Ethics, ecology and evolution of Indonesian slow lorises (*Nycticebus spp.*) rescued from the pet trade

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Ethics, ecology and evolution of Indonesian slow lorises (*Nycticebus* spp.) rescued from the pet trade

By

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Abstract

Slow lorises (*Nycticebus* spp.) are small-bodied nocturnal primates found throughout South-east Asia. All slow lorises are threatened by habitat loss and trade for pets and traditional medicine. They are easily distinguishable from other primates by a myriad of unique morphological, behavioural, physiological and ecological characteristics, yet are amongst the least-known of all primates. During February 2010 and March 2011 I assisted a reintroduction programme for slow lorises initiated by International Animal Rescue (IARI) at their rescue centre in Java, Indonesia. Throughout the reintroduction process, I collected data that would enhance the reintroduction process, but also provide a deeper understanding of their behaviour, ecology and evolution.

I analyse data compiled by IARI over a four year period revealing demographic trends in slow lorises admitted to the rescue centre and discuss the role that rescue centres and reintroduction programmes have in regard to their contribution to conservation. Rescue centres working in collaboration with local governments have the potential to help mitigate trade through ensuring better enforcement and awareness campaigns. I conclude that they do have an important role in conservation. I examine the presence of stereotypic behaviours at IARI in relation to various intrinsic and extrinsic factors. 33% of slow lorises displayed stereotypies. Time in captivity and type of social group are shown to be significant predictors of stereotypies. For better welfare in captivity and for increased reintroduction success these findings should be addressed further. I monitored six reintroduced Javan slow lorises on Mount Salak, Java using radio telemetry. Of the feeding observations noted, floral nectar of *Calliandra calothyrsus* comprised 90% of the total. A combination of excessive flower visitation, non-destructive feeding and pollen observed on the faces of lorises suggests potential pollination of this species and reveals possible evolutionary implications. I analysed 89 photos of slow loris face masks in relation to anti-predator defence. I conclude that the pelage colours recorded have probably evolved for maximum signalling effect. When combined with the slow lorises' chemical defence mechanism I propose that the distinctive facemasks in slow lorises could serve as a form of aposematism. I postulate that the Javan and Bengal slow lorises actively mimic the spectacled cobra (*Naja naja*). Although the evidence appears to support this theory, more studies are necessary for validation. In conclusion, I believe that my study has shown that rescue centres are an untapped resource for conservation, awareness and learning. They often house a multitude of exotic and threatened species that are not common in zoos and difficult to study in the wild. By studying these animals in close proximity we can learn a great deal about improving captive welfare, conservation and evolution.

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My biggest regret is that my Mum is not around to witness the completion of this thesis. She passed away long before I began embarking on any sort of academic journey, when a Ph.D. was the last thing on my mind. I hope that she would have been proud of my achievement. It is in her memory that I dedicate this volume.

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List of abbreviations

ANOVA	Analysis of Variance
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
GHSNP	Gunung Halimun-Salak National Park
GPS	Global Positioning System
GIS	Geographical Information System
IARI	International Animal Rescue (Indonesia)
IUCN	International Union for Conservation of Nature,
JPEG	Joint Photographic Experts Group
KKH-PHKA	Biodiversity Conservation Office of the Directorate General of Forest Protection and Nature Conservation
MA	Million Years Ago
PCA	Principal Component Analysis
PPS Tegal Alur	Tegal Alur Wild Animal Rescue Centre
RGB	Red Green Blue
SD	Standard Deviation
SPSS	Statistical Package for the Social Sciences
DNA	Deoxyribonucleic acid
JATIM	Java, East Timur

1. General Introduction

"For 200 years we've been conquering Nature. Now we're beating it to death."
– Tom McMillan

1.1 Overview

1.1.1 Conservation status and threats

Slow lorises (Primates: Lorisidae: *Nycticebus* É. Geoffroy, 1812) are small-bodied nocturnal primates found throughout South-east Asia (Fleagle 1999). Analogous to many other primate species, slow lorises are at risk of extinction from habitat loss and illegal trade (Collins & Nekaris 2008; Nekaris et al. 2009; Shepherd et al. 2004). Trade in wildlife includes the sale or exchange of live or dead wild animals or plants, either as a whole or in part depending on the buyer's requirements. Wild animals are commonly sold as pets, for their decorative skins, for use in traditional medicine and for food (Nijman 2010; Shepherd et al. 2004). High demand for lorises as both pets and for traditional medicine, combined with the inability of a loris to escape from expert hunters due to their characteristic slow locomotion, leads to abundance in markets throughout their range (Nekaris et al. 2010a; Ratajszczak 1998; Starr et al. 2010). Irrespective of their recent placement on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix 1, which prohibits any international trade in this species, domestic sales of slow lorises persists openly in numerous local animal markets (Nijman 2009; Shepherd 2010; Shepherd et al. 2004). This is particularly the case in Indonesia where its three species are all considered threatened: greater slow loris (*N. coucang)* – Vulnerable (VU A2cd); Bornean slow loris (*N. menagensis*) – Vulnerable (VU A2cd); Javan slow loris (*N. javanicus*) – Endangered (EN A2cd) (IUCN 2011).

1.1.2 Rehabilitation and reintroduction

When enforcement does occur, the most likely destination for slow lorises is one of the numerous rescue centres established over the last decade (McGreal, 2007; Navarro-Montes, 2008). With such a high influx of slow lorises, many rescue centres have now reached full capacity and are investigating the possibility of reintroductions. International Animal Rescue recently established a rescue centre in Ciapas, Java (IARI), dedicated to rescuing confiscated lorises from the trade. IARI currently houses around 100 Indonesian slow lorises. With limited space and increasing numbers of animals arriving, combined with dwindling numbers in the wild, a release programme for some animals was proposed in 2007 (Collins & Nekaris 2008).

Table 1. Basic principles to consider when conducting reintroductions (IUCN 2002a)

	Basic Principles of Re-introductions
1	Identify the need for reintroduction and conduct a rapid overall assessment (determine if the key requirements - habitat, socioeconomic, financial, legal, management, release-stock suitability, veterinary, post-release monitoring-are likely to be met).
2	Define aims, objectives, and time frame.
3	Establish a multidisciplinary team.
4	Assess the proposed release-site habitat and determine its suitability.
5	Review the socioecological and behavioural data on the taxon of interest.
6	Determine if the socioeconomic, financial, and legal requirements can be met in the short and long terms.
7	Assess the suitability of the release stock.
8	Evaluate the genetic status of the release stock.
9	Ensure release stock has been cleared for release by a qualified veterinary team.
10	Develop strategy and time frame for transport and final release of animals.
11	Establish and enact post-release monitoring and other follow-up activities.
12	Document project outcomes on an on-going basis.

Unfortunately, reintroductions are notorious for low success and are often criticised regarding their viability (Beck et al. 1994; Fischer & Lindenmayer 2000; Seddon 1999). Some argue, if conducted correctly with minimal risks to the animals and the ecosystem into which they are being released, rehabilitation and reintroduction remains the only viable option for the increasing numbers of displaced threatened animals (Beck 2010; Carter 2003; Cheyne 2009; Cheyne et al. 2011).

As the reintroduction of animals is a decidedly complicated and sensitive affair (Cowlishaw & Dunbar 2000; Fischer & Lindenmayer 2000; Streicher 2004), the programme was designed to follow the guidelines compiled by the IUCN (IUCN 2002a, in prep, 1998) (Table 1, but see Appendix 1 for full guidelines). These guidelines only provide a 'best practice' model for reintroductions. As considerable differences are present between species, and even between individuals, the guidelines were deliberately customised to suit the ecological and behavioural needs of the slow lorises (IUCN 2002a, 1998). The reintroduction of slow lorises at IARI adhered to these following protocols:

- Assess the taxonomic status of captive lorises in IARI.
- Through observation of captive lorises in IARI, determine which lorises ostensibly possess adequate survival skills (foraging and social) required for release. This will also serve as a quarantine period (minimum 6-8 weeks).
- Conduct routine health checks with chosen lorises before release.
- Determine a release site based on the following criteria: habitat suitability, absence or low abundance of wild lorises, low likelihood of recapture by poachers
- Build a soft-release enclosure in the forest at the proposed release site, in order to monitor the lorises in a semi-wild setting before release. This process will help to establish further the chances of survival for the chosen individuals.
- Release the lorises that possess the necessary survival skills, into the wild at a site in close proximity to the soft release cage.
- Monitor the released lorises via radio-collars for a period of 6 months or more.

For animals involved in trade, a stint in captivity can hinder their potential to be reintroduced successfully back to their natural environment (IUCN 2002b; Mason et al. 2007; Shepherd 1990). Many rescue centres around South-east Asia are inundated with confiscated primates arriving at the centres, damaged both physically and mentally (Duy et al. 2010; Streicher 2004). During trade, slow lorises are regularly handled by traders and potential buyers, and are kept in cramped, crowded and noisy conditions (Nekaris et al. 2009). This environment undoubtedly has detrimental effects on their physical and psychological well-being. Consequently, recognising signs of abnormalities in slow lorises that may hinder their survival potential is critical in successful reintroduction programmes (Cheyne 2006).

1.1.3 Adaptation and Evolution

"Evolution has no long-term goal. There is no long-distance target, no final perfection to serve as a criterion for selection, although human vanity cherishes the absurd notion that our species is the final goal of evolution." – Richard Dawkins

Slow lorises (family Loridae; Gray, 1821) are among the least known of all primates (Izard et al. 1988; Nekaris & Bearder 2011; Trent et al. 1977). The ostensible lack of interest in this genus, and indeed family, is sometimes hard to comprehend considering their extreme specialisations and array of intriguing characteristics. They are easily distinguishable from other primates by a myriad of unique morphological, behavioural, physiological and ecological characteristics (Nekaris & Bearder 2011; Yoder et al. 2001). Accordingly, slow lorises form part of the most clearly recognisable clade in the whole primate radiation (Masters et al. 2005; Yoder et al. 2001). Their specialist adaptations for greater mobility during slow quadrupedal walking, climbing and suspensory movements in an arboreal setting include fewer caudal, but increased sacral and thoracic vertebrae with transpedicular foramina, large humeral and femoral articulations, and highly flexible ankles and wrist (Gebo 1989; Gebo 1987; Masters et al. 2005). For better grip on small substrates their hands and feet have reduced second digits, and for prolonged grip their limb arteries and veins form *retia mirabilia* (Ankel-Simons 1983; Osman Hill 1953). For location of mobile prey they possess frontated and upwardly rotated orbits (Schwartz 1986), and digestive specialisations and a slow metabolic rate for consuming toxic prey (Alterman 1995; Wiens et al. 2006). Perhaps the most curious loris trait of all, however, is its venomous attribute. Unique amongst primates, and extremely rare in mammals, lorises possess a brachial gland that secretes a chemical compound that when mixed with saliva becomes toxic (Alterman 1995; Hagey et al. 2007; Krane et al. 2003). Whilst the exact purpose of this function is yet to be discerned it has been associated with anti-predator defence and olfactory communication (Alterman 1995; Hagey et al. 2007). Despite this multitude of specialisations amongst Lorisidae, data on ecology and behaviour are only available on 18 species – less than half of those currently recognised – with a mere nine studies utilising radio-telemetry (Nekaris & Bearder 2011).

The evolutionary relationships between species in this taxon are also far from resolved both within this clade, and more broadly, with respect to other primates and mammals (Masters et al. 2005; Nekaris 2005; Rasmussen & Nekaris 1998; Roos et al. 2004). Indeed, some authors suggest that by studying members of Lorisidae, hotly-debated questions relating to primate origins may be elucidated. Lorises, for example, possess the greatest degree of orbital convergence amongst all primates, a trait often associated with prominent theories of primate evolution (Cartmill 1972; Cartmill 1992). Furthermore, numerous Lorisidae are known to feed on nectar. Adaptations to foraging amongst angiosperms in early primates, akin to those possessed by numerous extant Lorisidae, are another key feature linked with theories of primate origins (Rasmussen 1990; Rasmussen & Nekaris 1998; Sussman 1991; Sussman & Raven 1978).

1.2 Study taxa: slow lorises (*Nycticebus*)

1.2.1 Taxonomy and phylogeny

"Taxonomy is described sometimes as a science and sometimes as an art, but really it's a battleground." — Bill Bryson

In general, the taxonomic order of nocturnal primates has been subject to much revision over the last century (Grubb et al. 2003; Schwartz & Beutel 1995; Yoder et al. 2001). Their cryptic nature and similar appearance often hindered researchers, who after commencing studies of a single nocturnal primate species, unearthed numerous new species (Bearder 1999; Bearder 1995; Bickford et al. 2007). Once presumed to occupy broad geographic ranges, these new species were actually found to inhabit highly restricted ranges, making them more susceptible to habitat loss and hunting pressures (Ganzhorn 1997; Grubb et al. 2003). For slow lorises, a similar trend in increased diversity is suspected (Groves 1998; Groves 2001; Nekaris & Jaffe 2007).

Originally, nine species of slow loris were recognised (cf. Nekaris & Jaffe 2007), which were later united as one highly polymorphic species, *N. coucang* (Osman Hill 1953); and more recently, in the advent of genetic analysis techniques, apportioned back to five species (Groves 1998; Nekaris in prep; Roos 2003). This classification into five species is the one currently accepted, and consists of *N. bengalensis, N. pygmaeus, N. coucang, N. menagensis* and *N. javanicus* (Fig 1).

Slow lorises are Lorisiform primates, which together with the Lemuriformes, comprise the infra-order Strepsirrhini (Martin 1990) (Fig 2). Lorisiformes can be classified further into the family Lorisidae consisiting of Lorisinae (Lorises), Galaginae (galagos) and Perodicticinae (pottos and angwantibos), and again into sub-family Lorisinae comprising *Nycticebus* (slow lorises) and *Loris* (slender lorises) (Sussman 2003). Strepsirrhine primates are characterised primarily by having moist-rhinaria. Conversely, anthropoid primates and *Tarsius* possess dry rhinaria (Parga & Overdorff 2011). Strepsirrhine primates also possess a grooming claw on their second digit and, with the exception of the aye-aye (*Daubentonia madagascariensis*), tooth combs (Martin 1990). Tooth combs are needle-like dental structures, comprising four procumbent lower incisors and two lower canines. They are used in grooming, the procurement of plant exudates from tree trunks via gouging behaviour and potentially, in slow lorises, for administering venom (Fig 3) (Fleagle 1999; Hagey et al. 2007; Nekaris et al. 2010b).

Figure 1. Five currently recognised slow loris species (From left) *N. bengalensis, N. pygmaeus, N. coucang, N. menagensis* **and *N. javanicus*.**

Among the Lorisidae all members are strictly nocturnal and arboreal (Nekaris & Bearder 2011). Like other nocturnal strepsirrhines, Lorisidae possess an extra retinal layer known as a tapetum lucidum, which effectively recycles incoming light and enhances vision in low-light conditions (Fleagle 1999). Excellent night vision is accompanied by acute olfactory senses by which Lorisidae use to communicate with conspecifics (Alterman 1995; Ambrose

2003; Fisher et al. 2003). Unlike the Galaginae, which are fast runners and agile leapers with long tails, Lorisinae and Perodicticinae are comparatively slow and deliberate movers (Walker 1969). Although relatively fast speeds have been observed in some species of Lorisinae whilst quadrupedal walking, they always maintain at least one point of contact with the substrate and are unable to jump (Ishida et al. 1992; Nekaris & Stevens 2007; Walker 1969).

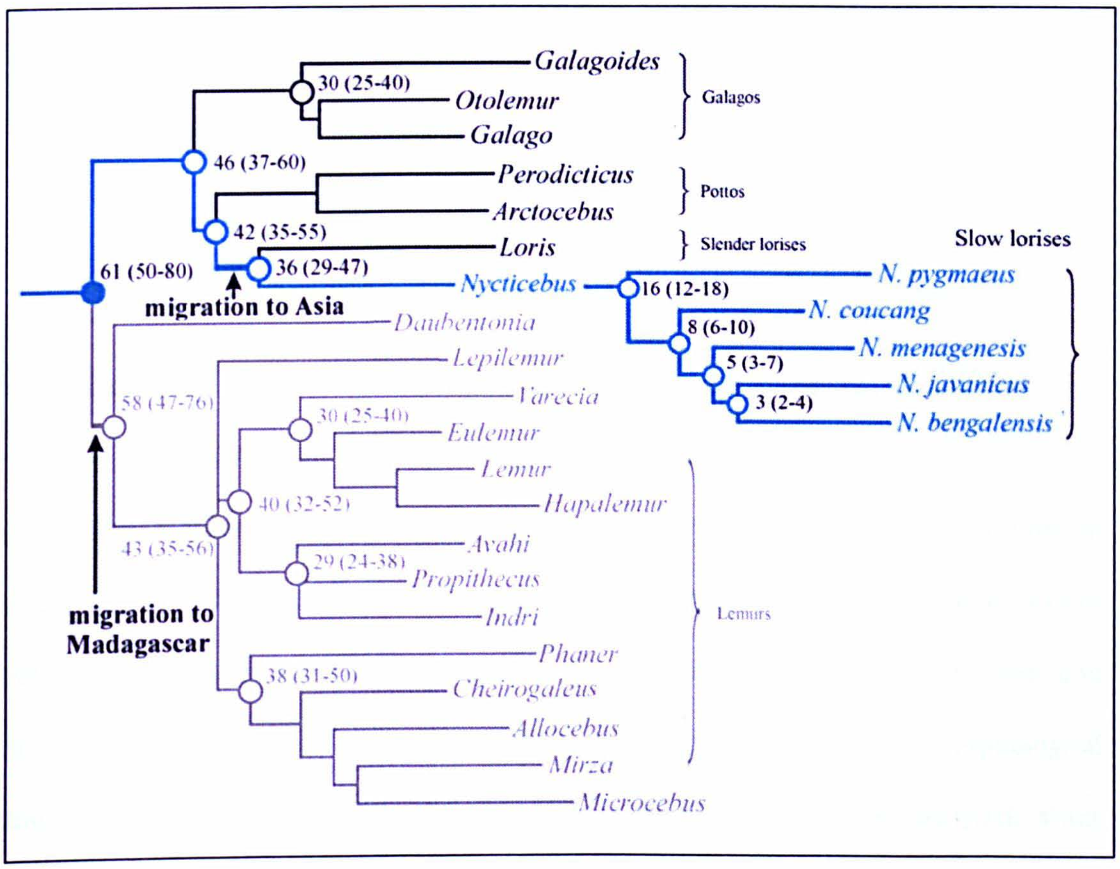

Figure 2. Phylogenentic tree for strepsirrhine primates adapted from Roos et al. (2004) and Nekaris et al. (in prep). The filled blue circle indicates the divergence between Lorisiformes and the Malagasy Lemuriformes and Chiromyiformes 61 (50–80) Ma. Open circles and their respective numbers (in Ma) refer to divergence ages between main groups as estimated from mitochondrial sequence data.

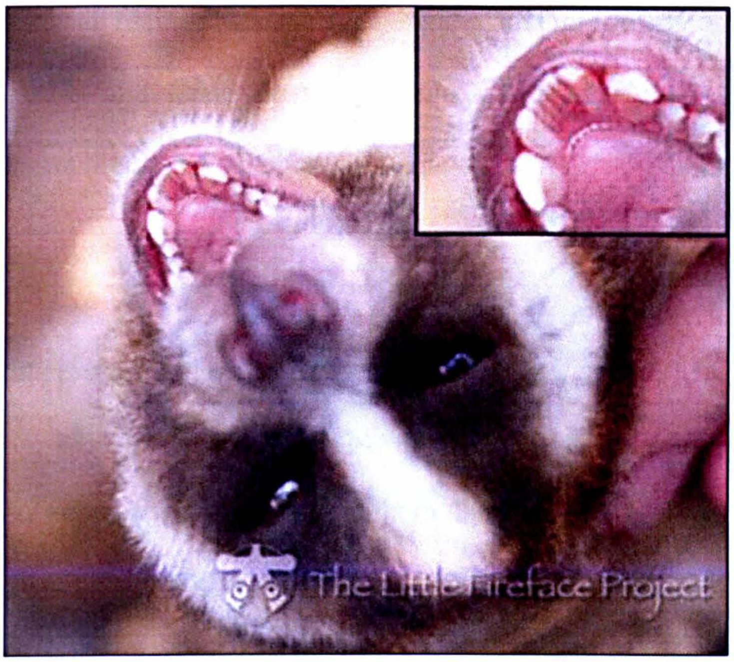

Figure 3. Javan slow loris displaying its tooth comb (a dental structure present in strepsirrhine primates) (Photo by the Little Fireface Project, 2012)

The evolutionary history of the lorisiform primates remains somewhat unresolved. Until recently, an East African ancestry in the Miocene was generally thought most likely (Rasmussen & Nekaris 1998). The uncovering of two new fossils in Egypt, however, provide evidence for an earlier origin during the late Eocene (Seiffert et al. 2003). Although earlier behavioural studies appeared to support a closer relationship between *Loris* and *Perodicticus* (Bearder et al. 2002; Pimley 2002), the current consensus from morphological and molecular evidence indicates that the sub-family Lorisidae is a monophyletic sister clade to Galigidae (Nekaris in prep; Roos 2003; Roos et al. 2004). An alternative scenario places galagos, pottos and lorises in three separate monophyletic groups, all with a common ancestor (Yoder et al. 2001). Nevertheless, the currently unresolved complex relationships within this group will no doubt be unravelled with further studies. A proposed explanation for the speciation among lorisiformes relate to different feeding strategies (Nekaris & Rasmussen 2003; Rasmussen & Nekaris 1998). Galagos primarily hunt evasive, fast-moving prey that requires them to have good auditory ability and fast leaping, compared to pottos and lorises that rely more on olfactory and slow, calculated movements to locate their less agile toxic prey.

1.2.2 Geographic range

The Bengal slow loris (*N. bengalensis*) boasts the largest geographic range among *Nycticebus*, found across northeast India, southern China, Burma, Bhutan, northern China, Cambodia, Laos, and Vietnam (Fig 4). The range of the pygmy slow loris (*N. pygmaeus*) overlaps with much of the range of *N. bengalensis* occurring in China, Laos, Vietnam and Cambodia. The greater slow loris (*N. coucang*) is found in southern Thailand, Malaysia and Indonesia and overlaps the range of the pygmy slow loris in the north of Malaysia and southern Thailand. The Bornean slow loris (*N. menagensis*) occurs across Borneo in Indonesia, Malaysia and Brunei and extends into the Philippines. The Javan slow loris (*N. javanicus*) is restricted to western Java (IUCN 2011).

1.2.3 Behaviour and ecology

Traditionally, the primate order was divided into two groups: nocturnal and diurnal species. This division loosely resembled the strepsirrhine/haplorhine divide with the former being predominantly nocturnal and the latter diurnal (Curtis 2006). This division was later found increasingly inadequate as some species were active at certain periods both day and night (e.g. *Eulemur fulvus rufus, E. f. collaris* and *Aotus azarai*) (Curtis et al. 1999; Donati & Borgognini-Tarli 2006). This behavioural pattern is known as cathemerality (Tattersall 2006).

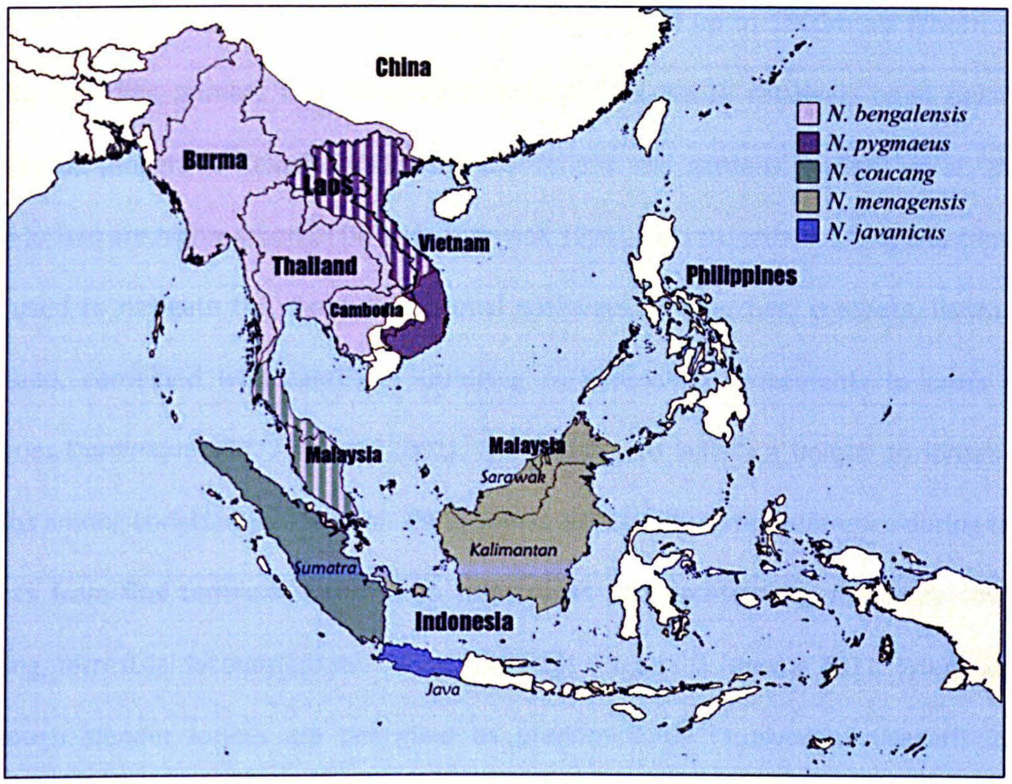

Figure 4. Broad geographic distribution of the five recognised species of slow loris (*Nycticebus*) across South-east Asia. Distributions in accordance with the IUCN (2011).

All members of *Nycticebus*, as indeed all Lorisidae, are exclusively nocturnal (Nekaris & Bearder 2011). As with numerous other nocturnal or cathemeral species (e.g. *E. f. rufus*, *A. azarai*, *Dypodomys merriami* and *Meles meles* (Bowers 1990; Cresswell & Harris 1988; Donati et al. 2001; Wright 1989), however, behaviours of some Lorisidae are influenced by moon light. In *Galago moholi* and *G. zanzibaricus* activity patterns increase with moonlight (Bearder et al. 2002; Bearder et al. 2006). Conversely, *N. coucang* and *L. tardigradus* were found to decrease high activity behaviours and increase inactive behaviour (Radhakrishna & Singh 2002; Trent et al. 1977). Such behavioural differences are often associated with predator avoidance (Nash 2007).

Slow lorises utilise a range of habitat types at altitudes of up to 1800m asl (Thorn et al. 2009), including primary and disturbed forests (Wiens 2002), relatively open savannah grasslands (Rogers & Nekaris 2011), and plantations and gardens (Nekaris et al. 2009). Slow lorises are highly arboreal (Walker & Nowak 1999). Quadrupedal walking and climbing are used to navigate the three-dimensional pathways of branches, creepers, lianas and bamboo, combined with cantilever (bridging or extending) movements to cross gaps (Charles-Dominique 1977; Nekaris 2001). The inability to leap is a unique to lorises and pottos among Lorisidae (Ishida et al. 1992; Sellers 1996). Substrate preference during travel ranges from fine terminal branches to tree trunks and occasionally, if canopy cover is lacking, terrestrial locomotion over short distances (Rogers & Nekaris 2011; Wiens 2002). Although slender lorises are described as predominantly faunivorous (Nekaris 2005; Nekaris & Rasmussen 2003), slow lorises in contrast, appear to have a more varied diet feeding on nectar, gum, sap, fruit as well as arthropods (Barrett 1984; Nekaris & Bearder 2011; Nekaris et al. 2010b; Swapna et al. 2010; Wiens et al. 2006). Some variation in diet is apparent, both between and within species, and is also dependent on location, habitat type and season (Nekaris & Bearder 2011). For example, Bengal and pygmy lorises show a preference for gum during certain times of the year when other foods are scarce (Nekaris et al. 2010b; Swapna et al. 2010). No long-term published studies have documented feeding behaviour in any of the Indonesian slow loris species, although a craniometric study postulates that the Bornean slow loris is the most faunivorous (Ravosa 1998).

1.2.4 Sociality

"People knew that animals were nocturnal but they didn't really know what they did because they couldn't see them. – David Attenborough

Nocturnal primates are often erroneously labelled as being 'solitary', as is the case with many nocturnal mammals (Charles-Dominique 1978; Kays 2003; Nekaris & Bearder 2011).

The anthropocentric tendency to assume that an animal is solitary, or indeed cryptic, just because we find it difficult to locate, does not consider the highly specialised adaptations nocturnal species have developed for use in complex communication (Bearder 1999; Kays 2003). Nocturnal primates, for example, can communicate via vocalisations at frequencies inaudible to humans and rely on olfactory senses to convey information to conspecifics and heterospecifics (Alterman 1995; Bearder 2007; Bolen & Green 1997; Braune et al. 2005). Visual phenotypic clues may also play an important role especially low light (Bearder 1999; Penteriani et al. 2007). For the less conspicuous mammal species, such as slow lorises, the intra- and sometimes inter-specific variation in facial patterns, to the human eye, appear superficial, but on closer inspection reveal intricate pattern and colour deviations (Bearder 1995; Nekaris & Munds 2010). The function of this variation, especially amongst ostensibly similar-looking nocturnal species, may serve in individual recognition between species or mate-recognition within species (Bearder et al. 2006; Couldridge & Alexander 2002).

Recent studies – especially since the advances in radio-telemetry – have revealed that many previously presumed solitary nocturnal mammals are actually highly social in their activities (Gehrt & Fritzell 1998; Nekaris 2006; Nekaris 2003; Wiens & Zitzmann 2003b). Slow lorises are no exception, and have been observed to sleep in social groups of up to seven individuals and have ranges that extensively overlap (Wiens 2002; Wiens & Zitzmann 2003b). With only nine previous studies that have focussed on behaviour in *Nycticebus*, our understanding of the complex social interactions will only be improved with increased study effort.

1.2.5 Framework of objectives

Evidently, there is much to be gained by studying the intriguing and enigmatic slow lorises – both in regards to welfare and conservation, but also regarding their specialist adaptations and evolutionary history. The reintroduction programme at IARI provided me with the perfect opportunity to gain a better understanding in some of these areas. Systematic observations during the pre- and post-release phases of the IARI reintroduction programme provided the ideal scenario to study these primates in both a close-up captive setting and also in the wild. Particularly for such a lesser-known and threatened taxon, this information served to (1) facilitate the rehabilitation and reintroduction programme for Indonesian slow lorises; (2) augment the currently limited knowledge of slow loris behaviour and ecology – vital in the construction of future conservation plans; and (3) provide insights into the evolutionary processes which have contributed to the moulding of the slow loris behavioural and morphological specialisations they possess today.

1.2.6 Main aims and layout of study

Although this study focusses predominantly on the three Indonesian species of slow loris, mention of the other non-Indonesian species appear frequently and are therefore included in the introduction. Furthermore, as none of the Indonesian species have been studied previously in any depth, comparisons with studies of their closely related sister-taxa are of vital importance to making any valid conclusions or assumptions.

The topics covered in this thesis fall generally into three different disciplines: conservation, welfare and evolution. Whilst the inclusion of these three rather different disciplines may appear slightly arbitrary at first glance, I believe that I demonstrate during the thesis that they do overlap enough to produce a single comprehensive, yet sufficiently interlinked body of work with Indonesian slow lorises as the common theme. My primary aim was to provide much needed information that would aid in the conservation and welfare of this Endangered species, which I hope will also pave the way for future studies. As my fieldwork at IARI was focussed on initiating the slow loris reintroductions, much of the data I collected was associated with maintaining welfare and increasing conservation efforts, which is evident in the first half of the thesis. The final part of the thesis takes a more evolutionary approach to understanding some of the slow loris' unique and unusual characteristics. Although perhaps not so obviously linked to conservation and welfare, I do believe that a better comprehension of the selection forces and subsequent adaptations, which occurred during the slow loris' evolutionary history, can help us to understand their complex ecological needs today.

The first section of this thesis primarily deals with the problems associated with rehabilitation and reintroductions at IARI; both in respect to the criticism such programmes receive (chapter 3) and the difficulties faced during the rehabilitation process (chapter 4). Chapter 5 provides the bridge from welfare and conservation into more evolutionary based studies. It combines feeding behaviour of reintroduced slow lorises, providing the first ecological data on semi-wild Javan slow lorises, but also sheds light on more evolutionary aspects of their adaptive feeding ability. Chapter 6 investigates visual communication in slow lorises, specifically relating to the function of the face masks; this study builds on an earlier study undertaken by Nekaris and Munds (2010). Chapter 7 investigates further aspects of visual communication, but this time from the perspective of mimicry, used in anti-predator defence. The final chapter provides summaries and conclusions.

2. General Methods

"He who seeks for methods without having a definite problem in mind
seeks in the most part in vain." - David Hilbert

2.1 Study site

2.1.1 Indonesia

Spanning the equator from 6° N to 11° S, the Indonesian archipelago consists of over 17,000 islands that extend from Sumatra in the North to New Guinea in the South (Djoko & Walter 2006; Supriatna et al. 2001). Indonesia is on the border of two zoogeographical regions: the more westerly Paleotropical Realm is separated from the eastern Notogean (Australian) Realm by a transitional zone known as Wallacea (Kingston 2009; Myers et al. 2000) (Fig 5). A complex geological history involving the fission and fusion of these two distinct biological realms, and an abundance of island speciation centres, have contributed to the high levels of species richness and endemism present in the region today (Hall 2001; Kingston 2009). Boasting nearly 12% of the world's vertebrates and 10% of the world's vascular plants, Indonesia is one of the most biologically rich countries in the world. Here, endemic species account for 45% of all amphibians, 32% of the mammals, 28% of the birds, and a massive 60% of the vascular plants (Kingston 2009). Indonesia encompasses the aptly named Sundaland and Wallacea Biodiversity Hotspots (Mittermeier et al. 1999; Myers et al. 2000; Supriatna et al. 2001).

West of the Wallacea transitional zone lies the Sunda Shelf: a south-eastern extension of the Southeast Asian continental shelf, which is partially submerged beneath the Java and South China Sea (Harrison 2006) (Fig 5). Fluctuating sea levels caused by the melting and freezing of continental glaciers at higher latitudes, combined with shifting tectonic plates throughout the Cenozonic, resulted in the formation of intermittent land bridges between

Figure 5. Map of Australasia showing extent of the Sunda and Sahul continental landmasses with Wallacea in between. Biogeographical lines of Wallace, Huxley, and Lydekker are indicated, as is the Isthmus of Kra (Harrison 2006)

islands in the Sunda region (Heaney 1991; Meijaard 2004a, b). During periods of lower sea levels, the connections between islands facilitated the spread of plants and animals from the Asian mainland onto previously inaccessible islands. These species were later isolated again as sea levels rose and promoted *in situ* (endemic evolution) (Harrison 2006; Meijaard 2004a; Morwood et al. 2008). Other island groups situated in the deeper trenched Wallacea region, however, remained isolated despite changing sea levels and promoted endemism in the few species that managed to cross the oceanic barrier (Kingston 2009).

Coinciding with the land bridges around the time of the last glacial maximum, 18,000 years ago, the climate was beginning to cool. Lower temperatures caused changes in habitat in the Sundaic region. A band of drier more seasonally adapted woodland ran from north of the Malay Peninsula down as far as Java replacing the more tropical forests (Heaney 1991; Morley & Flenley 1987). For some species this habitat alteration may have benefitted them in allowing an easier migration south towards Java through the more savannah-like landscape, but for others it acted as a barrier possibly isolating some species and preventing gene flow (Harrison 2006; Meijaard 2004a, b).

2.1.2 Java

The island of Java was formed during the Miocene (Whitten et al. 1997). It is almost entirely volcanic in origin and consequently characterised by strong altitudinal gradients (Backer & Brink 1963). Vegetation types range from lowland swamp forests along river courses to sub-alpine vegetation in mountainous regions (Sémah & Sémah 2012). The west of Java has a tropical wet climate, which was once dominated by rain forest. In comparison, the east is more seasonal with a dry season lasting from four to six consecutive months (Sémah & Sémah 2012). Generally, the vegetation types in the east reflect the drier conditions, resulting in less dense forest and even patches of savannah (Heaney 1991; Sémah & Sémah 2012)

Although the entire land area of Java only comprises 7% of Indonesia's total, 67% of Indonesia's population reside there (Lavigne & Gunnell 2006). Java is the political and industrial centre of Indonesia and one of the most densely populated areas in the world (Whitten et al. 1997). Java's huge population and its accompanying demand for raw materials has contributed to the extensive clearance of the indigenous forests (Grow et al. 2010; Smiet 1992). Only 10% of the original forest now remain and are generally confined to mountainous areas (Lavigne & Gunnell 2006; Smiet 1992). Forests have been replaced by residential housing, agricultural land, cash crop plantations (e.g. sugarcane and rice) and forest plantations (e.g. teak and rubber) (Verburg et al. 1999; Whitten et al. 1997). Although 23% of Java's forests are classified as state forests, 16% of this is actually for production, with only 7% being of protected or reserved status (Lavigne & Gunnell 2006). Production forest and agriculture is largely of the monoculture variety. The simplifying of ecosystems through intensive farming of a single crop can lead to loss of diversity and richness, leaving the fragile environment susceptible to pests, flood hazards, slope instability and soil erosion (Lavigne & Gunnell 2006). Even in the more remote areas, forests are not completely free from exploitation, and experience – often despite protective measures – pressure from local people collecting firewood, timber and fodder (Moore 2011; Smiet 1992).

Trade in wildlife is another huge threat to Indonesia's biodiversity (Davies & Goodall 2005; Nekaris et al. 2010a; Nijman 2009; Nijman 2010; Nijman et al. 2010; Shepherd et al. 2004). Java and Bali are suspected to be the central hubs of the Indonesian wildlife trade (Davies & Goodall 2005; Malone et al. 2004; Shepherd et al. 2004). Unfortunately, the keeping of exotic pets in Indonesia is extremely popular and often associated with social status or economic success: the rarer the animal, the higher the status. Indeed, a strong positive correlation was found between household income and pet species of conservation concern (Jepson 2002; Jepson & Ladle 2009). To satisfy the demand for exotic pets and traditional medicines individuals are gathered by hunters throughout Indonesia and subsequently transported to Java or Bali to be sold in one of the numerous animal markets (Malone et al. 2004; Shepherd et al. 2004). Despite the illegalities of trading or possessing protected species (Indonesian Law 5/1990), people involved in trade are often motivated to break the law because of the financial rewards. People who benefit range from local people near source populations to market vendors to regional dealers (Malone et al. 2004). The high prices paid for such species may also include extraction and transport costs, and bribes to local officers to avoid receiving penalties (Malone et al. 2004). Markets in Javan cities such as Jakarta and Surabaya are open daily in designated areas and often have protected species on display (Nekaris et al. 2010a). Clearly, adequate enforcement of the illegal trade from local officials is lacking.

Figure 6. Mount Salak study site and the location of International Animal Rescue centre where the captive studies were conducted. Radio tracking of slow lorises occurred on the north face of Mount Salak.

2.1.3 Mount Salak, Bogor

I conducted the study between December 2009 and March 2011. Part of my study was conducted on the north face of Mount Salak in the Gunung Halimun-Salak National Park (GHSNP) (6°41'S, 106°44'E) and the other part at the IARI rescue centre on the periphery of GHSNP (6°39'S, 106°43'E) (Fig 6). GHSNP comprises the Halimun range, Mount Salak, Mount Endut and other forests adjacent to Halimun. Originally established in 1992 as the Halimun National Park, the park boundaries were extended in 2003 to include Mount Salak, and subsequently became known as GHSNP. The park covers an area of 113,357 ha (~400 – 2211 asl) and is the largest remaining forested area in Java (Kim et al. 2011). Mount Salak consists of lowland, submontane and montane forest and covers an area of approximately 76,000 ha (Supriatna 2006). Primary forest is still present at higher altitudes, but secondary forest dominates the lower regions (Gjershaug et al. 2004), which is where the study was conducted. Mean monthly minimum and maximum temperatures have a narrow range of 17 to 27 °C (Roosita et al. 2008) (Fig 7). High annual rainfall reaches 4000–5000 mm, which is an important water catchment area (Gjershaug et al. 2004) (Fig 8). Despite Mount Salak being within a protected area, locals collecting firewood and cattle fodder, and hunters regularly use the park, suggesting proper policing is lacking (Fig 9) (Moore 2011).

Mount Salak is home to all five species of non-human primates present in Java: Javan gibbons (*Hylobates moloch*), grizzled leaf monkeys (*Presbytis comata*), ebony leaf monkey (*Trachypithecus auratus*), long-tailed macaques (*Macaca fascicularis*) and Javan slow lorises (*Nycticebus javanicus*) (Collins 2007; Prawiladilaga et al. 2008). Other mammals present include leopards (*Panthera pardus*), leopard cats (*Prionailurus bengalensis*), common palm civets (*Paradoxurus hermaphrodites*), Javan stink-badgers (*Mydaus javanensis*) (Prawiladilaga et al. 2008) and Javan small-toothed palm civets (*Arctogalidia trivirgata trilineata*) (Moore 2011).

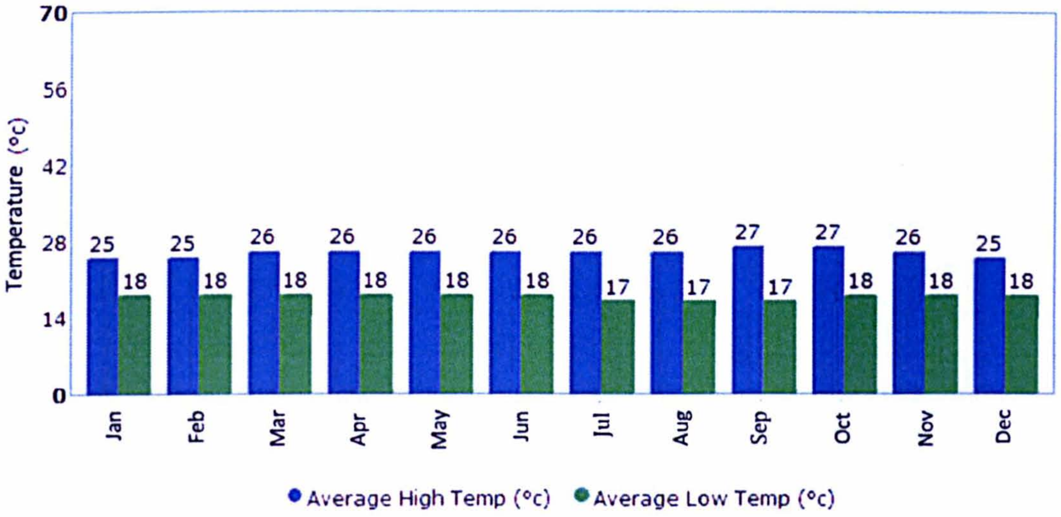

Figure 7 Mean monthly temperatures for Bogor, Indonesia (http://www.worldweatheronline.com)

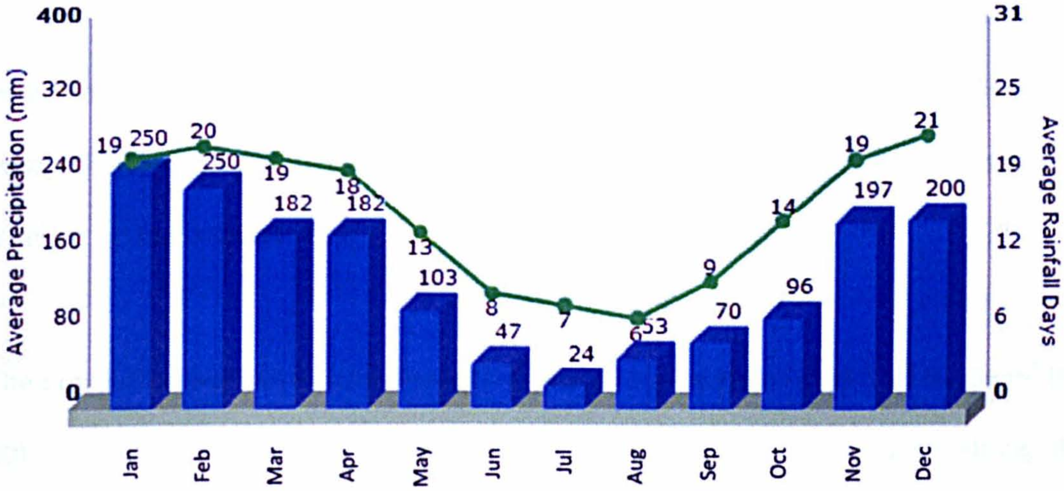

Figure 8 Mean monthly precipitation for Bogor, Indonesia (http://www.worldweatheronline.com)

2.1.4 International Animal Rescue

IARI is situated on the north face of Mount Salak and currently houses long-tailed and pig-tailed macaques (*Macaca fascicularis* and *Macaca nemestrina*) and all three species of Indonesian slow lorises (*N. coucang, N. menagensis* and *N. javanicus*). The centre was built

Figure 9. Local villagers collecting fire wood (left), and hunters trapping birds for sale in markets (right).

in 2006 and started receiving slow lorises in 2008. The centre has a fully operational veterinary clinic, a quarantine area, and three full time veterinarians. Each animal that enters the centre is given a medical check-up, screened for all known diseases, and spends a period of time in quarantine.

The slow lorises are kept in semi-natural enclosures ranging in size from 8 m^3 to 156 m^3 (Fig 10). Trained animal keepers are responsible for feeding, cleaning and socialising the animals in the cages following the animals' period in quarantine. Although enclosures vary in their furnishings, each is minimally equipped with nest boxes and weaved bamboo tubes for sleeping, feeding trays and other feeding enrichment devices, substrates (both live and artificial) for climbing, and water containers. Enclosures are made from wire mesh, are semi-covered, and illuminated with dim red lighting on a rotating schedule. Red light does not appear to disturb the lorises (Nekaris 2003) owing their monochromatic vision, which does not allow for discrimination of the colour red (Perry et al. 2007). Lorises are provisioned with enrichment on a weekly basis. Lorises are given three main feeds and two enrichment feeds per night and provisioned with water daily. The area is restricted from visitors.

Figure 10. Slow loris cages at IARI (left) and typical layout of enrichments and substrates in one of the cages (right)

2.2 Methods

2.2.1 Rehabilitation and reintroduction process

Approximately 100 animals were housed at IARI during my study period. The selection process for the slow loris reintroduction programme was based on a number of factors: the animal's health and condition, the period of time it had been at the centre, and its ability to perform species-typical behaviours deemed necessary for survival in the wild. All animals are checked thoroughly when they enter the centre by the IARI veterinarians. Potential candidates were chosen based on the veterinarian's report (i.e. if the slow lorises were in good health, free of disease and still possessed teeth). Slow lorises were then chosen based on the length of time they had been at the centre. A captive environment can detrimentally affect the behaviour and psychological wellbeing of wild animals over time. Animals recently admitted are more likely to still possess natural behaviours associated with fitness compared to animals that have spent a long time in captivity (Elsbeth McPhee 2004; Jule et al. 2008). Accordingly, slow lorises that had been received in the last year were selected over individuals that had been at the centre for longer. Finally, these selected slow lorises were monitored in their captive environment for a minimum of 30 hours each in order to assess their suitability for reintroduction.

An activity budget for each slow loris was generated based on the observational data and compared to wild studies of closely related species (Barrett 1984; Swapna 2008; Wiens 2002) in order to assess whether the slow lorises were exhibiting relatively normal behavioural patterns. Behavioural data were collected using 5-minute instantaneous focal sampling (Martin & Bateson 2007) and followed ethograms by Fitch-Snyder et al. (2001) and Glassman and Wells (1984) (Appendix 2). Other information collected during the scans included: postural position, angle of substrate, size of substrate, height of animal and speed of travel (Nekaris 2001). Slow lorises displaying a full range of natural species-specific behaviour and limited stereotypic or abnormal behaviour were chosen for the reintroduction programme. Species-specific behaviour included the ability to catch live prey, gouging, vocalising and affable social interactions (Nekaris & Bearder 2011). The ability to catch live prey and recognise appropriate food items is not considered innate behaviour in slow lorises (Wiens 2002; Wiens & Zitzmann 2003a), therefore the absence of this learned knowledge may seriously restrict their survival potential post-release.

The north face of Mount Salak in Gunung-Halimun National Park was chosen as the release site and the necessary permits from the Indonesian Forestry Department were subsequently obtained. Based on data obtained from previous spot-light surveys by Collins (2007) and the IARI team in 2011 (totalling 109 km of transects) only four Javan slow lorises were sighted, suggesting that whilst they are present, they occur at low densities. Although the site is not completely free of disturbance (Moore 2011), its protected status enabled the reintroduction/monitoring team to inform the Forestry Department when hunters entered the park. Of the hunters encountered on Mount Salak, the majority were trapping birds and only once were they accompanied by dogs; although what they were hunting was unknown (Moore 2011). Nevertheless, to the arboreal slow loris, dogs are unlikely to constitute a threat. Furthermore, the steep treacherous terrain on Mount Salak, combined with the high continuous canopy layer, makes hunting arboreal mammals relatively difficult. The close proximity of the release site to the IARI rescue centre provided a good base for spreading awareness through the neighbouring villages regarding the reintroduction programme and slow loris conservation.

Slow lorises selected for the reintroduction programme were subsequently fitted with Biotrack VHF radio collars (Biotrack, Dorset, UK) weighing approximately 15.5 g (< 2 % of the animals' body weight) (Gursky 1998). The fitting of collars occurred at least two weeks prior to the animals leaving the centre. This trial period served to give the slow lorises time to adapt to wearing the collars and to determine whether the collars restricted their movements or feeding to any degree (Streicher & Nadler 2003). After a final medical check, the slow lorises were taken in pairs up to the pre-determined release site, where they spent a period of time (ranging from 5 to 104 days) in a pre-constructed habitation cage (5m x 4m x 3m) (Fig 11). During the slow lorises' period in the habituation cage, they were provided with food and guarded at all times. This habituation process allowed the animals to adapt to the new environment and has been termed a soft-release by the IUCN (IUCN 1998; Streicher & Nadler 2003). Animals were monitored during their active periods following the same behavioural sampling techniques as used for assessing behaviour in captivity.

Figure 11. Habituation cage built at the release site on Mount Salak

2.2.2 Radio-tracking

After sufficient time had passed for the animals (n = 11) to ostensibly adapt to the new environment ($\bar{X}$ = 27 days, SD = 36) they were released from the cage either in pairs or singularly during the night (from 2000-2200h). Longer durations were preferred for lorises in the habituation cage, but this was not always possible owing to time restraints of the release permits issued by the forestry department. The first four lorises were released in pairs. Owing to difficulties monitoring two animals simultaneously when they travelled far apart on the mountain, the next seven animals were released singularly. Monitoring of the slow lorises began immediately after release. The animals were tracked using red halogen Petzl-zoom lamps by two teams in 6-hour shifts: an evening shift (1800-0000h) and a late shift (2400-0600h) in order that researchers maintained stamina in the field. R1000 Com-Spec receivers and Biotrack antennas were used to track the slow lorises with the fitted collar frequencies between 151 – 152 MHz. The same 5-minute instantaneous behavioural scan sampling was conducted on the released slow lorises. In addition, 15-minute GPS locality fixes were taken using a GPS Map60 CSX (Garmin Ltd.) in order to monitor ranging behaviour. Data on feeding and positional behaviour presented in Chapter 5 derived from the radio-tracking of six rehabilitated and reintroduced Javan slow lorises from April 2010 to March 2011 for periods ranging from two weeks to three months per animal.

The use of radio-telemetry has been vital in the studies of nocturnal and cryptic species. Without such technology, finding and following small animals at night in thick vegetation is virtually impossible. Radio-telemetry allows the analysis of how wild animals use space and time in response to different environmental factors (Naef-Daenzer et al. 2005). One of the benefits of radio telemetry is that it permits sampling on demand and consequently reduces the chance of bias (Millspaugh & Marzluff 2001). The radio-tracking of reintroduced animals is highly recommended during post-release monitoring phases as it enables: an assessment of the release methods and animal survival rates; an opportunity to compare pre- and post-release behaviours; an insight into how the animal is adapting to its new environment; and the ability to assess any impact the animal is having on its habitat (Cheyne 2008; IUCN 2002a).

2.2.3 Ecological data collection

I followed six rehabilitated and reintroduced Javan slow lorises on Mount Salak. I recorded feeding observations using focal animal instantaneous point sampling at five minute intervals (Altmann 1974; Martin & Bateson 2007) following ethograms by Fitch-Snyder et al. (2001) and Glassman and Wells (1984) (Appendix 2). I identified flora food items to the species level, but for live prey items, to the ordinal level owing to visual difficulties. Lorises use a variety of different substrates and capture methods to acquire prey, so in order to quantify these actions, I recorded their exact position, the size of the substrate and method of food acquisition in each case (Glassman & Wells 1984; Nekaris 2005) (Appendix 2). These included: whether the loris was in a quadrupedal position or in suspension; the size of the substrate (terminal, small but still flexible, medium and sturdy or trunk), and the food manipulation/capture technique (one hand, two hands or directly from mouth). When considering the consumption of floral parts and fruit, I noted whether hands were used in the manipulation of the flower/fruit stem during feeding; therefore, whilst the food item itself was not directly placed into the mouth using the hand, the stem was manipulated with the grasping extremities.

2.2.4 Obtaining demographic data

Since the IARI centre was established in 2006, records of every animal received have been stored in a database including information on species, sex, origin and condition on arrival. I used four different categories for classifying the origin of the animal: confiscations, transit, surrendered and captive born. I defined confiscations as police raids on pet markets. Transit raids were also police confiscations but occur before the animals reached their market destination. Surrendered animals can derive from people who have bought the animal, unaware of the illegalities of doing so, or from owners who no longer want to care for the animal, and subsequently donated the animal to the centre. Captive born lorises were born whilst at the centre: as lorises are provided with contraceptive drugs, the captive lorises usually only occur if the animal is pregnant on arrival. When possible, the people surrendering the lorises were briefly questioned. Questions included: reason for buying, market price and reason for surrendering. IARI gave me permission to have access to their database. Using these data, demographic trends for the past four years (2008-2012) were evaluated in Chapter 3.

2.2.5 Observations of stereotypies

As part of the pre-release phase in a reintroduction programme underway at IARI since January 2010, I systematically monitored IARI's captive slow lorises. 99 Indonesian lorises were present during this period including: *Nycticebus javanicus*, (n = 41) *N. coucang* (n = 42) and *N. menagensis* (n = 7) (Table 4). During a six month behavioural scan sampling period prior to the start of the survey, I became accustomed to the forms of stereotypic behaviour exhibited, observing and noting all behaviours deemed highly patterned, repetitive, and ostensibly afunctional. For 30 days in November 2010 I observed 90 of the 99 lorises at the rescue centre (nine were being treated at the IARI clinic) for one hour, three times a night at 2100h, 0000h and 0300h, and recorded any stereotypic behaviour displayed using the 'one-zero' (presence-absence) sampling technique (Altmann 1974). No attempt was made to record frequency or intensity of the behaviour. I chose the one-zero sampling method as it is less time consuming than other methods (Altmann 1974) and could be conducted between the regular pre-release observations, (which were necessary for lorises involved in the rehabilitation process). The study followed the methodology of other studies of stereotypic behaviour in strepsirrhines (Tarou et al. 2005) and giraffes (Bashaw et al. 2001). I excluded nine animals receiving medical treatment from the study. I measured each enclosure, and recorded the species, number of individuals and sex ratio (group composition) in each. Using data from medical records provided by IARI I also noted date each slow loris had arrived at the centre, their place of origin, and condition of the teeth, (as lorises often have their teeth cut by traders to avoid being bitten).

I observed three types of stereotypic behaviour: pacing, rocking and circling. Pacing involved walking to and fro along the ground, (defined by a minimum of three consecutive turns), and could last for periods of up 31 minutes with no breaks. Pacing covered a distance between 50 cm to 3 m. Rocking involved the individual crouching on hind legs and swaying from side to side against the cage, (defined by a minimum of three consecutive sways), and could last for up to 54 minutes uninterrupted. The hands of the loris would lightly brush the cage or the ground during motion to keep balance. Both pacing and rocking individuals usually used an area of the cage that provided visibility to the outside. Circling involved the loris engaging in a series of about 1 m^2 circles (defined by a minimum of three consecutive revolutions), whilst suspending from the roof of the enclosure. Lorises moved gradually around the roof of the cage, whilst rapidly circling, producing one circle after the next, occasionally using the sides of the cage too.

Occasionally other conspecifics would approach or interact with an individual engaged in any of the three stereotypies, and this would result in either an aggressive or passive display depending on dominance. If the conspecific had departed the loris would resume the behaviour immediately. If, however, the stereotypic individual was aggressively moved from the preferred area, it would leave the area and come back once the conspecific had moved away. Despite long durations, performance of stereotypies never resulted in observable injuries.

2.2.6 Photo capture

I took photos of Indonesian slow loris facemasks from live animals currently housed at IARI. I took all photos on a Panasonic Lumix TZ7 digital camera with an effective pixel count of 10.1 megapixels. I took all photos at the fine quality setting delivering images in Joint Photographic Experts Group (JPEG) format with approximately 3648x2736 pixels in each photo. All photos were taken outdoors at around midday utilising only natural lighting and were taken within an hour of each other to reduce variation in exposure caused by changes in the sun's position and brightness (Davis & Castleberry 2010). I took all photographs at a consistent one metre distance from the animal, used the same angles to shoot each photo, and faced the same direction to minimise any lighting variation. I used manual settings for aperture and shutter speed, and the white balance was set to daylight (Bergman & Beehner

2008). Based on the histogram in the camera's LCD display, any photo that was not consistent in lighting (either over- or under-exposed) was disregarded.

2.2.7 Photo analysis

I imported all images into Photoshop CS2 (Adobe Systems, San Jose, CA) where they were trimmed to display only the facemask of each individual. Using a Gretag-MacBeth ColorChecker chart and the inCamera 4.0.1 filter plug-in for Adobe Photoshop I created a colour profile that was then applied to all images (Bergman & Beehner 2008). I made colour and light adjustments where necessary using the Auto Levels, Auto Curves and Exposure functions (Beuchel et al. 2010). To convert each image into monochromatic colours I used the Greyscale function in Photoshop. To achieve a dichromatic colour conversion I used the Vischeck Plug-in for Windows, which produces a colour deficit simulation (Fig 12). Colour blindness type was set to deuteranope with gamma levels at 500. Finally, I made my colour measurements on each image using the Measure Regions function in FoveaPro v4. I selected fourteen areas (40 x 40 pixels each) using the Fixed Marquee tool in Photoshop. For each individual, I measured eight dark areas and six light areas at specific points on the face (forehead, circumocular region, preauricular region, median stripe etc.). The exact same fourteen locations on the monochromatic and dichromatic images for the same images were measured accordingly. In each selection FoveaPro calculates the mean red, green and blue (RGB) scores, which I then used to compare between individuals.

2.2.8 Repeatability of photo measurements

I photographed a subset of the slow lorises (n=8) twice under the same conditions, approximately 30 seconds apart. Using the aforementioned methods, I measured the colour in exactly the same areas of the face in both photographs. I measured the repeatability of the scores (Lessells & Boag 1987) using the reliability analysis function in

SPSS (Field 2005). The intra-class correlation coefficient yielded high repeatability ($r_i = 0.72$, $p < 0.05$) (Martin & Bateson 2007).

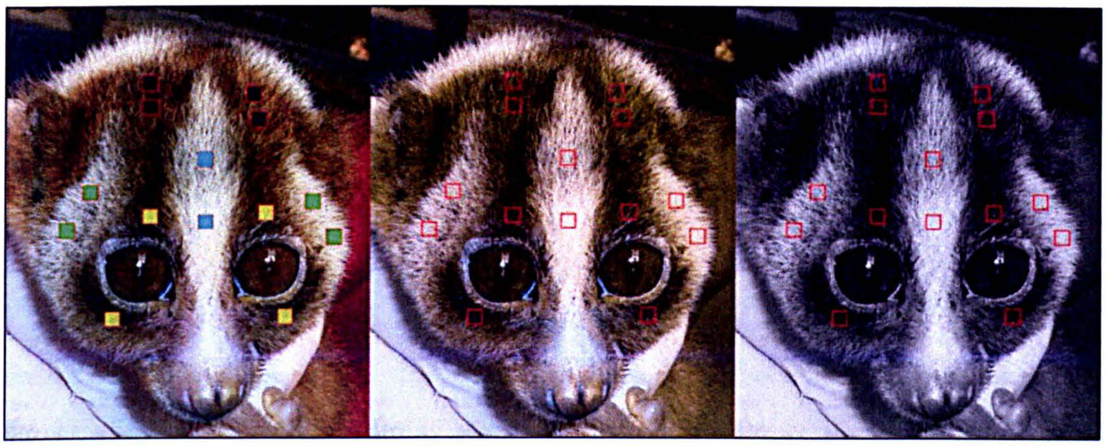

Figure 12. Normal, dichromatic and monochromatic versions of a digitally photographed Javan slow loris facemask used in my analysis. The squares indicate areas used for colour measurements. (Black squares = forehead, yellow = circumocular, blue = median stripe and green = pre-auricular)

2.2.9 Statistics

I used a combination of parametric and non-parametric statistics depending on the type of data being analysed. I ran Kolmogorov-Smirnov tests to assess if the data were normally distributed. I used parametric tests on normally distributed data with a sufficient sample size to fit the validity assumptions (Zar 1999). For nominal data, I used non-parametric tests. I conducted most statistical analyses using SPSS 17 (SPSS, Inc). All reported probabilities are two-tailed and statistical significance was accepted at the $p \leq 0.05$ level, unless stated otherwise (Zar 1999). Data are reported as means and standard deviations (SD).

I used non-parametric Chi-squared, Kruskal-Wallis and Spearman's Rank tests to analyse the demographic data in chapter 4 owing to the presence of nominal and categorical data. I used a binary logistic regression model in order to predict possible causes for the occurrence of stereotypies based on the range of intrinsic and extrinsic variables. I chose this method as the dependent variable was binary and categorical, and the independent variables featured a mix of both categorical and continuous data. I set the criterion value of 0.10 for inclusion of a variable (Tabachnick & Fidell 2007). I used diagnostics tests in the linear regression model to test for multi-collinearity. Tolerance values less than 0.1 and Variance Inflation Factor values greater than 10 were discarded (Field 2000; Menard 1995). I used SPSS 17 for all analyses and accepted significance when $p < 0.05$ (Zar 1999).

For analysis of the colour data in chapter 6, I used descriptive statistics to visualise the means of the variance for the measured colours in each region. As the colour data (scores for RGB) were highly correlated ($p \leq 0.001$) I applied a Principal Component Analysis (PCA) on these data in order to compile one composite variable from all three data sets for each separate facial region (Clough et al. 2009; Stevens et al. 2009). Only one variable for each region was produced as the values explaining the variance in the first component were consistently high compared to component two. I investigated the intra-specific variation on the PCA scores using analysis of variance test (ANOVA) from which *Nycticebus menagensis* was removed from owing to the small sample size. ANOVA was subsequently used to examine colour variation across species in relation to sex, species and age (sub-adult, adult and old), where age was estimated by the IARI vets according to teeth colour and wear, colour and texture of hand pads pelage condition (Dunbar & Dunbar 1975). As age increased teeth become darker and increasingly worn; hand pads become darker and scalier; and fur loses condition. I conducted Friedman tests to analyse differences between photo-types. Bonferroni corrections to the alpha level were applied when multiple tests were conducted (Quinn & Keough 2002).

3. Ethics of rehabilitation and reintroduction

3.1 Introduction

The existence and well-being of approximately one quarter of all mammal species are threatened by a rapidly growing human population, with species declining at a rate 100 times faster than before the emergence of *Homo sapiens* (Wilson 1996). Deforestation combined with excessive hunting for medicine, meat, body parts and the capture of wild animals for a burgeoning pet trade are among the main causes behind this rapid depletion of wildlife (Cheyne 2008; Foley et al. 2011; Shepherd et al. 2004; Starr et al. 2011; Still 2003). Evidence of this egregious phenomenon is highlighted by the rising numbers of threatened species housed in rescue centres around the world (Chapman & Peres 2001; Cheyne 2009; Cheyne 2008; Defler et al. 2003; Nijman 2009). Whilst habitat loss and degradation are certainly prominent factors in the gradual demise of many species, the impact of trade - both legal and illegal - appears previously underestimated (Nekaris & Nijman 2007; Nijman 2010; Nijman et al. 2010; Shepherd et al. 2004). Here, from a conservation view point, the adverse repercussions of over-harvesting threatened species are amalgamated with the welfare issues of animals being inhumanely treated during their stint in trade (Clark et al. 2008; Nekaris et al. 2009).

When confiscations by law enforcement officials are made, the most likely terminus for these animal refugees is either government holding facilities, zoos or one of the numerous rescue centres established over the past two decades (McGreal 2007; Nekaris et al. 2009; Nijman et al. 2010; Streicher 2004). Dependent on availability of space, suitable housing and funding for long-term care at such sanctuaries, the fates of these confiscated animals, involuntarily embroiled in trade, are resigned to one of a few less than desirable outcomes: euthanasia, a lifetime in captivity or at best the rather ambiguous probability of successful reintroduction back to the wild (Ashraf & Menon 2005; Bennett 1992; Cooper & Cooper 2006; Harcourt 1987; Kirkwood 2005). Deciding on which option to take is no simple task and frequently raises controversial and conflicting opinions depending on the intentions of those involved (Harcourt 1987; IUCN 2002b; Kirkwood 2005; Tutin et al. 2001).

Of all species affected by trade, primates are among the most ubiquitous (Nijman et al. 2011; Shepherd 2010). In 2006, a specialist rescue centre was established in Bogor, Java by International Animal Rescue (IARI) to accommodate displaced Indonesian primates: specifically, macaques (*Macaca fascicularis* and *M. nemestrina*) and slow lorises (*Nycticebus coucang, N. menagensis* and *N. javanicus*). These taxa receive little media attention compared to major flagship species such as rhinos, orang-utans, elephants and tigers, and consequently suffer reluctance by funding agencies to assign financial aid to both conservation and welfare initiatives (Cheyne 2009; Clucas et al. 2008; Ware 2001). Akin to numerous other Asian primates, the slow loris (*Nycticebus*), a small, relatively unknown nocturnal strepsirrhine primate, is under particular pressure from trade, as it regularly appears in the region's notorious animal markets owing to the high demand as pets and for traditional medicine (Nekaris et al. 2009; Shepherd et al. 2004; Starr et al. 2010).

The aptly named 'slow' loris with its meticulous locomotion devoid of rapid movement, and with an anti-predator response of simply freezing in position, does not fare well against expert human hunters who can easily pluck them off branches (Ishida et al. 1992; Nekaris et al. 2009). From market survey data and evidently diminishing extent of suitable habitat, the current rate of harvesting this slow-reproducing primate is hardly sustainable (Fitch-Snyder & Thanh 2002; Nekaris & Nijman 2007; Ratajszczak 1998; Thorn et al. 2009). Justifiably, in 2007, owing to raised international concern, this genus was transferred to

CITES Appendix 1 thereby banning all international trade in this genus. Unfortunately, irrespective of improved sanctions in trade regulation, efforts to improve law enforcement and raised international awareness, no sign of retardation in this trend is apparent (Cheyne 2008; Nijman et al. 2010; Shepherd et al. 2004). In Indonesia, for example, trade in slow lorises and other low-profile protected species persists openly in numerous bird markets with traders displaying little or no conformity to the strict local legislations. The traders' absence of fear of legal action suggests adequate enforcement is lacking (Nijman 2009; Shepherd 2010).

Rescue centres primarily function to rehabilitate wild animals: offering refuge to animals which are victims of human persecution. Rescue centres undoubtedly hold vast potential to offer a viable alternative, regarding both conservation and welfare, to an otherwise bleak future for many displaced animals (Beck 2010; Cheyne 2008; Teleki 2001). The sheer volume of animals in trade, however, ensures most rescue centres reach carrying capacity within only one to two years (Bennett 1992; Nijman et al. 2010; Teleki 2001; Ware 2001). Notwithstanding their obvious noble intentions, public opinions on the value of rescue centres are mixed, predominantly owing to a paucity of tangible information regarding the work that they undertake (Carter 2003; Cheyne 2009; Farmer & Courage 2008; Kabasawa 2011; Yeager & Silver 1999). With only anecdotal information available, the slow process of trial and error is often repeated every time a new centre is established (Teleki 2001). Indeed, even in developed countries no legislation exists to set the standards for the running of such centres and the associated treatment of wildlife (Kirkwood 2005). The goals of each centre are thus determined by the owners – often based on personal judgement – in isolation from other centres (Carter 2003; Farmer & Courage 2008; Teleki 2001). Scientists sometimes criticise the methods employed by rescue centres, yet rarely offer practical alternatives (Carter 2003; Teleki 2001). Arguments can stem from the ostensibly conflicting fields of conservation biology and welfare science, whereby the former focuses on assisting the plight of the species, the latter on the welfare of the individual (Albrecht 2003; Fraser 1999; Kabasawa 2011). Some conservation biologists assert that rescue centres squander funding that could be better used elsewhere (cf. Bennett 1992; Carter 2003; Kabasawa 2011; MacKinnon 1977; Oates 1999; Ware 2001). Cheyne (2009), however, indicates that funding for conservation and welfare usually derives from different sources. Rescue and rehabilitation centres are a consequence of law enforcement (Rijksen et al. 1999). In an ideal world, all wildlife and their encompassing habitats would be sufficiently protected, thus rendering rescue centres redundant (Beck 2010; Ware 2001). Unfortunately, owing to the current worsening environmental situation and the exponential growth in human population, this ideal, for now, may only be regarded as wishful thinking.

The reintroduction or translocation of animals is a further topic of contention and often raises controversial issues relating to the viability of success in such projects and the issues of animal welfare post-release (Soorae 2007). A reintroduction is defined as 'an attempt to establish a species in an area that was once part of its historical range, but from which it has been extirpated or become extinct', and a translocation as 'the deliberate and mediated movement of wild individuals or populations from one part of their range to another' (IUCN in prep, 1998). From here on, the term reintroduction will be used to cover both aforementioned aspects unless otherwise stated. Reintroductions are renowned for low success (Beck et al. 1994; Fischer & Lindenmayer 2000; Seddon 1999); however, a few notable instances reveal that success can be achieved if the programmes are properly planned and executed (Spalton et al. 1999). Once again, a major criticism of reintroduction programmes is the lack of documentation and subsequent publication of results into the scientific community (Beck et al. 1994; Carter 2003; Fischer & Lindenmayer 2000; Soorae

2007; Yeager & Silver 1999). The reasons for lack of communication appear to be related to fear of condemnation by authorities or funding agencies concerning failure or improper implementation of such projects (Farmer & Courage 2008; Teleki 2001). Nevertheless, without such information, progression in the field of reintroduction science is undoubtedly hampered by a lack of comparable data – both successful and unsuccessful – from which modifications to new methodologies can be made accordingly (Fischer & Lindenmayer 2000; Seddon et al. 2007; Soorae 2007; Stoinski et al. 2003).

Using the case of Indonesian slow lorises as an example, here I attempt to reconcile the absence of transferable data and to promote transparency in the activities of the IARI rescue centre. I review demographic trends of slow lorises arriving at the centre since its opening in 2008, including their origins (either from confiscations or donations), condition, and mortality. I present the methods and results for the slow loris "reinforcement" reintroductions, defined as 'the addition of individuals to an existing population' (IUCN in prep, 1998) that have occurred in the past 18 months, assessing the outcomes in terms of both success and failure. Similarly to many other rescue centres dealing with traded animals, IARI is at full capacity. With a large percentage of animals unable to be released owing to various health and behavioural problems, an obtrusive question is raised: what is the most viable option regarding *both* conservation and welfare, for animals that cannot be released? I tackle this question and discuss the ethical issues raised for each possible option for slow lorises received, and relate this to current welfare and conservation goals. Finally, I propose guidelines for other rescue centres dealing with similar situations.

3.2 Methods

See chapter 2

2.2.4 – Obtaining demographic data

2.2.9 - Statistics

3.3 Results

3.3.1 Demographics

In 2008, IARI began receiving slow lorises from the pet trade. Over these four years a total of 180 individuals were admitted. The first two years observed a large influx of lorises, when admissions peaked at 82 individuals in 2009, but was then followed by a sharp decline until 2011 (Fig 13). The total number of lorises housed at IARI steadily climbed until 2009 and remained stable until 2011 ($\bar{X}$ = 94 ± 6). Mean annual mortality over four years was 14 deaths (22%) (n = 61). Mortality was highest in 2010 with 26 cases (26%) and lowest in 2008 with three (14%). Lorises surrendered to IARI by the public over the four years comprised 37% of all lorises received (Fig 14). Lorises from government rescue facilities such as PPS Tegal Alur (Tegal Alur Wild Animal Rescue Centre) comprised 35% and are suspected to be predominantly derived from market confiscations whilst in trade. Confiscations conducted by BKSDA JATIM etc. that occurred in transit before animals reached comprised 21%. Captive born animals constituted 6% of lorises at IARI. In 2009, IARI received significantly more lorises from confiscations than in other years ($\chi^2 = 59.3$, df = 6, $p \leq 0.001$). *Nycticebus javanicus* from Java was the most common loris species to be received at IARI, making up 55% of the total, with *N. coucang* from Sumatra and *N. menagensis* from Borneo comprising a further 41% and 4% respectively (Fig 15). Owing to difficulties in the identification of *N. coucang* and *N. menagensis*, however, the percent of *N. menagensis* may be slightly underestimated.

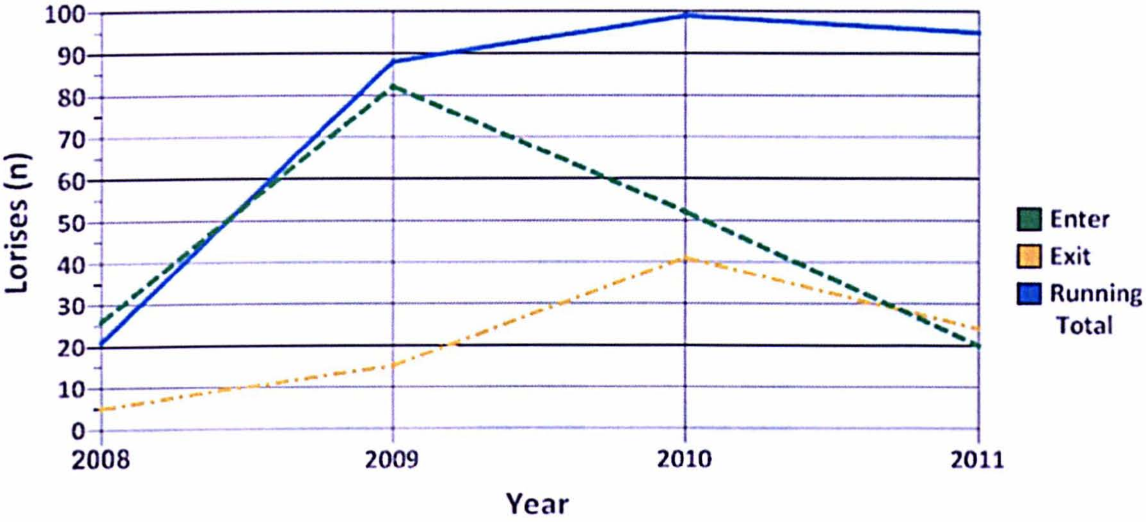

Figure 13. Graph displaying slow lorises entering, exiting and the running total at IARI over a four year period from 2008 to 2011. A high influx of animals in the first two years followed by a sharp decrease in numbers received once at full capacity is apparent.

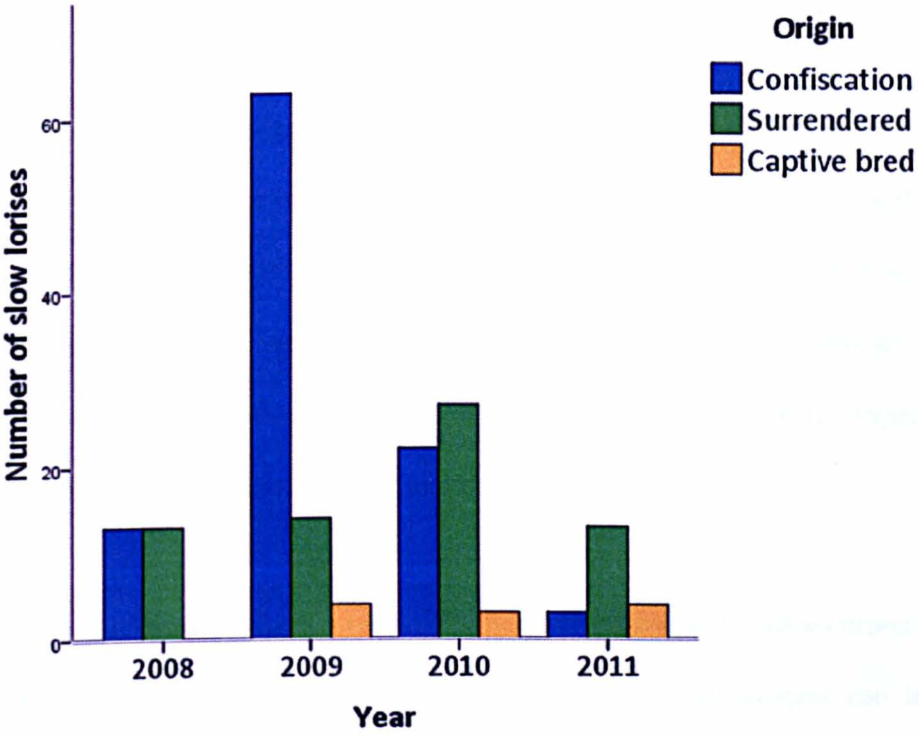

Figure 14. Graph displaying the number of slow lorises admitted to IARI over four years from 2008 to 2011 and from where they originated: confiscations, surrendered, transit or captive born. High numbers of admissions are apparent in 2009 followed by a subsequent decrease.

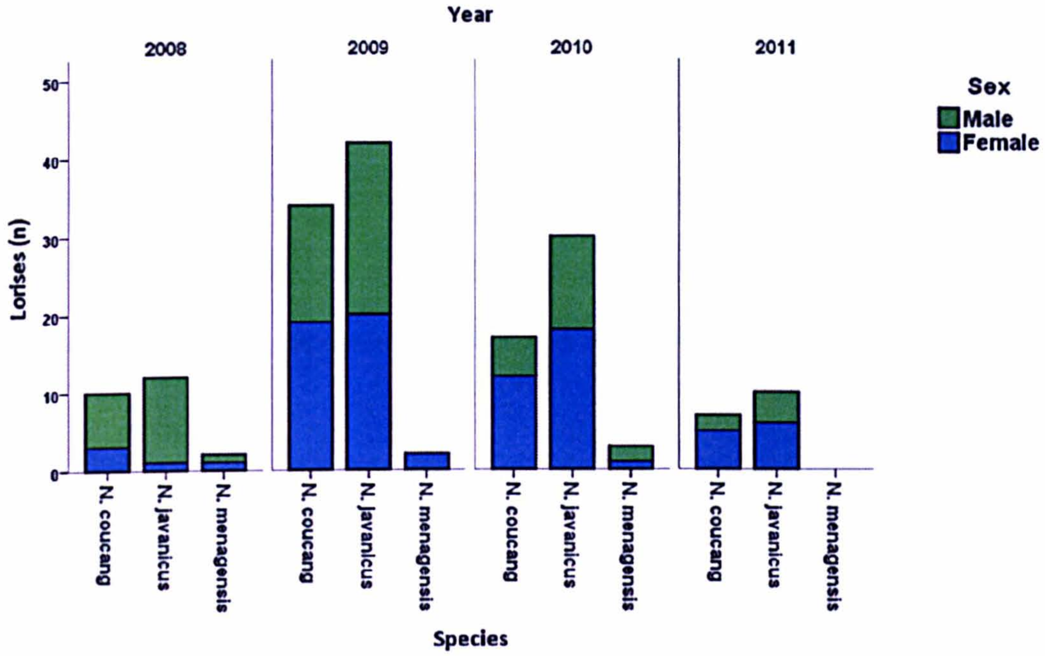

Figure 15. Graph displaying counts of the three slow loris species admitted to IARI over four years, and their respective sex.

Of the ten people who surrendered lorises to IARI, nine reported that they were unaware that the species was slow loris; traders often mislead the purchasers into believing they are buying a similar-looking species called a cuscus (Family: Phalangeridae). Subsequently, these buyers discovered the legal restrictions on keeping lorises on the internet, which prompted them to contact IARI. Prices of lorises bought in the markets ranged from 300,000 to 1,000,000 Indonesian Rupiahs (approximately £21 to £71).

Market traders are known to cut the teeth of lorises, often using pliers, wire cutters or nail clippers, to avoid being bitten when handling the animals. This process can lead to abscesses and severe gum disease, and even death. Reconstructive-endodontic dental work is carried out on the affected lorises where possible, but often removal of the broken teeth is the only option. Approximately 64 % of all lorises received have had their teeth damaged to some degree. 100% of lorises originating from the transit raids associated with BKSDA have their teeth intact, or are only partially cut. No significant differences were found between mortality rates, over the four years since IARI's establishment, and species ($\chi^2 = 0.195$, df = 2, p = 0.91) or origin ($\chi^2 = 3.44$, df = 4, p = 0.49). Females, however, had significantly higher mortality within the first year at IARI than males ($\chi^2 = 6.089$, df = 2, p = 0.05).

3.3.2 Reintroductions

Since April 2010, eleven slow lorises have been included in the systematic IARI R&R programme: ten *N. javanicus* and one *N. coucang* (Table 2). The *N. javanicus* were released into the protected Gunung Halimun-Salak National Park, West Java and the *N. coucang* into the Batutegi Nature Reserve, Lampung, Sumatra. All animals were tracked following release for a minimum period of three months, unless death, sickness or movement into an unsafe area occurred.

Of the eleven slow lorises released, five died. Paloma and Tengah died of unknown causes (owing to the rapid decomposition of the cadavers in the hot and humid forest conditions despite their retrieval after approximately three days). For this reason, post-mortem examinations were not possible; however, no visible signs of predation were observed. Paloma was discovered dead on the ground in a forest clearing, suggesting that she was travelling terrestrially when she died. Tengah was retrieved from the top of a pine tree – approximately 25 m high – his body was sprawled out over horizontal, terminal branches.

Table 2. Details and outcomes of the rehabilitation and reintroduction of eleven slow lorises from International Animal Rescue Centre between 2010 and 2011. The *N. javanicus* were released into the Gunung Halimun-Salak National Park, and the *N. coucang* was released at Batutegi Reserve in Lampung, Sumatra. Wilis and Bromo (*N. javanicus*) are still under observation.

#	Name	Sex	Days in habituation	Date of release	Days survived	Date rescued	Reason for rescue	Date of death	Cause of death	Reason for stopping	Status
1	Paloma	F	5	18.4.10	22	10.5.10	Travel into village				Dead
	Paloma*	F	0	7.6.10	10			17.6.10	Unknown		
2	Tengah	M	5	18.4.10	16			4.5.10	Unknown		Dead
3	Baluran	M	7	21.5.10	61	21.7.10	Visible weakness	14.8.10	*Klebsiella pneumoniae*		Dead
4	Marta	F	7	21.5.10	27	17.6.10	Travel into village				Rescued
5	Silje	F	10	30.8.10	94					Collar irritation	Survival?
6	Moni	F	50	10.11.10	31	11.12.10	Visible infection				Dead
	Moni*	F	9	28.1.11	25			22.2.11	Unknown		
7	Lupe	F	85	25.2.11	12	9.3.11	Visible weakness	30.6.11	Septicaemia		Dead
8	Leuser	M	6	27.4.11	146					Collar battery finished	Survival?
9	Fani	F	4	26.6.11	80					Collar bitten off	Survival?
10	Wilis	M	16	3.5.11	205 +						Survival
11	Bromo	M	104	4.10.11	59 +						Survival

*Paloma and Moni were released again after being recaptured owing to their movement out of the forest into the village.

Baluran died of bacterial sepsis. In post mortem examination septicaemia and military abscesses were found in liver, lungs, spleen and lymph nodes. The bacterial culture from post-mortem lesions resulted on the isolation of *Klebsiella pneumonieae* (samples for diagnostic purposes were sent to "Prodia Laboratorium Klinic", Jakarta. *Klebsiella pneumonieae* is considered an opportunistic pathogen with characteristics that allow circumvention of host defence mechanisms, allowing colonisation and survival in affected organs (Quinn et al. 2011). *Klebsiella pneumonieae* can induce local and systemic changes including inflammatory responses, pyrexia, endothelial damage and microthrombosis. This pathogen is generally found in individuals with a weakened immune system (Quinn et al. 2011) and is reported to be virulent in prosimians (Junge 2003). It is one of the most commonly isolated bacteria in post mortem samples from lorises at IARI facility. Before his rescue, Baluran was observed to be visibly weak and struggling to move; therefore, was captured and brought back to IARI, where he later died despite medical treatment

Lupe was returned to the clinic after release because of weakness and disease. She was considered an old individual. After further attempts to re-release, Lupe was brought back to IARI owing to bad health. She spent a few months back at the centre before she died. Post mortem changes indicated septicaemia. Various bacteria (*Escherichia coli, Enterococcus sp.* and *Pseudomona aeruginosa*) were isolated from samples tested at the "Prodia Laboratorium Klinik".

Moni died of unknown reasons. One of the lesions found at post-mortem macroscopic examination was pulmonary oedema, which is a build-up of abnormal fluids in the abdomen and often caused by low protein in the blood (Mazzaferro 2010). Possible causes of oedema include viral infections, hypersensitivity reactions and septicaemia. Moni was found dead on the forest floor appearing to have fallen from a tree. In the preceding nights, Moni had travelled into an inaccessible steep-sided ravine, and so post-release monitoring was not possible on these days.

Leuser was followed for 147 days before the collar was taken off as the battery was about to finish. After suffering a massive head wound inflicted by a resident loris soon after his release, the wound visibly healed, and Leuser continued to feed and range freely. When the collar was taken off his condition was good.

After their initial release, Paloma and Marta travelled down the mountain out of the forest, through plantations, across roads, and were located deep inside human-habituated areas. As this area was deemed unsafe, owing to the risk of recapture, both were caught and brought back to the centre. After a medical check, Paloma was later released higher up the mountain. Marta spent a longer period of time back in captivity, although is planned to be re-released in a different area.

Silje was followed for 94 days. The collar was due to be replaced, so she was recaptured. Owing to an irritation of the collar around the neck, the collar was removed, checked by IARI vets and she was subsequently released. Until this time, she had been monitored continuously and had been feeding and ranging freely. Fani was monitored for 80 days until her collar was found on the ground. The collar revealed bite marks and appeared to have been chewed off. Two nights earlier, Fani had been observed grooming with a resident loris, so it was assumed this latter loris was responsible for the removal.

Wilis and Bromo are currently under observation. Wilis has been monitored now for 205 days and Bromo for 59. Both are feeding and ranging freely and appear to be well adapted to life in the forest.

3.4 Discussion

Demographic data from IARI reveal a rapid increase in lorises admitted to the centre in the first two years, and then a steep decline in 2010 and 2011. This trend is consistent with the predictions by Nijman (2009) and Teleki (2001) who suggest that there is an initial peak in animals taken in until capacity is reached – in approximately two years - followed by a rapid decline. Indeed, after reaching full capacity, IARI was forced to reduce numbers of lorises being received owing to space restrictions. Mortality was lowest in 2008 with three deaths (14%) and highest in 2010 with 26 (26%). These occurrences can probably be attributed to the lower numbers of animals housed in 2008 compared to successive years. With more lorises housed there is likely to be higher chances of the spreading of parasites and disease (Bernacky et al. 2002). Lorises deriving from transit raids arrived with much better teeth than ones that had already spent time in the markets, suggesting that the teeth clipping procedure occurred during this time. At IARI, 64% of lorises have had their teeth severely or completely cut and are thus unsuitable candidates for reintroduction owing to difficulties feeding on certain harder bodied food items such as gum, small reptiles and large arthropods.

The IARI reintroduction programme is still in its infancy. Despite thorough planning and execution of this programme, whilst adhering to the reintroduction guidelines put forward by the IUCN, the initial results mirror numerous other reintroduction attempts with mixed survival success (Bennett 1992; Britt et al. 2004a; Kleiman et al. 1986; Konstant & Mittermeier 1982; Streicher 2004). Of the eleven lorises released, five died, one was rescued and five are either currently surviving or were surviving when post-release monitoring stopped. Similar proportions of mortalities were recorded during releases of pygmy slow lorises (*N. pygmaeus*) in Vietnam (Streicher & Nadler 2003), where four out of ten died, and in the release of ruffed lemurs (*Varecia variegata variegata*) in Madagascar

(Britt et al. 2004a; Britt et al. 2004b) where eight out of thirteen died. Interestingly, predation was a major cause of mortality in pygmy slow loris (50 %, n = 4) and ruffed lemur (62 %, n =8) releases, which was not a factor in any of the slow loris releases. The causes of death in the slow lorises during the IARI reintroduction programme were presumed to be related to malnutrition, which subsequently weakened immune systems and made them more susceptible disease. Provisions of food were left near to the release cage during the first four releases, however, the lorises quick and unpredictable movement away from the area meant that they never came into contact with food. So far, no significant associations between any of the measures taken to ensure success, and the length of survival in this current study were found, but could merely be due to the small sample size, or factors not included in this analysis such as temperature and altitude, or whether there were sufficient food resources at the release site.

The low success rates in reintroduction programmes are one of the arguments against their usefulness in conservation plans, especially so as these programmes are extremely costly and labour intensive (Bennett 1992; Fischer & Lindenmayer 2000). Without such programmes, the only other options for these animals appear to be a life time in captivity either in zoos, biomedical research facilities or rescue centres, or euthanasia; none of which, from a conservation or welfare related perspective appear particularly beneficial (Beck 2010; Bennett 1992). Indeed, many animals, such as primates, bears (Ursidae), civets (Viverridae), turtles (Testudines) and otters (Lutrinae) currently housed in rescue centres around the world, some of which are threatened (IUCN 2011), could potentially offer the last chance to save these species through captive breeding and reintroduction, once extinct in the wild.

With the IARI rescue centre at full capacity for lorises, of which at least 64% cannot be released owing to dental defects, and with reintroductions yielding mixed success in their preliminary stages, I now discuss the alternatives to the question raised earlier: what is the most viable option regarding both conservation *and* welfare, for the animals that cannot be released (Fig 16).

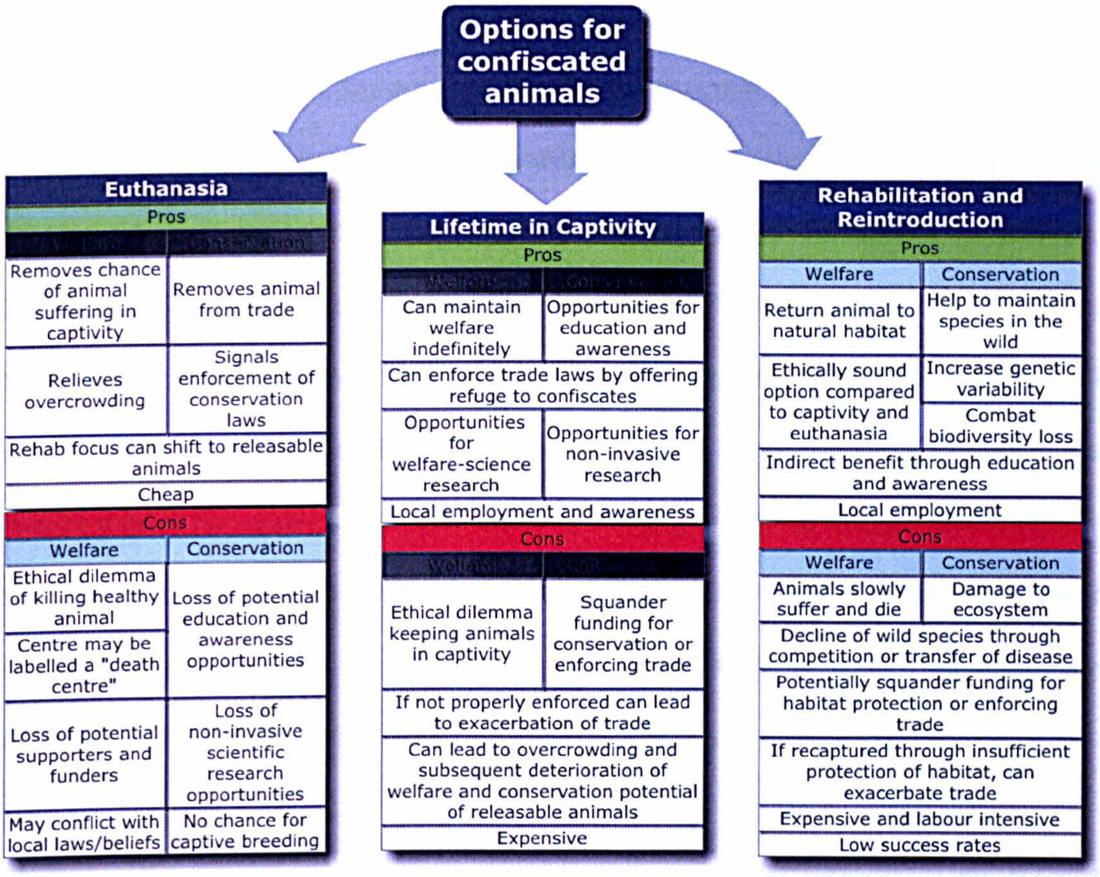

Figure 16. Possible options for confiscated animals highlighting the pros and cons for each

3.4.1 Euthanasia

Euthanasia involves humanely terminating the life of an animal for its own benefit (Broom 2007), and its primary justification is to prevent further suffering. Depending on local attitudes and religions, euthanasia can be met with substantial hostility and is perhaps the most sensitive and controversial option (Ashraf & Menon 2005; Bacon 2008; Bennett 1992; Ware 2001). Local laws can prohibit euthanasia and some religious beliefs deem it inappropriate, both of which have detrimental implications on the welfare of the animal as well as to public safety (Bacon 2008; Ware 2001), for example, when an animal is diagnosed with the zoonotic disease tuberculosis. Wild animals susceptible to tuberculosis include primates, carnivores, small mammals, marsupials, ungulates, cervids and marine mammals (Miller 2008).

Further controversy regarding euthanasia can arise when the rescued animals are threatened with extinction. Some conservationists believe that practising euthanasia limits potential conservation opportunities when using captive animals for restocking dwindling wild populations (Beck 2010; Carter 2003; Harcourt 1987). Euthanasia of animals, Endangered or otherwise, does remove the potential for the animal to be traded further, thus reducing future demand; although this option should perhaps only be considered if all others have been exhausted (Beck 2010; Harcourt 1987). Some contend that euthanasia may be a more favourable option than captivity. Keeping an animal with no chance of ever being released can be deemed as stressful and inhumane, especially for those kept in small crowded cages, in unnatural social organisations, and with no chance to reproduce (Bennett 1992; Rosen & Byers 2002).

Restrictions on conducting euthanasia can also create problems indirectly in the form of overcrowding. A rescue centre at capacity is not a problem in itself if sufficient funds are available to ensure adequate welfare to all the animals. A dilemma arises if other potentially fit and releasable animals must be refused because of lack of space, with vital resources being used on housing and feeding animals that are unable to leave captivity. If the goal of the centre is to rehabilitate animals, overcrowding will only hinder this process (Cheyne 2009).

3.4.2 Captivity

Rescue centres and zoos around the world provide shelter for confiscated animals (Carter 2003; Defler et al. 2003; Russon 2009). In situations where the release of an animal is not possible and euthanasia has been decided inappropriate, housing an animal indefinitely is the only other option. Arguably the main issue in contention is whether housing confiscated animals actually contributes to the trade that was effectively responsible for their initial capture. Trade can be exacerbated when members of the well-meaning, yet naive, public purchase the animal out of pity and then surrender it to a nearby facility (Beck 2010; Farmer & Courage 2008; Harcourt 1987; Karesh 1995). Furthermore, if rescue centres and zoos inadvertently create a humane outlet for the confiscated animals, they potentially reduce pressure on the respective governments to deal with the perpetrators and consequences of the trade, allowing their focus to shift elsewhere (Cuarón 2005; Harcourt 1987; Sumrall 2009).

Enforcement of environmental laws is normally dealt with by the government and the allocation of funds to this cause is often limited (Cuarón 2005), which prompts the question: would available funding for housing confiscated animals be better utilised in the prevention of trade in lieu of dealing with the after effects (Bennett 1992; Cheyne 2009; Ware 2001)? Leighton and Whitten (1984) argue that illegal trade is actually reduced by the establishment of rescue centres, and suggested that as confiscations increase, trade will naturally decline. This supposition is seemingly a consequence of improved efforts by government officials in the confiscation of animals owing to increased space in rescue centres in which to send them (Nijman 2009). In Indonesia, for example, there is an ostensible relationship between rescue centres receiving displaced gibbons and the frequency of confiscations taking place. As rescue centres reach capacity, a reduction in confiscations is observed (Nijman 2009; Nijman et al. 2010). Logically, only when confiscations are backed up sufficiently by local authorities ensuring perpetrators always face legal penalties, can rescue centres help in directly quelling the trade (André et al. 2008; Beck 2010).

Nevertheless, with little supporting evidence, only a tenuous link exists that rescue centres actually exacerbate trade in animals. If all rescue centres closed tomorrow and all captive animals were euthanized, would trade persist? Closing rescue centres would probably not stop animals being hunted and traded for traditional medicine, the biomedical industry or for bush-meat as these animals are killed before transportation. Even in countries where wild animals as pets are an important contributor to trade, such as Indonesia (Shepherd et al. 2004), there is no guarantee that the governments would be forced to take stronger action against trade if animals were not offered refuge. By closing all rescue centres there would be a reduction in outlets for these animals and therefore a reduced future potential for breeding threatened animals if the situation becomes critical (Harcourt 1987); although captive breeding is not without its limitations (cf. Rahbek 1993; Snyder et al. 1996) and should not be used as an excuse to avoid the preservation of habitats (Rahbek 1993). Furthermore, the suffering of animals being traded will be greatly increased, with authorities having to find alternative options for the confiscated animals. Trade and confiscation laws, including the Convention on International Trade in Endangered Species (CITES), may be left redundant without an outlet for the confiscated animals (André et al. 2008; Beck 2010).

3.4.3 Reintroduction

The principal justifications for reintroduction appear to be four-fold: firstly, for the conservation benefits of reintroducing or restocking Endangered populations (MacKinnon & MacKinnon 1991; Seddon 1999; Stanley Price & Soorae 2003); secondly, from a welfare perspective in giving the animals the freedom they deserve (Albrecht 2003; Swaisgood 2010); thirdly, to resolve human-wildlife conflicts (Fischer & Lindenmayer 2000); and finally, a more controversial motive – one strongly discouraged – for reintroducing animals to relieve overcrowding in captivity (Beck 2010; Bennett 1992; IUCN 1998).

Assessing the potential viability of reintroductions has been extensively covered elsewhere (Faria et al. 2010; Fischer & Lindenmayer 2000; Seddon 1999; Stanley Price & Soorae 2003) so will not be discussed here. The fact of the matter is, as long as animals are hunted, displaced or traded there will continue to be animal refugees; and organisations, both conservation and welfare, will continue to conduct reintroductions (Ware 2001). Whilst conservationists see reintroduction as a means of conserving populations, welfare groups see reintroduction as a means to help individual animals have a chance to live wild again (Albrecht 2003; Swaisgood 2010; Wickins-Dražilová 2006). Either way, both parties should be conducting the same procedures to ensure success – whether it be saving a species or saving an individual. The welfare of the animal and the welfare of the ecosystem into which the released animals are entering need to be preserved, best achieved by following the tried and tested protocols for reintroductions (IUCN in prep, 1998). Yet still some groups and individuals choose to ignore these guidelines (Table 3).

The release of an animal back into the wild, one that has been victim of trade and is otherwise faced with a lifetime in captivity, or euthanasia, may appear the ethically correct action to take: giving an animal the chance it deserves to live back in its original habitat or benefitting the species preservation (Albrecht 2003; Wickins-Dražilová 2006). Extreme caution is needed that we are not merely conducting releases for the purpose of our own human gratification (Albrecht 2003). For organisations conducting reintroductions, the

Table 3. Recent loris releases with inadequate monitoring, despite the publication of guidelines that discourage un-prepared reintroductions. These actions can be detrimental to both the welfare of the released animal and to the ecosystem at the release site (adapted from Doughty et al. 2010)

Species	n	Location	Date	Pre-release	Post-release	Source
N. bengalensis	2	Koh Kong, Cambodia	07/07/2008	Uncertain	No	1
N. menagensis	1	Matang, Malaysia	17/05/2009	No	No	3
N. pygmaeus	1	Thanh Hoa, Vietnam	30/05/2011	Uncertain	No	4
N. menagensis	1	Brunei	17/09/2007	No	No	5
N. bengalensis	1	Xishuangbanna Dai, China	29/08/2011	Medical check	No	6
N. bengalensis	1	Meghalaya, India	17/05/2005	No	No	7
N. bengalensis	1	Assam, India	31/12/2005	No	No	8
N. bengalensis	1	Assam, India	26/08/2009	No	2 days	9
N. bengalensis	1	Assam, India	07/02/2001	Medical check	1 week	10
Loris lydekkerianus	1	Chennai, India	13/08/2011	Uncertain	Uncertain	11
N. menagensis	4	Brunei	29/10/2005	Uncertain	uncertain	12
Loris lydekkerianus	1	Karnataka, India	07/02/2011	Medical check	Uncertain	13
N. pygmaeus	1	Da Nang, Vietnam	27/05/2011	Uncertain	Uncertain	14
N. coucang	1	Pala-U, Thailand	18/05/2010	Medical check	No	15
N. pygmaeus	2	Thailand	11/12/2010	Yes	Uncertain	16

difficulties faced are often in the pre-release phases, and on release of an animal can feel a sense of success and fulfilment. For the animal, however, this is where the difficulties and harsh realities start (Yeager & Silver 1999). Released into an unknown habitat the animal is suddenly forced to contend with predators, aggressive conspecifics defending their territories and the finding of sufficient and appropriate food; all of which may lead to a slow and painful death from attacks, starvation, or stress induced diseases (Beck 2010; Yeager & Silver 1999) (Fig 17).

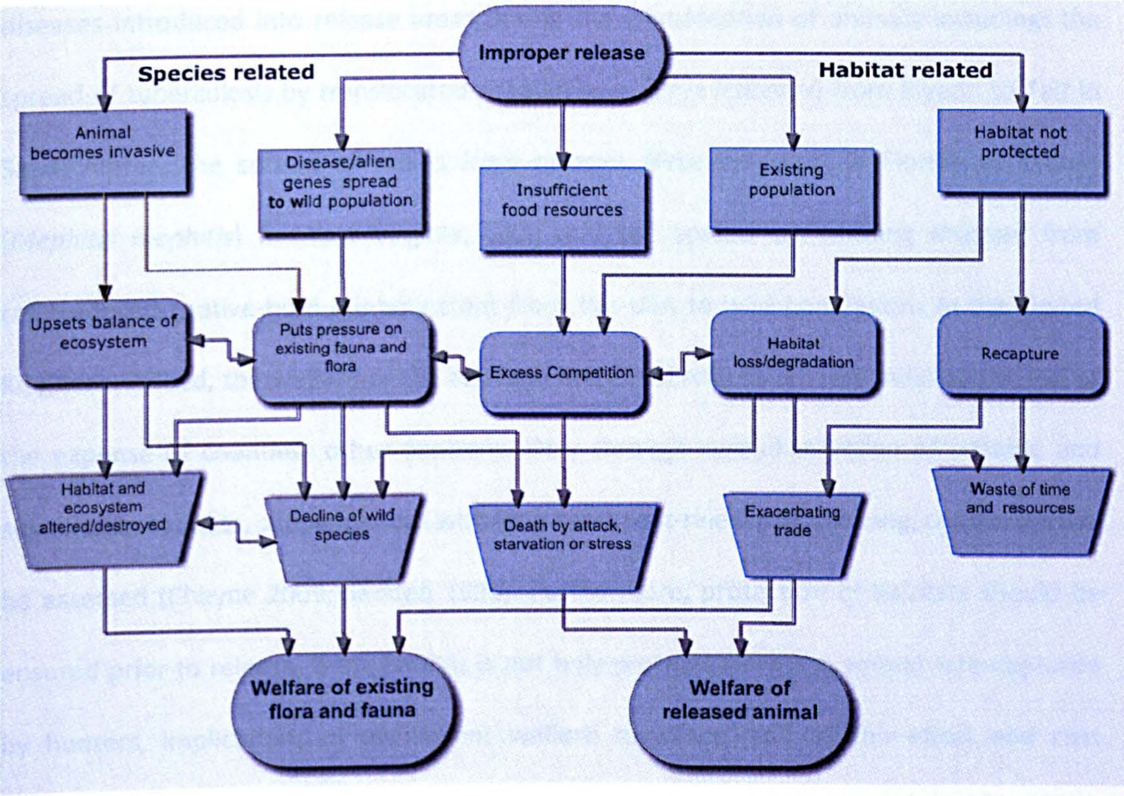

Figure 17. Consequences of improper releases

The advent of the post-release monitoring of animals has allowed such monitoring of survival, and has consistently revealed the occurrence of comparably undesirable fates (Bennett 1992). If we are taking it upon ourselves to give the animal a second chance, we should at least ensure we are providing it with the best fighting chance possible. If the animals released just slowly deteriorate and die, this option is analogous to merely killing them (Harcourt 1987), and perhaps euthanasia is a more humane option.

Further consideration of welfare and conservation implications of the ecosystem at the release site is also necessary. Releasing an animal into an already stable habitat has the latency to disrupt the balance of the ecosystem, and to potentially threaten other species of flora and fauna through competition or transfer of disease (Beck 2010; Burgman et al. 1998; Teleki 2001; Yeager & Silver 1999). Woodford (1993) provides hi-profile examples of diseases introduced into release areas during the translocation of animals including: the spread of tuberculosis by translocated Arabian oryx (*Oryx leucoryx*) from Riyadh to Taif in Saudi Arabia; the spread of rabies from racoons (*Procyon lotor*) in Florida to skunks (*Mephitis mephitis*) in West Virginia, USA; and the spread of 'whirling disease' from reintroduced captive-bred rainbow trout from the USA to wild populations in the United Kingdom. Indeed, the welfare of the released individual may have been maintained, but at the expense of countless other denizens. Only through careful selection of suitable and sustainable habitats, supplemented with long-term post-release monitoring, can these risks be assessed (Cheyne 2009; Seddon 1999). Furthermore, protection of habitats should be ensured prior to release. If the habitat is not fully protected and the animal is re-captured by hunters, implications of insufficient welfare resurface, and all the effort and cost involved in the project are wasted – and the trade is carelessly exacerbated (Wickins-Dražilová 2006).

3.4.4 The situation at IARI

Euthanasia at IARI is currently employed only when an animal is critically sick or injured. Indonesian rehabilitation guidelines state that euthanasia must not be carried out on protected species. Permission may be granted from BKSDA or KKH-PHKA (**Biodiversity**

Conservation Office of the Directorate General of Forest Protection and Nature Conservation) for euthanasia of animals in extreme pain, or with transmissible or incurable diseases, but not to simply alleviate overcrowding (Sanchez, pers. com). Situated in a predominantly Islamic country, the centre generally opts against euthanasia of healthy animals to avoid provoking any negative sensibilities from the local community and any corresponding authorities.

Initially, IARI did not employ a triage system on receiving animals, and thus accepted all slow lorises, either as donations from the public or from government confiscations. With space in captivity now at a premium owing to the large volume of lorises in trade, the centre is forced to regulate its intake. The lorises currently accepted are restricted to individuals free from injury and disease, and ostensibly possessing sufficient health and fitness to be included in the reintroduction programme. Without this regulation, the welfare of the animals already housed may suffer; as too may their rehabilitation potential. Centre veterinarians provide guidelines on the proper care to the owners of those lorises not able to be accepted.

For the lorises presently at the centre with no possibility of ever being released, IARI is faced with the onerous task of finding humane solutions to this situation. The construction of a large, permanent, semi-natural enclosure for the slow lorises is one option being considered. Here the lorises could live indefinitely, being closely monitored and receiving provisions from the centre's staff. The long-term financial costs of this are high, but can be alleviated by income from groups who might use the facility for education and research. Another option is the donation of lorises to other welfare and conservation organisations that have the facilities to house a slow loris humanely, but there is at present a paucity of sufficient space and resources.

Whatever the solution, it is essential that education and awareness are incorporated into the plans. For those lorises destined to live out their lives in captivity, they can at least become ambassadors for the species and their lamentable situation can benefit their conspecifics in the future. Furthermore, the horrors of the trade can be exposed to the world and unsustainable harvesting can be discouraged. Without enlisting these lorises in such a way, this cycle of events may continue indefinitely: captured from the wild, mutilated in the markets, rescued by police and condemned to a lifetime in captivity.

Indeed, much of the work in which IARI are currently involved focuses on education and awareness. The reintroduction programme is no exception. Supplemented with IARI's local and international advertising campaigns, news reports, television documentaries and seminars, the reintroduction programme has worked to promote empathy for the plight of the lorises and also in generating funding. With predominantly local staff involved in the running of both the pre- and post-release phases of the programme, the enhancement of local awareness is an inevitable offshoot. Students from national and international universities have undertaken research on the lorises during the programme and contribute to awareness further afield.

The reintroduction programme is still in its infancy and has yielded mixed results in terms of viability. Undeniably, success in such projects can take time as each species is unique and thus requires an understanding of the relevant factors necessary to augment successful reintroduction. Nevertheless, as such well-meaning, conservation-driven programmes can actually be ecologically detrimental; care and planning are paramount to ensure that this paradox is resolved. The decision by IARI to conduct the releases in a systematic and controlled manner obviates this risk. By adhering to these methods, I believe that rehabilitation and reintroduction can contribute to the overall conservation of this species.

The role that rescue centres can play in welfare, conservation and law enforcement is evident from my study. This role can be greatly enhanced by adhering to a few general guidelines.

- The dissemination of transferable data into the scientific community and to other centres and organisations is vital to the development in the operation of rescue centres, welfare science and reintroduction science.
- Only through the collaboration with other centres, local people, local authorities and governments can the necessary steps be made to ensure the safety and future of many threatened taxa.
- Working with local authorities to ensure that perpetrators of illegal trade are always prosecuted is an important factor in curbing trade; only when harsh and tangible deterrents are present will traders refrain from their lucratively illegal actions.
- Education and awareness play an equally integral role in the abatement of trade, specifically from the buyers' point of view.
- Reintroductions can be a viable method of maintaining both welfare and conservation, but must be conducted responsibly, with due consideration of the potential dangers to the released animals and the ecosystem.

4. Captive welfare and the occurrence of stereotypic behaviours

4.1 Introduction

The illegal wildlife trade in South-east Asia poses a serious threat to many species (Lee et al. 2005; Sodhi et al. 2010; Wagener 2001). Seizures by enforcement officials from hunters and traders ensure a steady flow of wild animals being admitted into the numerous rescue centres throughout the region (Cheyne 2009; Nijman et al. 2010). During their period in the trade, and subsequently, on reaching captivity, these wild, confiscated animals are subjected to environments radically different from those which they would normally occupy (Nekaris et al. 2009). In order to adapt to confinement, certain changes in the animal's behavioural repertoire are inevitable (Hogan & Tribe 2007; Mallapur & Choudhury 2003). Indeed, drastically different environments, such as those encountered in captivity, can trigger the manifestation of certain novel behaviours never displayed in the wild (Carlstead 1998; Pazol & Bloomsmith 1993).

In captivity, frustration or boredom in animals often develops because of inadequate space, unnatural or deprived social situations, inappropriate or scheduled feeding, excessive disturbance and lack of stimulation (Mason 1991; Shyne 2006; Trollope 1977). Frustration can lead to stress-related behaviours such as abnormal aggression, overgrooming, appetitive behaviours, inappropriate social interactions and stereotypic behaviours (Novak et al. 2006; Tarou et al. 2005). Stereotypic behaviours are described as behaviours that are repetitive and invariant in form, with no apparent function, for example, pacing, rocking and somersaulting, and can vary considerably between species (Carlstead 1996; Novak et al. 2006; Ridley & Baker 1982). Occurrence of stereotypic behaviours are high in captivity but are rarely observed in wild free-ranging animals (Carlstead 1998; Hogan & Tribe 2007).

Previously, most studies of stereotypic behaviours focused on domestic and laboratory animals (Lawrence & Rushen 1993); however, this last decade has seen attention turn to studies of wild animals held in captivity (Rushen & Mason 2006). Rescue centres are a fairly recent phenomenon and may differ from other captive institutions as many wild animals arrive with mental and physical defects owing to the insufficient care and housing conditions in trade (Cheyne 2006; Duy et al. 2010; Nekaris et al. 2009).

A myriad of studies have focused on primates and their adaptive abilities in captive situations (Finlay & Maple 1986), yet few featured strepsirrhine primates (Tarou et al. 2005). In a primate survey of 108 zoos, Bollen and Novak (2000) found approximately 7% of all individual strepsirrhines exhibited stereotypies. More recently, Tarou et al. (2005) reported that 13.2% of strepsirrhines (n = 440) displayed stereotypic behaviour across 48 captive institutions, and within the genus *Nycticebus* two out of the 13 individuals sampled displayed stereotypies.

The prevalence of *Nycticebus* in trade allows for the first study of the response of a large sample of wild slow lorises to a captive environment, and to use statistical models to predict when stereotypies are more likely to develop and in what setting (Swaisgood & Shepherdson 2005). I focus on three Indonesian loris species *N. javanicus, N. coucang and N. menagensis* housed at IARI.

Little is known about the ecology and behaviour of slow lorises (Genus: *Nycticebus*) in the wild with only few studies to date (Barrett 1984; Starr et al. 2011; Swapna et al. 2010; Wiens 2002). Information yielded from these and studies of slender lorises (Genus: *Loris*) in Sri Lanka and India indicates that within the Order Primates lorises have relatively large home ranges for their body size (0.1 – 2.5 kg) of up to 35 ha (Nekaris 2003; Nekaris &

Bearder 2011; Wiens & Zitzmann 2003b; Wiens et al. 2006), spend large percentage of their activity budget engaged in active behaviours (e.g. forage and travel is 77% ± 12, n = 4) (Nekaris 2001; Nekaris 2003; Nekaris et al. 2005; Wiens 2002; Wiens & Zitzmann 2003b), and can travel over 300 m per night (Bearder et al. 2006; Kar Gupta 2007). Comparisons of primate body sizes and home ranges are covered elsewhere (cf. Harvey & Clutton-Brock 1981; Milton & May 1976), but generally reveal a positive association between body size and home range size. Although not always the case, many primate species with home range sizes less than that of lorises ($\leq$ 35 ha) possess substantially larger body sizes, including: *Presbytis obscura* (6.6 kg), *Symphalangus syndactylus* (10.8 kg) and *Macaca fascicularis* (5.9 kg) (Campbell et al. 2011; Harvey & Clutton-Brock 1981). Despite previously being labelled as predominantly solitary animals (Bearder 1987; Charles-Dominique 1977), researchers have revealed regular social encounters between lorises, with sleeping groups of up to seven individuals (Nekaris 2006; Nekaris 2003; Wiens & Zitzmann 2003b), and substantial overlapping of territories; however, rarely between adults of the same sex (Wiens & Zitzmann 2003b). The diet of lorises is varied and comprises plant sap and gum, floral nectar and flowers, fruits, and animal prey (Nekaris 2005; Wiens et al. 2006). If Indonesian lorises are at all akin to their closest relatives in terms of behaviour and sociality, the constraints of captivity are potentially likely to elicit adverse behaviours, especially when considering such a wide-ranging, highly-active and social nocturnal primate (Clubb & Mason 2003a; Hosey 2005; Mallapur 2005). The process of removing slow loris' teeth by traders to avoid being bitten (Nekaris et al. 2009) may have ramifications on their ability to access preferred foods.

Based on the ecological data available I predict higher incidences of stereotypies in slow lorises housed in the smallest cages; in social groups with sex composition most dissimilar to that seen in the wild; and in social groups with number of conspecifics most dissimilar to that seen in the wild. I relate these conditions to length of time in captivity, teeth condition, and place of origin. Isolating the causes of stereotypies could have important implications for the welfare of these taxa and for developing protocols for their reintroduction. I also foresee parallel implications for other taxa impacted by the pet trade – those with relatively small body size, large home ranges and complex social behaviour, yet are confined in restricted spaced in rescue centres.

4.2 Materials and Methods

See chapter 2

2.2.4 – Obtaining demographic data

2.2.5 – Observations of stereotypies

2.2.9 – Statistics

4.3 Results

4.3.1 Demographic data

IARI has been receiving slow lorises since September 2008, with 18 of the studied lorises arriving in 2008, 38 in 2009, and 34 in 2010. Mean cage sizes for the three species were 62 m^3 (SD ± 65) for *N. coucang*, 26 m^3 (SD ± 16) for *N. javanicus* and 13 m^3 (SD ± 12) for *N. menagensis* (Table 4). Mean cage area per individual loris was $8m^3$ (SD ± 4) in *N. javanicus*, $16m^3$ (SD ± 25) in *N. coucang* and $3m^3$ (SD ± 3) in *N. menagensis*. IARI houses all species separately and group compositions consisted of: lorises kept singularly (13.3%), with the same sex (18.9%) or in mixed sex enclosures (67.8%) (Table 5). IARI kept lorises in group sizes ranging from 1 – 9 individuals, with group sizes as follows: 1 – 3 individuals (53%), 4 – 6 individuals (29%), and more than 6 (17%). Though all lorises were rescued from the pet trade, their origins varied: 47% derived from government holding facilities after police raids on traders in animal markets; 34% were surrendered by pet owners after discovering the illegal position of keeping them; 18% were seized in transit to animal markets; only 1% was captive bred from a loris pregnant on arrival. Origins before seizure in transit or placement in government holding facilities, along with total duration in trade, were not available. 80% of the lorises arrived with their teeth damaged or removed.

Table 4. Survey results for intrinsic and extrinsic factors chosen as possible predictors of stereotypic behaviour.

Species	n	Sex		Origin (%)				Years at centre (%)		
		M	F	Market	Pet owner	Transit	Captive bred	<1	1-2	2-3
N. coucang	42	50	50	57.1	28.6	11.9	2.4	33.2	47.6	19.2
N. javanicus	41	46	54	31.7	41.5	26.8	0	41.5	39	19.5
N. menagensis	7	57	43	71	29	0	0	42.9	28.6	28.5

Table 5. Survey results for more extrinsic predictors of stereotypic behaviour, together with percentages of stereotypies recorded in each species

Species	Mean cage size (m)	Cage composition (%)			Teeth damage (%)	Stereo (%)	Type of stereotypies (%)		
		Single	Mix	Same			Pace	Rock	Circle
N. coucang	62 ±65	14.3	64.3	21.4	74	31	77	8	15
N. javanicus	26 ±16	14.6	65.9	19.5	83	34	79	21	0
N. menagensis	13 ±12	0	100	0	100	43	66	34	0

4.3.2 Description of observed stereotypic behaviours

Regarding stereotypic animals per cage, 13% of cages revealed all animals engaging in stereotypies, 53% of cages had some individuals displaying stereotypies, and 44% had none. Of the 90 lorises observed 33% displayed at least one form of stereotypic behaviour and 6.6% displayed two, no lorises displayed all three. Pacing was significantly more prevalent (76.7%), followed by head rocking (16.7%) and circling (6.7%) ($\chi^2 = 25.8$, df = 2, $p \leq 0.001$).

No significant difference was found between species and the frequency of stereotypic behaviour observed ($\chi^2 = 0.401$, *df* = 2, *p* = 0.819), or between sex and frequency ($\chi^2 = 0.022$, $df_{\text{Yates}} = 1$, *p* = 0.881). Variance of stereotypic behavioural type across species was also not significantly different ($\chi^2 = 3.51$, *df* = 2, *p* = 0.173).

4.3.3 Predictors of stereotypies

I ran a binary stepwise logistic regression analysis using the stepwise "Forward Wald" method to assess the difference each dependent variable had on the predictability of the presence or absence of stereotypic behaviour between individuals. As I found multi-collinearity between number of lorises per cage and cage size (*r* = 0.587), I removed cage size and replaced it with the variable "lorises per cubic metre" by dividing cage size by number of lorises per cage. The overall model produced was statistically significant (χ^2 = 9.797, *df* = 3, *p* = 0.007) after step 1, and became increasingly significant after step 2 (χ^2 = 14.138, *df* = 3, *p* = 0.003). Hosmer and Lemeshow values implied the model was a good fit (step 1: *p* = 1; step 2: *p* = 0.16), with a Nagelkerke R^2 value of 0.279. The model predicted 71.1% of the values correctly.

Table 6. Logistic regression analysis of stereotypic behaviours as a function of extrinsic variables. Only time at the centre and cage groupings were significant

Variables	Wald/score	*df*	*P*
Cage composition	8.156	2	0.02
Number of conspecifics	3.701	1	0.05
Sex	0.018	1	0.89
Species	0.440	2	0.80
Origin type	1.263	3	0.74
Length of time at centre	1.873	2	0.39
Lorises per cubic metre	0.071	1	0.79
Teeth cut	0.039	1	0.84

Cage composition (p = 0.02) and number of conspecifics (p = 0.05) were the only two variables showing significance (Table 6). The model revealed that 14% of the variability explained in the dependent variable was influenced by cage groupings in step one, and 20% by cage groupings and number of conspecifics together in step two. Within the variable cage groupings, single and mixed sex groupings (Wald = 4.430, df = 1, p = 0.030) had a more significant influence on stereotypies than same sex groups (Wald = 2.624, df = 1, p = 0.100). A negative correlation was found between number of conspecifics and stereotypic behaviour (r = -0.254, p = 0.016) suggesting that as group size increased the presence of stereotypies decreased.

4.4 Discussion

At IARI 33% of the lorises housed at the centre displayed stereotypic behaviour. This figure is almost double that of the findings by Tarou et al. (2005) who reported that 15.4% of individual *Nycticebus* (n = 13), and 13% of all prosimians in the captive surveys exhibited stereotypies. Owing to the difficulties in captive breeding lorises (Izard et al. 1988; Welker & Welker 1989) and the persistently high numbers in trade (Shepherd et al. 2004), the lorises at IARI are undoubtedly wild caught animals. Captivity generally poses greater challenges to wild caught than to captive-bred individuals (Honess & Marin 2006), and consequently, could also be a causal factor in the higher levels of stereotypic behaviours in my study.

Pacing was the most prevalent form of stereotypy observed in my study (cf. Swaisgood & Shepherdson 2005; Tarou et al. 2005). A primary contributor to stress in captivity is the effect of restricted movement and confinement in small spaces (Clubb & Mason 2003a). Other authors have found positive correlations between home range size and stereotypies, particularly pacing, indicating a potential link between enclosure size and the animal's natural history (Clubb & Mason 2003a; Clubb & Mason 2003b; Clubb & Mason 2007; Lutz et al. 2003; Mason 1991). As Lorises have relatively large home ranges with regards to their body size for primates and can travel long distances in a night, I predicted small cage size would increase the occurrence of stereotypies. The results from the logistic regression analysis were not consistent with this prediction. Only 13% of enclosures revealed all animals engaging in stereotypies whereas in 44% of enclosures no animals engaged in them. If environmental factors such as cage size affect the prevalence of stereotypies (cf. Tarou et al. 2005), they only do for a proportion of individuals. Even moving an animal to a larger cage may have little to no effect on occurrence of stereotypies (Kaufman et al. 2004; Line et al. 1990).

When a loris engaged in pacing and rocking, it usually occurred along a cage side with a view outside. Vickery and Mason (2004) reported similar behaviour in Asiatic black bears (*Ursus thibetanus*) and suggested three possible reasons for this: a representation of territorial patrolling; to provoke interactions from nearby conspecifics; or simply as it offered the greatest sensory stimulation. In my study, the same rationale could apply: lorises actively defend home range boundaries so this behaviour represents a form of patrol; enclosures are in close proximity, so lorises may be signalling to others; or the view outside the cages, even if not to interact with other lorises, may provide the best sensory stimulation. Further experimental scenarios in the centre would need to be implemented to explore these hypotheses further.

The intrinsic variable sex was not found to be a significant predictor of stereotypies (Tarou et al. 2005), contrary to the findings of Lutz et al. (2003) and Hogan and Tribe (2007) where male animals displayed more stereotypic behaviour than females. Tarou et al. (2005)

reported the intrinsic variable genus to be a significant predictor of stereotypic behaviour. Whilst all animals in my study were of the same genus, I found no significant difference between species. Even closely-related species can, however, vary in the amount of stereotypic behaviour displayed (Mason 2010), and suggests a possible genetic disposition, as documented in other species (Schoenecker & Heller 2000; Schwaibold & Pillay 2001).

I predicted that certain extrinsic factors would influence the presence of stereotypies (Bashaw et al. 2001; Mallapur 2005; Tarou et al. 2005). Results from the logistic regression analysis revealed that cage composition along with number of conspecifics were significant predictors of stereotypies. Furthermore, lorises were less likely to display stereotypies in same sex cages, compared to mixed sex or in solitary cages, and solitary lorises had the highest occurrence of stereotypies. Indeed, as numbers of conspecifics decreased so did the presence of stereotypies.

Unnatural social groupings of animals in captivity are also a known source of stress (Morgan & Tromborg 2007; Stoinski et al. 2001). Sexual dimorphism in slow lorises and bite wounds found on many wild caught males imply an active defence of territories and/or contest competition (Wiens & Zitzmann 2003b). The sex of conspecifics in close proximity, therefore, could potentially affect the animals' well-being owing to an inability to escape from situations of conflict (Morgan & Tromborg 2007). Animals kept in social groups not usually occurring in the wild often show signs of social tension, reduced natural activity and stereotypic behaviour (Mallapur 2005; Morgan & Tromborg 2007). My findings regarding the low occurrence of stereotypies in same sex groups, therefore, is perhaps surprising owing to the natural social organisation of wild loris populations, where it is rare for adult ranges of the same sex to overlap (Wiens & Zitzmann 2003b). In same sex social groupings at IARI, however, there is perhaps less necessity for sexual competition or the need to assert dominance over same sex rivals. Moreover, where food availability is not limited and predators are lacking, resource conflicts and territorial defence are unnecessary. With less social tension and therefore potentially less stress, the manifestation of stereotypies may be less likely to occur. Animals keepers at IARI will move animals if repeated incidents of severe aggression occur, and strive to maintain group harmony. Irrespective of the difference from the social groupings in the wild, the results presented here would suggest same sex groups could promote less stereotypic behaviours.

The number of conspecifics in each cage was negatively associated with occurrence of stereotypies. Although previously assumed to be predominantly solitary, recent reports have shown that lorises can sleep in social groups of up to eight individuals (Nekaris 2006; Nekaris 2003; Wiens & Zitzmann 2003b), which may suggest why lorises were less likely to display stereotypies in groups of up to nine individuals. Indeed, for many species, isolation in captivity can be stressful (Mason 1991; Morgan & Tromborg 2007). As lorises maintain regular social contact with conspecifics in the wild, effective solitary confinement is likely to have adverse effects on their well-being, and consequently, could trigger the onset of stereotypies. Not all solitary lorises exhibited stereotypies, however, indicating that other factors may be influencing this behaviour.

As stereotypies are often (but not always) used as a measure of welfare in captive environments (Broom 1983; Mason & Latham 2004), the high incidence at IARI is potentially a cause for concern. As IARI maintains high levels of animal welfare in the form of natural enrichment and diet, close monitoring of health, and limited human contact, loris welfare would not appear to be compromised. The lack of significant relationships between cage size and occurrence of stereotypies corroborates this supposition. Caution is necessary when linking welfare to stereotypies as a wide range of influencing factors have been associated with this behavioural mode other than the animals current welfare conditions (Beringer et al. 1996; Hogan et al. 2010). For example, the origin of an animal can affect its welfare in captivity (Honess & Wolfensohn 2010). As IARI is a housing facility for wild animals rescued from trade, the high numbers of animals displaying stereotypies could be the result of previous experiences in suboptimal environments (Cheyne 2006; Duy et al. 2010; Swaisgood & Shepherdson 2005). Although my findings do not suggest a significant association between origin and stereotypies, I cannot rule this out. Data pertaining to exact origin previous to confiscation was not available, however, and therefore analyses could not incorporate total time spent in the markets or how well the animals had been treated previously.

My study assessed the prevalence of stereotypic behaviour in captive Indonesian slow lorises at IARI. I described the behaviours witnessed and attempted to predict the occurrence of stereotypies. I found sex composition and time at centre to be associated with stereotypic behaviour, although not in all cases. Many factors were not controlled in this study, which I recommend future studies should address. The association between stereotypic behaviour and extrinsic variables is complex and a combination of numerous interconnecting factors could influence them, rather than a one-to-one relationship (Mason & Mendl 1993; Mason 1991; Mason & Latham 2004). Even a genetic disposition to stereotypies is observed in some animals (Schoenecker & Heller 2000; Schwaibold & Pillay 2001), which may explain the discrepancies here. Uncovering the causes behind the manifestation of stereotypies is of vital importance to welfare in captivity, the rehabilitation process and survival in the wild of reintroduced slow lorises. Findings from such studies may also benefit other little known, small bodied carnivores commonly found in rescue centres, for example, binutrongs (*Arctictis binturong*), leopard cats (*Prionailurus bengalensis*) and Asian small-clawed otters (*Aonyx cinerea*). These taxa are also relatively understudied in the wild and are not common in zoos (IUCN, 2011). With little information on adequate captive care for these taxa, information yielded from this study of lorises may instigate a revision of captive management practices.

5. Ecology of reintroduced Javan slow lorises with evolutionary implications

5.1 Introduction

Nectar, a product of angiosperms, or flowering plants, is consumed by several species of non-flying mammal including marsupials, rodents and primates (Carthew & Goldingay 1997; Janson et al. 1981; Johnson et al. 2001). Nectar is a resource high in sugar, water, and to a lesser extent, amino acids (Baker et al. 1998; Lüttge 1977), and provides an important food source and possible water supply to many species, especially in habitats characterised by distinct seasonality (Ferrari & Strier 1992; Garber 1988; Goldingay 1990; Johnson et al. 2001; Nicolson 2007; Smith 1982).

Accumulating evidence provides support for the theory, first proposed by Porsch (1934), that non-flying mammals can play an active role in pollination of angiosperm plants whilst feeding on plant products (Carthew & Goldingay 1997; Cunningham 1991). For successful pollination to take place pollen has to be transferred by the animal from one flower, to the stigma of another, preferably during a non-destructive feeding bout (Carthew & Goldingay 1997; Johnson et al. 2001). Unfortunately, obtaining evidence of this process is notoriously difficult, which is subsequently hindered by the fact that many of the species involved are nocturnal and cryptic (Carthew 1994; Kress et al. 1994).

In a review by Carthew and Goldingay (1997), 59 species of non-flying mammals were observed to regularly visit flowers, 28 of which were primates. Of the primate species associated with nectar feeding, as opposed to directly consuming flowers, small-bodied primates predominated (Carthew & Goldingay 1997; Ferrari & Strier 1992). The high energy, yet often patchily distributed, nectar supplies probably favour smaller-bodied primates, which benefit from high energy and easily digestible food resources, owing to their comparatively high metabolic rate (Ferrari & Strier 1992; Isbell 1998; Martin et al. 2007).

Amongst small-bodied strepsirrhine primates, numerous lemuriformes are at least partially nectarivorous (See Gould et al. 2011; Sussman & Raven 1978), an adaptation that has been linked with potential pollination of angiosperms (Kress 1993; Kress et al. 1994; Overdorff 1992; Sussman & Raven 1978). In comparison, within the lorisformes, only *Sciurocheirus gabonensis* (Charles-Dominique 1977), *Nycticebus coucang coucang* (Wiens 2002; Wiens et al. 2006) and *N. bengalensis* (Swapna 2008) are currently recognised as partially nectarivorous. Only *N. c. coucang* in Malaysia had a considerable proportion of nectar in its diet, which made up 31.7% of total feeding time (Wiens 2002; Wiens et al. 2006). Studies of lemuriformes, however, are substantially more ubiquitous than those of lorisiformes, with only nine detailed studies of lorisiform feeding ecology to date. This paucity of studies, therefore, may be an influencing factor in the fewer records of nectarivory in this suborder (Nekaris & Bearder 2011). Indeed, evidence from recent studies of an unnamed taxon of galago in southeastern Tanzania suggests nectar consumption is regular, as does recent data from *N. pygmeaus* in Cambodia (Nekaris & Bearder 2011).

Lorisine and perodicticine primates (lorises and pottos) are known for their characteristic slow, deliberate mode of locomotion and inability to leap (Charles-Dominique 1977; Ishida et al. 1992; Miller 1943). Instead of leaping, lorises and pottos use their long bodies and flexible limbs to stretch across canopy gaps in a manoeuvre known as cantilevering (Nekaris & Bearder 2011). Lorises and pottos exhibit a wide range of postural modes including quadrupedalism on horizontal substrates, and multiplane spinal movements and antipronograde postures during more acrobatic behaviours like climbing, cantilevering and suspensory activities (Charles-Dominique 1977; Nekaris 2001, 2005; Stern 1975). This array of locomotor capabilities in lorises and pottos are made possible by certain specialised morphological adaptations. These include relatively long limbs and transversely oriented lumbar zygapophyses for bridging, climbing and reaching and *retia mirabilia* of the limb vessels and shortened second digits in the hands and feet for grasping (Bishop 1962; Rasmussen & Nekaris 1998; Shapiro 2007).

Within the Order Primates arboreality, particularly in the fine branch niche, and foraging amongst angiosperms, is associated with a number of hotly debated theories regarding primate origins (Rasmussen 1990; Sussman 1991). The earliest fossil evidence for euprimates comes from the early Eocene period, approximately 55 million years ago (Martin et al. 2007; Soligo & Martin 2006). Whilst interpretations of behaviour based on morphology of euprimates differ, the general consensus is that they were nocturnal, undergoing a transition from reliance on olfaction to vision with increasingly enhanced stereoscopy (Cartmill 1992; Martin 1990; Martin & Ross 2005; Ross et al. 2006); although some authors argue that they were diurnal or cathemeral (Ni et al. 2004; Tan & Li 1999; Tan et al. 2005). Nevertheless, they were adapted to foraging in the terminal branches of trees, with fossil postcrania implying a shift toward manipulative abilities such as grasping hands, utilising their opposable halluxes and nails replacing claws (Cartmill 1992; Martin 1990; Sargis 2001). Stereoscopic vision and ability to grasp are two key features purported to distinguish the primate order from other eutherian mammals (Le Gros Clark 1959; Martin 1990).

These primate-like features were initially thought to be adaptations to a life of arboreality (Le Gros Clark 1959). More recently, however, morphological studies on other tree-dwelling mammals often revealed an absence of these characteristics, and suggest whilst arboreality was certainly a factor, alternative selection pressures prompted their manifestation (Cartmill 1972; Lemelin 1999; Sussman 1974; 1991). Cartmill's (1972) 'Visual Predation Hypothesis' proposed that euprimate traits were adaptations to the capture of insects, primarily through vision, in the terminal branch niche. He identified that grasping hands are advantageous to habitual foragers in terminal branches, allowing food item manipulation whilst in suspension, and that orbital convergence is a common characteristic in predatory animals that rely on vision to locate prey.

Sussman and Raven (1978) and Sussman (1991) in their 'Angiosperm Co-evolution Hypothesis' postulated that euprimates, analogous to some extant to the nectar-feeding prosimians, were adapted to a period spent foraging in amongst angiosperms, which were reputed to have emerged around the same time from the Eocene period onwards. The radiation of angiosperms provided a wealth of small food items such as flowers, nectar, pollen and fruits, which also attracted insects for the coevolving euprimates that were beginning to utilise grasping hands, with or without stereoscopic vision, to exploit this new niche.

Rasmussen (1990) suspected that the characteristics, grasping hands and nails replacing claws, were the initial adaptations to foraging angiosperm products in the terminal branch milieu, and that stereoscopy evolved as adaptations to hunting live prey in this environment, where reliance on hearing or smell may not have been effective in the fine flexible branches. Rasmussen (1990) believed that the two previous hypotheses were not mutually exclusive and were likely to influence each other as a driving force for evolution.

Here I investigate further the notion of potential non-flying mammals as pollinators, and consider the role that terminal branch feeding in primates has shaped their evolution. With a paucity of data on lorisiformes to date, I focus on feeding and positional behaviour of six rehabilitated and reintroduced Javan slow lorises (*N. javanicus*). I investigate the amount of floral nectar in their diet in the Gunung-Halimun Salak National Park, West Java, Indonesia. I assess the position and movements of the Javan slow loris in the fine branch milieu in relation to its feeding behaviour and relate this to the known hypotheses regarding primate evolution.

5.2 Methods

See chapter 2

2.2.2 – Radio tracking

2.2.3 – Ecological data collection

2.2.9 - Statistics

5.3 Results

I collected 386 hours of data over 101 days. I witnessed 897 feeding observations during the focal instantaneous point sampling. The percentage of each food type consumed was: flowers (nectar and pollen) 89.97%; animal prey, 4.46%; fruit 3.32 %; and exudates 2.34% (Table 7). Lorises consumed floral parts significantly more than other food groups ($\chi^2 = 1952.08$, df = 3, p = ≤ 0.001), and amongst the flower species, *Calliandra calothyrsus* was the preferred food item consumed ($\chi^2 = 1903.53$, df = 3, $p \leq 0.001$). Foraging on flowers was significantly more common in terminal branches ($\chi^2 = 477.563$, df = 2, $p \leq 0.001$) and comprised 66% of incidences. When all feeding incidences are considered, foraging in terminal branches was also significantly more common ($\chi^2 = 788.40$, df = 3, $p \leq 0.001$), making up 60% of incidences. Foraging on small branches comprised 33%, on medium branches 6% and on the trunk 1% (Fig 18). Lorises were exclusively arboreal foragers, only coming to ground occasionally in order to travel when canopy cover was lacking.

During bouts of flower feeding, lorises would systematically move around the whole tree visiting every flower, using primarily vision to identify their next floral candidate. Scent was used when approaching the flower, but seemingly only after the loris had already located it visually. On sighting a flower, the loris would proceed to move quickly towards that flower.

Table 7. Breakdown of food items consumed by lorises during the focal animal scans (n = 897).

Food item/ species	Sundanese name	Family	n	Within Group Percent	Overall Percent
Flower (n = 807)					
Calliandra calothyrsus	Kaliandra	Fabaceae	652	80.79	
Plectocomia elongata	Bu buay	Arecaceae	91	11.28	
Cecropia peltata		Moraceae	52	6.44	
Piper aduncum	Seuseureuhan	Piperaceae	8	0.99	
Caryota rumphiana	Suwangkung	Arecaceae	4	0.50	**89.97**
Animal Prey (n = 40)*					
Lepidoptera	Kupu-kupu		8	20.00	
Hymenoptera	Semut		5	12.50	
Unidentified			27	67.50	**4.46**
Fruit (n = 29)					
Bellucia axinanthera	Jambu Tangkalak	Melastomataceae	6	20.69	
Dissochaeta gracillis	Ki Korong	Melastomataceae	11	37.93	
Villebrunea rubescens	Ki Nangsi	Urticaceae	10	34.48	
Maesopsis eminii	Kayu Afrika Manii	Rhamnaceae	2	6.90	**3.23**
Exudates (n = 21)					
Angiopteris evecta		Marattiaceae	12	57.14	
Paraserianthes falcataria	Jeungjing	Fabaceae	3	14.29	
Pinanga coronata	Bingbin	Arecaceae	5	23.81	
Unidentified			1	4.76	**2.34**

* Animal prey was identified to ordinal level where possible

If no direct route was available, the loris would move back towards the tree trunk into the sturdier branches, locate the branch the flower was on, and then move out into the terminal branches again to feed. When feeding on flower parts, one hand was used to manipulate the stem or flower in 53% of incidences, two hands were used 38% of incidences and just orally 9% (n = 797). Lorises engaged in significantly more suspensory

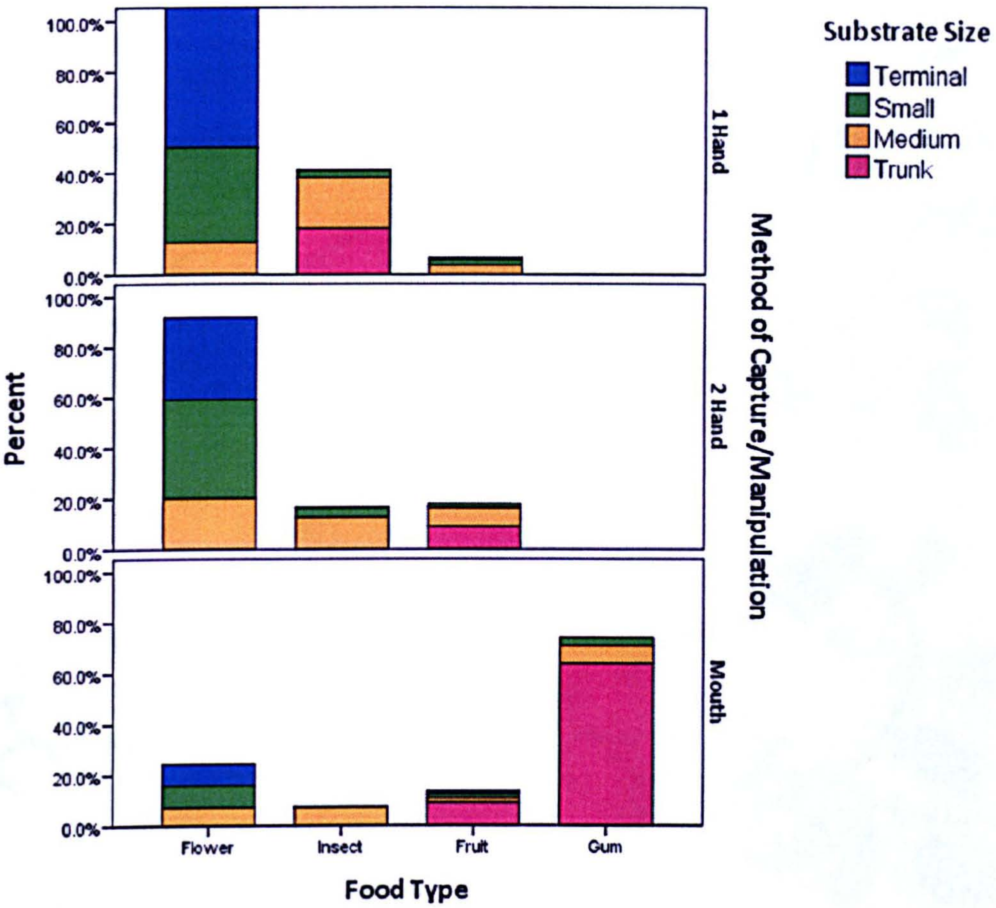

Figure 18. Bar chart displaying percentages of the four different substrate sizes utilised by lorises whilst obtaining different food types in relation to the method of capture employed.

positions whilst flower feeding ($\chi^2 = 29.95$, $df_{Yates} = 1$, $p \leq 0.001$), and also when considering all feeding incidences combined ($\chi^2 = 31.09$, $df_{Yates} = 1$, $p \leq 0.001$). The trunk was never used during flower consumption. For flowers located on terminal branches out of immediate reach, the loris was observed to grab the stem with one hand, pull it in, and then walk its hands up the stem until the flower was close enough to reach with the mouth (Fig 19).

A similar action involving manipulation of terminal branches was observed whilst bridging gaps between flower trees and has also been reported by Charles-Dominique (1977) in pottos and Nekaris (2001) in slender lorises. Lorises are unable to leap, however on numerous occasions when a break in canopy was encountered this particular bridging

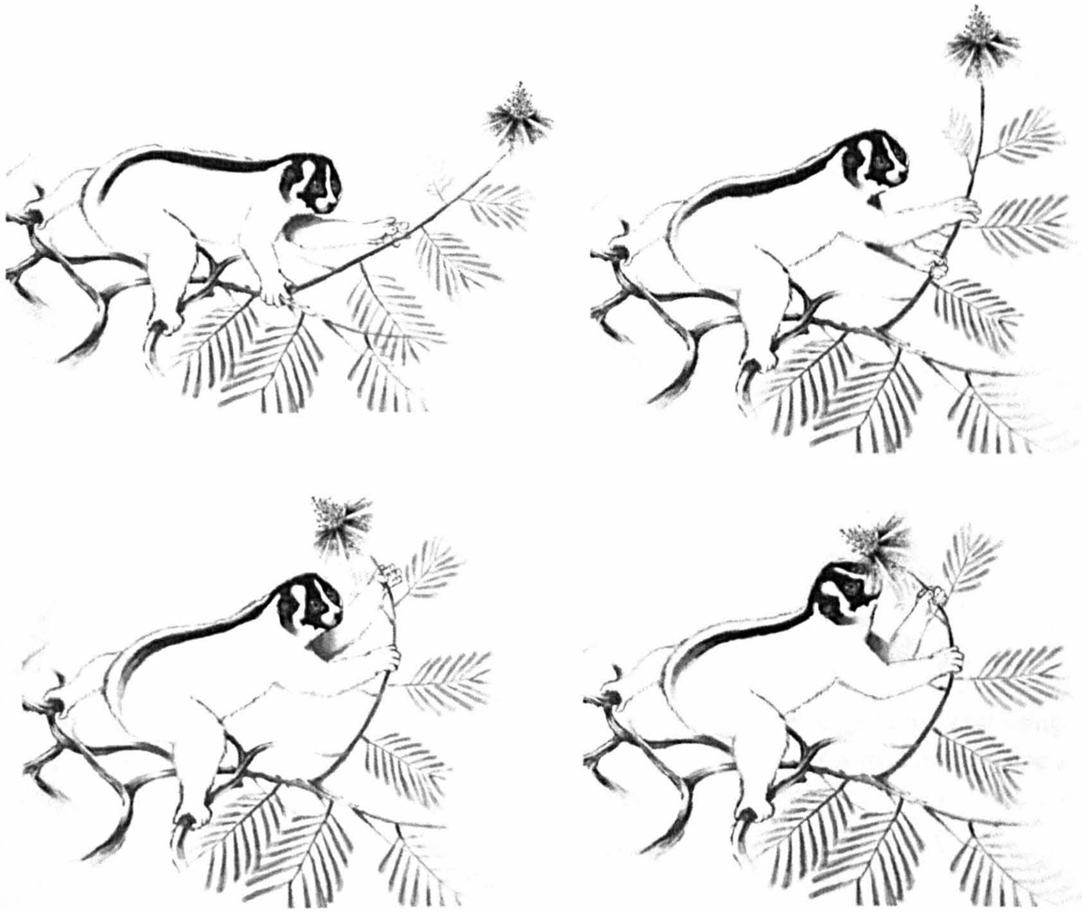

Figure 19. Illustration of a Javan slow loris foraging in terminal branches for the nectar of *Calliandra calothyrsus* using a controlled regulated grip to lure in the flower without damage (Illustrations by Anargha Setiadi).

manoeuvre was employed (Fig 20). Whilst its hind feet were securely fixed in a cantilever position, the loris would lunge its body forward with arms stretched out, either swinging the branch forward manually, or by utilising gusts of wind to increase its reach. On grasping a terminal branch on the opposite side of the gap, the loris would then pull this branch in, walking its hands up the branch until it became large enough to support its weight. The loris then released a hind leg from the previous branch, stretching it up to 180° horizontally, and positioning it on the new branch. When the loris was stable, it would release the remaining leg, often plummeting downwards under its weight, but still holding the branch. The loris would then climb up the branch once it had ceased swinging.

Figure 20. Illustration of the technique used by Javan slow loris to bridge across gaps using regulated hand manipulation to pull in the desired terminal substrates whilst maintaining a cantilever position. (Illustrations by Anargha Setiadi).

Nectar was the desired flower part in all cases of feeding from *C. calothyrsus*. Lorises fed on a single flower for a mean duration of 17 seconds (SD ± 12.7, n = 33). Feeding on *C. calothyrsus* was observed all year round, although seasonal differences were not investigated here. The flower was never observed to be damaged during feeding. On three separate occasions, pollen was observed on the face of the loris.

Whilst catching animal prey, sturdier small and medium substrates were preferred to the terminal branches and trunks ($\chi^2 = 39.340$, df = 3, $p \leq 0.001$). One-handed and two-handed grabs were employed to catch live prey significantly more times than directly by mouth ($\chi^2 = 11.40$, df = 2, $p \leq 0.01$), with one-handed grabs being the preferred option comprising 49% of incidences. Consumption of arthropods was prevalent in the animal prey category, although many could not be identified. Feeding on Hymenoptera (ants) was the only animal prey taken directly by mouth on all occasions. After feeding on ants the loris was occasionally observed to violently shake its head, presumably from the biting ants crawling over the loris' face. Outside the scans, lorises were observed to consume lizards on two occasions (Order: Squamata), and on one occasion the attempted capture of a small roosting bird was observed, but was unsuccessful.

Consumption of fruit was undertaken using all three food capture/manipulation techniques with no significant preference towards any one method ($\chi^2 = 0.545$, df = 2, $p \geq 0.05$). Small branches were utilised significantly more whilst feeding on fruits ($\chi^2 = 10.52$, df = 3, $p \leq 0.05$) and whilst suspensory positions were employed more often than not (61% to 39% respectively, n = 33) there was no significant difference ($\chi^2 = 1.485$, $df_{Yates} = 1$, $p \geq 0.05$).

Feeding on exudates only constituted a small proportion of the diet, and this action never involved any hand manipulation. Exudates consisted predominantly of sap from already open tree wounds, which were consumed orally. On only one occasion the loris was observed scraping hardened gum from an unidentified tree. Choice of substrate use during exudates consumption was not significant ($\chi^2 = 1.9$, df = 2, $p \geq 0.05$), although terminal branches were never used. Suspensory positions were employed significantly more when feeding on exudates (85% to 15% respectively) ($\chi^2 = 9.8$, $df_{Yates} = 1$, $p \leq 0.01$).

5.4 Discussion

The reintroduced Javan slow lorises consumed a variety of foods; however, they fed significantly more on the floral nectar of *C. calothyrsus* than on other food types. Although seasonality in flower feeding was not assessed, nectar feeding was observed throughout the year. An unpublished study of *N. javanicus* also reported regular feeding on *C. calothyrsus* in Java, although frequencies were not recorded (Arisona 2008). *Nycticebus c. coucang* in Malaysia displayed similar behaviour where a substantial proportion of the feeding time (31%) was devoted to floral nectar, specifically, the Bertram palm (*Eugeissona tristis*), which constituted 41% of all counts (Wiens 2002; Wiens & Zitzmann 2003b).

Compared to other species of loris, however, feeding behaviour was not analogous with my findings. Slender lorises (Lorisinae), for example, forage almost exclusively on animal prey (Nekaris 2005; Nekaris 2003) whereas Bengal and pygmy slow lorises reveal a preference for exudates (Nekaris et al. 2010b; Swapna et al. 2010). Whilst these food types were consumed by Javan slow lorises, they only constituted a small proportion of the overall diet. This inconsistency in findings, however, may be a consequence of different sampling techniques (Rose 2000). In the study by Nekaris (2005), all occurrence sampling was used, compared to the focal animal instantaneous sampling in this study. Capture and consumption of animal prey by lorises can be a very swift process (MacNeilage 1990; Nekaris 2005), therefore, all-occurrence sampling may be better suited to recording this type of rapid event. Indeed, outside of the instantaneous point sampling, insects were observed to be eaten regularly. Focal animal instantaneous point sampling was chosen in this study primarily for comparative purposes with other similar loris studies (Nekaris & Rasmussen 2003; Starr et al. 2012; Swapna et al. 2010), but also because of the difficulties in conducting continuous and all-occurrence sampling in dense undergrowth and over rough terrain (Altmann 1974). Whilst following lorises on Mount Salak there were some areas within the lorises range that could not be accessed owing to steep-sided ravines; therefore, caution is needed when considering the interpretation of these data.

Javan slow lorises foraged significantly more in the terminal branches than in other substrate categories comprising 60% of all feeding incidences. Lorises appeared highly adapted to the fine branch milieu displaying a number of postures and techniques that allowed them to exploit this niche readily. In accordance with slender lorises, at least two limbs were always in contact with a branch during flower/fruit stem manipulation or hunting of animal prey (Nekaris 2005; Nekaris & Rasmussen 2003). One-handed manipulation or grabs were the preferred method of food acquisition, although two-handed manipulation and grabs were also common. Indeed, slender lorises and pottos also forage live prey in this manner (Nekaris 2005; Pimley 2002). Two lorises were observed briefly travelling terrestrially, but never to forage. In both cases, it was to cross a cleared area where canopy was lacking. They descended to the ground and swiftly made their way across to the next tree.

Vision appeared to be the most important sense in location of *C. calothyrsus* flowers from a close range, not only in locating flowers, but also in choosing an appropriate route to get there. Olfaction may be of use to locate the flowering trees from a distance, although this would need to be confirmed. Once amongst the flowers, however, owing to their position and sheer abundance, other senses may not be as effective as vision. Audition is obviously ineffective in locating flowers, and olfaction may be hampered by short distances between flowers. Strong gusts of wind could disperse the scent from the flowers, and also cause the branches to move vigorously, therefore, confusing the origin of the smell. Capture of live prey also involved vision and is comparable to the findings in slender lorises (Nekaris 2005) and pottos (Pimley 2002) and reinforces the importance of vision as the predominant sense in the feeding ecology of these primates.

Calliandra calothyrsus trees were abundant at the Mount Salak study site (Mirmanto et al. 2008) and the lorises would actively search them out. Depending on tree size and profusion of flowers, the lorises would remain in the same tree or group of trees until all flowers had been visited. The Bertram palm flowers fed on by *N. c. coucang* during a study by Wiens and Zitzmann (2006) comprised several hundred flowers in one inflorescence and often contained copious amounts of nectar in a localised area. In comparison, flowers of *C. calothyrsus* are patchily distributed, located on the outermost tips of the branches, and undoubtedly require a great deal more movement in the terminal branches to access.

The genus *Calliandra* is native to Mexico, Central and South America, and *C. calothyrsus* was first introduced to Indonesia from Guatemala in 1936 by Dutch botanists (Chamberlain & Hubert 2001; MacQueen 1992). *Calliandra calothyrsus* is used principally as a source of cattle fodder and fuel wood, but also for manure, erosion control and honey production (Chamberlain & Hubert 2001; Moore 2011). Numbers of flowers per inflorescence range from 1 – 34, open over a period of 60 -90 days, and can be found from the base to the tip. If sufficient moisture is available the *C. calothyrsus* can flower throughout the year, although peaks between November and January (Chamberlain & Hubert 2001). Continuous flowering, therefore, potentially provides a constant food source to lorises and other flower visitors.

Calliandra calothyrsus becomes florally receptive during late afternoon and nectar is produced during the night, suggesting an evolved dependence on nocturnal visitors for pollination. Whilst bees and wasps are known to visit this flower, they are only regarded as "nectar robbers", as the morphology of the flower allows them access to the nectar without coming into contact with the reproductive parts (Chamberlain & Hubert 2001). Larger insects or mammals such as bats that would rub against the stamen whilst feeding are therefore the more likely pollinating candidates. Indeed, MacQueen (1992) suggested nectar feeding or long-tongue bats (*Glossophaga* spp.) were the primary pollinators of *C. calothyrsus* in Honduras. The bats regularly came into contact with the staminal brush, and pollen could be seen clearly on the underside of their bodies.

Javan slow lorises on Mount Salak appear to be highly dependent on nectar as a food source throughout the year. Lorises fed on nectar from many flowers a night, from different trees, and without damaging the flowers. When combined with the facts that pollen was observed on the face of the loris, and that the flower morphology of *C. calothyrsus* could accommodate small mammals, the available evidence appears to support the theory by Porsch (1934) that non-flying mammals are potential pollinators of angiosperms. Whether resident lorises are the sole pollinators of *C. calothyrsus* in this region is unlikely. Various species of nectar feeding bat (Family: Macroglossinae and Pteropodidae) also inhabit Mount Salak (Prawiladilaga et al. 2008), and bats are known pollinators of this species elsewhere (MacQueen 1992). Bats were never observed visiting *C. calothyrsus* flowers during my study.

Sussman's Angiosperm Co-evolution Hypothesis suggested that grasping hands and possibly stereoscopic vision were euprimate adaptations for foraging on nectar, flowers and fruit, which emerged during a co-evolution period with angiosperms. Rasmussen's synthesised view incorporated both the Angiosperm Co-evolution and Cartmill's Visusal Predation hypotheses. Arboreal, highly nectarivorous and potential pollinators of *C. calothyrsus*, the behaviours of Javan slow lorises in the present study do appear to support to the angiosperm related hypotheses of Sussman and Rasmussen. Although, as *C. calothyrsus* is a non-native flower to Indonesia, any possibility of co-evolution between these two species can be immediately disregarded. However, as my study site is located in secondary forest, the nectarivorous habits observed here may also feature in the diet of Javan slow lorises in less disturbed forests, but involving more archaic native species.

Cartmill (1992) had criticised the Angiosperm Co-evolution hypothesis arguing that stereoscopic vision would not be a prerequisite when foraging for sedentary items such as flowers or fruit. Javan slow lorises in this study reveal how marked optic convergence may be of use in locating appropriate flowers in a three-dimensional network of swaying terminal branches where smell is overwhelming and hearing is irrelevant. Indeed, some species of nectarivorous megachirpoteran bats also possess a degree of optic convergence with primate-like visual components in the brain (Barclay 2002; Pettigrew et al. 1989; Sussman 1995).

Cartmill (1992) also noted that the dental anatomy of the predominantly nectarivorous bats are in no way comparable to euprimate dentition, which indicate fruit, insect or leaf eating adaptations. Martin (1979), however, suggested that not all dietary habits of a species would be represented in the dentocranial morphology, and should only be used tentatively when assigning diets to species in this way. Indeed, some primate species with the same dental morphology can differ in diet owing simply to their location in a different habitat (Sheine & Kay 1982). Moreover, in the absence of dental indications of nectarivory, 'evolutionary inertia', where morphological adaptations can trail behind actual behavioural traits, may be a factor (Martin 1979). Rapid changes in behaviour or diet often coincide with environmental changes, whereas changes in dental morphology are not so rapid (Richard 1985). Nevertheless, whilst loris dentition may not directly suggest nectarivory, an area needing investigation is slow loris tongue morphology. Preliminary reports suggests different tongue lengths within slow loris species, some of which feature brush-like feathered tongues as seen in nectar feeding red-bellied lemur (*Eulemur rubriventer*) (Overdorff 1992).

Sussman (1991) proposed that grasping hands were an adaptation to fruit eating as it enabled euprimates to cling and feed amongst the terminal branches without needing to return back to sturdier supports. Javan slow lorises, comparable to cheirogaleid primates and woolly opossums (*Caluromys* spp.), frequently hang in suspension whilst extensive food manipulation occurs (Lemelin 1999; Rasmussen 1990; Schmitt & Lemelin 2002). Orkin and Pontzer (2011), however, based on their comparative study of Eastern Gray squirrels (*Sciurus carolinensis*), argued that grasping hands are unnecessary in terminal branches when feeding on seeds and buds. They proposed that adaptations to this niche have been overstated, unless when combined with certain other pressures involved in terminal branch feeding. Cartmill (1992), also noted that fruit-bearing plants occurred much later in the Cenozoic, which would not have coincided with earlier fossil evidence of grasping capabilities in the Cretaceous. Could long-stemmed, difficult-to-reach flowers, present in the Cretaceous, therefore, have been the evolutionary driver for primate prehensile extremities? Lorisiformes are renowned for their whole-hand power-grip, with forceps-like design, applied during the capture of animal prey or whilst firmly gripping branches (Bishop 1962; MacNeilage 1990; Napier 1960; Runestad 1997), but far less so for dexterous manipulation of food items. During flower stem manipulation in this study, Javan slow lorises exhibited a precise and delicate gripping ability whilst slowly luring the flower towards them. This action clearly demonstrates grip regulation, as opposed to the often 'stereotypically performed' power-grip observed in other lorisiforms (Bishop 1962; MacNeilage 1990). Perhaps the fundamental difference in feeding on flowers compared to fruit is that, from a reproductive perspective, if a flower is destroyed or consumed the plant's fitness is reduced. If co-evolution between primates and angiosperms has occurred, I would expect the flower to be left unharmed by the primate after feeding. The delicate precision grip, as observed in Javan slow lorises, helps to ensure the flower is not damaged during feeding. Whether this manipulating ability arose during a period of co-evolution is uncertain and these preliminary findings certainly warrant further investigation.

6. Face mask diversity and associated functions

6.1 Introduction

The diversity in skin and pelage colouration across the animal kingdom is significant and has stimulated considerable research into the understanding of its ultimate and proximate functions (Ortolani 1999). Colouration of external features originates from pigments that are transported along lengthy physiological pathways towards the skin: a costly process that requires energy (Frost-Mason et al. 1994; Margalida et al. 2008). Colour patterns, however, are generally construed to be advantageous, facilitating camouflage, communication and thermoregulation (Endler 1990, 1981; Guilford 1988; Hamilton 1973; Walsberg 1983). Such valuable traits are likely, therefore, to have evolved, at least partially, under natural selection (Wollenberg & Measey 2009).

Mammal colouration is generally restricted to browns, greys, blacks and whites (Davis & Castleberry 2010) with only a handful of species displaying more striking reds, yellows and blues (Clough et al. 2009; Newman et al. 2005). Diurnal primates, for example, are one such group that boasts an array of flamboyant hues – frequently, exhibiting clear distinctions between sexes (Bradley & Mundy 2008). Such intra-specific sexually dichromatic traits are commonly perceived to be a result of the influence of sexual selection, whereby females prefer brighter coloured males (Gerald et al. 2007; Kappeler & Schaik 2004; Setchell 2005). In many cases, however, owing to a myriad of distinct environmental and genetic factors interacting at various levels, the exact biological significance of the pigmented phenotype is often difficult to determine (Caro 2005; Davis & Castleberry 2010; Slominski et al. 2004; Stevens et al. 2009).

Previously, most studies of animal colouration have focussed on the visibly ostentatious animal taxa such as birds and insects; consequently, the more modestly coloured mammals have received less attention (Clough et al. 2009; Newman et al. 2005; Stevens et al. 2009). Typically, mammal colouration follows Gloger's rule, where darker colours are present in riparian (forested river course) habitats with lighter colours more common in open areas. Such colouration is thought to provide benefits in the form of camouflage and thermoregulation in the respective habitat type (Hamilton 1973). For the less conspicuous mammal species the intra- and sometimes inter-specific variation, to the human eye, appear superficial, but on closer inspection reveal intricate pattern and colour deviations (Bearder 1999; Bearder 1995; Clough et al. 2009; Nekaris & Munds 2010). The function of this variation, especially amongst ostensibly similar-looking nocturnal species, may serve in individual recognition between species or mate-recognition within species (Bearder 1995; Bearder et al. 2006; Couldridge & Alexander 2002; Kingdon 2007). Alternatively, colour variation possibly occurs as a response to light differences across habitats (Endler 1993; McNaught & Owens 2002). In 'closed habitats' such as dense forest, for example, orange and red colours are presumed better for signalling because these colours reflect the long wavelength light found in such environments and contrast starkly against the dark vegetation (Endler 1990, 1993). Vocalisations and olfactory signalling were thought to be the primary methods of communication amongst many nocturnal species; however visual phenotypic clues may also play an important role, especially in ambient lighting such as crepuscular or moon light (Penteriani et al. 2007). Intra-species colour variation may also be related to fitness (Clough et al. 2009; Dungle et al. 2008; Swaddle 1996) dominance (Gerald 2001; Palmer et al. 1981) and age (Bradley & Mundy 2008).

One particularly intriguing and relatively common pattern that occurs across numerous mammal species is the existence of black and white markings juxtaposed against each other (see Ortolani 1999). These contrasting markings can occur across the whole body, or are restricted to particular areas such as the tail, the face, or the trunk (Caro 2009; Guthrie & Petocz 1970; Newman et al. 2005; Ortolani 1999). The functions of these relatively conspicuous markings vary depending on which part of the body they occur. Different areas of the body can be viewed by conspecifics, predators or prey, under different conditions, from a range of distances, and thus affect the selection pressures at work (Caro 2009; Caro & Stankowich 2009; Ortolani 1999). In general, contrasting colour markings appear to reduce the cryptic properties of an animal and so are perceived to have more of an aposematic role (Cott 1940; Inbar & Lev-Yadun 2005; Ruxton 2010). Animals with aposematic colouration either possess or mimic attributes that are potentially harmful to predators (Cott 1940; Darwin 1871). Such traits include toxins, spines, horns and noxious odours, and can function either to make the animal unpalatable to predators, or to convey a warning that if attacked the perpetrator is likely to be injured (Caro 2009; Cott 1940; Inbar & Lev-Yadun 2005; Ruxton 2010).

The available literature that tackles variation in mammal colouration is sparse (Caro 2009; Caro & Stankowich 2009; Newman et al. 2005; Ortolani 1999; Stoner et al. 2003), and even fewer studies have focused on intraspecific variation (Davis & Castleberry 2010). Primate colouration has received more attention in the last few decades although most studies have focussed on skin colour, as opposed to pelage (Bradley & Mundy 2008; Clough et al. 2009). Nocturnal prosimians are perhaps the least known of all primates, and yet display great, albeit subtle, variation between and within species (Nekaris & Bearder 2011). This has been demonstrated in galagos (Bearder 1999) and in slow lorises (Nekaris & Jaffe 2007; Nekaris & Munds 2010). Slow lorises possess a multitude of distinguishing features including morphological characteristics and pelage colour. The reasons for this inter- and intraspecific variation is yet to be discerned, although Nekaris and Munds (2010) proposed the distinctive facemasks apparent in this genus aid primarily in individual recognition, with a possible secondary function of aposematism. The Javan slow loris (*N. javanicus*) in particular, possesses the striking black and white contrasting markings characteristic of this trait.

In this study, I investigate the variation found in facemask colour in three species of Indonesian slow lorises. I employ a quantitative approach to measuring colour, using digital photography and associated computer software. The perceived colour of a certain display depends on perhaps most importantly the visual abilities of the observer (Bradley & Mundy 2008; Endler 1990). As slow lorises are monochromatic (Malmström & Kröger 2006) seeing only black and white, with the majority of their potential predators being dichromatic (Bradley & Mundy 2008; Jacobs 1993) seeing a reduction in colour vision, images were adjusted to display the respective colour types for what each animal group would perceive.

I constructed hypotheses based on the information available. Nekaris and Munds (2010) suggest that *N. javanicus* was highly distinguishable from the other Indonesian slow loris species owing to its striking black and white fork-marked face mask. Therefore, I predicted that greater variation of colour would occur between the face masks of *N. javanicus* when compared to *N. coucang* and *N. menagensis* than between *N. coucang* and *N. menagensis*. As primate intra-specific sexually dichromatic traits are often the result of sexual selection (cf. Bergman & Beehner 2008; Davis & Castleberry 2010; Setchell & Jean Wickings 2005) I predicted loris face-mask colour variation would also be influenced by age and sex. Nekaris and Munds (2010) proposed facemasks of slow lorises may have an aposematic function. As the potential predators of slow lorises are predominantly dichromatic, I predict colours will contrast more in dichromatic view, when compared to monochromatic for maximum signalling effect.

6.2 Methods

See chapter 2

2.2.6 – Photo capture

2.2.7 – Photo analysis

2.2.8 - Statistics

6.3 Results

Of the 89 Indonesian slow lorises photographed: 40 were *N. javanicus*, 45 were *N. coucang* and four were *N. menagensis*. The sex ratio was 47 males to 42 females. Four lorises were classified as young, 65 as adult and 20 as old individuals. Colour scores measured ranged from 0 – 255 where lower numbers represent darker colours. Red scores for the dark facial markings – classified as the forehead and the circumocular regions – in all species, ranged from 17.4 to 153; light patches – the pre-auricular and median stripe regions – ranged from 134 – 250 (Fig 21).

Table 8. PCA results displaying percentage of variance explained for each different region and photo-type (for component one). Variance for monochromatic were 100% owing to the scores for each RGB category being the same in the black and white image.

	Photo-type		
Region	**Normal**	**Dichromatic**	**Monochromatic**
Forehead	88.2	82.2	100
Circumocular	85.5	82.5	100
Median stripe	95.7	94.8	100
Pre-auricular	94.8	94.1	100

I applied PCA analyses on all regions for each photo-type (Table 8). As the monochromatic scores were the same for each colour, it rendered the PCA results unusable for cross-image comparisons. Therefore, ANOVA colour analyses were conducted only on normal images. Between all species, when considering all regions, a significant variation in colour was present (Table 9). When focusing on individual regions, all but median stripes were significantly different to each other when considering the effect of species (Table 9). Post-hoc Tukey tests revealed only *N. javanicus* and *N. coucang* were significantly different in each pairwise comparison ($p \leq 0.001$).

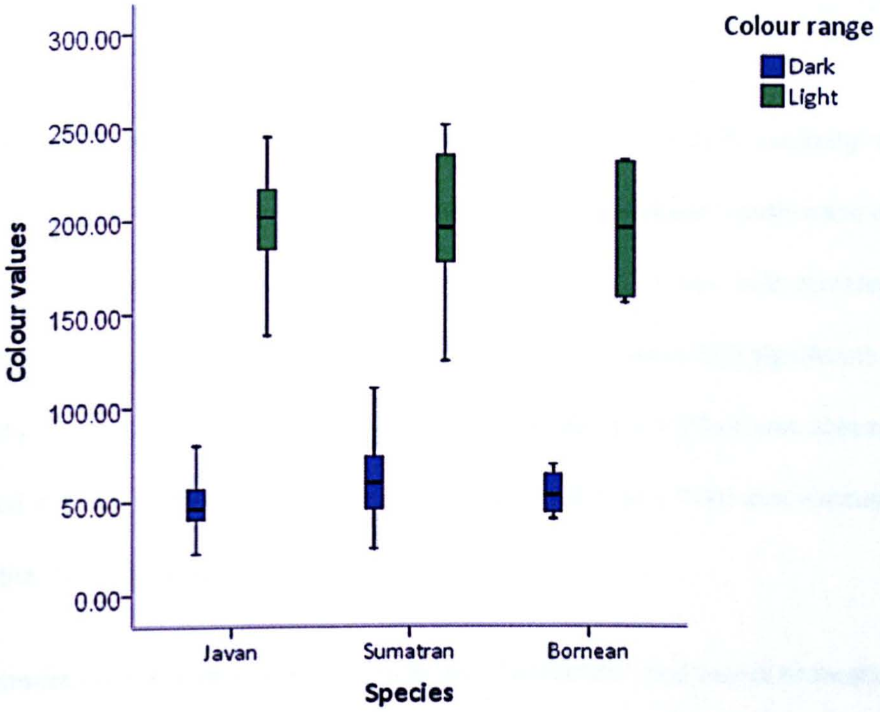

Figure 21. Box plot displaying a comparison of the red scores for the dark and light regions in all three species. (Dark regions: forehead and circumocular; light regions: median stripe and pre-auricular.) Red scores for dark patches ranged from ranged from 17.4 to 153; light patches ranged from 134 – 250.

When the effects of species, sex and age were considered simultaneously in the ANOVA model, only the circumocular region yielded significant results. In this model, age had the most significant effect on pelage colour ($F_{1,86} = 7.12$, $p = 0.004$). The model was statistically significant ($p = 0.001$) and explained 35% of the variance.

Table 9. ANOVA scores for significant results in colour variation analyses

Region	*df*	*F*	*p*
All regions	2,353	8.12	≤ 0.001
Forehead	2,86	10.54	≤ 0.001
Circumocular	2,86	10.35	≤ 0.001
Pre-auricular	2,86	6.59	≤ 0.002

Intra-species variation was explored in both *N. javanicus* and *N. coucang* where the influence of age and sex were measured. In *N. javanicus* significant results were reflected in the forehead colour scores in relation to sex ($F_{1,120}$= 5.03, $p = 0.02$), with females generally lighter than males (Fig 22). The circumocular colour scores were also significant in relation to age ($F_{2,120} = 7.87$, $p = 0.003$), where a gradual lightening of colour was observed as age increased (Fig 23). Both models produced were significant ($p > 0.01$) and explained 11 and 27% of the variation respectively.

When comparing the colour variation between dichromatic and monochromatic images, I used the red values for comparison owing to the non-applicable monochromatic PCA results (Fig 24). Significant differences were revealed for red scores between the image types ($\chi^2 = -16.3$, $p \leq 0.001$).

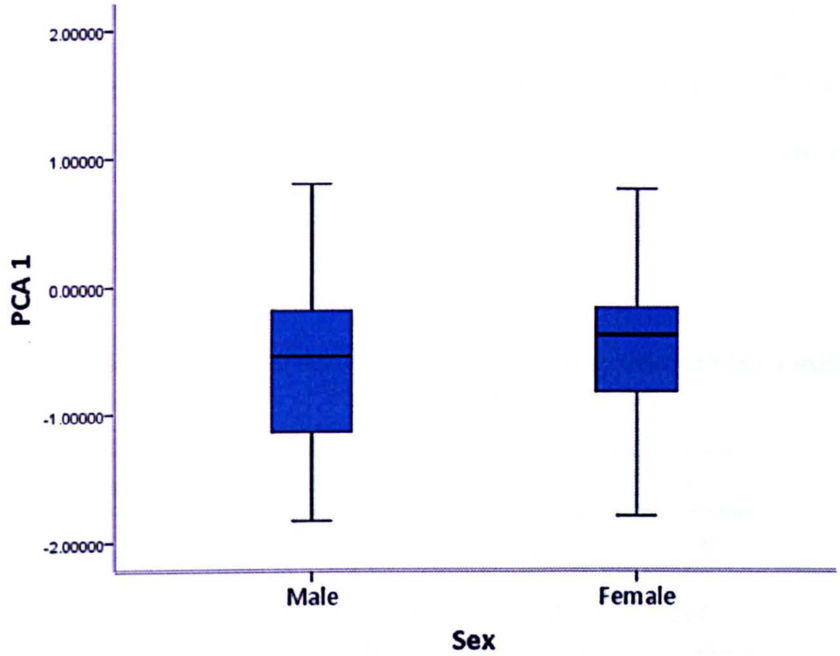

Figure 22. Box plot displaying the results for colour scores on the forehead of *N. javanicus* and *N. coucang* in relation to sex. Forehead scores in males were significantly lighter than females.

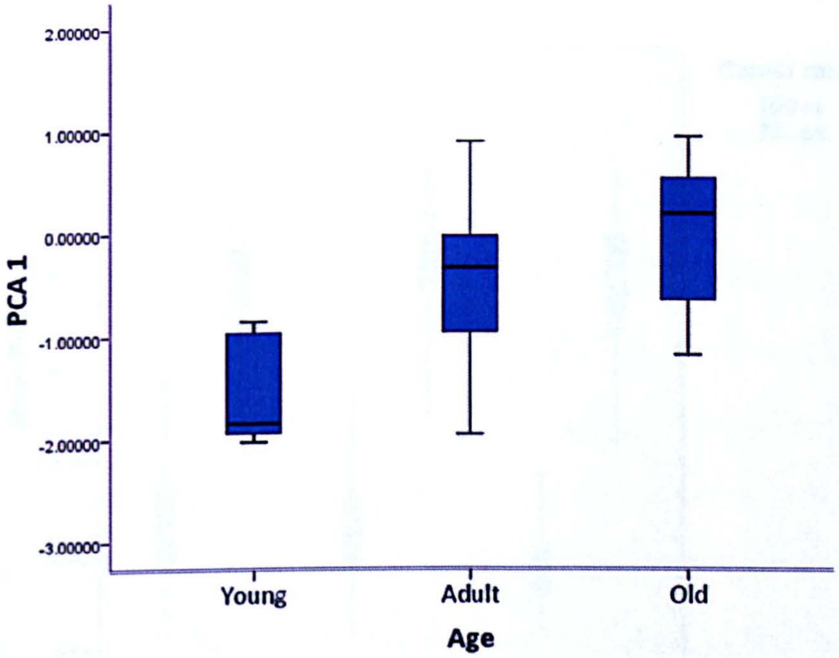

Figure 23. Box plots displaying the significant results for colour scores on the circumocular region of *N. javanicus* and *N. coucang* in relation to age. A gradual lightening of colour scores was observed as age increased.

When only the dark regions were considered significance was also reached ($\chi^2 = -11.5$, $p \leq 0.001$) and similarly when light regions were compared ($\chi^2 = -11.6$, $p < 0.001$). Lower means were observed in the monochromatic images. The difference between the mean scores was 142 for dichromatic and 148 for monochromatic (Table 10).

Table 10. Means of red colour scores of dichromatic and monochromatic images depending on region type.

Region	Image type	Mean	SD	n
Dark	Dichromatic	64.3	27.3	114
	Monochromatic	41.9	19.5	114
Light	Dichromatic	206.6	26.9	114
	Monochromatic	190.4	31.5	114

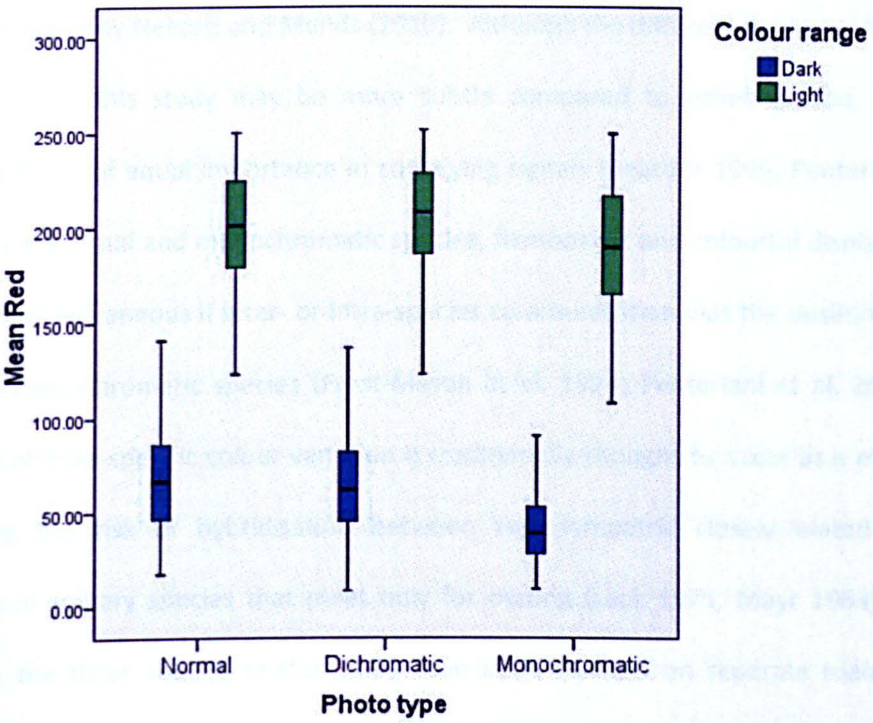

Figure 24. Box plot displaying the ranges of dark and light red colour scores for the three image types. Significant differences were found between the colour scores of each image type.

6.4 Discussion

A paucity of information is available on why colour variation occurs between and within species of slow lorises, or indeed other closely related nocturnal primates. I aimed to quantify the variance observed in the facial colour of three species of Indonesian slow loris in order to understand the associated proximate functions. Despite the procedures undertaken to minimise error in my study, owing to the absence of strict laboratory conditions with uniform lighting at the time of image capture, some caution is necessary when interpreting the results. These possible errors may be a contributing factor in the low percentages of variation explained by the ANOVA models for intra-species differences, which should also be interpreted tentatively. Further caution is needed when considering results featuring *N. menagensis* owing to the small sample size.

Inter-specific variation in colour was significant across all three species, which is consistent with the findings by Nekaris and Munds (2010). Although the differences between the slow loris species in this study may be more subtle compared to other species, they will undoubtedly be of equal importance in conveying signals (Bearder 1995; Penteriani et al. 2007). For nocturnal and monochromatic species, flamboyant and colourful displays would be costly and extraneous if inter- or intra-species communication was the desired function for these monochromatic species (Frost-Mason et al. 1994; Penteriani et al. 2007). The existence of inter-specific colour variation is traditionally thought to occur as a method of minimising the risk of hybridisation between two sympatric closely-related species; especially in solitary species that meet only for mating (Lack 1971; Mayr 1963; Wallace 1889). As the three species in this study have been isolated on separate islands (Java, Sumatra and Borneo respectively) – probably since the end of the Pleistocene when the last connecting land bridges between the islands disappeared (Harrison 2006) – this variance in colour between species may indeed be a relict of a time before the species became separated. It is perhaps more likely that speciation occurred after its separation, and consequently transformations in colour happened simultaneously. Furthermore, whilst inter-species comparative studies investigating this hypothesis are scarce, available evidence offers little support for this hypothesis (McNaught & Owens 2002), which suggests other pressures may be responsible.

A more contemporary theory proposes that colour variation is more closely associated with the amount of light present in an environment and therefore poses different selection pressures depending on habitat type (Andersson 2000; Endler 1993; McNaught & Owens 2002). The function of the colouration in this case, may be for camouflage, communication, aposematism and/or mimicry, with colours adapted for maximum effect to suit the ambient light (Bradley & Mundy 2008; Edmunds 1974; Hamilton 1973; Ruxton 2010). This theory certainly appears feasible for slow lorises and is supported by evidence in other species (Marchetti 1993; McNaught & Owens 2002; Zahavi & Zahavi 1997). In the absence of studies regarding habitat types for any of these species (Nekaris & Bearder 2011), it is difficult to validate at this time.

As predicted, there was a more significant difference between *N. javanicus* and the two other species, than between *N. coucang* and *N. menagensis*, which is again consistent with the study by Nekaris and Munds (2010). Further corroboration is provided by a recent genetic study that suggested *N. javanicus* and *N. bengalensis* (which occurs further North in the Indo-China region) are more closely related than to either *N. coucang* or *N. menagensis* (Nekaris in prep). Despite the close distance geographically, *N. javanicus* in an evolutionary context, is more distant. The significant colour difference in *N. javanicus* is potentially associated with previous climatic and habitat alterations that occurred within its range, but not in the ranges of the other two species. Heaney (1991) proposed that with cooling temperatures during the last glacial period, substantial areas of tropical forest disappeared, forming a savanna corridor that stretched from Java North towards the equator, which ran between the islands of Borneo and Sumatra. This change from tropical forest to savanna may have been responsible for different selection pressures that would have effected *N. javanicus,* but were absent in the other two species.

Intra-species colour variation in both the dark and light regions was extremely large, particularly in *N. coucang*, where an overlap between these two regions was observed (fig 17). A reason for the large variance in colouration observed within species, however, may be a result of the fact that we are actually dealing with a number of yet-to-be-recognised species. In the past, the three Indonesian slow loris species currently recognised today were lumped as one species (*N. coucang*). In 2006, based on genetics and morphology, the already recognised sub-species of Indonesian *Nycticebus* were elevated to species status (Nekaris et al. 2009). It is highly possible that the unearthing of yet more species may occur; such has been the case in lemurs, galagos and tarsiers (Bearder 1995; Mittermeier et al. 2008; Nietsch & Kopp 1998). Indeed, Nekaris and Jaffe (2007) provide convincing evidence for the recognition of even more species within this group.

The effects of sex and age on colour variation in *N. javanicus* and *N. coucang* were only significant in *N. javanicus*. Measurement of forehead colour in *N. javanicus* revealed that males were generally darker in colour than females. The exact reason why only this particular region should display variance in relation to sex is unclear, but is perhaps one of the most effective places for other conspecifics to view the desired signal as they are approaching in terms of both its anterior position and also to catch the light (Baylis 1979; Caro 2009; Ortolani 1999). Similar results regarding colour in relation to sex have been recorded in other primate, mammal and bird species (Bergman & Beehner 2008; Caro

2005; Davis & Castleberry 2010; Gerald 2001) and is often presumed to have numerous communicative functions (Caro 2005; Caro 2009; Hamilton 1973; Stephenson & Stewart 1955). In contrast to inter-specific colour variation which primarily serves to aid in species recognition and concealment, intra-specific variation conveys different messages to conspecifics. Colours are often used as signals of quality, where individuals communicate information regarding their genetic and phenotypic makeup to potential mates or indeed conspecific competitors (Dale 2006; Dale et al. 2001; Olson & Owens 1998; Setchell et al. 2006). Colour may also convey signals of dominance or status, especially in males (Bergman & Beehner 2008; Gerald 2001; Setchell & Jean Wickings 2005), but is also thought to represent honest signals of the individual's quality of health, immune system, absence of parasites or foraging capabilities (Andersson 1994; Dale 2006; Hamilton & Zuk 1982; Zahavi & Zahavi 1997).

In *N. javanicus*, age was also found to be a significant predictor of colour in the circumocular region, where lighter colours were found in older individuals. This trend has been observed in the closely related *Loris lydekkerianus* nordicus (Schulze pers. comm) and in Galagidae (Bearder, pers. comm). This trend, when combined with the sexual dichromatism observed, is perhaps also linked to signalling honesty in terms of health, fitness or even fighting ability in males (Dale 2006; Setchell & Jean Wickings 2005), where young and adult individuals are generally healthier, fitter and stronger than older individuals. Slow lorises are sexually dimorphic and are known to defend territories actively occasionally resulting in severe bite wounds from conspecific attacks (Nekaris, pers. comm; (Wiens & Zitzmann 2003b). As physical fighting poses a risk to all involved (Maynard-Smith 1982), the ability to recognise the opponent's ability may help to determine the best response in that situation and subsequently reduce chance of injury (Cott 1940; Preuschoft & van Schaik 2000).

Perception of colours by the intended receiver is an important aspect in understanding their respective functions (Bradley & Mundy 2008; Stephenson & Stewart 1955). On analysis of the two image types, I found that monochromatic colour scores were consistently lower than the dichromatic. Despite the lower values for monochromatic scores, the difference in scores between the light and dark regions remains similar (Table 9) suggesting that the overall effect of the contrasting colours does not change between the perceptions of conspecifics and potential predators. The darker colour scores recorded in monochromatic images have probably evolved and adapted for maximum signalling effect when perceived through monochromatic eyes; however, there are probably other evolutionary drivers at work creating a trade-off between intra- and inter-species communication, anti-predator defence (aposematism versus camouflage) and anti-glare adaptations (Bradley & Mundy 2008; Broom et al. 2006; Caro 2009).

Caro (2009) proposed that the contrasting colour of the slow loris facemask was not an aposematic adaptation to predation, but function to reduce glare, where the dark eye patches prevent dazzling by light reflected off the fur at dawn and dusk. This theory is certainly feasible and has been reported previously (Burtt 1981; Ficken et al. 1971). Caro (2009) compared the slow loris to other tree dwelling nocturnal arboreal species that possess a similar facial pattern and colouration: primarily the feather-tailed possum (*Distoechurus pennatus*) and the fork-marked dwarf lemur (*Phaner furcifer*) (Fig 25). He observed that not all species that possess conspicuous facemasks have the necessary defensive attributes – such as a formidable bite, spines or a noxious gas secretion – and therefore cannot be regarded as having aposematic functions. Slow lorises, however, do have a form of defence, one extremely rare in mammals and perhaps overlooked by Caro (2009) – the ability to administer a venomous bite. The venom derives from a brachial gland exudate, which when mixed with saliva becomes toxic (Alterman 1995; Hagey et al.

2007; Krane et al. 2003). The primary function of this venomous attribute is still debated, but has been suggested as a form of defence – either from conspecifics or predators, to provide a medium for olfactory communication or to function as an anti-parasite mechanism amongst others (Alterman 1995; Hagey et al. 2007; Rasmussen 1986).

Figure 25. Images displaying the parallel evolution of similar facial markings in three separate nocturnal mammals (from the left: fork-marked lemur *Phaner furcifer*, Pen-tailed possum *Distoechurus pennata* and the Javan slow loris *Nycticebus javanicus*).

(*Phaner furcifer* - http://m.tin247.com/15_loai_moi_phat_hien_doc_dao_nhat-12-21778712.html)
(*Distoechurus pennata* - http://img.wired.jp/gallery/201010/20101007111121-4.jpg)

Based on this evidence, it appears highly likely that the distinctive facemasks in slow lorises could serve as a form of aposematism, either against predators or conspecifics. However, as other nocturnal arboreal species have similar markings, but are devoid of such a defence, the original manifestation of these colour patterns were probably not the result of an aposematic adaptation. The initial impetus may have been sexual selection or as an anti-glare mechanism, which was subsequently modified for the dual use of aposematism and/or communication. Similarly, the toxin present in slow lorises may have originated as an anti-parasitic defence for example, but later adapted to use as defensive venom. If the slow loris became less cryptic as a result of sexual selection – therefore counteracting natural selection and making them more visible to predators – strong selective pressure for a form of secondary defence would have begun to act.

7. Mimicry in the Javan and Bengal slow loris

"...I heard the regular breathing sound made by a cobra when he inflates and deflates his body... The sound came from my room, where, although it was dusk there was still plenty of room to kill a snake." [On entering the room] *"...I saw the outline of a cobra sitting up with hood expanded, and threatening a cat who crouched about six feet away. This was the loris, who, with his arms and shoulders hunched up, was a sufficiently good imitation of a cobra to take me in, as he swayed on his long legs, and every now and then let out a perfect cobra hiss... I may mention that I have kept snakes, including a cobra, and am therefore the less likely to be easily deceived by a bad imitation"* (Still 1905).

7.1 Introduction

Still's (1905) was the first anecdotal account of the uncanny resemblance of his pet slender loris (*Loris sp.*) to a cobra. Other authors have since remarked on the slender and slow loris' (*Lorisidae*) snake-like characteristics in regards to their aversive pant-grunt calls, their defensive postures (Elliot & Elliot 1967; Schulze & Meier 1995) and serpentine gait (Gebo 1987; Osman Hill 1953; Walker 1969; Walker & Nowak 1999). Furthermore, the Javan slow loris (*Nycticebus javanicus*) and the Bengal slow loris (*Nycticebus bengalensis*) display facial markings undeniably akin to the eyespots and accompanying stripes of the formidable spectacled cobra (*Naja naja*) (Fig 26). The dark contrasting dorsal stripe of these two species also closely resembles the body of a snake, particularly when viewed from above. We address here for the first time whether this collection of intriguingly imitative traits merely evolved coincidentally with no combined function, or whether they do in fact benefit slow lorises, also intriguingly the only known venomous primate (Hagey et al. 2007).

Deception provides the basis for mimicry in nature. Many animals possess protective colouration that deceives predators by masquerading as something else (Behrens & Whitson 1976; Stevens 2007). Mimicry is common among insects (Ruxton et al. 2004; Wickler 1968), with many caterpillars (Lepidopteran larvae) displaying extremely

Figure 26. Images displaying potential mimicry between slow lorises and spectacled cobras (1). Javan slow loris (2) Spectacled cobra (rear view) (3) Spectacled cobra (front view) (4) Bengal slow loris.

convincing imitations of various species of snake, both in appearance and behaviour (Janzen et al. 2010; Stephenson & Stewart 1955). Mimicry among vertebrates is less common (Robinson 1893; Wickler 1968), and in mammals extremely rare (Pough 1988). Although the potential mimicry in the Javan and Bengal slow loris may not be as striking as in other cases, across the natural world imperfect mimicry is widespread (Edmunds 2000).

In order to gain protection, a mimic need not perfectly replicate its model, as long as it is similar enough to cast uncertainty in the mind of the predator (Edmunds 2000; Harper & Pfennig 2007; Pough 1988; Ruxton 2010). Mammalian mimicry, such as proposed in aardwolves (*Proteles cristatus*) mimicking striped hyaenas (*Hyaena hyaena*) (Gingerich 1975) and cheetah (*Acinonyx jubatus*) infants mimicking honey badgers (*Mellivora capensis*) (Eaton 1976) generally appears to be less precise than that of invertebrates; auditory and olfactory mimicry that may enhance the proposed visual similarities are often overlooked (Barber & Conner 2007; Camazine 1985; Pough 1988). Moreover, the rather surprising affinity of *Naja naja* to *Nycticebus javanicus* and *Nycticebus bengalensis* may initially seem coincidental if comparing the markings alone, but when examined in its respective ecological context and by assessing to which predators the defence is most effective, the mimetic potential may gain plausibility.

I hypothesise that *Nycticebus javanicus* and *Nycticebus bengalensis* do gain an adaptive advantage through mimicking *Naja naja.* As lorises are themselves a toxic species, we further contend that this is to at least a degree, a form of Müllerian mimicry. Müllerian mimicry is the mimicking of another species warning signals consequently reducing the threat of attack (Charlesworth 1994; Wickler 1968). To test this hypothesis, an understanding of the evolutionary processes towards the selection of mimetic traits is necessary. For Müllerian mimicry to be effective, it is crucial that the animal mimic is recognised by a predator (or dupe) as another unpalatable or noxious model it is imitating. For the predator to recognise the animal as an unpalatable prey species, the predator must already be aware of the other species undesirable characteristics (Charlesworth 1994). Accordingly, at some point in time, the ranges of the mimic, the model and the dupe would have overlapped (Harper & Pfennig 2007; Pfennig et al. 2001; Pough 1988). For mimicry to occur in one species, but not in other closely related species, would indicate a specific ecological pressure was driving the selection of mimetic traits in only that species, and which was absent in the others (Ruxton 2010; Ruxton et al. 2004; Wickler 1968).

Slow lorises rely primarily on crypsis as their anti-predator strategy with subtly coloured pelages aiding in their ability to forage unnoticed (Charles-Dominique 1977; Petter & Hladik 1970). The striking facial colouration and markings in *Nycticebus javanicus* and *Nycticebus bengalensis* appear to contradict this notion. If indeed, these two species are utilising mimicry, it would suggest that they have more to gain from increased conspicuousness rather than crypsis utilised in the other species (Charlesworth 1994; Ruxton 2010; Ruxton et al. 2004).

I postulate that the *Nycticebus javanicus* and *Nycticebus bengalensis* mimicry evolved during a period of co-existence with *Naja naja*, at a time when environmental pressures would have favoured its selection. I examine the evidence for this proposed mimicry and discuss each mimetic characteristic in regards to its evolution and ecological role. I discuss the potential gain in relation to anti-predator strategies employed by these two species, and discuss how the foraging activities of *Nycticebus javanicus* and *Nycticebus bengalensis* may differ from the other species in *Nycticebus*. As the mimetic traits appear to have been maintained into contemporary times, I propose that *Nycticebus javanicus* and *Nycticebus bengalensis* still currently benefit from their mimetic properties. While *Nycticebus bengalensis* occurs sympatric with strongly patterned *Naja* types, the *Naja* forms found sympatric with *Nycticebus javanicus* are not strongly patterned in most of the range.

7.2 Overlapping ranges

Based on studies of mitochondrial DNA, the present genus *Naja* appears to have originated and diversified in Africa, subsequently travelling into Eurasia and across to the Orient around 16 million years ago (Ma) (Kelly et al. 2009; Wüster et al. 2007). These dates roughly correspond to the occurrence of a continuous land bridge from Africa to Asia in the early Miocene (Gheerbrant & Rage 2006). The origin of *Naja naja* in Asia is estimated at approximately ten Ma, and it still persists today in India, Pakistan, Sri Lanka and Bangladesh (Wüster 1998; Wüster et al. 2007). The earliest fossil record of lorises (*Lorisidae*) present in Asia dates back to 8 Ma (Rasmussen & Nekaris 1998). Molecular data for the currently recognised five slow loris species imply a close monophyletic relationship between *Nycticebus javanicus* and *Nycticebus bengalensis* within the clade of *Nycticebus* (Roos 2003). The divergence of these two species is estimated at 2.6 Ma with *N. menagensis* branching off earlier at 4.77 Ma (Nekaris in prep).). As only *Nycticebus javanicus* and *Nycticebus bengalensis* share the cobra-like markings, the mimicry appears to have evolved after the divergence of *Nycticebus menagensis*, but before *Nycticebus javanicus* migrated to Java where *Naja naja* has never been present. The dates of the period that the last common ancestor to *Nycticebus javanicus* and *Nycticebus bengalensis* and *Naja naja* were present on the mainland Asia, therefore, ostensibly coincide with the evolution of the mimetic traits.

Like numerous other mammalian species where a Javan taxon is more closely related to an Indochinese one than a Sundaic island form (cf. Hassanin & Ropiquet 2007; Meijaard 2004a, b). *Nycticebus javanicus,* restricted to Java, is most closely related to the Indochinese *Nycticebus bengalensis*. This allopatric distribution is probably explained by the existence of intermittent land bridges that ran between Java and the Malay Peninsula during the early to middle Pleistocene (approximately 2.6 Ma), enabling migrating species access to Java from the Asian mainland (Meijaard 2004a, b).

Around the time of the divergence of *Nycticebus javanicus* and *Nycticebus bengalensis*, the climate in the Southeast Asia underwent a number of dramatic fluctuations, largely altering the vegetation (Bird et al. 2005; Heaney 1991; Voris 2000). Coinciding with the intermittent land bridge formations in the Pleistocene, a band of drier more seasonally adapted woodland ran from north of the Malay Peninsula down as far as Java replacing the more tropical forests (Heaney 1991; Morley & Flenley 1987). This habitat alteration may have benefitted some animals in allowing an easier migration south through the more savannah-like landscape, but for others it acted as a species isolation barrier (Harrison 2006; Meijaard 2004a, b).

For *Nycticebus javanicus* and *N. bengalensis* this change in habitat to a more open savanna-like environment and a different array of predators may have provided the initial selection impetus towards mimicry. As Java generally consisted of more open and drier habitat than the neighbouring Borneo and Sumatra (Meijaard 2004a), possibly the mimetic pre-adaptations to this type of environment allowed *Nycticebus javanicus* to exploit the resources and subsequently settle there. Despite being outside of the range of *Naja naja* the nature of the striking markings could still act to startle predators that are unaware of *Naja naja* (Ruxton et al. 2004; Stack & Plant 1982; Stevens et al. 2008). Furthermore, many animals carry an almost innate fear of snakes, so even without encountering *Naja naja* before, may still be tentative to attack something that resembles a snake (Isbell 2006; Robinson 1893).

7.3 Visual mimicry

"Let us take as a starting point the strange instinctive terror of the serpent which nearly all animals exhibit... The other day I transformed a savage old male rhesus macacus which was tearing at his cage to get at me, with crimson face and gnashing canines, into a limp and pallid coward by the exhibition of a Japanese toy snake which I had in my pocket (Robinson 1893)"

7.3.1 Eye spots

Many animals possess protective colouration that deceives predators by masquerading as something else (Behrens & Whitson 1976; Stevens 2007). One example of mimicry is patterns of concentric circles present on the bodies of animals that resemble the vertebrate eye (Stevens et al. 2008; Vallin et al. 2011). Known as "eyespots", these features are common amongst butterflies, fish, frogs and birds (Brakefield et al. 1996; Davison 1983; Neudecker 1989; Stack & Plant 1982; Wickler 1968), and function to deter predators outright, startle them to allow time for an escape, or misdirect the attack to a less vital body part (Cott 1940; Stevens 2005). Eyespots are not exclusively restricted to vulnerable or defenceless animals, but are also present in more formidable fauna. The markings of *Nycticebus javanicus* and *N. bengalensis* appear to mimic the eye-spots of *Naja naja*. As these markings reveal a distinct deviation away from crypsis, I postulate an environmental setting that would favour their evolution.

Lorises (*Lorisidae*) are highly arboreal primates (Schwartz 1986; Walker & Nowak 1999), but when no continuous canopy is available, will occasionally venture over ground to breach a gap (Nekaris 2001; Rogers & Nekaris 2011; Streicher & Nadler 2003). Terrestrial travel undoubtedly increases predation risk and is normally only attempted when no other option is present (Nekaris 2001; Wiens & Zitzmann 1999). For lorises in more open habitats terrestrial travel appears to be more of a necessity than a choice, although for *Nycticebus bengalensis* the presence of long grass in dry dipterocarp forests can act as a partial cover during movement between trees (Rogers & Nekaris 2011).

The climatic changes during the Pleistocene and the associated succession in vegetation from tropical forest to a more open savanna grassland environment may have increased the need for early *Nycticebus javanicus* and *N. bengalensis* to travel over ground. Consequently, the change in predation pressure caused by this adaptive shift may have triggered the move towards mimicry, whereby an advantage from mimicking a predator like *Naja naja* was gained. For aerial predators in particular, with their vision hampered by long grass, glimpses of the unmistakeable markings of a spectacled cobra meandering across the ground between trees may have been enough to deter or at least postpone their intended attack.

7.3.2 Dorsal stripe

The dorsal stripe of *Nycticebus javanicus* and *N. bengalensis* bears resemblance to the body of a snake (fig 27). The primary function of this attribute is presumed to have developed as a form of camouflage in an arboreal setting (Bradley and Mundy, 2008) and is observed in other *Lorisidae* (Groves 1998; Nekaris 2003; Nekaris & Jaffe 2007). It is not uncommon, however, for such features to have dual functions (Alterman 1995; Ruxton 2010) and in *Nycticebus javanicus* and *N. bengalensis* may enhance the mimetic potential. Intriguingly, the gait of a slow loris as it moves over ground has also been described as serpentine (Gebo 1987; Osman Hill 1953; Walker 1969; Walker & Nowak 1999). This distinctive gait is present in numerous other prosimian primates, although most pronounced in *Nycticebus* (Shapiro et al. 2001). The exact reason for the lateral spinal bending is uncertain, but is presumed to be an adaptation to locomotion on fine branch supports (Shapiro et al. 2001). Moreover, as the selection process for mimetic traits can only work on external visual characters, any major morphological adaptations such as bone structures would not be affected (Cott 1940; Ruxton 2010). Nevertheless, such sinuous movements observed in slow lorises may enhance the effectiveness of the dorsal stripe as a potential cobra mimic, especially when on the ground and observed from above.

7.4 Acoustic mimicry

> *"Is it not strange that, throughout all nature, from the desolate swamp to the opera-house radiant with electric light, a hiss is an imitation of hostile intent?... One can easily understand that a prowling carnivore which anticipated the presence of something edible in a hole would consider twice before inserting a 'privy paw' when he heard that blood-curdling threat"*(Robinson 1893).

Acoustic mimicry has received little attention compared to visual mimicry over the years despite its obvious role in warning or aposematism (Barber & Conner 2007; Masters 1979). Aposematic traits signal to a potential predator that they might be harmed if they attempt an attack (Cott 1940; Darwin 1871). Many anecdotal accounts of acoustic snake mimicry have reported its presence in a variety of species ranging from honey bees to burrowing owls (*Athene cunicularia*) that mimic the sound of a rattle snake (Barber & Conner 2007; Robinson 1893; Rowe et al. 1986). In snakes, the noisy expirations emitted during a forward attacking strike enhance the aposematic display (Gans & Maderson 1973; Young 2003). Similar snake-like calls emitted during threatening displays are common in reptiles and mammals such as bats (Chiroptera), cats (Felidae), birds (*Athene cunicularia and Parus carolinensis*), lizards (*Pristidactylus volcanensis*) and alligators (*Alligator mississippiensis*) (Alcock 1975; Andrew 1963; Kushlan & Kushlan 1980; Labra et al. 2007; Martin 1973; Robinson 1893; Sibley 1955) and appear to be an archaic call type, which evolved from an aversive respiration sound (Andrew 1963).

The distinctive expiratory pant-grunt produced during aggressive encounters in other slow lorises (*Nycticebus*) (Daschbach et al. 1981; Elliot & Elliot 1967; Zimmermann 1985) and slender lorises (*Loris*) (Schulze & Meier 1995; Still 1905) resembles perfectly the raspy hiss of a cobra during threatening displays (Gans & Maderson 1973). Whilst such acoustic mimicry is yet to be documented in *Nycticebus javanicus* and *N. bengalenis,* this pant-grunt call has been observed in both (pers. obs.) and was accompanied by fast, forward lunges towards its opponent. Such aggressive snake-like behavioural displays with accompanying vocal threats are present in other species (e.g. salamanders, owls and cats) (Brodie 1978; Robinson 1893). The threat of this cobra-like strike is undoubtedly enhanced by the simultaneous emission of the sibilant sound.

7.5 Olfactory mimicry

Odours are used by some animals to advertise their unpalatability (Krall et al. 1999; Marples et al. 1994; Sword et al. 2000), some of which reportedly mimic the odours of others (Czaplicki et al. 1975; Wickler 1968). *Perodicticus potto,* a small nocturnal prosiman and close relative of *Nycticebus,* may also employ olfactory mimicry to attract insect prey (Cowgill 1966). All species of *Nycticebus* produce an exudate from a brachial gland located near the elbow, which when mixed with saliva creates a toxic compound (Alterman 1995; Hagey et al. 2007; Krane et al. 2003). Although the exact purpose of this characteristic remains unclear, proposed functions include olfactory communication and defence against predators (Alterman 1995; Hagey et al. 2007; Rasmussen 1986). Alterman (1995) reported that a number of large predatory mammals immediately retreated when presented with a swab of slow loris toxin. Although recognising it as an obvious deterrent to these species, Alterman conjectured that the odour is unlikely to provide slow lorises with defence from their primary predators, viz raptors and reptiles, which possess different olfactory pathways to mammals. Presumably Alterman was implying the makeup of the olfactory organs in reptiles and birds would be unable to detect this toxic odour. In fact, some snakes and birds are not impassive to olfactory cues, which can illicit behavioural and physiological responses (Greene & Mason 2005; Marples et al. 1994; Mason & Parker 2010; Weldon & Schell 1984). The noxious odour produced by slow lorises, therefore, may also work as a deterrent to these non-mammalian species. Alterman (Alterman 1995) further proposed that the noxious odour produced from the slow loris brachial gland exudate may function to mask the smell left from normal scent marking activities, which could otherwise conveniently lead predators straight to them. Consequently, masking their normal scent with a noxious odour would confuse or discourage predators from pursuing.

If indeed, the lorises do produce a noxious odour to ward off predators, or even to administer a venomous bite if cornered, could this be an additional form of cobra mimicry? Intriguingly, snakes possess two glands near to the cloacal orifice that release secretions containing glandular, volatile and potentially communicative information. During disturbances snakes more often release this volatile and odorous secretion, which is suspected to function as a deterrent or as alarm pheromones (Graves & Duvall 1988; Mason 1992). Olfactory mimicry is far less common than visual mimicry in animals, but certainly exists (Czaplicki et al. 1975; Kaiser 2006; Wickler 1968). Mimicry works on external features only, so the initial evolution of the chemical producing parts in *Nycticebus* would not have been selected for mimicry (Cott 1940; Ruxton 2010). The acquisition of these traits could have been selected for intra-specific communication primarily (Alterman 1995; Hagey et al. 2007; Rasmussen 1986), later to be utilised for mimicry.

7.6 Conclusion

I have discussed the evidence for the evolution of the proposed Müllerian mimicry in *Nycticebus javanicus* and *N. bengalensis*. The fact that both the ranges of mimic and model potentially overlapped at around the time when I predicted the mimicry had arisen, appear to support my hypothesis. Moreover, the dramatic changes in environment coinciding with this coexistence may have created the necessary trigger towards the manifestation of mimicry, which was not present in other *Nycticebus*.

For each of the snake-like mimetic traits discussed, there appears to be a corresponding adaptive advantage gained through mimicry. Some of the potentially mimetic traits are shared by all species of *Lorisidae* and some are present (or are at least more prominent) only in *Nycticebus javanicus* and *N. bengalensis*. As little is known about predation threats to slow lorises, it is difficult to determine here to which predators the mimicry is most effective. Nevertheless, *Nycticebus javanicus* and *N. bengalensis* do appear to inhabit more open habitats compared to the other members of *Nycticebus* (Meijaard 2004a). In the absence of tree cover slow lorises are potentially more vulnerable to predators such as raptors and ground snakes. In a recent study, *Nycticebus bengalensis* was often observed travelling over ground between trees with only long grass as cover (Rogers & Nekaris 2011). Indeed, *N. javanicus* also travels short distances and even forages when on the ground (pers. obs.). However, *Nycticebus pygmaeus* and *N. coucang* also utilise the ground for foraging and travel (Streicher & Nadler 2003; Wiens 2002), raising the question: why did mimicry did not evolve in these species too? The evolution of mimicry primarily requires a threat from a visually orientated predator and the presence of a suitably formidable model to imitate (Ruxton et al. 2004). If either one of these requisites was absent, mimicry would not occur. As *Nycticebus javanicus* and *N. bengalensis* form a close monophyletic group, it is plausible to assume that a certain environmental or predation pressure was lacking in the other species.

Whilst the theoretical framework discussed in this paper provides some support to my hypothesis that *Nycticebus javanicus* and *N. bengalensis* actively mimic *Naja naja*, validation of this hypothesis requires more work. Detailed information on the ecology, habitat use and phylogenetic relationships of slow lorises is still scarce, and future studies may help to shed light on this topic. A closer examination of slow loris predator-prey interactions is vital to unravelling the complex network of selection pressures that have influenced the slow loris phenotype we see today. For example, by identifying which type of predator pose the greatest threat (e.g. aerial, terrestrial or arboreal), in what setting (e.g. arboreal or terrestrial), and in what type of lighting (full moon versus new moon), the exact role of the mimetic traits – particularly when considering the intended dupe – may become apparent. Finally, a better understanding of the function of the slow lorises toxin could provide new clues to their anti-predator strategies and how this evolved.

8. Summary

The research I undertook was based around the IARI slow loris rehabilitation and reintroduction programme that began in 2010. I collected data at different stages of the programme, which particularly for such a lesser-known and threatened taxon, served to (1) facilitate the rehabilitation and reintroduction programme for Indonesian slow lorises; (2) augment the limited knowledge of slow loris behaviour and ecology; and (3) provide insights into the evolutionary processes which have contributed to the moulding of the slow loris behavioural and morphological specialisations they possess today. The first part of my thesis (chapters 3 and 4) deals with issues pertaining to rehabilitation, reintroduction, welfare and conservation. Chapter 5 moves into ecology with subsequent evolutionary implications. Chapters 6 and 7 remain with the evolutionary theme and investigated aspects of slow loris diversity and morphology in relation to mate recognition, communication and anti-predator strategies.

In chapter 3, I present and analyse data compiled by IARI over a four year period revealing demographic trends in slow lorises admitted to the rescue centre. The trends follow those of other rescue centres, where a peak in animals is observed in the first two years, followed by a rapid decline owing to the centres reaching full capacity (Nijman, 2009; Teleki, 2001). One common problem rescue centres face is quickly reaching full capacity owing to an influx of animals admitted in the first two years of opening. Whilst reintroductions can provide some relief to overcrowded centres, the numbers entering usually far outweigh the numbers leaving. Until the trade of animals is reduced, this problem is likely to be on-going. I review the options for animals in rescue centres and discuss possible solutions. I propose that if the animals cannot be released and are destined to a lifetime in captivity, they could be used to promote awareness and subsequently aid in the plight of their wild conspecifics.

Reintroductions can be a sensitive and often controversial affair, and I discuss the numerous issues involved with reintroduction programmes. I provide recommendations to help mitigate the potentially detrimental consequences of conducting reintroductions. Whilst guidelines for reintroductions are already in place (IUCN, 2002), I aim to provide more comprehensive and manageable advice to all parties involved, which considers the respective viewpoints of each.

Chapter 4 of this thesis focusses on describing and predicting the occurrence of stereotypic behaviours in slow lorises at the IARI rescue centre. I hope that by isolating the causes of stereotypic behaviours, we can gain a better understanding of how to mitigate these potentially detrimental behaviours and increase rehabilitation and reintroduction success. My study revealed that around a third of slow lorises displayed at least one type of stereotypy. Pacing was the most prevalent form. I found sex composition and length of time at centre to be associated with stereotypic behaviour, although not in all cases. Slow lorises were less likely to display stereotypies in same-sex cages, compared to mixed sex or in solitary cages; solitary lorises had the highest occurrence of stereotypies. Moreover, lorises recently admitted to the centre were more likely to display stereotypies, which could reflect the stresses of being extracted from the wild and spending time in trade. Despite the results of this preliminary study not being fully conclusive, and revealing that other influencing factors may be responsible for the presence of stereotypies, my findings highlight some aspects of captive management that should be reviewed further. The experiences that slow lorises encounter before reaching IARI is somewhat out of our control; however, improving the welfare of the animals whilst in captivity through better management of social groupings may help to alleviate certain stress related behaviours. By uncovering the causes behind the manifestation of stereotypies the findings could be equally important to other lesser-known species equally impacted by trade.

Chapter 5 of this thesis investigates the ecology of Javan slow lorises in the first ever radio-tracking study of this species. In particular, I examine how the specialist feeding adaptations and potential pollination of angiosperms displayed by Javan slow lorises may provide further evidence to support certain prominent theories of primate evolution. Based on the feeding observations, floral nectar of *Calliandra calothyrsus* comprised 90% of the total. Feeding occurred predominantly in terminal branches whilst in suspensory positions, where flowers were located visually, slowly lured in for feeding manually and subsequently released without damage. This combination of excessive flower visitation, non-destructive feeding and pollen observed on the faces of lorises suggests that Javan slow lorises are potential pollinators of angiosperms. Whilst *C. calothyrsus* is non-native to Indonesia theories of Angiosperm Co-evolution with primates can be disregarded between these two species, co-evolution with other more archaic native species in other areas is possible. Strepsirrhines are renowned for their often 'stereotypically' performed power-grip, however, less so for precise and delicate manipulation of objects. In the three-dimensional world of the fine branch milieu where scent is overwhelming and audition is irrelevant, I propose that stereoscopy and grasping may have developed in response to swaying floral food.

Chapter 6 of my study focusses on the variation in colour between the three slow loris species at IARI and their potential function in mate recognition, communication and anti-predator defences. I analysed 89 photos of Indonesian slow loris facemasks from live animals currently housed at IARI. Variation in colour within species was large and supports the findings by Nekaris and Jaffe (2007) that there may in fact be more species than currently recognised. As slow lorises are monochromatic (Malmstrom and Kroger, 2006) seeing only black and white, with the majority of their potential predators being dichromatic (Bradley and Mundy, 2008; Jacobs, 1993) seeing a reduction in colour vision, I adjusted images to display the respective colour types for what each animal group would perceive. My study built on the suggestions of Nekaris and Munds (2010) that the distinctive facial markings of slow lorises may have aposematic functions. My analysis of the monochromatic and dichromatic image types indicates that monochromatic colour scores were consistently lower than the dichromatic and have probably evolved and adapted for maximum signalling effect when perceived through monochromatic eyes. Furthermore, when combined with the slow lorises toxic attributes, I argue that the distinctive facemasks in slow lorises could serve as a form of aposematism.

In chapter 7, I take a more hypothetical view of anti-predator defences in slow lorises; in particular the Javan and Bengal slow loris. As already partially discussed in chapter 6, the rather conspicuous nature of the face masks of these species appears to serve to deter predators. I postulate that the Javan and Bengal slow lorises actively mimic the formidable predator, the spectacled cobra (*Naja naja*). Whilst the similarities between the facial patterns of Javan and Bengal slow lorises and the spectacled cobra are uncannily similar, I found many other aspects of the slow loris anatomy resemble snakes. Similarities between these species included defensive behavioural postures (Elliot & Elliot 1967; Schulze & Meier 1995), gait (Gebo 1987; Walker 1969; Walker & Nowak 1999) and chemical defence/communication (Alterman 1995). Furthermore, it is possible that ranges of the ancestors of the spectacled cobra and the Javan and Bengal slow loris overlapped previously, at a time when environmental pressures may have provided the impetus for slow loris evolution towards mimicry.

9. Conclusions

In numerous countries across South-east Asia, the future appears particularly bleak for the unfortunate animal species that have high demand as pets and for traditional medicine (Nekaris & Nijman 2007; Nijman 2010; Nijman et al. 2010; Shepherd et al. 2004). Many of these animals are being harvested at extremely unsustainable rates and could face extinction in the near future unless immediate action is taken to curb the trade and protect their habitats (Shepherd et al. 2004). Working alongside law enforcement agencies and governments in countries where trade is a severe threat to biodiversity rescue centres possess a significant potential to facilitate a reduction in this trend (Beck 2010; Cheyne 2008; Teleki 2001). I believe that this potential should be recognised and, perhaps more importantly, acted upon. Rescue centres and welfare groups often come under attack from conservation biologists who contend that valuable funding is wasted on the well-meaning, yet often uninformed and potentially disadvantageous activities of such organisations (Carter 2003; Cheyne 2009; Farmer & Courage 2008; Ware 2001). Conversely, conservationists are often criticised by welfare groups for their lack of compassion for individual animals. Such disputes can only restrict progress. The disputes between these two parties (discussed in chapter 3) focus more on criticism of the immediate outcomes of the respective groups and less so on finding common ground and a way to resolve the pending environmental catastrophe.

Rescue centres provide an outlet for the confiscated animals when law enforcement occurs (André et al. 2008; Beck 2010). Without cooperation between rescue centres and governments, the confiscated animals would have nowhere to go and enforcement may be reduced (Nijman 2009; Nijman et al. 2010). Until such time that conservation efforts manage to fully protect an animals' habitat, the threats from hunting and deforestation will remain. Furthermore, as numbers of threatened species continue to diminish in the wild, the animals housed in rescue centres may provide a last resort to save a species from extinction (Harcourt 1987). If conservation efforts fail to prevent habitat loss and subsequently fail to protect the species residing in them, other avenues including the role of rescue centres have to be explored.

Rescue centres should not be criticised in their work, but diplomatically encouraged with helpful advice. Similarly, conservationists need to be made more aware of individual animal suffering albeit for the good of the species. Both sides need to compromise. Both conservationists and welfare groups have honourable motives behind their actions, and these should not be mutually disparaged. With no obvious abatement in animal trade and the forests fast becoming empty, rescue centres present an untapped resource for conservation when, and even before, the situation becomes critical. Indeed, the work many centres have already started, such as at IARI, is beginning to focus more on conservation. The welfare of individual animals relies to a large degree on providing them with adequate habitat, and this can only be achieved through habitat conservation efforts. With an increasing number of rescue centres around the world housing a variety of threatened species, maybe now is the time for both parties to join forces. Welfare groups should recognise the importance of conservation, and conservationists should realise the potential of rescue centres.

The IARI reintroduction programme has yielded mixed results in terms of viability. Success in such projects can take time as each species is unique and thus requires an understanding of the relevant factors necessary to underpin successful reintroduction. Whether or not reintroduction is a viable solution to the drastic reduction in wild populations and overcrowded rescue centres caused by the burgeoning pet trade remains debatable. Ideally, the nettle must be grasped; the actual source of the problem needs to be resolved. Reducing demand for slow lorises, for example, can be approached through awareness campaigns and enforcing the law with the help of local governments. In the meantime, and until the trade is stopped, reintroductions are a method of supplementing wild populations and provide a chance to assess the overall viability of such projects. If conducted in a completely controlled manner, the risks associated with reintroductions can be minimised.

Unfortunately, not all species receive the same amount of attention from scientists, conservationists and funding bodies (Cheyne 2009; Clucas et al 2008; Ware 2001); consequently, many species are slipping rapidly towards extinction. Reintroductions may not be supported by all stakeholders, but owing to the increasing numbers of displaced animals and dwindling wild populations, they will continue to be conducted (Ware, 2001). In this case, I propose that reintroductions can provide an opportunity to observe lesser-known species in the wild, both in terms of behaviour and ecology, but also from an evolutionary perspective. Learning how an animal behaves in the wild, what resources it requires, and how it has adapted to its environment over time are questions fundamental to the construction of more successful conservation initiatives (Clemmons 1995).

Similarly, whilst captivity is obviously not an ideal scenario from a welfare or conservation perspective, there are situations where many animals cannot be released and where euthanasia is not an option. If a lifetime in captivity is the only option for these animals, is it not in our interests to learn as much as we can from these animals in close proximity before it is too late? Many animals housed in rescue centres are not common in zoos and are difficult to observe in the wild owing to their cryptic nature or general rarity. By taking this opportunity to learn about these species we can increase our scientific knowledge of biological and behavioural aspects of their lives. All of which may improve our current understanding of how we care for them when in captivity or conserve them when in the wild.

My study in Chapter 4 of this thesis, for example, attempted to uncover some of the underlying factors behind the manifestation of stereotypies. The occurrence of these behavioural anomalies are often linked to welfare in captivity (Broom 1983; Mason & Latham 2004). By revealing the main predictors of stereotypies, I hoped to facilitate more adequate captive care for the slow lorises at IARI and elsewhere. Access to a large sample size of captive slow lorises at the centre enabled me to potentially enhance the impact of my findings. Unfortunately, whilst my study did yield some significant results, as is often the case with such studies, the questions set out to resolve were only answered with more questions. Nevertheless, I do feel that this preliminary research into welfare issues does have considerable value to future work and should demonstrate to others, the potential opportunities for studies in rescue centres and other captive facilities.

Likewise, through being involved in the IARI slow loris reintroduction programme, the opportunities of collecting data during the various phases of the programme led to some interesting, albeit preliminary, ecological findings that may be applied to conservation initiatives. In the first semi-wild study of Javan slow lorises, reintroduced lorises on Mount Salak were observed to feed heavily on the nectar of angiosperm plants, particularly *Caliandra callothyrsus* (Chapter 5). Whilst definite pollination of *C. callothyrsus* needs to be confirmed, the evidence put forward in this study appears to support this notion. If future studies can validate the pollination of certain angiosperm plants by slow lorises, their ecological role may actually be of greater significance to maintaining the balance within the ecosystem than was previously assumed. Slow lorises may even become potential candidates for catalysers in forest regeneration programmes via the pollination of angiosperms (Andresen 1999; Bravo 2012; Carthew & Goldingay 1997; Ferrari & Strier 1992).

The past few decades have witnessed a shift in conservation approaches from an emphasis on a single species to that of the whole ecosystem (DeBoer 1979; Lambeck 1997). A better understanding of the intricate network of plant and animal relationships, and in this case, the ecological importance of slow lorises, will no doubt lead to better suited and more comprehensive conservation efforts. The removal of a single species from an intact ecosystem has the potential to disrupt the balance, leading to marked decreases in, and even the extinction of, numerous other associated species (DeBoer 1979). Putting forward new arguments for the ecological significance of slow lorises, based on data collected from IARI, could provide support for increased conservation efforts in maintaining biodiversity. Indeed, slow lorises could be used as an 'umbrella species', or species whose conservation will confer protection to other naturally co-occurring species (Lambeck 1997; Roberge & Angelstam 2004).

The data collected during the time spent at IARI both in captivity and in the wild during the post-release monitoring also offered an opportunity to investigate more evolutionary based questions. Utilising the same ecological data collected from the post-release monitoring phase (Chapter 5), but by interpreting it in a different way, enabled me to make inferences pertaining to the adaptive behaviour and morphology of slow lorises. My study discussed the significance of these new findings in relation to some of the most hotly-debated questions in primate evolution. The observed reliance on angiosperm plants, and the method of acquisition used by slow lorises to obtain nectar, provided novel information on which to test the current evolutionary hypotheses. Owing to the difficult terrain encountered on Mount Salak, there were obviously some obstacles and consequent limitations in data collection, and therefore the major conclusions in my discussion must still be interpreted with caution. However, I hope that this study has helped to highlight the evolutionary importance of studying wild slow lorises, and that future studies can address this exciting and much contested topic.

The regular health checks of all individuals at IARI gave me a brief opportunity to be in close proximity to every slow loris housed at the centre. During this time I was able to photograph each slow loris from numerous angles in order to assess the subtle variation within and between individuals. This study (Chapter 6), as with other studies of slow loris morphological diversity (Nekaris & Jaffe 2007; Nekaris & Munds 2010) was designed to investigate the role of visual communication in relation to the distinct facial markings they possess. In the previous studies (Nekaris & Jaffe 2007; Nekaris & Munds 2010), relatively subjective methods were used to assess and measure colour variation, so here I attempted to employ, for the first time in slow lorises, a more complex and scientific technique to quantitatively measure the variation in colour between individuals. The findings, although not entirely conclusive, perhaps owing to errors in my own sampling techniques, still yielded a number of interesting results. One of which was that the function of the face mask was possibly an aposematic adaptation to predation – a point that had previously been disregarded by Caro (2009). I hope this intriguing finding, together with the others yielded from this study, will be investigated further and that my innovative methods will provide the building blocks for more quantitative studies of slow loris colouration and their associated functions. Whilst this study was primarily focussed on the adaptive significance of such traits, I believe that the methods used here could also be applied in a more conservation related practices. For example, as a method used by law enforcement officials to accurately and efficiently identify species confiscated from markets. Also for rescue centres to ensure that the slow lorises they receive can be housed together with the correct species whilst in captivity to avoid hybridisation.

During the analysis of slow loris colour I happened to notice a fairly striking resemblance of the slow loris face mask to a species of snake, the spectacled cobra (*Naja naja*). On closer examination, I found numerous other characteristics in slow lorises that were remarkably serpentine in appearance. Mimicry is an exciting topic in biology and the study of evolution and so it was with delight that I embarked on this research, which attempted to explain this unusual collection of snake-like loris traits. This particular study was highly theoretical in its structure and certainly needs to be validated further through the conduction of controlled experiments; however, I believe I have provided sufficient background information for these future studies to address. Ultimately I have managed to draw further attention to the uniqueness of slow lorises and have highlighted the dearth of reliable information about the species.

Arguably these theoretical, evolutionary-based studies may not be linked directly to conservation, but I do propose that any study of any aspect of their intriguingly unique and specialised lives will help to bring awareness of their plight. Like other similar rain forest species, the slow loris is indeed on the frontline between conservation and commerce. Only by generating focussed interest through more exciting and thought-provoking studies can we, in the short term, urge funding bodies to support such research and, for the future, hope to achieve a cultural change both towards an abatement of the pet trade and a concomitant affirmation of the welfare of these animals.

10. References

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APPENDIX 1

Reintroduction Guidelines (IUCN, 2002)

BIOLOGY

(i) Feasibility study and background research

- An assessment should be made of the taxonomic status of individuals to be reintroduced.

They should preferably be of the same subspecies or race as those which were extirpated, unless adequate numbers are not available. An investigation of historical information about the loss and fate of individuals from the re-introduction area, as well as molecular genetic studies, should be undertaken in case of doubt as to individuals' taxonomic status. A study of genetic variation within and between populations of this and related taxa can also be helpful. Special care is needed when the population has long been extinct.

- Detailed studies should be made of the status and biology of wild populations(if they exist) to determine the species' critical needs. For animals, this would include descriptions of habitat preferences, intraspecific variation and adaptations to local ecological conditions, social behaviour, group composition, home range size, shelter and food requirements, foraging and feeding behaviour, predators and diseases. For migratory species, studies should include the potential migratory areas. For plants, it would include biotic and abiotic habitat requirements, dispersal mechanisms, reproductive biology, symbiotic relationships (e.g. with mycorrhizae, pollinators), insect pests and diseases. Overall, a firm knowledge of the natural history of the species in question is crucial to the entire re-introduction scheme.
- The species, if any, that has filled the void created by the loss of the species concerned,

should be determined; an understanding of the effect the re-introduced species will have on the ecosystem is important for ascertaining the success of the re-introduced population.

- The build-up of the released population should be modelled under various sets of conditions, in order to specify the optimal number and composition of individuals to be released per year and the numbers of years necessary to promote establishment of a viable population.
- A Population and Habitat Viability Analysis will aid in identifying significant environmental

and population variables and assessing their potential interactions, which would guide long-term population management.

(ii) Previous Re-introductions

- Thorough research into previous re-introductions of the same or similar species and wide-ranging contacts with persons having relevant expertise should be conducted prior to and while developing re-introduction protocol.

(iii) Choice of release site and type

- Site should be within the historic range of the species. For an initial re-inforcement there

should be few remnant wild individuals. For a re-introduction, there should be no remnant population to prevent disease spread, social disruption and introduction of alien genes. In some circumstances, a re-introduction or re-inforcement may have to be made into an area which is fenced or otherwise delimited, but it should be within the species' former natural habitat and range.

- A conservation/ benign introduction should be undertaken only as a last resort when no

opportunities for re-introduction into the original site or range exist and only when a significant contribution to the conservation of the species will result.

- The re-introduction area should have assured, long-term protection (whether formal or otherwise).

(iv) Evaluation of re-introduction site

- Availability of suitable habitat: re-introductions should only take place where the habitat and landscape requirements of the species are satisfied, and likely to be sustained for the for-seeable future. The possibility of natural habitat change since extirpation must be considered. Likewise, a change in the legal/ political or cultural environment since species extirpation needs to be ascertained and evaluated as a possible constraint. The area should have sufficient carrying capacity to sustain growth of the re-introduced population and support a viable (self-sustaining) population in the long run.
- Identification and elimination, or reduction to a sufficient level, of previous causes of decline: could include disease; over-hunting; over-collection; pollution; poisoning; competition with or predation by introduced species; habitat loss; adverse effects of earlier research or management programmes; competition with domestic livestock, which may be seasonal. Where the release site has undergone substantial degradation caused by human activity, a habitat restoration programme should be initiated before the reintroduction is carried out.

(v) Availability of suitable release stock

- It is desirable that source animals come from wild populations. If there is a choice of wild populations to supply founder stock for translocation, the source population should ideally be closely related genetically to the original native stock and show similar ecological characteristics (morphology, physiology, behaviour, habitat preference) to the original sub-population.
- Removal of individuals for re-introduction must not endanger the captive stock population or the wild source population. Stock must be guaranteed available on a regular and predictable basis, meeting specifications of the project protocol.
- Individuals should only be removed from a wild population after the effects of translocation on the donor population have been assessed, and after it is guaranteed that these effects will not be negative.
- If captive or artificially propagated stock is to be used, it must be from a population which has been soundly managed both demographically and genetically, according to the principles of contemporary conservation biology.
- Re-introductions should not be carried out merely because captive stocks exist, nor solely as a means of disposing of surplus stock.
- Prospective release stock, including stock that is a gift between governments, must be subjected to a thorough veterinary screening process before shipment from original source. Any animals found to be infected or which test positive for non-endemic or contagious pathogens with a potential impact on population levels, must be removed from the consignment, and the uninfected, negative remainder must be placed in strict quarantine for a suitable period before retest. If clear after retesting, the animals may be placed for shipment.
- Since infection with serious disease can be acquired during shipment, especially if this is intercontinental, great care must be taken to minimize this risk.
- Stock must meet all health regulations prescribed by the veterinary authorities of the recipient country and adequate provisions must be made for quarantine if necessary.

(vi) Release of captive stock

- Most species of mammal and birds rely heavily on individual experience and learning as juveniles for their survival; they should be given the opportunity to acquire the necessary information to enable survival in the wild, through training in their captive environment; a captive bred individual's probability of survival should approximate that of a wild counterpart.
- Care should be taken to ensure that potentially dangerous captive bred animals (such as large carnivores or primates) are not so confident in the presence of humans that they might be a danger to local inhabitants and/or their livestock.

SOCIO-ECONOMIC AND LEGAL REQUIREMENTS

- Re-introductions are generally long-term projects that require the commitment of longterm financial and political support.
- Socio-economic studies should be made to assess impacts, costs and benefits of the reintroduction programme to local human populations.
- A thorough assessment of attitudes of local people to the proposed project is necessary to ensure long term protection of the re-introduced population, especially if the cause of species' decline was due to human factors (e.g. over-hunting, over-collection, loss or alteration of habitat). The programme should be fully understood, accepted and supported by local communities.
- Where the security of the re-introduced population is at risk from human activities, measures should be taken to minimise these in the re-introduction area. If these measures are inadequate, the re-introduction should be abandoned or alternative release areas sought.
- The policy of the country to re-introductions and to the species concerned should be assessed. This might include checking existing provincial, national and international legislation and regulations, and provision of new measures and required permits as necessary.
- Re-introduction must take place with the full permission and involvement of all relevant government agencies of the recipient or host country. This is particularly important in reintroductions in border areas, or involving more than one state or when a re-introduced population can expand into other states, provinces or territories.
- If the species poses potential risk to life or property, these risks should be minimised and adequate provision made for compensation where necessary; where all other solutions fail, removal or destruction of the released individual should be considered. In the case of migratory/mobile species, provisions should be made for crossing of international/state boundaries.

PLANNING, PREPARATION AND RELEASE STAGES

- Approval of relevant government agencies and land owners, and coordination with national and international conservation organizations.
- Construction of a multidisciplinary team with access to expert technical advice for all phases of the programme.
- Identification of short- and long-term success indicators and prediction of programme duration, in context of agreed aims and objectives.

- Securing adequate funding for all programme phases.
- Design of pre- and post- release monitoring programme so that each re-introduction is a carefully designed experiment, with the capability to test methodology with scientifically collected data. Monitoring the health of individuals, as well as the survival, is important; intervention may be necessary if the situation proves unforseeably favourable.
- Appropriate health and genetic screening of release stock, including stock that is a gift between governments. Health screening of closely related species in the re-introduction area.
- If release stock is wild-caught, care must be taken to ensure that: a) the stock is free from infectious or contagious pathogens and parasites before shipment and b) the stock will not be exposed to vectors of disease agents which may be present at the release site (and absent at the source site) and to which it may have no acquired immunity.
- If vaccination prior to release, against local endemic or epidemic diseases of wild stock or domestic livestock at the release site, is deemed appropriate, this must be carried out during the "Preparation Stage" so as to allow sufficient time for the development of the required immunity.
- Appropriate veterinary or horticultural measures as required to ensure health of released stock throughout the programme. This is to include adequate quarantine arrangements, especially where founder stock travels far or crosses international boundaries to the release site.
- Development of transport plans for delivery of stock to the country and site of reintroduction, with special emphasis on ways to minimize stress on the individuals during transport.
- Determination of release strategy (acclimatization of release stock to release area; behavioural training - including hunting and feeding; group composition, number, release patterns and techniques; timing).
- Establishment of policies on interventions (see below).
- Development of conservation education for long-term support; professional training of individuals involved in the long-term programme; public relations through the mass media and in local community; involvement where possible of local people in the programme.
- The welfare of animals for release is of paramount concern through all these stages.

POST-RELEASE ACTIVITIES

- Post release monitoring is required of all (or sample of) individuals. This most vital aspect may be by direct (e.g. tagging, telemetry) or indirect (e.g. spoor, informants) methods as suitable.
- Demographic, ecological and behavioural studies of released stock must be undertaken.
- Study of processes of long-term adaptation by individuals and the population.
- Collection and investigation of mortalities.
- Interventions (e.g. supplemental feeding; veterinary aid; horticultural aid) when necessary.
- Decisions for revision, rescheduling, or discontinuation of programme where necessary.
- Habitat protection or restoration to continue where necessary.
- Continuing public relations activities, including education and mass media coverage.
- Evaluation of cost-effectiveness and success of re- introduction techniques.
- Regular publications in scientific and popular literature.

APPENDIX 2

Basic ethogram used for captive and wild data collection, adapted from ethograms by Fitch-Snyder et al. (2001) and Glassman and Wells (1984).

Code	Behaviour	Description
AC	Active	No movement, eyes open
IN	Inactive	No movement, eyes closed
FE	Feed	Feeding
FO	Forage	Searching for food
TR	Travel	Travelling
GR	Grooming	Groom oneself
SO	Social	Interactions with conspecifics
OT	Other	Other behaviours not included above

Breakdown of behaviours listed in basic ethogram (above)

FEED		
	FM	Feeding directly from mouth
	FH	Feeding using hand (1 or 2)
	DM	Lap water with tongue
	DH	Drink using hand
SOCIAL		
	SGA	Allo-groom
	SAP	Approach conspecific
	SAPP	Approach conspecific and pass
	SFW	Follow conspecific
	SDP	Depart from conspecific
	SMO	Mount attempt
	SCO	Copulation
	SEX	Social Explore - sniff a conspecific
Play	**PL**	Play
	PS	Solicit play behaviour
	AT	Attack a conspecific
Aggressive	**ADE**	Defensive threat from conspecific attack
	ATH	Threaten a conspecific
	ASU	Submissive position
	ARE	Retreat - fast movement away from conspecific
GROOM		
	GL	Self-groom - lick or use tooth comb
	GS	Self-groom - scratch with grooming claw
	GFA	Self-groom - facial rubbing using arms
	GFO	Self-groom - facial rubbing using object
OTHER		
	FZ	Freeze - for >3 seconds at sign of disturbance
	RA	Run away from stimulus
	BA	Back away from stimulus
	DEF	Defecation
Stereotypic	**STEP**	Stereotypic - Pacing
	STEH	Stereotypic - Rolling of head
	STEC	Stereotypic - Circular locomotion on cage
Olfactory	**SMT**	Scent mark via urine Trail
	SMD	Scent Mark via urine Dab
	SN	Sniff - apply nose to objects
Vocal	**VO**	Sound emitted from mouth

APPENDIX 3

Postural and locomoter modes adapted from Glassman and Wells (1984) and Nekaris (2005)

Postural Mode	Description
P4	Quadrupedal stand
P2	Bipedal stand
P3	Triplets
PS	Sit
PC	Crouch
PS4	4 limb Suspension
PS3	2 limb suspension
PS2	3 limb suspension
PS1	1 Limb suspension
PT	Postural transition
PSP	Sleeping ball
PB	Bridge

Locomotor mode	Description
L	Quadrupedal walk
LC	Climb ascent
LD	Climb descent
LSH	Locomote horizontally on vertical substrate
LB	Bridge whilst locomoting
LCB	Locomote bridge climb
LDB	Locomote bridge descend
LP	Pull-up
LS	Locomote suspensory
LSC	Locomote suspensory climb
LSD	Locomote suspensory descend
LSB	Locomote suspensory bridge
LO	Other

Information relevant to postural and locomotor modes
Substrate angle: Horizontal, 30, 60, 90
Substrate Type: BH=branch, T=terrestrial, C=cage, NB=nestbox, FT=Feeding trough, BR=Black Rubber
Substrate size: Branch = small < 10cm, Medium 10-20, Large >20