physiology and behaviour*, P. Charles-Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, A. Schilling and J.J. Petter (eds.), pp. 41-73. Academic Press, New York, USA.

Isbell, L.A. 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* **3**: 61-71.

Izard, M.K., Weisenseel, K. and Ange, R. 1988. Reproduction in the Slow Loris (*Nycticebus coucang*). *American Journal of Primatology* **16**: 331-339.

Kappeler, P.M. and van Schaik, C.P. 2002. Evolution of primate social systems. *International Journal of Primatology* **23**: 707-740.

Lavigne, F. and Gunnell, Y. 2006. Land cover change and abrupt environmental impacts on Javan volcanoes, Indonesia: a long-term perspective on recent events. *Regional Environmental Change* **6**(1-2): 86-100.

Manley, G. 1966. Reproduction in lorisoid primates. *Proceedings of Symposium of the Zoological Society of London* **15**: 493-509.

Moore, R. 2012. Ethics, ecology and evolution of Indonesian Slow Lorises (*Nycticebus* spp.) rescued from the pet trade. PhD dissertation, Oxford Brookes University, UK.

Moore, R.S., Nekaris, K.A.I. and Eschmann, C. 2010. Habitat use by western purple-faced langurs *Trachypithecus vetulus nestor* (Colobinae) in a fragmented suburban landscape. *Endangered Species Research* **12**: 227-234.

Nash, L.T. and Harcourt, C.S. 1986. Social organization of galagos in Kenyan coastal forests: II. *Galago garnettii. American Journal of Primatology* **10**: 357-369.

Nash, L., Gursky, S.L. and Nekaris, K.A.I. 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: Illuminating possible anti-predator efforts. **In**: *Primate anti-predator strategies*, S.L. Gursky and K.A.I. Nekaris (eds.), pp. 173-205. Springer, New York, USA.

Nash, L.T. and Burrows, A. 2010. Advances and remaining sticky issues in the understanding of exudativory in primates. **In**: *The Evolution of Exudativory in Primates*, A.M. Burrows and L.T. Nash (eds.), pp. 1-24. Springer, New York, USA.

Nekaris, K.A.I. 2001. Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkerianus*): Implications for slow climbing locomotion. *Folia Primatologica* **72**: 228-241.

Nekaris, K.A I. 2012. Lethal loris. *BBC Wildlife*. Feb: 52-56.

Nekaris, K.A.I. and Bearder, S.K. 2011. The lorisiform primates of Asia and mainland Africa: Diversity shrouded in darkness. **In**: *Primates in perspective*, C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder and R.M. Stumpf (eds.), pp. 34-54. Oxford University Press, Oxford, UK.

Nekaris, K.A.I. and Munds, R. 2010. Using facial markings to unmask diversity: the Slow Lorises (Primates: Lorisidae: *Nycticebus*) of Indonesia. **In**: *Indonesian Primates*, S. Gursky and J. Supriatna (eds.), pp. 383-396. Springer, New York, USA.

Nekaris, K.A.I., Rode, E.J. and Nijman, V. 2014. Javan Slow Loris *Nycticebus javanicus* É. Geoffroy Saint-Hilaire, 1812. **In**: C. Schwitzer, R. A. Mittermeier, A. B. Rylands, L. A. Taylor, F. Chiozza, E. A. Williamson, J. Wallis and F. E. Clark (eds.), Primates in Peril: The World's 25 Most Endangered Primates 2012–2014, pp. 20–21. IUCN SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), and Bristol Zoological Society, Arlington, VA, USA.

Nekaris, K.A.I., Llano Sanchez, K., Thorn, J.S., Winarti, I. and Nijman, V. 2009. Javan Slow Loris *Nycticebus javanicus* E. Geoffroy, 1812, Indonesia. **In**: *Primates in peril. The world's 25 most endangered primates 2008-2010*, R. A. Mittermeier, J. Wallis, A.B. Rylands, J.U. Ganzhorn, J.F. Oates, E.A. Williamson, E. Palacios, E.W. Heymann, M.C.M. Kierulff, L. Yongcheng, J. Supriatna, C. Roos, S. Walker, L. Cortes-Ortiz and C. Schwitzer (eds.), pp. 44-46. IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), and Conservation International (CI), Arlington, US.

Nekaris, K.A.I., Campbell, N., Coggins, T.G., Rode, E.J. and Nijman, V. 2013a. Tickled to death: Analysing public perceptions of 'cute' videos of threatened species (Slow Lorises - *Nycticebus* spp.) on Web 2.0 Sites. *PloS one* **8**:e69215.

Nekaris, K.A.I., Shekelle, M., Wirdateti, Rode, E.J. and Nijman, V. 2013b. *Nycticebus javanicus*. **In**: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1 <www.iucnredlist.org>. Downloaded on 1 March 2014.

Pliosungnoen, M. and Savani, T. 2008. *Spatial and feeding behavior of the endangered Bengal Slow Loris, Nycticebus bengalensis in Khao Angrunai Wildlife Sanctuary, Thailand*. Unpublished Report to the Primate Society of Great Britain, UK.

Pliosungnoen, M., Gale, G. and Savini, T. 2010. Density and microhabitat use of Bengal Slow Loris in primary forest and non-native plantation forest. *American Journal of Primatology* **72**:1108-1117.

Porter, L.M., Garber, P.A. and Nacimento, E. 2009. Exudates as a fallback food for *Callimico goeldii. American Journal of Primatology* **71**: 120-129.

Rode, E.J., Stengel, C.J. and Nekaris, K.A.I. 2013. Habitat assessment and species niche modelling. **In**: *Primate ecology and conservation*, E. Sterling, N. Bynum and M. Blair (eds.). Oxford University Press, Oxford, UK.

Rode-Margono, E.J. and Nekaris K.A.I. 2014, in press. Lunarphobia in a venomous mammal, the Javan slow loris (*Nycticebus javanicus* Geoffroy, 1812). *Contributions to Zoology*.

Rogers, L.D. and Nekaris, K.A.I. 2011. Behaviour and habitat use of the Bengal Slow Loris *Nycticebus bengalensis* in the dry dipterocarp forests of Phnom Samkos Wildlife Sanctuary, Cambodia. *Cambodian Journal of Natural History* **2011**: 104-113.

Schwitzer, C., Glatt, L., Nekaris, K.A.I. and Ganzhorn, J.U. 2011. Responses of animals to habitat alteration: an overview focussing on primates. *Endangered Species Research* **14**: 31-38.

Schwitzer, C., Leus, K., Byrne, M., Lorca, L. and Yaxley, M. 2010a. Feeding. **In**: *EAZA husbandry guidelines for Callitrichidae*, E. Ruivo, B. Carroll and A. Demoulan, A. (eds.), pp. 80-110. EAZA Executive Office, Amsterdam, the Netherlands.

Schwitzer, N., Clough, D., Zahner, H., Kaumanns, W., Kappeler, P. and Schwitzer, C. 2010b. Parasite prevalence in blue-eyed black lemurs *Eulemur flavifrons* in differently degraded forest fragments. *Endangered Species Research* **12**: 215–225.

Shepherd, C.R. 2010. Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in north Sumatra. *Endangered Species Research* **11**: 201-205.

Shepherd, C.R., Sukumaran, J., Wich, S.A. and Asia, T.S. 2004. *Open season: An analysis of the pet trade in Medan, Sumatra, 1997-2001*. TRAFFIC Southeast Asia, Kuala Lumpur, Malaysia.

Smiet, A. 1990. Forest ecology on Java: conversion and usage in a historical perspective. *Journal of Tropical Forest Science* **2**(4): 286-302.

Smiet, A.C. 1992. Forest ecology on Java: Human impact and vegetation of montane forest. *Journal of Tropical Ecology* **8**(2):129-152.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P. and Brook, B.W. 2010. The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation* **19**: 317-328.

Starr, C., Nekaris, K.A.I. and Leung, L. 2012. Hiding from the moonlight: luminosity and temperature affect activity of Asian nocturnal primates in a highly seasonal forest. *PloS one* **7**:e36396.

Starr, C.R. and Nekaris, K.A.I. 2013. Obligate exudativory characterises the diet of the pygmy Slow Loris *Nycticebus pygmaeus. American Journal of Primatology* **75**: 1054-1061.

Streicher U. 2009. Diet and feeding behaviour of pygmy lorises (Nycticebus pygmaeus) in Vietnam. *Vietnamese Journal of Primatology* **3**: 37-44.

Streicher, U. 2004. Aspects of ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam. PhD dissertation, Ludwig Maximilian University, Munich, Germany.

Streicher, U., Collins, R., Navarro-Montes, A. and Nekaris, K.A.I. 2013. Exudates and animal prey characterize Slow Loris (*Nycticebus pygmaeus, N. coucang, N. javanicus*) diet in captivity and after release into the wild. **In**: *Leaping Ahead: Advances in Prosimian Biology*, J. Masters, M. Gamba and F. Genin (eds.), pp. 165-172. New York: Springer.

Swapna, N., Radhakrishna, S., Gupta, A.K. and Kumar, A. 2010. Exudativory in the Bengal Slow Loris (*Nycticebus bengalensis*) in Trishna Wildlife Sanctuary, Tripura, Northeast India. *American Journal of Primatology* **72**: 113-121.

Tan, C.L. and Drake, J.H. 2001. Evidence of tree gouging and exudate eating in pygmy Slow Lorises (*Nycticebus pygmaeus*). *Folia Primatologica* **72**: 37-39.

Vinyard, C.J., Wall, C.E., Williams, S.H. and Hylander, W.L. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. *American Journal of Physical Anthropology* **120**:153-170.

Voskamp, A., Rode, E.J., Coudrat, C.N.Z., Wirdateti, Abinawanto, Wilson, R.J. and Nekaris, K.A.I. 2014. Modelling the habitat use and distribution of the threatened Javan slow loris Nycticebus javanicus. *Endangered Species Research* **23**: 277-286.

Waser, P.M. and Jones, W.T. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology* **58**: 355-390.

Wiens, F. 2002. Behavior and ecology of wild Slow Lorises (*Nycticebus coucang*): social organization, infant care system, and diet. PhD dissertation, University of Bayreuth, Germany.

Wiens, F. and Zitzmann, A. 2003. Social structure of the solitary Slow Loris Nycticebus coucang (*Lorisidae*). *Journal of Zoology* **261**:35-46.

Wiens, F., Zitzmann, A. and Hussein, N.A. 2006. Fast food for Slow Lorises: is low metabolism related to secondary compounds in high-energy plant diet? *Journal of Mammalogy* **87**:790-798.

Winarti, I. 2003. Distribusi dan struktur vegetasi habitat kukang (*Nycticebus coucang* Boddaert, 1785) di desa Marga Mekar, kecamatan Sumedang selatan, Sumedang, Jawa Barat. BSc dissertation, Universitas Padjadjaran Bandung, Indonesia.

Winarti, I. 2011. Habitat, populasi, dan seberan kukang Jawa (*Nycticebus javanicus* Geoffroy 1812) di talun Tasikmalaya dan Ciamis. MSc dissertation, Jawa Barat Sekolah Pascasarjana, Bogor, Indonesia.

Wirdateti. 2012. Sebarandan habitat kukang Jawa (*Nycticebus javanicus*) di perkebunan sayur Gunung papandayan, Kabupaten Garut. *Berita Biologi* **11**:113-120.

Wright, P.C., Arrigo-Nelson, S.J., Hogg, K.L., Bannon, B., Morelli, T.L., Wyatt, J., Harivelo, A.L., Ratelolahy, F., Huffman, M.A. and Chapman, C.A. 2009. Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. **In**: *Primate parasite ecology. The dynamics and study of host-parasite relationships*, C. Chapman and M.A. Huffman (eds.), pp. 311-330. Cambridge University Press, Cambridge, UK.

Zhou, J., Wei, F., Li, M., Zhang, J.F., Wang, D. and Pan, R.L. 2005. Hainan black-crested gibbon is headed for extinction. *International Journal of Primatology* **26**: 453-465.

Appendix 1. Ethogram for Javan Slow Loris.

	Behaviour	Definition
1	Alert	Remain stationary like in “rest” but active observation of environment or observer
2	Feed	Actual consumption of a food item
3	Forage	Movement associated with looking for food (often includes visual and olfactory searching)
4	Freeze	Interrupt locomotion to maintain motionless, rigid posture in standing or sitting position for at least three seconds, extremely slow movement not associated with foraging
5	Groom	Autogroom, lick or use tooth comb on own fur
6	Rest	Remain stationary, often with body hunched, eyes open
7	Sleep	Remain stationary in huddled position with head between the knees, or eyes visible but closed
8	Social	All interactions with conspecifics, including aggression, allogrooming, play and other social behaviours
8a	Aggression	Fight, bite (including attempts), threat, chasing; often accompanied by agonistic vocalizations
8b	Allogroom	Lick or comb with toothcomb other loris’ face or fur - usually while clasping him or her
8c	Play	Behaviours serving no immediate, definable purpose, including friendly attempted bites or manual attacks and clasping, dangle by feet, wriggle body with arms over head. No vocalizations as when fighting
8d	Other social	Social activity while being in contact or close proximity (<5 m), like mating, social follow, sniffing, social explore
9	Travel	Continuous, directed movement from one location to another
10	Other	Other behaviours not included above

Note: based on observations in this study and from Nekaris, 2001, Fitch-Snyder et al., 2001 and Daschbach et al., 1983.

Appendix 2. List of plant species that were used by Javan Slow Loris during this three month study, their use by local people and the percentage of samples: used by Slow Lorises (n=1,875), and presence in transects (n=261).

	Scientific name	Family	English common name	Trees used for	% used	% random
1	*Gigantochloa apus* (Schult.) Kurz, *Gigantochloa atter* (Hassk.) Kurz	POA	String Bamboo, Sweet Bamboo	2, 5	**37**	4
2	*Melaleuca leucadendra* (L.) L.	MRT	Cajeput Tree	3, 4, 5	22	39
3	*Acacia decurrens* (Willd.)	FAB	Green Wattle	6	**9**	2
4	*Persea Americana* (Mill.)	LAU	Avocado	1, 3	9	9
5	*Calliandra calothyrsus* (Meisn.)	FAB	Red Calliandra	6, 7	**7**	4
6	*Toona sureni* (Blume) Merr.	MEL	Suren, Indonesian Mahogany	3, 4	5	10
7	*Grevillea robusta* (A.Cunn. ex R.Br.)	PRT	Silky Oak	3, 4	3	3
8	*Artocarpus heterophyllus* (Lam.)	MOR	Jackfruit	1, 3, 8	2	2
9	*Diospyros kaki* (L.f.)	EBN	Japanese Persimmon	1, 3	1	3
10	*Coffea Arabica* (L.)	RUB	Arabica Coffee	1, 6	<1	<1
11	*Casuarina junghuhniana* (Miq.)	CAS	?	3	<1	4
12	*Musa acuminata* (Colla)	MUS	Banana	1, 9	<1	7
13	*Schima wallichii* (Choisy)	TEA	Needle Wood	3	<1	<1
14	*Dendrocalamus asper* (Schult.) Backer	POA	Giant Bamboo	2, 5	<1	
15	*Maesopsis eminii* (Engl.)	RHM	Umbrella Tree	3, 4	<1	4
16	*Chromolaena odorata* (L.) R.M.King & H.Rob.	CMP	Siam Weed, Christmas Bush	6, 7	<1	<1
17	*Ageratina riparia* (Regel) R.M.King & H.Rob., *Lycianthes denticulata* (Blume) Bitter, *Gaultheria sp.*(L.)	CMP, SOL, ERI	Mistflower, ?, ?	6	<1	
18	*Gigantochloa sp.* Kurz ex Munro	POA	Clumping Bamboo (genus)	2, 5	<1	<1
19	*Cestrum aurantiacum* (Lindl.)	SOL	???	7	<1	
20	*Citrus aurantiifolia* (Chrism.) Swingle	RUT	Key Lime (?)	1	<1	<1
21	*Aleurites moluccanus* (L.) Willd.	EUP	Candlenut	1, 3	<1	
22	*Arenga pinnata* (Wurmb)	PAL	Sugar Palm	1, 3, 9	<1	
23	*Calliandra tetragona* (Willd.) Benth.	FAB	White Calliandra	6, 7	<1	
24	*Brugmansia suaveolens* (Humb. & Bonpl. ex Willd.) Bercht. & J.Presl	SOL	Angel Trumpet	5, 7	<1	
25	*Eriobotrya japonica* (Thunb.) Lindl.	ROS	Loquat	1, 6	<1	
26	*Camellia chinensis* (Sims) Kuntze	TEA	Tea	1, 6	<1	
27	*Manglietia blumei* Prantl	MAG	?	3		3

28	*Cinnamomum burmanni* (Nees & T.Nees) Blume	LAU	Indonesian Cinnamon	1, 3, 4		1
29	*Carica papaya* (L.)	CRC	Papaya	1		1
30	*Anthocephalus cadamba* (Roxb.) Miq.	RUB	Common Bur Flower, Kadamb	3, 4		<1
					n=1875	**n=261**

Bold numbers indicate that tree species were used significantly more often by lorises than expected by chance, numbers underlined indicate that the trees were used significantly less often. 1=Consumption (including smoking), 2=construction material, 3=house (including traditional roof), 4=furniture, 5=garden (flower, fence, stable), 6=fire wood, 7=natural prevention of erosion, 8=mortar, 9=packing material.

Asian Primates Journal 4(2), 2014

A KEY ROLE OF THE SOUTHERN PIG-TAILED MACAQUE *Macaca nemestrina* (Linnaeus) IN SEED DISPERSAL OF NON-CLIMBING RATTANS IN PENINSULAR MALAYSIA

Nadine Ruppert[1*], Asyraf Mansor[2] and Shahrul Anuar M.S.[3]

School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden, Pulau Pinang, Malaysia.[1]E-mail: n.ruppert@usm.my, [2]E-mail: asyrafm@usm.my, [3]E-mail: sanuar@usm.my,
*Corresponding author

ABSTRACT

Primates play an important role in the seed dispersal of a multitude of plant species, including rattans (Calamoideae). Here, camera-trapping was used as a means of identifying mammal rattan fruit predators of two non-climbing rattan species, *Calamus castaneus* Griff. and *Daemonorops calicarpa* (Griff.) Mart., at a lowland dipterocarp forest of West Malaysia. Of a total of 25 resident frugivorous and mainly terrestrial mammal species at the study site, only Southern Pig-tailed Macaques *Macaca nemestrina* (Linnaeus) were found responsible for rattan fruit removal at ground level. Video recordings allowed the analysis of fruit handling behaviour, of which the most frequent was firstly peeling of skin and sucking of pulp, and subsequently ingesting the pulp and seeds (38.3% of N=148). Cheek pouch feeding (34.0%) and ingestion of the whole fruit (27.7%) also occurred frequently. These behaviours might not lead to the destruction of the seed and indicate seed dispersal rather than predation. As both rattan species have a low tendency to form clonal clusters, they might very much rely on animal seed dispersers for successful reproduction. This has implications for conservation efforts, as there seems to be no redundancy in seed dispersers for local acaulescent rattans, and a decline in *M. nemestrina* abundance might therefore severely affect rattan genetic diversity and population dynamics. Thus, *Macaca nemestrina* might be considered a single-species seed disperser for these two rattan species at the study site.

Keywords: acaulescent rattans, Calamoideae, *Calamus castaneus*, *Daemonorops calicarpa*, seed dispersal, seed predation, Segari Melintang Forest Reserve, Perak.

INTRODUCTION

Ninety percent of primates found in tropical regions are dependent on the forest (Mittermeier & Cheney, 1987) where they have significant effects on seed dispersal of up to 75% of plant species (Howe & Smallwood, 1982; Terborgh et al., 2002; Beckmann & Muller-Landau, 2007; Dirzo et al., 2007; Levey et al., 2002; Nuñez-Iturri & Howe, 2007; Stoner et al., 2007; Wang et al., 2007; Wright et al., 2007; Stevenson et al., 2008). Primates comprise around 40% of the frugivore biomass in tropical forests (Eisenberg & Thorington, 1973; Chapman, 1995) where they consume large quantities of fruits and defecate or spit high numbers of diverse seeds (Lambert, 1999). Moreover, they can add positive effects on seed germination, which are caused by the passage of seeds through their digestive system (Samuels & Levey, 2005; Robertson et al., 2006; González-Di Pierro et al., 2011). Seed swallowing is by far the most common means of primate seed dispersal in the Neotropics. In the Palaeotropics seed spitting by cheek-pouched monkeys (Cercopithecinae) is more common. Cheek pouches, which have nearly the same capacity as the stomach, allow monkeys to extract pulp without having to invest in digesting swallowed seeds (Lambert, 1999).

The plant-primate interaction determines the variation in seed shadows, which influences plant demography and spatial distribution. Primate seed-handling strategies depend on factors, such as the interactions between their digestive system and traits of the fruiting species, and there is a wide variation in the shape of seed shadows generated by primates (Chapman & Russo, 2007). In addition, the response of a primate to a fruiting species is mediated by many factors, such as its social structure, foraging decision, digestive anatomy, seed-handling strategy, or ranging behaviour, whereas the distribution and abundance of fruit resources influences daily foraging speeds and distances (Chapman & Russo, 2007).

There is a high variability among primate species, and according to Chapman & Russo (2007) there is no such thing as one "primate seed syndrome" for fruiting plant species. It seems that primates tend to ingest and disperse more smaller than larger seeds (Corlett & Lucas, 1990; Lambert, 1999), and more ovoid than round seeds (Garber, 1986; McConkey, 2000); and some, but not all primates, might be rather selective, for example orangutans preferred high pulp mass (Leighton, 1993), whereas Long-tailed Macaques *Macaca fascicularis* (Raffles) did not select on the basis of seed or fruit size (Corlett & Lucas, 1990). Ingested seeds may become dispersed over longer distances than spat seeds (Lambert, 1999, 2001), and spat or dropped seeds are more likely to be deposited on the forest floor singly because fruits are handled individually (Lambert, 1999).

Countries with primate populations are losing approximately 125,000 km^2 of forest each year (Chapman & Peres, 2001) and habitat fragmentation and hunting are further reducing primate populations. The reduction in primate abundance may have severe impacts on plant communities (Redford, 1992; Chapman, 1995) as it was shown that hunted primate populations in a fragmented habitat produce altered seed dispersal patterns (Pacheco & Simonetti, 2000; Wright et al., 2000; Chapman, Chapman et al., 2003; Chapman, Lawes et al., 2003; Cordeiro & Howe, 2003). Most importantly, there is simply not enough redundancy in fruit disperser species to compensate for losses of one group, such as primates (Poulsen et al., 2002). Thus, with the loss of primate species in fragmented areas, seed dispersal rates may decrease and seed shadows may become more stereotyped, which can eventually lead to changes in plant population densities and reduction of diversity of plant communities (Chapman & Russo, 2007).

Primates are considered to be, besides hornbills, the main dispersers of rattan seeds (Calamoideae, Arecaceae) in both Southeast Asia and Africa (Corlett & Lucas, 1990; Dransfield, 2001; Sunderland, 2001). Rattans are an important component of the primary and secondary forest vegetation of Malaysia and play an important role in the rainforest ecosystem: they can act as shelter, for example for ants (Sunderland, 2004); or as food source, such as for various insect groups that feed on their pollen (Henderson, 1986; Lee, 1995; Kidyoo & McKey, 2010); and mammals or birds that feed on fruits, seeds, or fresh shoots (Sunderland & Dransfield, 2002). In Peninsular Malaysia alone, 106 species of eight genera grow in the wild (Dransfield, 1979) and of the approximately 600 rattan species that can be found worldwide, 117 are now regarded as threatened to some degree (Walter & Gillet, 1998). The threats are manifold but habitat loss due to land conversion and overexploitation of rattans for the furniture industry must be considered the most hazardous ones. Rattans use two reproductive strategies: some rattan species have a high tendency to form big clusters with multiple clonal stems, whereas other species appear solitarily or in small clusters. These are widely represented by genetically different, seed-derived individuals (Dransfield & Sunderland, 2002).

There are two commonly observed strategies of rattan fruit handling by primates: either fruits are ingested as a whole and pass through the intestinal tract with the seed intact, or the pulp is sucked and the seed spat out (Corlett & Lucas, 1990; Pritchard & Davies, 1999). However, only a few studies address the role of primates in rattan seed dispersal (e.g. Corlett & Lucas, 1990; Tutin et al., 1994; Lucas & Corlett, 1998; Sunderland, 2001) and none of these were conducted in Peninsular Malaysia. Primates are the most important dispersers of larger-seeded plant species (Howe & Smallwood, 1982; Chapman & Chapman, 1995; Chapman & Russo, 2007) and most rattan species that were found at the study site have medium- to larger-sized seeds (c. 1 cm diameter).

However, in studies on African primates where gorillas, chimpanzees, bonobos, drills and mandrills were found to use rattan fruits as a food source (Tutin et al.,1994; Sunderland, 2001), their feeding habit seemed to lead to the destruction of the seeds. These larger primate species often chew before they swallow their food and this might inhibit the germination ability of the seed (Kingdon, 1997). Feeding experiments with African rattan seeds presented to those primate species showed that only fruits of the genus *Laccosperma*, which has small seeds (1 cm x 0.6 cm), were swallowed as a whole and thus stood the chance of being dispersed intact. Bigger seeds (diameter >1.5 cm) of the genera *Eremospatha* and *Oncocalamus* were either chewed and destroyed or spat out at the site (Sunderland, 2001).

Also in Southeast Asia, primates have been found to contribute to rattan seed dispersal (Dransfield, 2001). In Singapore, Long-tailed Macaques have been observed to feed on seeds of the genera *Calamus*, *Daemonorops* and *Korthalsia* in the wild. They were found to spit out or clean and drop the majority (up to 69%) of seeds of the ripe fruits they consume. This alternative "seed spitting behaviour" might be regarded as a means of dispersing viable seeds (Corlett & Lucas, 1990; Lucas & Corlett, 1998). Despite these efforts to better understand the role of primates in rattan seed dispersal, there is still a major lack of fundamental studies dealing with rattan seed dispersal mechanisms in general and the specific interactions of primate and rattan species of Peninsular Malaysia. This study was thus aimed at identifying mammal species that play a key role in seed dispersal of local non-climbing rattan species.This was conducted by means of camera trap surveillance of fruiting rattans during a two-year survey. Both primate species and small mammals were expected to predate on ripe rattan fruits. Seed handling strategies were analysed to assess the impact on seed survival.

METHODS

Study Site

The study site was located at the Western edge of the Segari Melintang Forest Reserve (SMFR), Manjung District, Perak, Peninsular Malaysia (4°19-20’N, 100°34-36’E) (Fig. 1). The SMFR originally comprised 4,566 ha (in the 1960s) but in 2010 only about 2,720 ha remained. 408 ha of the SMFR are strictly protected as a Virgin Jungle Reserve (VJR). The rest is a logged-over, regenerated Permanent Forest Reserve (PFR). Vegetation within the SMFR consists of coastal lowland mixed dipterocarp forest and areas with alluvial freshwater swamp forest, which are temporarily flooded. To the exclusion of a few emergents, the maximum height of the closed canopy is about 40 m and the SMFR extends from 20 m to 250 m above sea level (Wiens & Zitzmann, 2003).

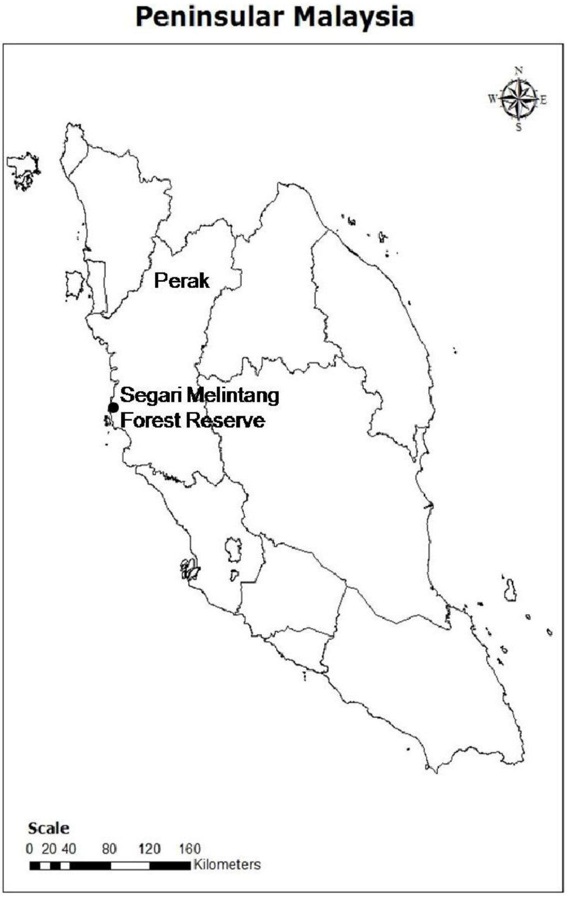


Fig. 1. Location of the Segari Melintang Forest Reserve, Manjung District, Perak, Peninsular Malaysia.

Camera trap survey

In order to identify rattan fruit consumers, ripe infructescences of *Calamus castaneus* Griff. and *Daemonorops calicarpa* (Griff.) Mart. were video monitored with motion-triggered infrared cameras specially designed for wildlife monitoring (Bushnell® Trophy Cam™). Altogether 15 individuals of *C. castaneus* were video monitored over a total time span of 13 months, and five fruiting individuals of *D. calicarpa* over three months. Videos triggered by approaching animals were recorded for 15 seconds with a 2-second interval allowing identification of fruit handling behaviour. Visitors were identified to species level by the authors, who at this same time also ran a long-term mark-and-recapture study for small mammals in the area, and were thus very familiar with the local small mammal species that are sometimes difficult to identify (Ruppert et al., 2012). The number and duration of visits of all animals were recorded. Video monitoring of rattan infructescences was performed continuously from July 2010 until December 2010 and again during several other fruiting events until the end of 2013. Camera trap locations comprised an area of around 1.5 km^2.

Fruiting events of rattans

Calamus castaneus produced fruits non-seasonally throughout the year and one individual would exhibit different fruiting stages (ripe, unripe, budding, flowering) all at the same time (Fig. 2C). *Daemonorops calicarpa* on the other hand is a hapaxanthic species, meaning that individuals only flower and fruit once in their lifetime and die subsequently (Fig. 2A) (Dransfield, 1979). Thus, recorded fruiting events of *D. calicarpa* at the study site occurred far more seldom than those of *C. castaneus*. Both species have fruits and seeds that are similar in size (seed: 1 cm x 1 cm) (Fig. 2B).

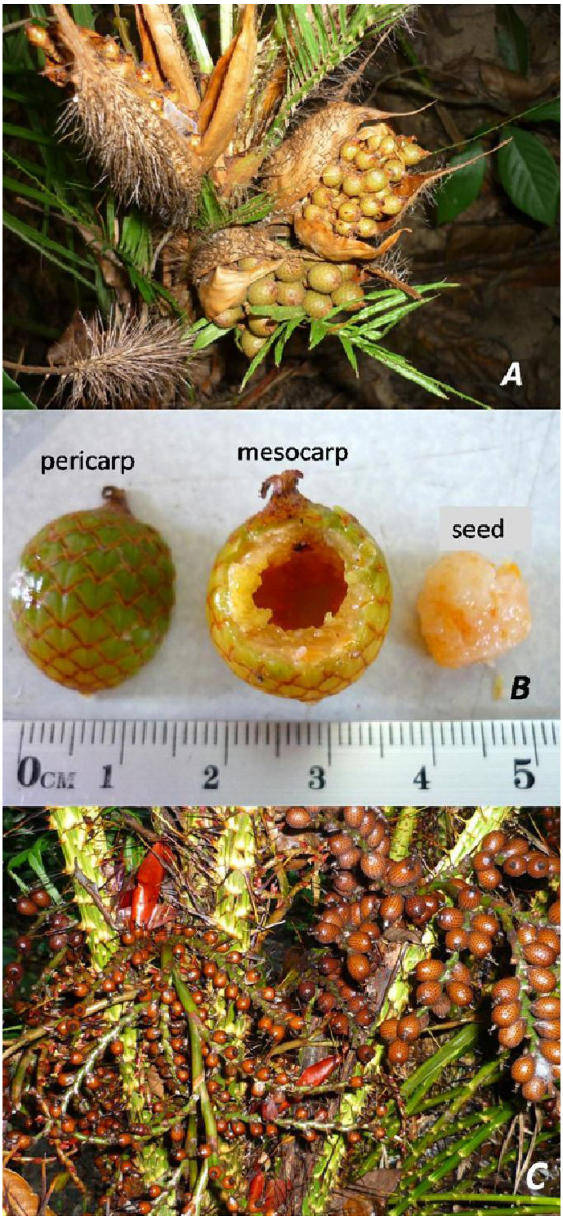


Fig. 2. (A) Infructescence of *Daemonorops calicarpa* (Griff.) Mart. (B) Fruit of *D. calicarpa* with pericarp, mesocarp and seed. (C) Infructescence of *Calamus castaneus* Griff. with different development stages (ripe, unripe, budding, flowering).

RESULTS

Frugivorous mammals at the study site

A total of 25 frugivorous diurnal and nocturnal mammal species (Table 1) were identified at the study site during the study period, either by camera trapping or live trapping (Ruppert et al., 2012). More species are probably present but escaped detection, for example several species of Sciuridae and Muridae that inhabit higher forest strata, or were missed due to low abundance.

Rattan fruit monitoring

During the video surveillance of ripe rattan infructescences a total of 485.1 minutes video footage was triggered by forest-dwelling animals moving by the infrared-sensor of the cameras. The majority of species in these recordings showed no interest in the rattan fruits, and individuals of some species (e.g. *M. fascicularis*, *Tupaia glis* [Diard], *Callosciurus notatus* [Boddaert]) would examine the fruits but subsequently not take any.

In all recorded footage, no other species but *M. nemestrina* was found responsible for any single recorded rattan fruit removal event. The species was recorded handling fruits for a total of 39.3 minutes, which corresponds to 8.1% of the overall recording time (Fig. 3).

Fruit handling strategies

During different recording events, a total of 41 different *M. nemestrina* individuals (including adult males and females, as well as subadults and juveniles) were found foraging on rattan fruits. Together they picked 148 different fruits. The most common fruit handling behaviour was: (1) peeling or opening the pericarp with teeth to get access to the mesocarp, and subsequently (2) sucking the pulp and ingesting the seed (38.3%). Cheek pouch feeding (34.0%) and ingestion of the whole fruit (27.7%) also occurred frequently. In only 2.1% of the recordings, picked fruits were discarded or seeds were spat out at site (Table 2). Juveniles not distinguishable by sex (34.4%) and adult males (29.3%) were most frequently recorded on rattans (Table 2), however adults males and females picked the most fruits (38.5% and 30.4%, respectively) (Fig. 4). During several examinations of the forest floor under fruiting rattans, opened fruits were found where the pulp and seeds had been removed and possibly ingested by primates (Fig. 5). No seeds were found at the site.

DISCUSSION

This study highlighted the importance of *M. nemestrina* for rattan seed dispersal in forests of the Malay Peninsula. Here, the fruits of two abundant, non-climbing (or acaulescent) rattans with low clustering ability (Dransfield, 1979), *C. castaneus* (here: 6.1 stems ha^{-1}) and *D. calicarpa* (here: 3.1 stems ha^{-1}), were found to be consumed solely by one primate species at the study site. Despite the presence of four other primate species and over 16 terrestrial obligate-frugivorous small mammal species, *M. nemestrina* alone was found responsible

Table 1. List of frugivorous mammal species observed at the study site during the study period.

ENGLISH NAME	SCIENTIFIC NAME
Muridae	
Sundaic Lenothrix	*Lenothrix canus* Miller, 1903
Chestnut White-bellied Rat	*Niviventer fulvescens* (Gray, 1847)
Red Spiny Red	*Maxomys surifer* (Miller, 1900)
Whitehead's Spiny Rat	*Maxomys whiteheadi* (Thomas, 1894)
Rajah Spiny Rat	*Maxomys rajah* (Thomas, 1894)
Polynesian Rat	*Rattus exulans* (Peale, 1848)
Malaysian Field Rat	*Rattus tiomanicus* (Miller, 1900)
Annandale's Rat	*Rattus annandale* Bonhote, 1903
House Rat	*Rattus rattus* (Linnaeus, 1758)
Long-tailed Giant Rat	*Leopoldamys sabanus* (Thomas, 1887)
Sciuridae	
Plantain Squirrel	*Callosciurus notatus* (Boddaert, 1785)
Prevost's Squirrel	*Callosciurus prevostii* (Desmarest, 1822)
Pale Giant Squirrel	*Ratufa affinis* (Raffles, 1821)
Black Giant Squirrel	*Ratufa bicolor* (Sparrman, 1778)
Shrew-faced Ground Squirrel	*Rhinosciurus laticaudatus* (Müller, 1840)
Low's Squirrel	*Sundasciurus lowii* (Thomas, 1892)
Tupaiidae	
Pen-tailed Treeshrew	*Ptilocercus lowii* Gray, 1848
Common Treeshrew	*Tupaia glis* (Diard, 1820)
Tragulidae	
Lesser Mousedeer	*Tragulus kanchil* (Raffles 1821)
Viverridae	
Common Palm Civet	*Paradoxurus hermaphroditus* (Pallas, 1777)
Lorisidae	
Sunda Slow Loris	*Nycticebus coucang* (Boddaert, 1785)
Cercopithecidae	
Dusky Langur	*Trachypithecus obscurus* (Reid, 1837)
Long-tailed Macaque	*Macaca fascicularis* (Raffles, 1821)
Southern Pig-tailed Macaque	*Macaca nemestrina* (Linnaeus, 1766)
Hylobatidae	
Agile Gibbon	*Hylobates agilis* F. Cuvier, 1821

Fig. 3. Juvenile *Macaca nemestrina* (Linnaeus) picking and ingesting fruits of *Calamus castaneus* Griff. (<1m above ground; still images taken from video of camera trap).

Table 2. Rattan fruit handling behaviour of different *Macaca nemestrina* (Linnaeus) individuals (N=41).

Behavior **# ID of the individual**[1]	**Pick fruit & discard**	**Peel pericarp**	**Suck pulp & ingest**	**Spit seed**	**Ingest as whole**	**Put in cheek pouch**	**n**
SA♂	-	1, 2, 16, 21	1, 2, 16	-	16, 40	21	4
SA♀	-	-	-	-	-	-	0
A♀	37[2]	4, 13, 25, 34, 35, 37	4, 25, 34, 35, 37	-	4, 5	13, 25, 30, 34	7
A♂	-	11, 14, 18, 28, 29, 36	11, 14, 18, 28, 29, 36, 38	28	11, 14, 18	3, 7, 9, 11, 12, 22	12
Juv♀/♂	-	19, 26, 27, 31, 32, 36	19, 26, 27, 31, 32, 36	-	6, 33, 36, 39, 41	10, 20, 23, 24	14
Unidentified	-	17, 20	17, 20	-	8, 15	17	4
Frequency of behaviour	1	24	23	1	13	16	

[1] ID numbers refer to numerical order of recorded individuals on camera trap.

[2] #37 picked whole infructescence and discarded some fruits and ingested others.

for rattan fruit removal and ingestion. Similar findings might be expected in forests of Peninsular Malaysia with similar mammal species composition. It should be pointed out that the study site lacks any bigger herbivorous mammal species, like tapirs or elephants. Effects of macaques on seed dispersal might thus vary in forests where competition for fruits is higher (also in regard to the presence of orangutans in Borneo or Sumatra).

According to the IUCN Red List *Macaca nemestrina* is classified as Vulnerable (Richardson et al., 2008) and its possible role as the single species seed disperser for acaulescent rattan species may have far-reaching consequences for conservation efforts, also from the plant perspective. It might be argued that, whilst having a low clustering ability, the high output of fruits, especially in *C. castaneus* (see Fig. 2C), and the high abundance *C. castaneus* point towards an effective seed dispersal strategy, likely facilitated by *M. nemestrina* at the study site.

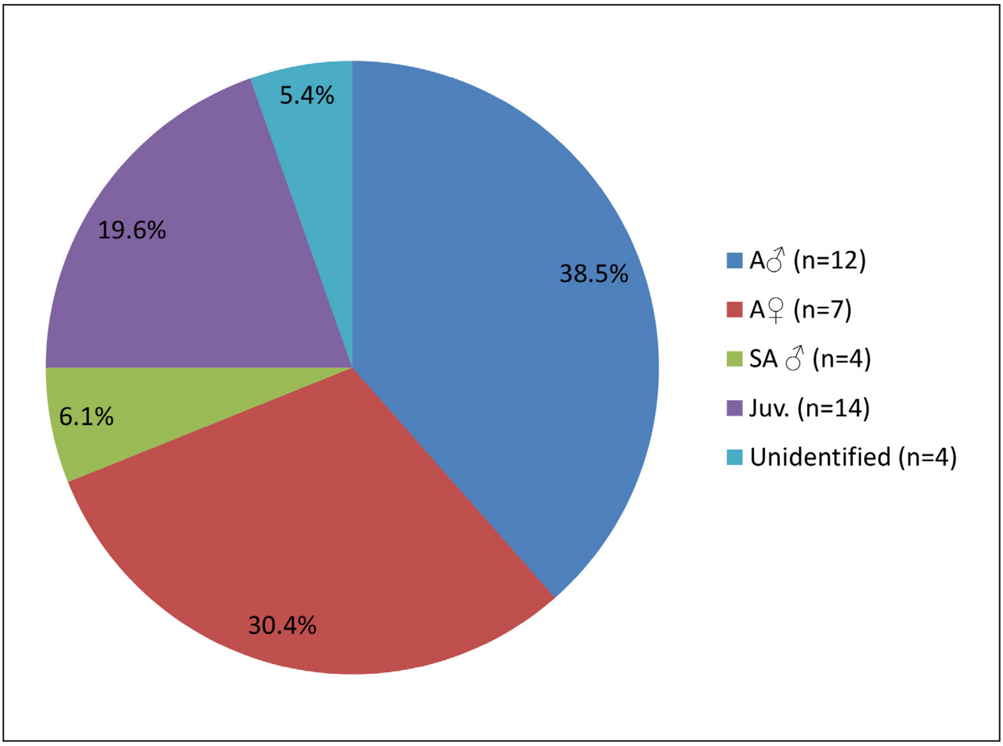


Fig. 4. Total number of rattan fruits (N=148) ingested by *Macaca nemestrina* (Linnaeus) according to age and sex.

There might be several reasons why other primate or small mammal species at the study site did not engage in rattan fruit removal. For the more arboreal primate species (*Hylobates agilis* F. Cuvier, *Trachypithecus obscurus* Reid and *M. fascicularis*) low-growing rattans of the understorey vegetation might simply be growing outside their preferred niche. However, there were several recordings showing *M. fascicularis* and *T. obscurus* sitting next to fruiting rattans on the ground. One video showed the attempt of one *M. fascicularis* individual to reach for some rattan fruits, but it was chased away by an adult male *M. nemestrina* already present at the site. This does point towards competition for ground resources between these two species, where *M. nemestrina* seems to dominate this habitat type (Caldecott, 1986). On the other hand, peaceful interactions between groups of both species, resulting in mixed-species foraging cohorts, even leading to playful interactions between subadult members of both species, could be frequently observed (N. Ruppert, pers. obs.).

So there might also be other reasons unknown to the authors for why *M. fascicularis* could not be recorded feeding on rattan fruits at the study site. Slow lorises *Nycticebus coucang* (Boddaert), which are nocturnal and thus inhabit another ecological niche, could be expected to feed on ripe fruits (Wiens & Zitzmann, 2003). They were frequently recorded on videos monitoring Dull Bertam Palm (*Eugeissona tristis* Griff.) flowers at the study site (F. Wiens, in litt.) but not a single individual was caught on camera near rattans, for reasons unknown. Also nocturnal and diurnal rodents could not be associated with rattan fruit removal, which might be due to the seed size that is presumably too big to be handled by small mammal species (P.-M. Forget, pers. comm.). In general, not many studies on *M. nemestrina* have been conducted in the wild (e.g. Caldecott, 1986; Oi, 1990). These primates live in multi-male multi-female groups with a group number of up to 80 individuals (Caldecott, 1986). Usually higher ranking males gain prior access to food sources. Groups often split up during daily foraging tours, and adult males might wander solitarily over longer daily distances than females and juveniles (Caldecott, 1987). Here, it was shown that adult males contributed most to rattan fruit removal, and might thus also carry seeds over longer distances than females, who do not leave their group. Adults, in contrast to subadults, were responsible for the majority of 69% of rattan fruit removal.

Fig. 5. Examples of discarded rattan fruits (here *Calamus castaneus* Griff.) on the forest floor around fruiting rattan clumps. Pictures show the opened pericarp with pulp and seeds removed. No seeds were found on site.

Preliminary data on a habituated group of *M. nemestrina* at the study site indicates that the group travels between 1.5 km and 3.5 km (average 1,880 m) per day, with a mean travelling speed of 420 m h-1 during the active period" However, gut passage time between the sexes and age may differ, which complicates the prediction of dispersal distances, but there hardly exists any literature for this on wild macaques (e.g. Corlett, 2009 mentioned seed dispersal distances by macaques ranging between 10 m to 100 m). A study on captive *Macaca fuscata* (Blyth) indicated a mean retention time of larger seeds of 37-54 hours (Tsuji et al., 2010) with 4.4% of ingested seeds passing through the GI tract intact (Otani, 2004). Wild *Macaca leonina* (Blyth) ingested the seeds of at least 15 fruit species in Khao Yai, Thailand where some seeds were dispersed and others predated (Latinne et al., 2008). There, a variety of fruits were dispersed by over 25 different animal species, including macaques, but no close relationship between a particular fruit plant and a frugivore was found (Kitamura et al., 2002).

In order to study the impact of *M. nemestrina* on seed dispersal, more studies including experiments on gut passage time, daily foraging distances and effects of gut passage on seed germination correlated to gender and age must be conducted in the future. These preliminary results point towards a role of *M. nemestrina* as seed disperser rather than predator for acaulescent rattans. The fact that only *M. nemestrina* was found to consume rattan seeds does put extra weight on the need of acting towards protection of these primates. As there seems to be no redundancy in seed dispersal agents for non-climbing rattans, a decline in *M. nemestrina* abundance might directly influence rattan population dynamics and lead to an erosion of their genetic diversity.

ACKNOWLEDGEMENTS

This study was part of NR's PhD-project on the population dynamics of rattans, which was financed by USM Postgraduate Grant 1001/PBIOLOGI/843098, University Research Grant 1001/PBIOLOGI/811131 and Ministry of Higher Education Fundamental Research Grant 203/PBIOLOGI/6711223. The authors acknowledge the Perak Forestry Department for issuing respective permits. NR would like to thank Antje Engelhardt and another anonymous reviewer for valuable comments on the manuscript.

REFERENCES

Beckman, N.G. and Muller-Landau, H.C. 2007. Differential effects of hunting on pre-dispersal seed predation and primary and secondary seed removal of two Neotropical tree species. *Biotropica* **39**(3): 328-339.

Caldecott, J.O. 1986. An ecological and behavioural study of the pig-tailed macaque. **In**: *Contributions to Primatology*, Szalay, F.S. (ed.), pp.1-259. Karger, Basel, New York, USA.

Chapman, C.A. 1995. Primate seed dispersal: coevolution and conservation implications. *Evolutionary Anthropology* **4**(3): 74-82.

Chapman, C.A., Chapman, L.J., Vulinec, K., Zanne, A.E. and Lawes, M.J. 2003. Fragmentation and alteration to seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* **35**: 382-393.

Chapman, C.A., Lawes, M.J., Naughton-Treves, L. and Gillespie, T.R. 2003. Primate survival in community-owned forest fragments: are metapopulation-models useful amidst intensive use? **In**: *Primates in Fragments: Ecology and Conservation*, L.K. Marsh (ed.), pp. 63-78. Kluwer Academic/Plenum, New York, USA.

Chapman, C.A. and Peres, C.A. 2001. Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology* **10**: 16-33.

Chapman, C.A. and Russo, S.E. 2007. Primate seed dispersal. **In**: *Primates in Perspective*, C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S. Bearder. (eds.), pp. 510-525. Oxford University Press, New York. USA.

Cordeiro, N.J. and Howe, H.F. 2003. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* **15**: 1733-1741.

Corlett, R.T. and Lucas, P.W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* **82**:166-171.

Corlett, R.T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica* **41**(5): 592-598.

Dirzo, R., Mendoza, E. Ortíz, P. 2007. Size-related differential seed predation in a heavily defaunated Neotropical rain forest. *Biotropica* **39**(3): 355-362.

Dransfield, J. 1979. *A Manual of the Rattans of the Malay Peninsula*. Malayan Forest Records 29. Forest Department, Ministry of Primary Industries, Malaysia.

Dransfield, J. 2001. Taxonomy, biology and ecology of rattan. *Unasylva* **52**: 11-12.

Eisenberg, J.F. and Thorington, R.W. 1973. A preliminary analysis of a Neotropical mammal fauna. *Biotropica* **5**: 150-161.

Garber, P.A. and Paciulli, L.M. 1997. Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). *Folia Primatologica* **68**: 236-253.

González-Di Pierro, A.M., Benitez-Malvido, J., Mendez-Toribio, M., Zermeno, I., Arroyo-Rodriguez, Stoner, K.E. and Estrada, A. 2011. Effects of the physical environment and gut passage on the early establishment of *Ampelocera hottlei* stands in rain forest fragments. *Biotropica* **43**(4): 459-466.

Henderson, A. 1986. A review of pollination studies in the Palmae. *The Botanical Review* **52**(3): 221-259.

Howe, H.F., and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecological Systematics* **13**: 201-228.

Kidyoo, A.M. and McKey, D. 2012. Flowering phenology and mimicry of the rattan *Calamus castaneus* (Arecaceae) in southern Thailand. *Canadian Journal of Botany* **90**: 856-865.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, London, UK.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. and Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* **133**(4): 559-572.

Lambert, J.E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail-monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physiological Anthropology* **109**: 365-386.

Lambert, J.E. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and Strychnosmitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology* **22**(2): 189-201.

Latinne, A., Huyen, M.C. and Savini, T. 2008. Feeding ecology and seed dispersal of pigtail macaques (*Macaca nemestrina*) in KhaoYai National Park, Thailand. *Folia Primatologica* **79**(5): 348-348.

Lee, Y.F. 1995. Pollination in the rattans *Calamus subinermis and Calamus caesius* (Palmae: Calamoideae). *Sandakania* **6**:15-39.

Leighton, M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruitselection. *International Journal of Primatology* **14**: 257-313.

Lucas, P.W. and Corlett, R.T. 1998. Seed dispersal by long-tailed macaques. *American Journal of Primatology* **45**: 29-44.

McConkey, K.R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology* **52**: 13-29.

Mittermeier, R.A. and Cheney, D.L. 1987. Conservation of primates and their habitats. **In**: *Primate Societies*, B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.), pp. 477-490. University of Chicago Press, Chicago, USA.

Oi, T. 1990. Population organization of wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West-Sumatra. *Primates* **31**: 15-31.

Otani, T. 2004. Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Euryae marginata. Ecological Research* **19**(5): 495-501.

Pacheco, L.F. and Simonetti, J.A. 2000. Genetic structure of amimosoid tree deprived of its seed disperser, the spider monkey. *Conservation Biology* **14**: 1766-1775.

Poulsen, J.R., Clark, C.J., Connor, E.F. and Smith, T.B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* **83**: 228-240.

Pritchard, H.W. and Davies, R.I. 1999. Biodiversity and conservation of rattan seeds. **In**: *Rattan Cultivation: Achievements, Problems and Prospects*, R. Bacilieri and S. Appanah (eds.), pp. 51-60. International Co-operation Centre on Agrarian Research for Development (CIRAD), Malaysia.

Redford, K.H. 1992. The empty forest. *Bioscience* **42**: 412-422.

Richardson, M., Mittermeier, R.A., Rylands, A.B. and Konstant, B., 2008. *Macaca nemestrina*.The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 8 March 2015.

Ruppert, N., Asyraf, M. and Shahrul Anuar, M.S. 2012. *One year mark-and-recapture study on small terrestrial mammals at Segari Melintang Forest Reserve, Perak: assessing trap height and bait preferences and efficiency of different tagging methods for long-term identification*. **In**: Seminar on long-term ecological research in the EAP-region. 4th July 2012. Kuala Lumpur: Forest Research Institute Malaysia.

Stevenson, P.R. and Aldana, A.M. 2008. Potential effects of Ateline extinction and forest fragmentation on plant diversity and composition in the Western Orinoco Basin, Colombia. *International Journal of Primatology* **29**(2): 365-377.

Stoner, K.E., Riba-Hernandez, P., Vulinec K. Lambert, J.E. 2007. The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. *Biotropica* **39**(3): 316-327.

Sunderland, T.C.H. 2001. The taxonomy, ecology and utilization of African rattans (Palmae: Calamoideae). Ph.D. dissertation, University College, London, UK.

Sunderland, T.C.H. 2004. Ant and rattan associations in forest of tropical Africa. *Ghana Journal of Forestry* **15** & **16**: 13-19.

Sunderland, T.C.H. and Dransfield, J. 2002. Species profile rattan. **In**: *Rattan: Current Issues and Prospects for Conservation and Sustainable Development*, J. Dransfield, F.O. Tesoro and N. Manokaran (eds), pp. 9-22. Non-Wood Forest Products 14. FAO, Rome, Italy.

Terborgh, J., Pitman, N., Silman, M., Schichter, H. and Nunez, P. V. 2002. Maintenance of tree diversity in tropical forests. **In**: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, Levey, D. J., Silva, W. R., and Galetti, M. (eds.), pp. 351-364. CABI Publishing, New York, USA.

Tsuji, Y., Morimoto, M. and Matsubayashi, K. 2010. Effects of the physical characteristics of seeds on gastrointestinal passage time in captive Japanese macaques. *Journal of Zoology* **280**(2): 171-176.

Tutin, C.E.G., White, L.J.T., Williamson, E.A., Fernandez, M. and McPherson, G. 1994. List of plant species identified in the northern part of the Lopé Reserve. *Gabon Tropics* **3**(3/4): 249-276.

Wang, B.C., Sork, V.L., Leong, M.T. Smith, T.B. 2007. Hunting of mammals reduces seed removal and dispersal of the Afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica* **39**(3): 340-347.

Wiens, F. and Zitzmann, A. 2003. Social structure in the solitary slow loris *Nycticebus coucang* (Lorisidae). *Journal of Zoology* **261**: 35-46.

Wright, S.J., Hernandéz, A. and Condit, R. 2007. The bush meat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* **39**(3): 363-371.

Asian Primates Journal 4(2), 2014

SUMATRAN ORANGUTAN AS A FLAGSHIP FOR CONSERVING BIODIVERSITY AND PARKS: LESSONS LEARNT FROM NORTH SUMATRA CONSERVATION AWARENESS PROGRAMMES

Jatna Supriatna[1,2*], Erwin Perbatakusuma[3], Abdul Hamid Damanik[4], Hasbi Hasbulah[5], and Anton Ario[6]

[1]Department of Biology, University of Indonesia, Depok 16424, Indonesia. E-mail: jsupriatna@rccc.ui.ac.id

Conservation International, Indonesia. Jalan Pejaten Barat 16A, Jakarta, Indonesia. [2]E-mail: jatna.supriatna@unitedindiversity.org, [3]E-mail: adriawan2010@gmail.com, [4]E-mail: Abdul.Damanik@resources.net, [5]E-mail: h.hasbulah@conservation.org
[*]Corresponding author

ABSTRACT

Conservation International (CI) in Indonesia has developed three conservation awareness programmes since 1995; two programmes are still running, while one was discontinued due to funding issues. These conservation education programmes are part of a long-term plan by CI to prioritize large-scale efforts to conserve biodiversity in Indonesia by pulling together various stakeholders and partners. Through partnerships with local non-governmental organizations, the government, universities, the private sector and other donors, environmental education programmes can be sustained. Successes in terms of the conservation of flagship species have been achieved in some areas. For example, the Sumatran Orangutan *Pongo abelii* Lesson was used as a flagship species in education programmes at the Sibolangit Interpretive Centre. However, in local forest communities the use of the flagship-species approach was perceived to be effective only in conjunction with raising awareness of ecological services. Discontinuation of the Sibolangit Interpretive Centre occurred due to a lack of donor support, as has been the case for many conservation education programmes in Indonesia. Nationwide, few public awareness programmes focusing on species have endured and proven effective without relying on donors. A key to the success of the surviving programmes is engagement with a variety of partners that provide various skills, funding opportunities, and resources.

Keywords: Awareness programmes, conserving biodiversity and parks, Indonesia, orangutan.

INTRODUCTION

Globally, conservation awareness-raising has often been embedded within environmental education at the primary, secondary and tertiary levels of the formal education system, as well as within extra-curricular activities for children and adult education programmes. These activities include any type of educational programme about nature, wildlife and the environment with the underlying goal of developing the following outcomes: an appreciation for nature, knowledge of nature or participation in activities related to the protection of nature. These programmes aim to increase awareness and alter behaviour to contribute to conservation and decrease environmental destruction resulting from human practices. Although conservation education alone will not solve all environmental problems, effective education and communication programmes are a prerequisite for better natural resource management and, ultimately, for safeguarding the biosphere on which we all depend (Jacobson, 1995).

Indonesian environmental education programmes began in the late 1960s, mostly in schools, and gained momentum when the Government of Indonesia established the Ministry of the Environment in the early 1970s. Initiatives to educate Indonesians about the environment have mostly been embedded in curricula, biology books and related activities, such as nature clubs, at many universities. Non-governmental organizations (NGOs) have played a significant role by either developing conservation centres in or near parks or by proactively working with schools to develop the necessary biodiversity conservation content for their curricula (Indrawan et al., 2007; Supriatna, 2008).

Although public environmental education is not a new idea, it has previously had only a small-scale and short-term impact in Indonesia. The oldest environmental education facility is the Seloliman Forest Centre in East Java, which brings together students, educators, farmers, governments, businesses, women's groups and the general public to learn about the environment. Courses at Seloliman have included seminars to promote the integration of environmental education into school curricula, and workshops for local villagers to learn skills for environmentally friendly living. This centre is not only the oldest in Indonesia, but it has received many awards for successfully educating a wide range of stakeholders in environmental issues.

In 1995, World Wide Fund for Nature (WWF) Indonesia created an environmental awareness programme that departed from other such initiatives through a special project that included motor vehicles equipped with films and flyers for school children, communities and stakeholders in forested areas, such as national parks and other protected areas (WWF Indonesia, 2014). Another NGO, Conservation International (CI), initiated similar programmes in three locations in 1996. The first was Bodogol Conservation Education Centre (BCEC) in the Gunung Gede Pangrango National Park near Bogor, West Java, which is south of Jakarta, the capital city of Indonesia (Ario & Supriatna, 2015). The second was the Sibolangit Interpretive Centre (SIC), which was established in North Sumatra Province as an anchor for conserving parks and biodiversity over large areas, such as the Leuser Ecosystem (2.3 million ha). The third programme was located in the marine and coastal areas of Raja Ampat in West Papua. This programme continues to this day and utilizes a large ship called 'Kalabia' which means 'shark' in the local language, as a mobile classroom on the water.

In North Sumatra, CI awareness programmes were focused on saving parks that support the Sumatran Orangutan. The Sumatran Orangutan is one of the six closest relatives of humans, and is rapidly moving toward the brink of extinction (Rijksen, 2001). The Sumatran Orangutan population is concentrated in the northern part of the island, in the North Sumatra and Aceh provinces. There are several small parks in North Sumatra and Aceh between 1,000 and 10,000 ha in size, such as Dolok-Sipirok Protected Area (6,970 ha), Sibual-buali Protected Area (5,000 ha), Jantho Protected Area (8,000 ha), and only one large park, Leuser National Park, of 1.1 million ha (Supriatna et al., 2001). Sumatran Orangutan is found only in part of Leuser National Park and a few small protected areas in North Sumatra. Loss of natural habitat and poaching are the most significant factors contributing to the reduction of orangutan populations in North Sumatra. With current estimated rates of logging, habitat loss and the associated removal of orangutans, results from a Population and Habitat Viability Analysis (PHVA) indicated that only populations of 6,600 or more orangutans showed long-term viability, and that high logging rates of 10-20% annually will quickly drive populations to extinction (Singleton et al., 2004; Utami & van Schaik, 2010).

CI programmes on conservation awareness have been using 'flagship species', a term applied to a popular, charismatic species that serves as a symbol and rallying point to stimulate conservation awareness and action (Heywood, 1995). All the advantages of using flagship species may be reinforced by appropriate marketing that successfully enhances or highlights the species' charisma to serve a conservation campaign (Bowen-Jones & Entwistle, 2002). One notable example is the rehabilitation of the image of the Komodo Dragon *Varanus komodoensis* Ouwens, which used to be feared and hunted by local populations, but has become a strongly charismatic and even emblematic species for both local populations and tourists thanks to an ambitious conservation programme (Walpole & Leader-Williams, 2002). Many other species have been 're-designed' as charismatic species by such programmes.

In this paper, we review the CI conservation awareness initiatives that focused on educating the communities living in forested areas around parks, and used wildlife species as flagships, in SIC in the Sibolangit Nature Reserve of North Sumatra. The programmes were considered successful for a while, but have now stopped due to no further donor support. We analyze the awareness-raising activities in North Sumatra and compare them with the CI programme in West Java, and draw lessons for future environmental awareness programmes in Indonesia.

Programme Development of Sibolangit Interpretive Centre, North Sumatra

From 2001 to 2004, with funding from the Critical Ecosystem Partnership Fund (CEPF) and in partnership with the local office of the Ministry of Forestry, CI developed SIC, which was located approximately one hour's drive from Medan toward Berastagi. SIC used the Sumatran Orangutan as its flagship species to increase public awareness about natural resource management and biodiversity conservation. The centre was situated on the main road between Medan and Lake Toba in central North Sumatra near a large lake formed by the eruption of a super volcano (Fig. 1). It focused on conservation education and raising

Fig. 1. Sibolangit Interpretive Center, Leuser National Park and Batang Toru Protected Area.

public awareness within the communities surrounding Gunung Leuser National Park (Perbatakusuma et al., 2009).

SIC's staff was supported by volunteers from the surrounding communities, all of whom had undergone intensive training in nature interpretation. To reach audiences who otherwise might not have had the opportunity to learn about orangutan conservation, CI also operated the Orangutan Mobile Education Unit, which took the conservation message beyond the gates of Sibolangit to remote areas. These areas included villages of refugees from the Aceh Tsunami of December 2004 that had been created within the national park.

From 2005 to 2007, additional funding from USAID and a private donor was secured allowing the mobile unit to expand its coverage to West Batang Toru. The mobile unit travelled to remote villages and camped out for 3-4 days with regular return visits throughout the year. During visits, the CI team conducted informal learning sessions ranging from school visits and puppet shows to interactive games and daytime forest walks. The mobile unit was warmly received by local communities and was very effective in raising awareness among its target audiences. It reached villages and refugee camps in regencies in North Sumatra, and hundreds of people attended each session, particularly a popular, evening 'orangutan film series' (Fig. 2). The Mobile Education Unit was an integral part of conservation education and awareness-raising work in North Sumatra, and it also provided an important entry point for reaching local decision makers.

Interpreters play a very important role in conservation education and awareness-raising throughout the world, and through them, the public comes to under-

Fig. 2. The mobile unit.

stand nature and its role in supporting their livelihoods. Interpreters have the skill to communicate and translate the technical facets of the environment and its interactions to non-scientist audiences in a clear and comprehensible manner. Thus, good interpreters are a key component of successful conservation education and awareness programmes. Training materials for interpreters in this programme included the basics of ecology for nature guides or interpreters, conservation games, the basics of nature interpretation, communication for nature guides and interpreters, flora and fauna identification, jungle survival, and practice in the field.

As part of developing the education and awareness programme, the level of knowledge about orangutan conservation in the area surrounding Gunung Leuser National Park was assessed. Surveys were undertaken to evaluate the knowledge level, attitudes and behaviours of the community to provide a foundation for developing a targeted campaign strategy. The surveys were conducted in three sub-districts (Bohorok, Sibolangit and Tiga Lingga) bordering on or in proximity to orangutan habitats. There were a total of 360 respondents, 48 of whom were the formal and informal leaders of their communities. In addition to the surveys of communities, we conducted an assessment specifically designed to evaluate the knowledge, attitudes and behaviours of the decision makers (Perbatakusuma et al., 2009).

The survey results suggested that the communities in the sub-district of Tiga Lingga (Fig. 1) had the lowest level of knowledge about forests, orangutans, and the relationship between the two, even though the area is the nearest to orangutan habitat. In most of the study areas, the decline in clean water (both availability and quality) was the most important concern for the people interviewed. Most of the respondents identified their immediate welfare as their first priority, with forest destruction and orangutan conservation as a lesser concern.

Based on the responses from the target groups, three categories of educational activities were developed. The first category specifically targeted adult members of the general public, including the refugees in the park. It included the creation of illustrated informational materials in the form of fact sheets and posters, the production of sermon sheets, the development of information boards for the local cafe, and movie sessions and discussions. The sermon sheets were pages with information on the environment and biodiversity conservation, which were developed by the programmes in collaboration with priests and given out during Sunday prayer. SIC and the mobile unit staff also collaborated with partners to produce and distribute additional materials, such as video news releases, posters, T-shirts and a variety of souvenirs such as orangutan dolls.

From our present review of these two parallel programmes, SIC and the mobile unit team, in and around North Sumatra forests, we postulate that increasing public awareness of the important environmental services (e.g. watershed protection, erosion control) that forests provide may have been a key contributor to an observed slowing of illegal logging by smallholders in those areas visited by the mobile unit team (authors, personal observations), although data is lacking. Most of the content offered in both activities fitted with the idea of ecosystem services. In addition, appreciating how the survival of orangutans in Sumatra was linked to the forests in which they live, enabled communities and decision-makers to understand the importance of reducing further loss of habitat through cessation of logging or conducting habitat restoration, and through providing alternative livelihood opportunities for local communities.

Lessons learnt from the Conservation Awareness programmes

Conservation education and awareness-raising focused on flagship species is not new, but conducting this with a range of tools, as in this example, has not been carried out by many national or international organizations in Indonesia. Many organizations in Indonesia (WWF, CI, Birdlife International, Wildlife Conservation Society) have conducted conservation education programmes using charismatic flagship species. Such campaigns have commercial, ecological, promotional and practical advantages. The first advantage regards public communication, and the recognition that using a sympathetic or ‘charismatic’ symbol for conservation issues can generate interest and motivate public action for conservation (Lorimer, 2007).

In addition, using animals that are already recognized as sacred or traditionally symbolic can significantly increase cooperation of local populations and their willingness to respect restrictions and constraints that may be imposed by the conservation programme (Bowen-Jones & Entwistle, 2002; Schlegel & Rupf, 2010). It can also facilitate environmental education. In the case of our programme at BCEC in West Java, the Javan Hawk-eagle *Nisaetus bartelsi* (Stresemann) (‘Garuda bird’) was selected because it is a widely-understood symbol of Indonesia, while the Javan Gibbon *Hylobates moloch* (Audebert) was chosen because it is among the most ‘cute and loveable’ animals in the area (Supriatna & Ario, 2015).

One consideration in selecting flagship species regards the scope and definition of flagship species: if one defines it purely as the ‘symbolic construct of a marketing campaign’ without any consideration of other values such as the species’ role in the ecosystem (Verissimo, 2011), then charisma is likely to be the only parameter used to select a flagship species; the only aim of such an application is to maximize the generosity of potential donors for conservation in general (Walpole & Leader-Williams, 2002). In this case, the flagship is no more than a mascot, which must embody the entirety of the biodiversity crisis at a given scale (the panda – in the logo of WWF - being a major symbol of worldwide biodiversity). It need not be a keystone or umbrella species, nor even endangered (Walpole & Leader-Williams, 2002).

Why were flagship species used, and, in particular, why (at SIC) Sumatran Orangutan? Sumatran orangutan acted as an umbrella for all other forest species. It has been regarded as a flagship species that can raise conservation awareness to ensure survival of the forests that contain many other organisms (Utami & van Schaik, 2010). In Sumatra, many communities already knew that the habitat of the Sumatran Orangutan had decreased rapidly due to habitat conversion for commercial and subsistence agriculture, logging, open pit mining, forest fires, infrastructure development, local encroachment and many other factors. Sumatran forests were undergoing the highest rate of conversion in the world (Rijksen, 2001; Supriatna et al., 2002; Wich et al., 2008; Singleton et al., 2009), causing a loss of orangutan habitat.

Support for conserving Sumatran Orangutans has been very high among people outside Sumatra but this was not the case with North Sumatra villagers. In some cases, protection of orangutans in the forest may not have been the villagers’ concern, therefore, we had to put emphasis on the key environmental services (e.g. watershed, erosion control) that forests provide as a way to slow illegal logging and, ultimately, conserve orangutans. Thus the effectiveness of the flagship species approach per se was limited in these communities without a connection to their direct wellbeing. It is clear that without efforts to reduce fragmentation and link orangutan populations, continued habitat loss and losses to poaching will soon drive this species close to extinction. To counteract this threat, local communities must recognize the importance of the species and the forests in which they live (Conservation International Indonesia, 2007).

From our awareness-raising activities in both North Sumatra and West Java the success of the awareness programmes has depended on how the programmes have been set up: especially financial management. The awareness programme in BCEC, West Java used a collaborative financing strategy, in which all partners helped to develop a business plan and raise the money together; it was not dependent on particular bilateral or private donors. In North Sumatra, however, the programme was heavily dependent on two donors, CEPF and USAID. Once those two donors pulled out the programme stopped suddenly. At the end of 2004, a huge earthquake and tsunami hit Aceh Province, just a few hundred miles north of SIC, and many donors changed their priorities toward relief programmes. Thus the North Sumatra conservation awareness programme was discontinued due to a lack of donors, and CI's programme in Sumatra was also changed toward post-tsunami relief projects.

In the case of BCEC in West Java, because of the sustainable financing mechanism the programme continues until now. It features several packages for multi-day visits, which include programme fees, tickets, insurance, interpreters, accommodation, welcome drink, meals and transportation. The cost for these ranges from US$20 to $50 per person, and encompasses tailored themes for research tourism, family gatherings, 'outbound fun' adventure tourism, family camps and others. These tourist programmes not only promote conservation education, but also provide employment opportunities for members of communities around the park, providing food and transportation to visitors or working as field staff and interpreters.

The comparison of the two different models indicates that a conservation awareness programme will ultimately only be successful in the long term if it is supported, now and well into the future, with enough funding, either through donations or a financing model that raises funds from visitors, or a combination of both. A summary of the two conservation programmes is presented in Table 1.

SIC, which depended on donors rather than income from visitors and participants in its programs, was terminated in 2005 after CI handed it over to a local NGO. Unfortunately, the local NGO was unable to raise enough funding to sustain the education and awareness programme, after CI was able to give it support for just a one-year extension.

A number of educational methods were used, including fact sheets, posters, displays, and Powerpoint presentations, along with several editions of sermon sheets to promote the importance of protecting species and nature from the perspectives of both Islam in West Java and Christianity in North Sumatra. Each of these awareness-raising activities was preceded by an awareness needs assessment of the general public (including refugees in the park in the case of North Sumatra) and key decision makers such as local government officers and conservation officers.

The flagship species approach can only successfully reach larger audiences if it is set up by collaborating organizations with the respective park organization and local or indigenous organizations. Creating alliances requires building awareness and creating incentives for people to support conservation efforts. Creating such alliances, and disseminating information to people around parks and decision makers and to participating communities generally, have been used by CI Indonesia in the two examples reviewed here. These conservation education programmes have been successful in helping people understand the importance of ecosystems, the species in them and their role in livelihoods in West Java and North Sumatra.

ACKNOWLEDGMENTS

We would like to thank all of the former CI staff, including Iwan Wijayanto, Didi Wurjanto, Edy Hendras Wahyono, Akbar Aryo Digdo, Ismayadi Samsudin, Erwin Widodo, and many others; the current staff member, Ketut Sarjana Putra; and the manager of the North Sumatra Corridor. All of these individuals have helped to successfully implement conservation education. Some of us have retired from CI and for that reason the authors are grateful to those who have been helping this programme to be successful. To our colleagues at the Department of Biology at the University of Indonesia, we thank you for your advice and support. Thanks also to our donors that supported both sites financially or in kind: USAID, USFWS, CEPF, WB-GEF, and other private donors. Not least, we would like to thank the reviewers for improving the manuscript.

Table 1. Summary of conservation education and awareness programmes initiated by Conservation International in North Sumatra and West Java, Indonesia.

	North Sumatra	West Java*
Location	Sibolangit Tourism Park, Leuser National Park	Gunung Gede Pangrango National Park
Target audience	Communities around the Park and students from the city of Medan	Communities around the park, invited students, paying visitors and family gatherings, and people from the cities of Bogor, Sukabumi and Jakarta
Partner organizations	Conservation Office (BKSDA), CI, local NGOs, USAID	National Park, CI, local NGOs, Private sector
Outreach	Sibolangit Interpretive Centre (SIC) and villages around the Orangutan habitat. Plus a radio talk show series discussing conservation and other related topics, and radio spots or Public Service Announcements on conservation	Both at Bodogol Conservation Education Centre (BCEC) and people around the park
Flagship species	Sumatran Orangutan	Javan Hawk-eagle and Javan Gibbon
Equipment	Digital and film documentation and also working with the church and Muslim leaders	Digital film and working with Muslim boarding-school leaders
Infrastructure/ Vehicles	In the Park: SIC (1 office house, 1.5 km trails, several gazebos) Outside the Park: With 2 vehicles (4WD SUV and medium-size bus) travelling to villages and schools and churches around Leuser National Park and Batang Toru Forest	In the park: BCEC (2 rooms with 40 bunk beds, 1 class room, volunteer house, staff house, guard house, 2 gazebos, restaurant, canopy bridge, 2 km trails) Outside the Park: Working with Ford Company (SUV), travelling from school to school around the park, Islamic boarding school, villages around Gunung Gede Pangrango National Park
Funding	Critical Ecosystem Partnership Fund (CEPF), World Bank GEF and USAID	Collaborative partnership (park budget, local and international companies, sale of tickets, programme packages), Keidanren Foundation from Japan, companies (Mattel), and entrance fee and programme packages
Educators	CI staff and occasionally with park rangers at SIC. Two motor vehicles travelling with 3-4 crew went to several villages in the buffer zone of Leuser National Park	CI staff in collaboration with University of Indonesia, volunteers from NGOs and Park authorities developed education modules, flyers and digital information together
Duration	2001-2004, extended until 2007	1998 to present
Tag lines or Programmes	'Save the Orangutan'	'Discover the Secret of the Rainforest', 'Forest the Food Supplier', 'Forest, the Drug Store', and 'Life in the Canopy'

*from Ario & Supriatna, 2015

REFERENCES

Ario, A. and Supriatna, J. 2015. Developing conservation education programs in association with protected areas in Indonesia: Lessons learned from Gunung Gede National Park. **In:** *Symbion: Symposium on Biology Education; Edubiodiversity, inspiring education with biodiversity,* p. 46, Universitas Ahmad Dahlan, Yogyakarta.

Bowen-Jones, E. and Entwistle, A. 2002. Identifying appropriate flagship species: the importance of culture and local contexts. *Oryx* **36**(2): 189-195.

Conservation International Indonesia 2007. *Development of collaborative orangutan habitat protection in Batang Toru Watershed, North Sumatra.* Technical Report, CII, Jakarta.

Heywood, V.H. 1995. *Global Biodiversity Assessment.* Cambridge University Press, Cambridge.

Indrawan, M., Primack, R., and Supriatna, J. 2007. *Biologi konservasi.* Yayasan Obor, Jakarta, 502 pp.

Jacobson, S.K. 1995. Introduction: wildlife conservation through education. **In:** *Conserving Wildlife: International Education and Communication Approaches,* S.K. Jacobson (ed.), pp. xxiii-xxxi, Columbia University Press, New York, USA.

Lorimer, J., 2007. Nonhuman charisma: which species trigger our emotions and why? *Environment and Planning D: Society and Space* **25**(5): 911-935.

Perbatakusuma, E.A., Supriatna J., and Wijayanto, I., 2009. *Strengthening Biodiversity Conservation at Key Landscape Areas in the Northern Sumatra Corridor.* Report to GITI Tires, Conservation International Indonesia, Jakarta.

Rijksen, H. 2001. The Orangutan and the conservation battle in Indonesia. **In:** *Greater Apes and Humans: The Ethics of Coexistence,* B.B. Beck, T.S. Stoinski, M. Hutchins, T.L. Maple, B. Norton, A. Roan, E.F. Stevens and A. Arluke (eds.), pp. 57-70, Smithsonian Institution Press, Washington, D.C.

Schlegel, J., and Rupf, R. 2010. Attitudes towards potential animal flagship species in nature conservation: A survey among students of different educational institutions. *Journal for Nature Conservation* **18**(4): 278-290.

Singleton, I., Supriatna, J., and Wich, S.A. 2009. Sumatran orangutan. **In:** *Primates in Peril: the World's 25 Most Endangered Primates in 2008-2010,* R.A. Mittermeier and S. Nash (eds.), pp. 65-66. IUCN, IPS and CI, Switzerland.

Supriatna, J. 2008. *Melestarikan alam Indonesia (Saving of Indonesia's nature).* Yayasan Obor, Jakarta, 482 pp.

Supriatna, J., Manansang, J., Tumbelaka, L., Andayani, N., Indrawan, M., Darmawan, L., Leksono, S.M., Djuwantoko, Seal, U. and Byers, O. 2001. *Conservation Assessment and Management Plan for Indonesia Primates: Final Report.* Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, Minnesota, USA, 251 pp.

Supriatna, J., Wijayanto I., Manullang B.O., Anggraeni, D., Wiratno and Ellis, S. 2002. The state of siege for Sumatra's forest and protected areas: stakeholders view during devolution, and political plus economic crises in Indonesia. **In:** *Proceedings of the IUCN/ WCPA-EA-4 Taipei conference,* pp. 439-456, Taipei, Taiwan.

Utami, S.S. and C.P. van Schaik, 2010. The natural history of Sumatran Orangutan *(Pongo abelii)*. **In:** *Indonesia Primates, Development Primatology: Progress and Prospects,* S. Gursky-Doyen and J. Supriatna (eds), pp. 41-55, Springer, New York.

Verissimo, D., MacMillan, D.C., and Smith, R.J. 2011. Toward a systematic approach for identifying conservation flagships. *Conservation Letters* **4**(1):1-8.

Walpole, M.J., and Leader-Williams, N. 2002. Tourism and flagship species in conservation. *Biodiversity and Conservation* **11**(3): 543–547.

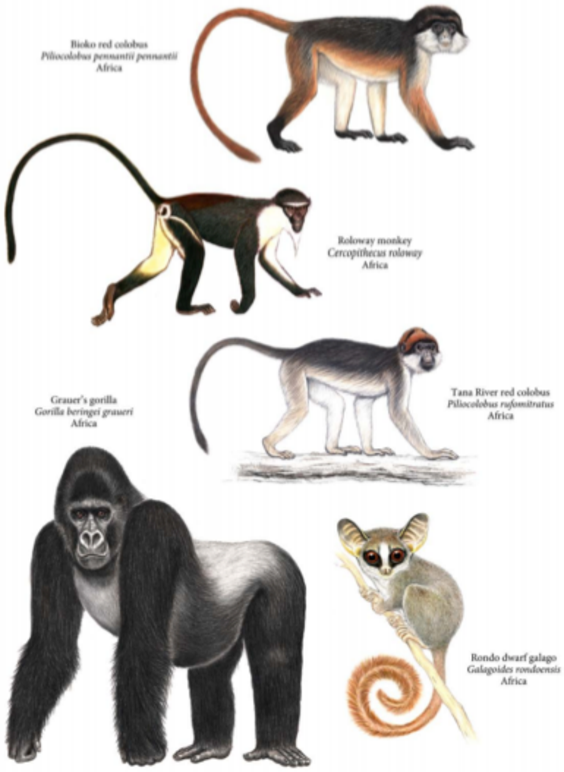
Wich, S.A., Meijaard, E., Marshall, A.J., Husson, S., Ancrenaz, M., Lacy, R.C., van Schaik, C.P., Sugardjito, J., Simorangkir, T., Traylor-Holzer, K., Doughty, M., Supriatna, J., Dennis, R., Gumal, M., Knott, C.D. and Singleton, I. 2008. Distribution and conservation status of the orangutan (*Pongo* spp.) on Borneo and Sumatra: how many remain? *Oryx* **42**(3): 329-339.

WWF Indonesia, 2014. Environmental Education (available from internet: /www.wwf.or.id/en/about_ wwf/ whatwedo/pds/whatwedo/ environmentaleducation). Downloaded on 14 September 2014.

The World’s 25 Most Endangered Primates 2012–2014

AFRICA		
Rondo dwarf galago	*Galagoides rondoensis*	Tanzania
Roloway monkey	*Cercopithecus roloway*	Côte d’Ivoire, Ghana
Bioko red colobus	*Piliocolobus pennantii pennantii*	Equatorial Guinea (Bioko Is.)
Tana River red colobus	*Piliocolobus rufomitratus*	Kenya
Grauer’s gorilla	*Gorilla beringei graueri*	DRC
Madagascar		
Madame Berthe’s mouse lemur	*Microcebus berthae*	Madagascar
Sclater’s black lemur	*Eulemur flavifrons*	Madagascar
Red ruffed lemur	*Varecia rubra*	Madagascar
Northern sportive lemur	*Lepilemur septentrionalis*	Madagascar
Silky sifaka	*Propithecus candidus*	Madagascar
Indri	*Indri indri*	Madagascar
ASIA		
Pygmy tarsier	*Tarsius pumilus*	Indonesia (Sulawesi)
Javan slow loris	*Nycticebus javanicus*	Indonesia (Java)
Pig-tailed snub-nosed langur	*Simias concolor**	Indonesia (Mentawai Is.)
Delacour’s langur	*Trachypithecus delacouri*	Vietnam
Golden-headed or Cat Ba langur	*Trachypithecus poliocephalus*	Vietnam
Western purple-faced langur	*Semnopithecus vetulus nestor*	Sri Lanka
Grey-shanked douc monkey	*Pygathrix cinerea*	Vietnam
Tonkin snub-nosed monkey	*Rhinopithecus avunculus*	Vietnam
Cao-Vit or Eastern black-crested gibbon	*Nomascus nasutus*	China, Vietnam
NEOTROPICS		
Variegated spider monkey	*Ateles hybridus*	Colombia, Venezuela
Ecuadorian brown-headed spider monkey	*Ateles fusciceps fusciceps*	Ecuador
Ka’apor capuchin	*Cebus kaapori*	Brazil
San Martín titi monkey	*Callicebus oenanthe*	Peru
Northern brown howler	*Alouatta guariba guariba*	Brazil

* The pig-tailed snub-nosed langur *Simias concolor* had previously been classified as *Nasalis concolor* and referred to as such in the 2012–2014 Top 25 Fact sheets


Bioko red colobus
Piliocolobus pennantii pennantii
Africa
Roloway monkey
Cercopithecus roloway
Africa
Tana River red colobus
Piliocolobus rufomitratus
Africa
Grauer's gorilla
Gorilla beringei graueri
Africa
Rondo dwarf galago
Galagoides rondoensis
Africa


Madame Berthe's
mouse lemur
Microcebus berthae
Madagascar
Sclater's black lemur
or Blue-eyed black lemur
Eulemur flavifrons
Madagascar
female
male
Northern sportive lemur
Lepilemur septentrionalis
Madagascar
Silky sifaka
Propithecus candidus
Madagascar
Red ruffed lemur
Varecia rubra
Madagascar
Indri
Indri indri
Madagascar


Pygmy tarsier
Tarsius pumilus
Asia
Pig-tailed
snub-nosed langur
Simias concolor
Asia
Grey-shanked
douc langur
Pygathrix cinerea
Asia
Tonkin snub-nosed monkey
Rhinopithecus avunculus
Asia
Western
purple-faced langur
Semnopithecus vetulus
nestor
Asia
Golden-headed langur
or Cat Ba langur
Trachypithecus
poliocephalus
Asia
Delacour's Langur
Trachypithecus
delacouri
Asia
Javan
slow loris
Nycticebus
javanicus
Asia


male
female
(front view)
female
(rear view)
Cao Vit or
Eastern black-crested gibbon
Nomascus nasutus
Asia
San Martin titi monkey
Callicebus oenanthe
Neotropics
male
female
dark variant
light
variant
Variegated or
Brown
spider monkey
Ateles hybridus
Neotropics
dark
variant
Ecuadorian brown-headed
spider monkey
Ateles fusciceps fusciceps
Neotropics
Ka'apor capuchin
Cebus kaapori
Neotropics
Northern brown howler
Alouatta guariba guariba
Neotropics

Instructions to Contributors

Scope

This journal aims to provide information relating to conservation of the primates of Asia. We welcome manuscripts on any relevant subject, including taxonomy and genetics, biogeography and distribution, ecology and behaviour, active threats and primate-human interactions. Submissions may include full articles, short articles and book reviews.

Submissions

Manuscripts and all editorial correspondence should be directed to Dr Ramesh Boonratana (rbz@loxinfo.co.th). Manuscripts are to be submitted to the journal on the understanding that they have not been published previously and are not being considered for publication elsewhere. The corresponding author is responsible for ensuring that the submitted manuscript has been seen and approved by all co-contributors, and the covering letter accompanying it should be signed to this effect. It is also the responsibility of the contributor to ensure that manuscripts emanating from a particular institution are submitted with the approval of the necessary authority. The editors retain the right to modify the style and the length of a contribution and to decide the time of publication; they will endeavour to communicate any changes to the contributors. The full name and address of each contributor should be included. Please avoid the use of unexplained abbreviations and acronyms.

Contributions

Manuscripts should be submitted in UK English. Manuscripts must be in electronic format in MS-Word or a compatible program, double-spaced and left-justified. The first page should include a concise title, up to seven keywords not found in the title, full names and addresses of all authors, current addresses if different, e-mail addresses, and indication to whom queries and proofs should be sent. In-text citations should use comma and ampersand and follow first chronological, then alphabetical, sequence: (Matsuzawa & MacKinnon, 1980; Marsh, 1998; Matsuzawa, 1998a, 1998b). All pages including tables should be numbered. Footnotes should be avoided.

Full articles will be sent out for peer-review and should contain significant new findings. They should not exceed about 20 pages in length (double-spaced), including references. Please include an abstract of no more than 200 words, placing the work in conservation context and summarising what it has contributed, and subheadings (e.g. Introduction, Methods, Results, Discussion, Acknowledgements, References) as appropriate.

Taxonomy

Scientific nomenclature should be used at first mention of any species or subspecies. Nomenclature should include taxonomic authority (at first mention) as currently recognised by IUCN, e.g. Northern Pigtailed Macaque *Macaca leonina* (Blyth) (see www.iucnredlist.org). Authors are referred to The Plant List (www.theplantlist.org) for up-to-date plant nomenclature.

Numbers

Measurements should always be metric, or where this is inappropriate, the metric equivalents given in parentheses. Time should be designated in the 24-hour system (as e.g. 17:30 h) and date in the European system (e.g. 7 December 2011). Summary statistics should include measures of both central tendency and dispersion where appropriate, e.g. means and standard deviations (SD). Reports of all statistical tests should include the name of the statistical test, the name and value of the test statistic, the degrees of freedom, the probability value used to determine significance and the authors' interpretation. Probabilities should be reported as exact values if not significant, otherwise rounded off to either $p<0.05$, 0.01 or 0.001.

Figures, maps and tables

Articles may include photographs, high-quality figures, high-quality maps and tables. Please keep these to a minimum. We stress the importance of providing maps which are *publishable*, with clear explanation of features shown, scale and orientation. Please number tables and figures (as Table 1, Fig. 1 etc.) and provide clear concise captions.

References

Examples of house style may be found in the latest volume of this journal. Please refer to these examples when listing references:

Journal article

Bynum, E.L., Kohlhaas, A.K. and Pramono, A.H. 1999. Conservation status of Sulawesi macaques. *Tropical Biodiversity* **6**: 123-144.

Chapter in book

Hohmann, G.M. and Fruth, B. 1995. Loud calls in great apes: sex differences and social correlates. **In**: *Current Topics in Primate Vocal Communication*, E. Zimmerman, J.D. Newman and U. Juergens (eds.), pp. 161-184. Plenum Press, New York, USA.

Book

Niemitz, C. 1984. *The Biology of Tarsiers*. Gustav Fischer, Stuttgart, Germany.

Thesis/Dissertation

Barrett, E. 1984. *The Ecology of some Nocturnal, Arboreal Mammals in the Rainforests of Peninsular Malaysia.* PhD dissertation, Cambridge University, UK.

Report

Eudey, A.A. 1987. *Action Plan for Asian Primate Conservation: 1987–1991.* IUCN/SSC (Species Survival Commission) Primate Specialist Group, Gland, Switzerland.

Electronic Database

Nadler, T., Timmins, R.J. and Richardson, M. 2008. *Trachypithecus germaini.* **In**: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 1 June 2012.

Asian Primates Journal

A Journal of the Southeast Asia, South Asia and China Sections of the IUCN/SSC Primate Specialist Group

Volume 4
Number 2
2014

EDITORIAL

ARTICLES