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The ecophysiology of seed dispersal by Orangutans in Bornean peat swamp forest

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UNIVERSITY OF
WOLLONGONG

Department of Biological Sciences

THE ECOPHYSIOLOGY OF SEED DISPERSAL BY ORANGUTANS IN A BORNEAN PEAT SWAMP FOREST

Students Full Name

Esther Tarszisz

"This thesis is presented as part of the requirements for the
award of the Degree of Doctor of Philosophy
of the
University of Wollongong"

Month and Year

March 2016

To Ethan and Avery – you are my eternal joys

ABSTRACT

The study of an ecosystem process like seed dispersal is at the forefront of the dynamic field of ecophysiology, the study of how animals and environments interact. Understanding spatial movements is essential to unravelling how animals interact with their ecosystem and tie animal ecology to ecosystem processes, particularly to animal mediated seed dispersal (zoochory). The movement of seeds through an animal gut (endozoochory), from one place to another is an essential driver of forest structure and is a complex process that depends on a variety of environmental and physiological factors. Seed dispersal is a crucial component of plant population dynamics, influencing plant populations and communities through both short and long distance dispersal. The spatial arrangement of seed deposition also contributes to at least half the gene-flow of plants, and their population genetic structure can be highly dependent on fauna-mediated seed dispersal, particularly in tropical regions.

A review on the role of physiology in conservation translocation was evaluated for over a decade worth of peer-reviewed studies (2000-2010) to highlight both the relative rarity of including physiological analyses in such a significant conservation undertaking, and the absolute essentiality of addressing this lack, especially in the face of todays changing world.

The data here link a number of stages in endozoochorous provision by the orangutan. In an *ex-situ* setting, the first ever measurement of the transit time of indigestible seed mimics was made, with study subjects that were fed a diet consisting largely of plant matter. Elimination pattern of seed mimics was measured, demonstrating a pulse dose excretion, often in one or two single defecation events, with smaller amounts both before and after this peak. The average transit time of seed mimics across all bead sizes was 76 hours, a figure that was later used to create a predictive model of faecal deposition patterns of seeds in an *in-situ* situation. Orangutans were shown to have the potential to provide very long distance dispersal from the parent plant due to their long transit times and large home ranges. Large bodied frugivores, such as the orangutan, are likely to be critically important seed dispersers as there are typically few animals that can effectively disperse large-seeded species. This has often lead to co-evolution of the plant-animal interaction particularly with regards to large seeds which many other frugivores cannot swallow intact.

The application of Time Local Convex Hull (T-LoCoH) is the first objective tool of its kind in orangutan ecological research in tropical peat swamp forest (TPSF), and the first application of T-LoCoH to ecological service provision anywhere. T-LoCoH is a new technique that models animal movement over both time and space. This modeling accurately predicted where orangutans would deposit faeces when compared to real-time data gathered in the Sabangau Forest, Central Kalimantan, Indonesia (Indonesian Borneo). This environment exhibits a relative lack of secondary seed removal and orangutans can be expected to play a disproportionate role in seed dispersal here, particularly of large sized seeds and over wide ranging areas. This method provides a basis to establish a training method to make *a priori* projections of seed dispersal dynamics in novel ecosystems.

Evaluation of post-defecation germination potential of seeds provided further insight into the orangutan;s role in dispersal of 13 different seed species. Surprisingly endozoochorous travel through the orangutan gut was not the most significant factor in germination as manually extracted seeds showed the highest rates of germination over both orangutan "gut-treated" seeds and whole fruits. However seeds passed intact via orangutan faeces still germinated and contributed to the primary dispersal of many plant species. Orangutans might also play a more important role in germination when seeds are moved, by spitting whole seeds out.

ACKNOWLEDGEMENTS

Firstly, the largest thanks goes to my supervisor Dr Adam Munn, for his guidance and encouragement. Even through adversity (on both sides), you've always been my support, through difficult times both in Borneo, Australia and even Antarctica, when I wanted to give it all up.

I am grateful to all the Indonesian authorities for granting me permission to undertake this research project in Sabangau: the Indonesian Institute of Sciences (LIPI), specifically the director of the research centre for Biology (Pusat Penelitian Biologi), Dr Siti Nuramaliati Prijono; the Indonesian Department of Forestry (PHKA); and OuTrop's (The Orangutan Tropical Peatland Project) sponsor, CIMTROP (Centre of International Co-operation in Management of Tropical Peatlands).

For financial support, a debt of appreciation goes to the Australian Commonwealth for granting me an Australian Postgraduate Award, which allowed me to carry out this research project. Also to the travel grant/UMAP Scholarship funds which allowed me to travel to Borneo the first time without dipping into project or personal money.

A big thanks goes to the staff at Taronga and Perth Zoos who were of paramount assistance in the *ex-situ* portion of my fieldwork. This work was made possible with support from many members of both Taronga and Perth Zoo's. At Taronga Zoo I would like to thank: Larry Voglenest, Rebecca Spindler; Paul Thompson; Katie Hooker, Michael Shiels and Louise Grossman; as well as all the other wonderful and helpful Taronga Zoo primate keepers and Jo Wiszniewski in the research office. At Perth Zoo I would like to thank: Katja Geschke; Holly Thompson; Kylie Bullo and all the other fantastic Perth Zoo primate keepers, and Caroline Lawrence in the research office.

Another big thank you goes to the OuTrop directors, particularly Dr Mark Harrison and Dr Helen Morrogh-Bernard. Mark especially pushed for this topic, recognising a knowledge gap on the ecosystem service provision of seed dispersal by orangutans.

I owe Professor Chris Dickman continual thanks for so many things over the years: Being a wonderful lecturer of biology as an undergrad vet student; support during my masters; during the inception of my PhD; for help editing my literature review which you graciously accepted an authorship for; and for countless references over the years for different jobs and grants..

My intense and forever gratitude to Dr Sean Tomlinson who provided invaluable help with the grappling and (somewhat) taming of the R programming language. I am not now, nor will ever be, a computer programmer, but you made it possible for me to conduct what I feel is the most adaptable and far reaching portion of my research. Editorial advice was also very much appreciated (no matter how much I complained). Our cross continental email hilarity was also appreciated. I fear (and like) that we know too much about each other, without having met…yet. There's some bourbon, a glass and an ear waiting for you here in Sydney when you stop by.

I have a great appreciation for the other PhD researchers at OuTrop whom I had the good fortune to meet and spend some time with especially my roomie Amanda Hoepfner, as well as Aimee Oxley and Megan Cattau. You guys provided me with sanity in an insane world.

A special thanks goes to my field assistant, Aman, for working with me and collecting my less than pleasant samples. Thank you to other OuTrop personnel including Pau Bongo who took me to hospital when I broke my finger. To all the interns who collected samples for me as well in particular Samantha Tesoriero, Helen Thompson, Hélène Birot, Claire Juliet Neale, Marina McMullin and others whose name I may have forgotten here and to the volunteers, particular Brooke Robertson, Bronwyn Eva and others who I may have forgotten who checked my darling little seeds for radicle emergence when I had to go to town.

Thank you to all the other OuTrop research assistants, Adul, Azis, Aziz, Ciscoes, Santi, Supian, Siswanto, Udin, whose sense of humour, camaraderie, and hard work made for a more rewarding and enjoyable experience. A special thanks to the chefs in the kitchen, Lis, Ibu Yanti, Ibu Jariah for getting up at stupid-o'clock-in-the-morning to make sure no one went in the forest hungry and keeping me sustained (and to the Ibu's for pounding out my disgusting, peat soaked clothes – you both are amazing!). Additional thanks goes to Riethma Yustiningtyas for her fantastic administration in town. Also thanks to the CIMTROP patrol team, especially Krisyoyo, Idrus, Bina and Yanto for their vital work in fighting forest fires around Sabangau and the effective protection of the research area. I would also like to thank Eja Hafiz at Lahuka, who worked diligently on my behalf in Jakarta ensuring I got my research permit and all the necessary documentation to go into the forest. An additional thank you to Rosalie Dench who sourced me first adrenaline vials and then the much more convenient form of it in an epi-pen after I discovered, the hard way, on my first day back of my second field season, that I am exceptionally, life-threateningly allergic to bees and wasps. Without those I would not have been able to safely head back out into the forest although thankfully it wasn't needed again. Oh and for introducing me to Sherlock!

A special thanks to all the orangutans – it was a privilege to follow you, and even to collect your…ahem…deposits. You make the forest go round, literally, and have provided me with some of my best wildlife experiences out of a pretty good list thus far.

Thank you also to anyone I may have forgotten or not had space to mention.

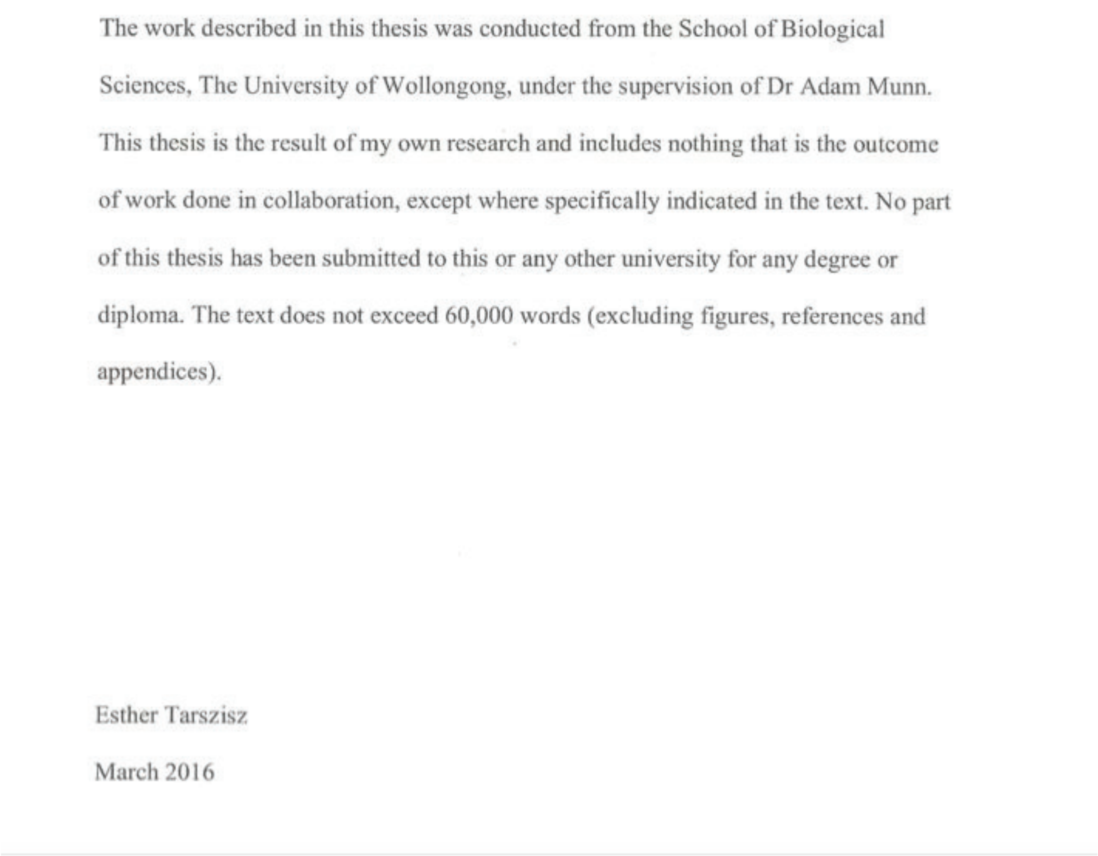
A special shout out to the crew at Davis Station, Antarctica who supported me through the last few months of my write-up in between elephant seal capture-and-tagging particularly Wade, Jenn, Sue, Louise and Clive. It's a strange place to finish a PhD whose field work was based in the tropics, but I always have to do things in odd ways it seems. A special thank you and remembrance to Dave Woods whose passing during my time there was an enormous tragedy. Your positivity inspired me to look, at myself and my place in the world, differently and for the better and I thank you and the team who worked so hard to rescue you.

To Ilana (+ Minty), not only have we been friends for coming up to 31 years, but you also opened your home to me during the last year of my write up, and charged me laughably low rent so I could finish up my PhD and not have to live off beans. To Anne (+ Michael, Phil & Hero) whose inspired shut-up-and-write sessions were the most productive times during my entire writing-up process. As well as just the love, support and friendship from you both as well as my other dear friends who have helped me debrief from PhD (and other) craziness both near and far away: Tal, Galya, Fletchy (+ MT & Ferguson), and Nicky.

Lastly and most importantly to my family, who have offered me endless support throughout my life. I think y'all will be as glad as I am that I'm finishing this thing. To The Reins: Marianne, Nigel, Gabi and Michael (+ Mia & Kenji) – you can now talk to me without me snapping at you. Even more so and importantly, to the Tushtons, firstly to Naomi and Phil (+ Beanie). You have housed, fed and loved me, even at my most unlovable, saddest and grouchiest. I will never be able to express my gratitude enough for your love and support. To your children, Ethan and Avery, to whom this document is dedicated to – you are the future and my future and I hope that I can leave the planet at least a tiny-weeny bit better off than I arrived on it, for you both. Last and mostly to my Mum and Dad who with their unwavering love, encouragement and faith. Without you I wouldn't be anywhere, ever. You have supported me through life and it was a toss up who to dedicate this too. You both know how much I love you plus you're not as cute as the little-un's so you lost out there. Also a mention goes to my grandparents: Zahava, Alan and Joan. I wish you could have been alive to have seen me become a vet, do a masters and now finish a PhD. I know you all would have been so proud.

And last but never least to Licorice, my true love, you are in my heart always.

PREFACE



The work described in this thesis was conducted from the School of Biological Sciences, The University of Wollongong, under the supervision of Dr Adam Munn. This thesis is the result of my own research and includes nothing that is the outcome of work done in collaboration, except where specifically indicated in the text. No part of this thesis has been submitted to this or any other university for any degree or diploma. The text does not exceed 60,000 words (excluding figures, references and appendices).

Esther Tarszisz

March 2016

AUTHORISATION OF STYLE 2

The candidate and the primary supervisor agree that Style 2 is the thesis format to be used for this thesis.

Esther Tarszisz PhD Candidate	Adam Munn Primary Supervisor

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1 ANIMAL MEDIATED SEED DISPERSAL

1.1 INTRODUCTION

Seed dispersal is an essential ecosystem function connecting individual plants to vegetation structure. It links adult plants with their offspring's potential establishment (Wang and Smith, 2002, Nathan et al., 2011, McConkey et al., 2012) as well as maintenance of heterogeneity (Wang and Smith, 2002, Bascompte and Jordano, 2007, Schupp et al., 2010, Côrtes and Uriarte, 2013). Seed dispersal is critical to ecosystem functioning and understanding of plant population dynamics (Jordano and Herrera, 1995, Schupp et al., 2010) and community structure and dynamics (Levin et al 2003, Howe & Miriti 2004). Primary seed dispersal forms part of the seed dispersal cycle (Wang and Smith, 2002, Stoner et al., 2007a), while preparing for seed predation and competition (Nathan et al., 2011) and further, secondary dispersal methods (Wang and Smith, 2002).

Dispersal of a plant's genetic offspring, the seed, away from the parent plant is believed to confer a number of possible advantages on the seed. It can potentially reduce the exposure of the seed/s to seed predators and pathogens (Levin et al. 2003), reduce competition with the parent plant, and also other offspring (Levin et al., 2003, Muller-Landau, 2007, Ruxton and Schaefer, 2012), and can thin the risk from stochastic events (Nathan, 2006). In this way, the continued viability of a plant ecosystem may be dependent on the populations of animals that it in turn sustains.

Primary seed dispersal is concerned with the initial seed dispersal event and it can occur through a number of mechanisms, both abiotic and biotic. Zoochory, or animal mediated dispersal, is the mode of dispersal we are most concerned with here and seed dispersal, particularly in the tropics, (Jordano, 2001, Stoner et al., 2007a) can largely be attributed to animals transporting seeds through their gastrointestinal system (endozoochory), and to a lesser extent seeds on their coats (epizoochory), e.g. (Blondel, 2003). Other methods of primary seed dispersal are either mediated by plant characteristics or abiotic mechanisms such as wind or water (Levin et al., 2003, Nathan, 2006).

1.1.1 An overview of zoochory – Animal mediated seed dispersal

Animal mediated seed dispersal (zoochory) has been demonstrated to have significant importance in many forest types. These include neotropic, paleotropic, Americas, Africa, and Indo-Malaysian regions (Corlett, 1998, Stoner et al., 2007a), with many studies finding mammal and bird species as the most important groups for seed dispersal in tropical regions (Jordano, 2001, Bascompte and Jordano, 2007, Stoner et al., 2007a). There have also been findings indicating that although different animal guilds may disperse some of the same plants, the patterns of how the guilds disperse seeds differ and rather than being redundant, are complementary (McConkey and Brockelman, 2011, Escribano- Avila et al., 2014). Tropical plant species have particularly high reliance on animals for their dispersal, with over 40-90% depending on animals for seed dispersal (Jordano, 2001, Bascompte and Jordano, 2007, Côrtes and Uriarte, 2013).

1.1.1.1 Endozoochory

Endozoochory is the process of ingestion and then subsequent defecation of seeds by animals (Traveset et al., 2007a, Herrera, 2009). Plants attract animals using their fruit as a lure, and generally speaking, plants dispersed by vertebrate endozoochory have edible components covering the seeds that are eaten and pass through the digestive tract to be deposited at a later time (Levin et al., 2003, Herrera, 2009). This is influenced by factors including food handling, ingestion and or regurgitation, physiological drivers such as satiety, behaviour, gut structure, and properties of ingesta affecting gut throughput and defecation (Cousens et al., 2010).

1.1.1.2 Epizoochory

Epizoochory is the transport of seeds outside of an animal on the animal's coat. This depends on the ability of the seed (or other dispersal unit/diaspora) to attach and be retained on an animal's fur (Will et al., 2007). This ability is due to two factors – the morphology of the diaspora and the structure of an animal's coat of hair/wool/feathers (Tackenberg et al., 2006, Cousens et al., 2010). Both these components influence the strength of attachment. Plant factors that impact on the number of seeds dispersed by epizoochory include the number of seeds available at any one time, their maturity, their height relative to the animal, location on an animal's coat, periods of hair growth and moult, and the frequency and location of animal grooming (Cousens et al., 2010).

Environmental and physiological factors related to an animal will also affect where, when and how many seeds are dispersed by epizoochory. Environmental factors include vegetation structure, water levels (Cousens et al., 2010) and cannot be wholly separated from how an animal moves through its environment. Furthermore, movement factors are themselves influenced by numerous physiological processes. I was not able to measure the impact of epizoochory on seed dispersal, however during 100s of hours of orangutan observations, seeds were rarely observed to cling to coats (when viewing orangutans through binoculars) as they travelled through the canopy.

1.1.1.3 Seed spitting

One aspect of animal-mediated seed dispersal that has oft been overlooked is that of seed spitting and carrying with subsequent spitting/dropping (McConkey and Brockelman, 2011). Spitting in particular may be quite important as often fruit pulp can contain germination inhibitors, and the processing of fruit in a primate's mouth (i.e. "cleaning" off the pulp) can result in germination deinhibition (Yagihashi et al., 2000, Robertson et al., 2006).

1.2 CURRENT TRENDS IN ZOOCHORY RESEARCH

The Janzen-Connell or 'escape' hypothesis, which has long been held as a stalwart in seed dispersal research (Janzen, 1970, Connell, 1971, Howe and Smallwood, 1982b, Howe and Miriti, 2000, Terborgh, 2012, Terborgh, 2013, Comita et al., 2014), advanced the notion that long distance dispersal from the parent trees improved survivability by protecting seeds and seedlings from density-dependent mortality from seed predators or pathogens (Howe and Smallwood, 1982b, Howe and Miriti, 2000). The 'escape' hypothesis has been shown to have relevance, with numerous studies and meta-analyses showing a degree of total density-dependent mortality as predicted by the Janzen-Connell hypothesis e.g. (Harms et al., 2000, Howe and Miriti, 2000), although some have shown none e.g. (Hyatt et al., 2003). Thus the Janzen-Connell hypothesis is relevant, but only for some plant species and for some of the time. Other influences can be involved in zoochory which depends on a myriad of factors and inputs into "the seed dispersal loop" (Wang and Smith, 2002).

Recently the call from seed dispersal researchers has been to move away from context-dependent models of seed dispersal and create more integrative approaches that allow for better predictions within changing conditions and landscapes (Cousens et al., 2010, McConkey et al., 2012, Ruxton and Schaefer, 2012, Côrtes and Uriarte, 2013). By and large, seed dispersal research has focused on data that relate to the time and place from which the data have been collected, rather than moving towards more processed-based models (Cousens et al., 2010, Côrtes and Uriarte, 2013). Seed deposition is related to animal movement that is itself influenced by the interplay of a wide range of physiological and environmental factors (Nathan et al., 2008a, Cousens et al., 2010, Côrtes and Uriarte, 2013). Connecting animal movement and the physiological drivers behind this movement to endozoochory has been deemed to be of prime importance in seed dispersal research (Cousens et al., 2010, Ruxton and Schaefer, 2012, Côrtes and Uriarte, 2013).

Animal movement is a complex area of study that has been making continuous advancements as global position systems (GPS) and tracking technology improve (Côrtes and Uriarte, 2013). While incorporation of random walk models into seed dispersal studies is an advancement to habitat use descriptions (Côrtes and Uriarte, 2013) its assumptions contain inherent flaws, as animals do not walk randomly. Rather, animals' movements can be determined by the interplay of numerous factors such as satiety, thirst, social factors, predator-prey interactions, and reproductive state (Cousens et al. 2010). Random walk models also have to be quantified under specific conditions, which can make their application to different situations of limited value (Cousens et al. 2010). Cŏrtes and Uriarte (2013) reviewed a number of studies where a greater degree of realism was incorporated into movement decisions in relationship to seed dispersal (Levey et al., 2005, Russo et al., 2006, Levey et al., 2008, Uriarte et al., 2011).

1.2.1 Primates and Primary Seed Dispersal

Primates have been documented throughout their taxa and ranges to play a significant role in primary seed dispersal (Wrangham et al., 1994, Chapman and Onderdonk, 1998, Poulsen et al., 2001, Chapman and Russo, 2003, Nuñez-Iturri and Howe, 2007). Primate contribution to seed movement in the tropics has been well researched in a number of species and locations e.g. the tantalus monkey (*Chlorecebus tantalus tantalus*) in Nigeria (Agmen et al., 2010), the woolly monkey (*Lagothrix lagothricha lugens*) in Colombia (Stevenson, 2000, Stevenson and Guzmán-Caro, 2010), the drill (*Mandrillus leucophaeus*) in Cameroon (Astaras and Waltert, 2010); tamarins (*Saguinus mystax* and *S. fuscicollis*) in Peru (Culot et al., 2010); and chimpanzees (*Pan troglodytes*) in Rwanda (Gross-Camp et al., 2009), among many others. However, information within tropical peat-swamp forest (TPSF has received limited attention (see section 1.3 for description of the ecological and environmental importance of PSF).

Evidence indicates that despite there being a broad variety of mammalian and avian taxa that disperse seeds, e.g. (Howe and Smallwood, 1982a, Corlett, 1998), primate extirpations do not necessarily lead to compensation in seed dispersal by other frugivores (Poulsen et al., 2002, Jordano et al., 2007, Wang et al., 2007, McConkey and Brockelman, 2011), suggesting that different taxa occupy different roles in seed dispersal (Poulsen et al., 2002, Jordano et al., 2007) and that different frugivores can complement rather than overlap in their roles (McConkey and Brockelman, 2011).

A number of studies in tropical forests have demonstrated that low densities of animal seed dispersers can eventually depress forest recruitment (Nuñez-Iturri and

Howe, 2007, Peres and Palacios, 2007, Stoner et al., 2007a, Melo et al., 2010). Primates, relative to their number, make up a disproportionally large part of a forest's biomass (Chapman and Russo, 2003, Wang et al., 2007) and thus have the potential to disproportionally contribute to seed dispersal relative to their numbers. It follows that the presence of primate species can be an important ecological contributor to the maintenance of forest structure and their absence can cause alterations of forest structure (Wrangham et al., 1994, Webb and Peart, 2001, Peres and Palacios, 2007, Wang et al., 2007), including reduction in forest plant community heterogeneity/biodiversity (Peres & Palacios 2007).

Primates of different sizes have been shown to handle different sized fruits and seeds in a way that can be predicted from their body size (Peres & Palacios 2007), as is typical of fruigvores across all taxa and accordingly, big seeded fruits are able to be passed intact through the gut in a smaller number of dispersers, with the largest seeds being dependent on a few species that may be highly vulnerable to habitat and hunting pressures e.g. (Corlett, 1998, Beckman and Muller-Landau, 2007, Corlett, 2007, Muller-Landau, 2007, Nuñez-Iturri and Howe, 2007, Stoner et al., 2007a, Terborgh et al., 2008, Bradford and Westcott, 2010, Ruxton and Schaefer, 2012, Vidal et al., 2013). Orangutans, as the largest-bodied arboreal frugivore in tropical peat swamp forest (and Asia) (Ancrenaz et al., 2008), likely have heightened potential for primary dispersal of large-seeded species, as well as small and medium sized species.

1.3 TROPICAL PEAT SWAMP FOREST: THE SABANGAU ECOSYSTEM

Tropical peat swamp forest (TPSF) is of significant importance to world carbon stores, containing up to 20% of global peat-soil carbon (Gorham, 1991). Of the CO_2

emissions caused by peatland destruction, 90% in Southeast Asia was reported to be emitted by Indonesia (Hooijer et al., 2006, Limpens et al., 2008).

Since TPSF comprises an important sink of global carbon stores, alteration to this habitat has the potential to affect the global climate. This was evidenced in 1997 when catastrophic fires (due to a combination of peat drainage, see 1.2.4 and drought caused by El Niño effects) released up to 40% of the total annual world carbon emissions from fossil fuels and lead to a major increase in global atmospheric CO_2 concentration since 1957, when recordings began (Page et al., 2002, Limpens et al., 2008). In addition to carbon storage, TPSF has other roles of environmental importance: high biodiversity; regulation of hydrology over large areas; and contains valuable sustainable forest products (Husson et al., 2001 , Page et al., 2008, Page et al., 2011, Posa et al., 2011).

Despite covering large amounts of Kalimantan, compared to other forest types, study of TPSF was minimal until the establishment of the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP) when these areas started to be explored e.g. (Rieley et al., 1997, Shepherd et al., 1997, Page et al., 1999, Page et al., 2002, Page et al., 2008, Page et al., 2011, Posa et al., 2011, Siegert et al., 2013).

The Sabangau Forest is a fully-ombrogenous deep-peat-swamp forest (PSF) (Page et al., 1999, Husson et al., 2009). Ombrogenous describes a system whereby the nutrient input is received wholly though rainfall, aerosols and dust (Page et al., 1999, Husson et al., 2009). An exception to this is the riverine areas which may receive nutrients during the wet season when the river floods (Shepherd et al., 1997).

1.3.1 Habitat and vegetation

TPSF structure and plant heterogeneity is determined by the interplay between peat thickness, hydrology, chemistry and organic matter (Page et al., 1999, Page et al., 2008). A salient feature of TPSF is its variable forest floor topography which is comprised of hummocks (raised areas) and hollows (depressions) (Page et al., 1999, Shimamura and Momose, 2005, Page et al., 2008) which may affect seedling recruitment and survival (Shimamura and Momose, 2005), as well as contributing to high tree species biodiversity via creation of habitat boundaries, or partitioning (Koponen et al., 2004, Shimamura and Momose, 2005). The arrangements of these microtopological features is thought to be due to an interplay of emerging pneumatophores as well as fallen trees and branches, differing growth and decay rates (Lampela et al., 2014) as well as large water level fluctuations and gentle slopes (Dommain et al., 2010). Lampela et al (2014) also found that the chemical composition of hummocks and hollows differed and thus may also play a role in tree species partitioning.

There are four distinct forest habitat sub-types: Mixed-swamp; low pole; tall interior and very-low canopy. Each area has been assessed for orangutan densities based on nest counts (Husson et al., 2009) and see Fig 1.1.

a) Mixed swamp forest (MSF)

The majority of Sabangau's orangutan population is found within MSF, at a density of 2.35 orangutans/km^2 (Husson et al., 2009) and almost all of my field research was conducted within this habitat. This is the most extensive habitat present in the Sabangau forest. It is positioned beyond riverine flooding limits and is on the margins of the peat dome (Page et al., 1999). Peat depth ranges from 2-6m, with 3 strata of trees: ground strata (7-12m), mid-level (12-20m) and a maximum canopy height of

35m, with pneumatophores (breathing tree roots) occurring frequently (Page et al., 1999). MSF mostly dries during the dry season and floods during the wet season (Page et al. 1999).

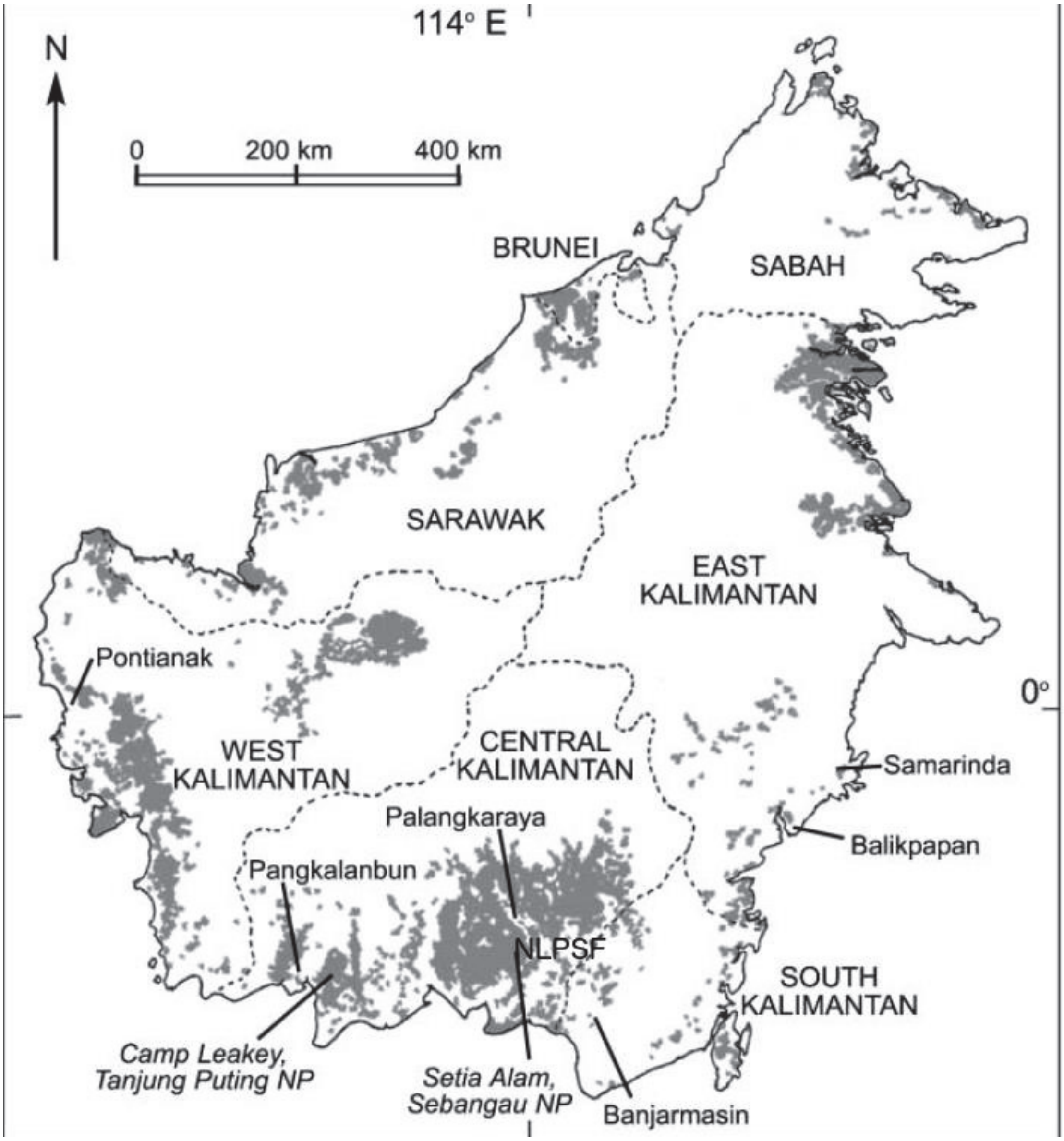

Fig 1.1a: Map of Borneo [Adapted from (Struebig and Galdikas, 2006)]

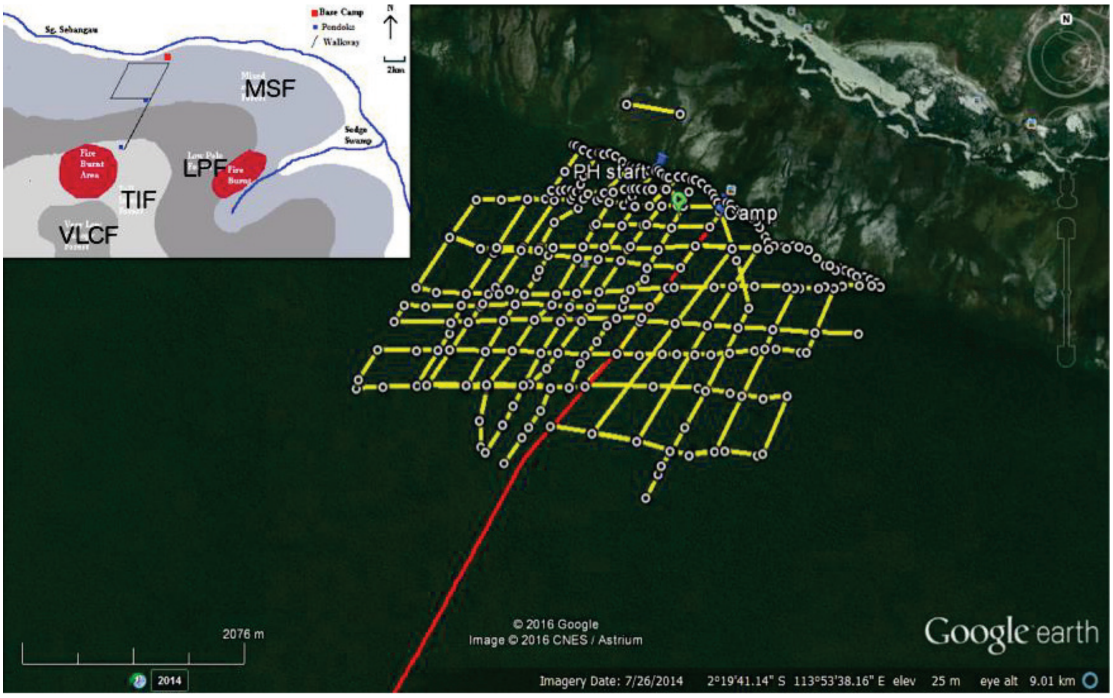

Fig 1.1b: Map of Natural Laboratory of Peat swamp forest. [Source: Google Earth, 2016, Grid points courtesy of OuTrop]. Inset showing map of forest sub-types, MSF= mixed swamp forest, LPF = low pole forest, TIF = tall interior forest; VLCF = very low canopy forest. [Map courtesy of OuTrop]

b) Low pole forest

Low-pole forest has the lowest orangutan density of 1.12 orangutans/km^2 (Husson et al., 2009). A small amount of my research was conducted here. Peat depth increased to 7-10m and remains consistently flooded throughout the year and has only two strata: the lower canopy (12-15m) and high canopy (maximum 20m) and pneumatophores are numerous (Page et al., 1999). *Pandanus*, *Freycinetia* and *Nepenthesis* spp. occupy all of the ground area and restrict small tree and sapling growth (Morrogh-Bernard et al, 2003). This habitat has low productivity, canopy height and plant diversity compared to all the other habitat types.

c) Tall interior forest

This area has the highest densities of orangutans, at marginally more than

MSF at 2.49 orangutans/km^2 (Husson et al., 2009). This exists at the peak of the peat dome and is therefore the furthest distance from the Sabangau River (Page et al., 1999). Due to its height (peat is 10-13m thick) the water table is below the peat surface year round and has four strata of trees with the tallest reaching up to 45m (Page et al., 1999). There are minimal pneumatophores due to the lack of flooding.

d) Very-low canopy forest

No orangutans have been found in this habitat type (Morrogh-Bernard et al., 2003). This occurs within the centre of the tall interior forest (Page et al., 1999). The canopy reaches a maximum of 15m with the habitat being open. It is very wet with small islands of vegetation in between large pools of water (ca. 200m wide and 1m deep, (Page et al. 1999)). Pneumatophores abound, projecting high above the surface of these pools. The open canopy allows in light and there is a high level of plant diversity (Page et al., 1999).

Additionally riverine forest was a 5th distinct habitat sub-type, which was flooded by river-water during the wet season and formed intermittent shallow pools across the forest floor in the dry season (Page et al., 1999). Fire and felling has destroyed most of this habitat sub-type which would have extended approximately 1km from the forest edge (Page et al., 1999) and it has now been replaced by sedge swamp, which is not utilised by orangutans (Morrogh-Bernard et al., 2003).

1.3.2 Fauna

The Sabangau TPSF sustains a numerous amount of biodiversity of both fauna and flora. Fauna taxa include mammal (63 species), birds (201 species), reptiles (40) and amphibians (9). Cataloguing of invertebrate species is ongoing forming a number of different projects. There are a number of endemic animal species with a number classified as endangered (IUCN, 2015-4) including my study subject the central Bornean orangutan (*Pongo pygmaeus wurmbii*).

1.3.3 Climate

The study site is two degrees south of the equator, which runs through the centre of Borneo. This region is classified as a tropical rainforest climate by the Köppen-Geiger climate system (Peel et al., 2007, McKnight and Hess, 2008) and is characterized by consistently high temperatures and precipitation above 60 mm (McKnight and Hess, 2008). Weather data has been collected at the study site since 2003 as follows. Temperature, maximum and minimum, readings are taken each morning, using a weather thermometer placed just inside the forest. A precipitation gauge, placed in an open area, measures rainfall and is collected at 0600 hr and 1800 hr and summed to create a daily total. The Sabangau has consistently high average year-round temperature (average minimum 22°C, average maximum 29°C), which can be seen in Figs 1.2, 1.3. The dry and wet seasons can start at slightly different times, but for the purposes of this study, and based on my data, I considered June-September the dry season and October-May the wet season. Annual rainfall for my study period was 3108 mm. For data collected between 2004-2012 the average annual rainfall was 3230 mm/year (SD = 707), my study period conforming to the average, rather than exceptional years such as 2006 (2187 mm/year) or 2010 (4555 mm/year). Even though intense rain can fall throughout the year, the forest floor is flooded during the wet season, and, for the most part, not flooded during the dry season.

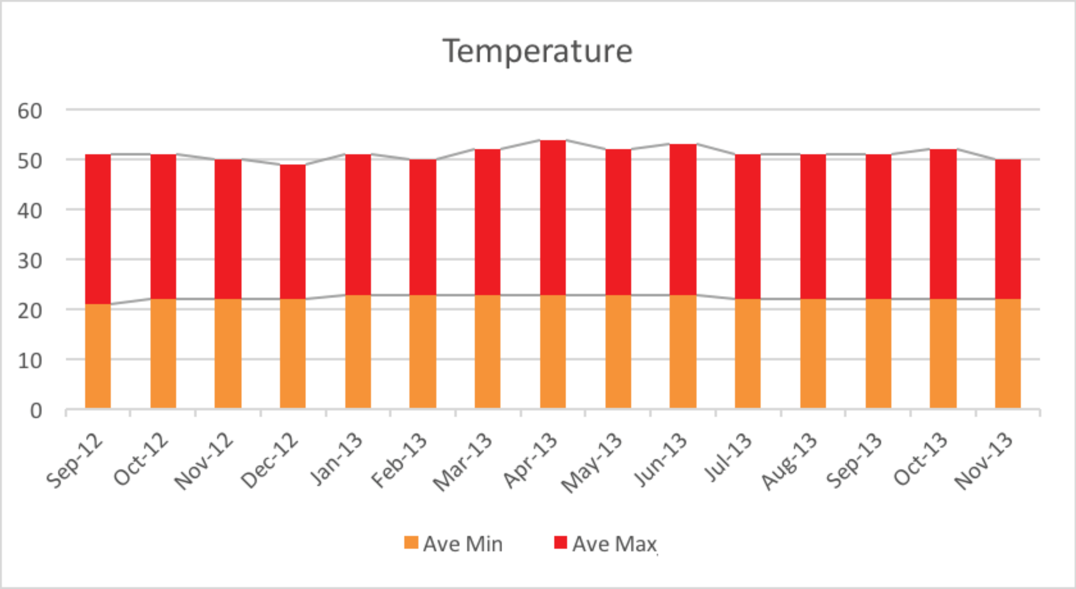

Fig 1.2: Average minimum and maximum temperatures for study period September 2012 - November 2013

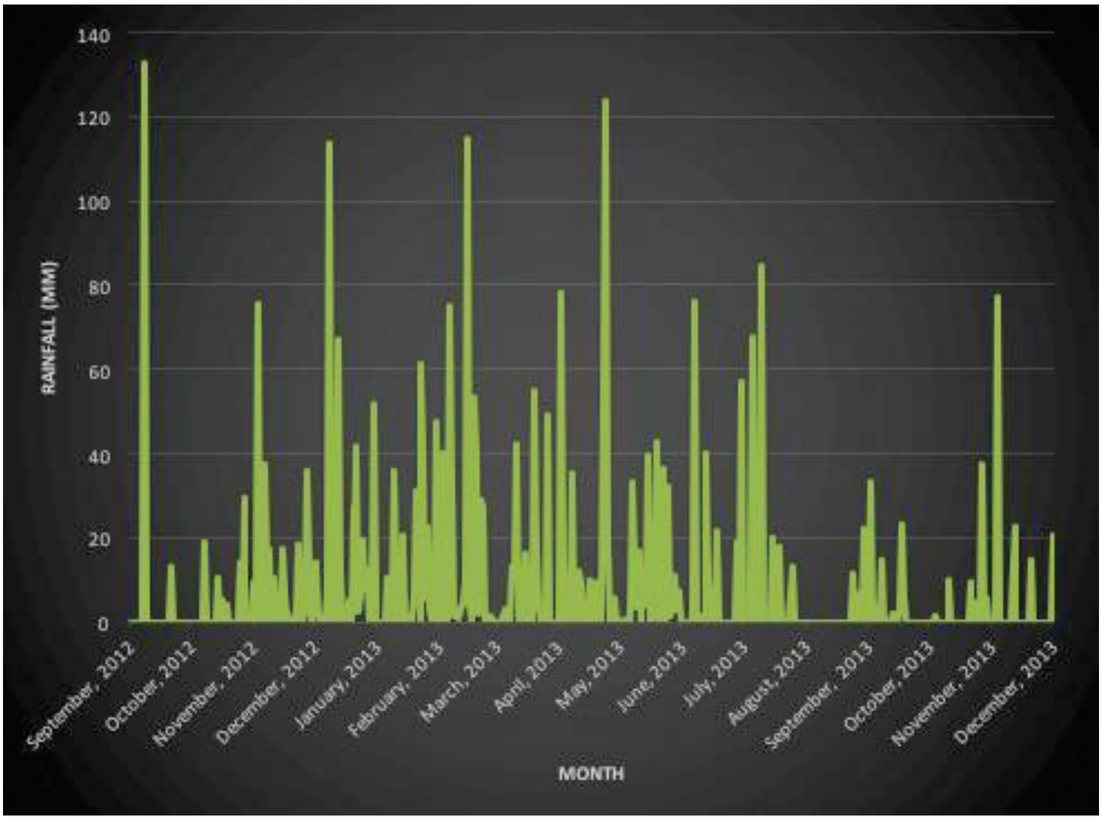

Fig 1.3: Rainfall (mm) for study period September 2012 - November 2013

1.3.4 Anthropogenic influence

Human activity, both legal and illegal, has had visible impacts on the Sabangau peat swamp forest. Logging concessions in the 1970s and late 1990s saw a large amount of tropical hardwood species sold, as well as smaller species felled to allow better forest access (Morrogh-Bernard, 2009). Selective logging, while less damaging than clear felling, changes the forest structure by creating gaps in the canopy (Morrogh-Bernard, 2009) which can alter both the feeding and movement of arboreal species such as the orangutan (van Schaik et al., 2001, Morrogh-Bernard et al., 2003).

Once the National Laboratory of Peat-Swamp forest (NLPSF, see 1.2.5, Fig 1.1a) was created and legal operations ceased, illegal logging operations commenced, creating significant damage (Morrogh-Bernard, 2009). Whereas previous selective logging had some controls on size and tree species, illegal logging was uncontrolled in all aspects (Morrogh-Bernard et al., 2003, Morrogh-Bernard, 2009). A canal network (over 1000 canals) was cut across the Sabangau allowing timber to be floated out of the forest (Morrogh-Bernard et al., 2003, Morrogh-Bernard, 2009). Large-scale logging was stopped by 2004, but the effects of the canal remain to this day, with the system acting as a drainage system causing a multitude of effects: peat collapse, lowering of the water table, and tree instability (Morrogh-Bernard, 2009). The culmination of damage of these effects is an increase in the frequency and severity of forest fires in the Sabangau (Morrogh-Bernard, 2009).

Major fires have occurred in the last 10 years (Morrogh-Bernard, 2009, Buckley, 2014) and most recently (after the cessation of my study) in 2015-2016 (pers. comms. and see (Dengate, 2015)). Smaller fires burn almost every year during the dry season. Peat-drainage is considered the single biggest threat to the orangutan population in the Sabangau (Wich et al., 2008b).

Various other anthropogenic disturbances occur within the forest including hunting (fruit bats, birds and pigs); wild latex or Jelutong (*Dyera lowii*) sap-tapping; bark harvesting of *Alseodaphne coriaece* and small-tree logging (for scaffolding).

1.3.5 Site background and study partners

My research was conducted at the Natural Laboratory of Peat-Swamp Forest (NLPSF), in the Sabangau ecosystem, Central Kalimantan, Indonesia (21^o 31' S and 113^o 90' E, Fig 1.1). The site is directed by the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP), which is a research and conservation institution based at the University of Palangka Raya (UNPAR). The orangutan tropical peatland project (OuTrop), initially an orangutan research project, was set up in 1999 by Simon Husson and Helen Morrogh-Bernard. It has since branched out into a multidisciplinary project that investigates an array of floral, faunal and biodiversity characteristics of TPSF.

The NLSPF occupies an area of 500km^2, representing a small fraction of the total 9,200 km2 of forest in Sabangau (Morrogh-Bernard et al., 2003). This area has government protection as a research area with development disallowed. The work reported in this study was conducted in a 2 x 2 km^2 area of the NLPSF, in which a grid system has been constructed for primate research. The NLPSF was previously a logging concession which ceased in 1997 after which illegal logging became widespread (Morrogh-Bernard, 2009), with researchers hearing chainsaws daily. This resulted in the formation of the CIMTROP Patrol Team, which effectively controlled logging inside the NLPSF since 2004 (Morrogh-Bernard, 2009). A 5780km^2 area of the Sabangau catchment (excluding the NLPSF) was set aside as the Sebangau National Park and is managed by the Indonesian Ministry of Forestry, Director General of Forest Protection and Nature Conservation.

1.3.5.1 The Setia Alam grid system

Almost all my orangutan research was carried out at the Setia Alam site, on a trail grid system, cut into an area of MSF, which is the most accessible and extensive of the habitat sub-types, with some forays “off-grid” with males (both flanged and unflanged). The western portion is ca. 900ha (3 x 3km), and the newer eastern portion is ca. 750ha (2.5 x 3km), see Fig 1.4a,b. It is bordered on the north and east by the forest edge (Fig 1.4a). An old, unused logging railway runs down the middle of the grid. This used to form the eastern border, until the additional eastern grid section was cut (Fig 1.4b).

The grid system (Fig 1.4a,b) has transects placed approximately 250m apart running north-south and east-west and was created to facilitate access for researchers (both orangutan and other) to this difficult forest terrain. Although topographically the peat surface in the cut transects is relatively flat, there is dense undergrowth of: lianas; thorny species (i.e. *Pandanus* spp., *Ceratolobus* spp., *Plectocomiopsis* spp.); exposed tree roots and fallen branches, all of which hamper foot travel. The wet season further impedes travel, with water in some areas reaching waist height. The logistics of travelling at this time can hamper both finding and following animals, as nests must be reached prior to dawn (approximately 0500 hrs). The challenging features of TPSF presented here can reduce usage of the full extent of the grid, with a large amount of follows within 400 ha and 200 ha closer to station in the dry and wet seasons respectively.

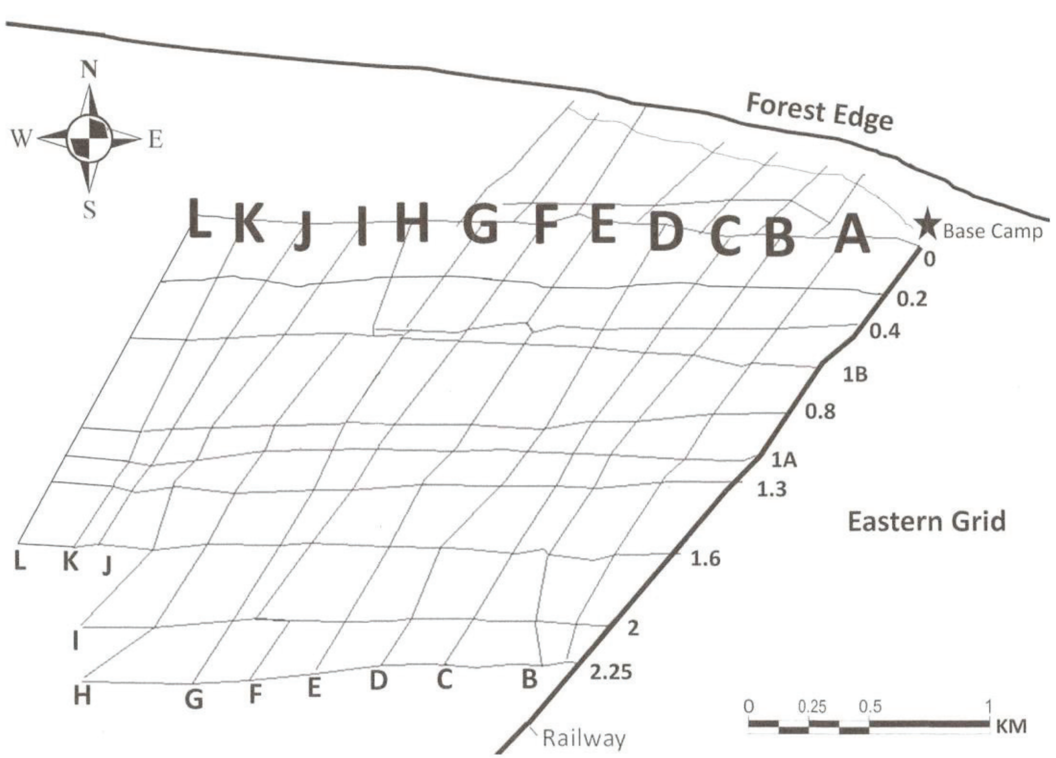

Fig 1.4a Map of the Setia Alam western grid section
Numbered transects run west from the old, disused railway and are labelled according to distance from camp
Lettered transects run south-west and are roughly 250m apart. The Sabangau River is to the north

Map courtsey of OuTrop.

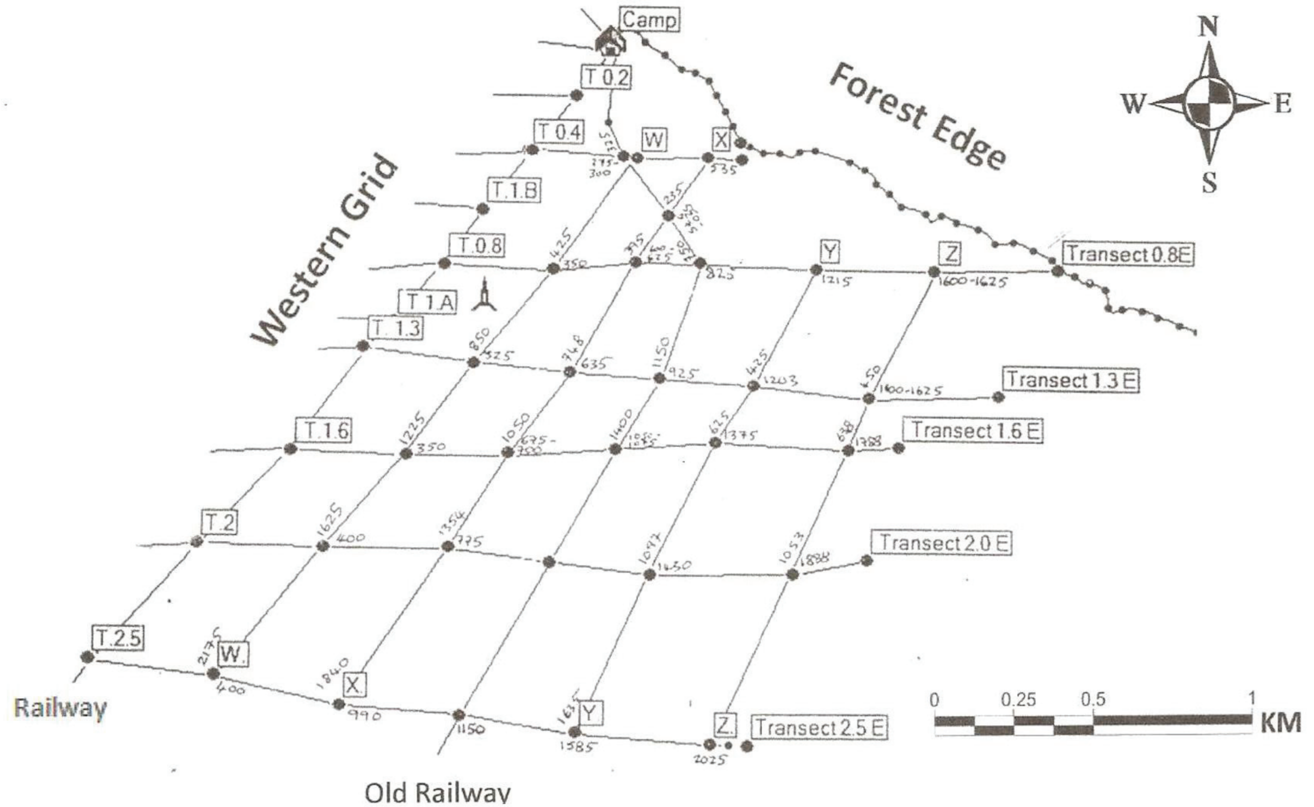

Fig 1.4b. The grid system extention (established in late 2010). Created to facilitate orangutan searching. Transect numbers relate to distancefrom camp and transect 0. Lettered transects run parallel to two disused railways.

Map courtsey of OuTrop.

1.3.6 The orangutan study population

Behavioural research on orangutans has been conducted at the NLPSF continuously since 2003, under the direction of Dr Helen Morrogh-Bernard, one of the founding directions of OuTrop. The behaviour team during my study time included field researchers, research assistants and interns. My fieldwork was conducted over September 2012 to December 2013.

The study population at this site consists of mature and immature orangutans. For my study, males are classed as mature /“flanged” (FM), and immature/”unflanged” (UFM). Both classes are sexually mature but only the flanged males have developed the characteristic cheek pads and throat sac with which they can make long-calls (Rijksen, 1978, Utami Atmoko et al., 2002, Mitra Setia and van Schaik, 2007). Females are separated into adult females (AF) and capable of reproduction, and nulliparous adolescent females, hereafter sub-adult females (SAF), with two SAF’s beginning to gain independence during the course of this study, whereby they were followed as focal animals and behavioural and ranging data were collected. Infants (suckling and travelling largely on mother) and juveniles (independent but not sexually active, suckling from mother 1+ times per day) were both visualized during this study but no data were taken.

1.3.7 Previous relevant ecological research

Research in the NLPSF initially concentrated on features of the peat and climate effects of carbon emissions (Rieley et al., 1997, Page et al., 1999, Page et al., 2002, Page et al., 2008, Page et al., 2011). Ecology research began in the late 1990s, describing the floral and faunal diversity of the NLPSF (Shepherd et al., 1997).

The formation of OuTrop in 1999, followed by the end of logging concessions in 2003, lead to more comprehensive ecological surveying. The Sabangau was found to house the world's largest contiguous orangutan population, with estimates at greater than 6000 individuals in 2003 (Morrogh-Bernard et al., 2003, Wich et al., 2008a). The behavioural ecology data collection started in 2003, collecting baseline data on: feeding; ranging; social interaction; activity patterns and the effect of anthropogenic disturbance e.g. (Husson et al., 2001 , Morrogh-Bernard et al., 2003, Morrogh-Bernard, 2009, Morrogh-Bernard et al., 2011). Detailed analysis of forest productivity, orangutan dietary composition, food selection, energy intake and nutritional metrics of the orangutan diet were conducted from 2005-2007 (Harrison, 2009b, Harrison et al., 2010, Harrison and Marshall, 2011, Harrison et al., 2015).

1.4 ORANGUTANS

1.4.1 Taxonomy

Orangutans (*Pongo* spp.) are part of the great-ape family (Hominidae), and the only member found in Asia (Wich et al., 2003). Other members of this family include the chimpanzee (*Pan troglodytes*), bonobos (*P. paniscus*) and gorillas (*Gorilla* spp.) as well as humans (*Homo sapiens*) that, apart from humans, all reside in Africa (Zhi et al., 1996, Greminger et al., 2014). They presently exist only in Borneo and Sumatra and until fairly recently orangutans were thought to consist of only one species, with Bornean and Sumatran sub-species. Following several genetic studies, they are now labelled as two separate species, the Bornean (*Pongo pygmaeus*) and Sumatran (*Pongo abelii*) (Xu and Arnason, 1996, Zhi et al., 1996, Groves, 2001, Goossens et al., 2009, Harrison, 2009a). Studies have shown orangutans to have the highest genetic diversity seen in great apes, including humans (Fischer et al., 2006, Goossens et al., 2009). Bornean orangutans have been further classified into subspecies, the Western Bornean (*P. p. pygmaeus*), and Southern Bornean (*P. p wurmbii*) (Brandon-Jones et al., 2004, Goossens et al., 2009). There are mentions of further sub-speciation of the Malaysian Sabah population to *P. p. morio* (Goossens et al., 2009) with strong indications that landscape features acting as barriers, such as rivers, could be the main contributors to shaping genetic structure within Bornean orangutan populations (Goossens et al., 2005, Jalil et al., 2008, Goossens et al., 2009).

1.4.2 Morphology

1.4.2.1 Gut morphology

The orangutan gastrointestinal morphology is similar to other mammalian herbivores that use colon-fermentation (Chivers and Hladik, 1980, Stevens and Hume, 1995, Caton et al., 1999a) with a simple stomach, long small intestine and enlarged colon (Chivers and Hladik, 1980, Stevens and Hume, 1995, Caton et al., 1999a). Detailed discussion of this can be found in Chapter 3.

1.4.2.2 Sexual morphology

Sexual dimorphism is highly pronounced in orangutans, as is male bimaturism (Utami Atmoko et al., 2002, Utami et al., 2009). Fully developed or “flanged” males can weigh over twice that of females (average 86.3kg for males, 38.7kg for females (Markham and Groves, 1990) and males continue to grow long after females cease (Utami et al., 2009). Flanged males are those with the fully developed secondary sex characteristics (SSC) of cheek pads, or “flanges” and throat sac as mentioned above. Unflanged males, while lacking both the size, being more similar to female body weights (Galdikas 1985, Utami Atmoko et al 2002), and the SSC of the flanged males, are still sexually mature and capable of siring offspring (Utami Atmoko et al 2002). It is believed that the extreme sexual dimorphism is driven by a combination of male-male competition and female choice (Utami Atmoko et al., 2002, Utami et al., 2009).

1.4.3 Social structure

Orangutans are a semi-solitary diurnal primate with large overlapping home ranges and long life histories (Delgado and van Schaik, 2000, Utami Atmoko et al., 2002, Utami et al., 2009). Their social interactions are infrequent, although increase in times of food abundance (Delgado and van Schaik, 2000, Wich et al., 2004, Marshall et al., 2009). There are also alternate forms of sociality found between Bornean and Sumatran orangutans with communities formed around a single dominant male in Sumatra and "roving male promiscuity" on Borneo, with strong inter-male competition (see (Delgado and van Schaik, 2000, Singleton and van Schaik, 2002, Utami Atmoko et al., 2009)).

The two male morphs exhibit alternate mating strategies as well as female-driven male-male competition (Utami Atmoko et al., 2002, Utami Atmoko et al., 2009, Utami et al., 2009). Flanged males may be approached by sexually active females around the time of ovulation (Knott et al., 2010). This constitutes a form of protection against harassment and forced mating by unflanged males (Galdikas, 1985, Fox, 2002, Utami Atmoko et al., 2002), the second male mating strategy. Studies on mating behaviours have observed females cooperating with mating by flanged males, and frequently (but not always) resisting forced mating by unflanged males (Galdikas, 1985, Fox, 2002, Utami Atmoko et al., 2002, Mitra Setia et al., 2009). Flanged males are the most solitary of orangutan age/sex classes; they are almost entirely solitary, apart from when "guarding" receptive females and when engaged in antagonistic interactions with other males (Fox, 2002, Utami Atmoko et al., 2002, Mitra Setia et al., 2009).

Females, however, exhibit a degree of philopatry, with related females forming clusters, as evidenced by recent genetic studies (Morrogh-Bernard et al., 2011, van Noordwijk et al., 2012). Related females showed greater range overlap than unrelated females (Singleton et al., 2009). This overlap or clustering is still looser than social relationships on Sumatra and has a relationship with forest productivity (Morrogh-Bernard et al., 2003, Marshall et al., 2009, Morrogh-Bernard, 2009). The female-infant dyad forms the strongest social unit (Mitra Setia et al., 2009). Females are still distributed widely, at least in Borneo, which prevents a monopolisation of females by a single male, and this accounts to some degree for the wide overlapping home ranges of males, as they search for and/or long call to advertise to, receptive females (Rijksen, 1978, Galdikas, 1985, Utami Atmoko et al., 2002, Mitra Setia and van Schaik, 2007, Delgado et al., 2009, Knott et al., 2010).

1.5 GENERAL METHODS

1.5.1 Finding orangutans

Orangutans were found by searching the grid system (fig 1.4a,b) along transects which are marked at 12.5m intervals with tags to assist in navigation and location. A minimum of two people were searching at any one time and in contact via mobile phone texting. Other researchers working on different projects would alert any orangutan researchers to their presence. Overwhelmingly, orangutans were found by auditory rather than visual cues i.e. hearing them moving through the canopy (usually crashing through); eating and dropping food on the forest floor, flanged males long calling or kiss squeaking at the observer. The duration of time it took to find orangutans varied greatly during my study, from approximately twenty minutes to 15 days, with numerous observers searching daily, and thus the variability of length of following as well as consistency following the same animals. Weather played an important role in this as finding orangutans in windy and/or rainy conditions impeded auditory and visual location and thus more orangutans were followed in the dry season, than the wet. Availability of searchers affected intensity of searching and also frequency of finding orangutans. Once an orangutan was found, it was followed until it nested for the night. Cotton was then attached from close to the nest to the nearest transect, enabling observers to return to the nest with relative ease the next day before dawn and then conduct a "full day" or nest-to-nest survey.

1.5.2 Following orangutans

Orangutan follows were conducted according to the standardized orangutan data collection protocol (Martin and Bateson, 1986, Morrogh-Bernard et al., 2002, Morrogh-Bernard, 2009) and are summarized here. Once orangutans were located along the grid transect in the NLPSF (fig 1.1a,b, 1.4a,b), they were followed by two-person teams for a maximum of six consecutive days. One person would collect behavioural and feeding data. This included instantaneous sampling every five minutes to record primary activities of feeding, travelling, resting and social interaction. Within the primary activities, secondary activities were also noted (Appendix A). Feeding data were recorded continuously every time the orangutan was observed to feed included start and finish of feeding bouts, food item eaten and if a plant foodstuff, then what part of this was ingested i.e. fruit (whole, skin, pulp, seed and combinations thereof), leaf (young or mature), bark or pith as well as feeding on other foods such as invertebrates or fungi. If an orangutan ceased feeding for one or more minutes on a particular foodstuff then recommenced, it was considered that this was a second feeding bout as per protocol (Morrogh-Bernard et al., 2002) and recorded as such.

Estimated height of the orangutan (0/ground, 1-5m, 6-10m, 11-15m. 16-20m, 21-25m, 26-30m) within the forest canopy were noted at the 5-minute mark. All data collectors, including myself had been tested in a sample transect with trees at known height and had achieved a 95% success rate, before recording this data on orangutan follows. A complete set of activities, primary and secondary, as well as types of food can be seen in a copy of the data sheets (Appendix A).

The second person on the follow recorded GPS data i.e. the location of the orangutan at the 5 minute sampling mark, identified and tagged feeding trees as well as collecting faecal samples for seed germination trials.

1.6 RESEARCH OBJECTIVES

In this study I examine the role of orangutans in endozoochorus transport of seeds. I aim to study the animal-mediated seed dispersal by combining the data gathered in the *ex-situ* work on gut transit times of indigestible seed mimics and relating this transit time to the movements of wild orangutans collected in the in the peat-swamp forest of the Sabangau River catchment in Central Kalimantan, Indonesia. By taking this two-step approach I propose to provide a holistic understanding of the role of orangutans in seed dispersal – including the type of seeds they disperse, the effects of digestion on seed germination and through attempting to create a mechanistic model to predict where they will deposit seeds. Ecosystem service provision, such as seed dispersal, by this charismatic flagship species was recognsied as a knowledge-gap at the research study site in the Sabangau forest.

In order to achieve this, I address the main research questions below with hypotheses that are more topic specific being given in each chapter. Research in this study was organised into 4 sections:

Chapter 2 is an in-depth look at the role of physiology in translocations and has been published prior to thesis completion. This chapter does not expressly fit in with the rest of the thesis content but was included for multifold reasons. 1. It highlights the role of physiology which is relevant to all forms of conservation. Evaluation of physiology broadly relates to endangered species management by understanding the interaction of speices and communities with their environments. This was deemed of paramount important in my specific study of orangutan seed dispersal.

2. Factors beyond my control (debilitating injury) led my initial project (involving a translocated species) to fall-through, necessitating switching projects to orangutan seed dispersal. The literature review on conservation translocation, for reasons outlined in 1., was considered of enough relevance to include in the current thesis manuscript.

Chapter 3 relates to ex-situ evaluation of transit time of indigestible seed mimics. I attempt to determine the transit time of different sized seed-mimics through the orangutan gut and discover if there are any patterns to excretion of said seed mimics. Previous research was done on this species using inert particulate and solute markers (Caton et al., 1999). However, I wish to ascertain how much larger markers (2-6mm) travel as these are the sizes that more closely relate to seeds in the wild.

The general research questions in this chapter are:

1. How long does it take for seed mimics to travel through the orangutan gut? I expect long transit times based on their large body sized and complex gut

structure (Stevens and Hume, 1995)

2. Does size of seed mimic matter? Do different sized seeds/seed-mimics spend longer in the gut than other sizes?
3. What is the pattern of seed-mimic elimination? Is it an even bell-curve distribution or discrete pulses or entirely random?

In **Chapter 4** I attempt to determine what orangutans eat in the wild, what seeds are defecated intact, and which are depredated. From those that are excreted intact, I aim to ascertain which germinate when compared to both non-handled seeds and intact fruit. The following research questions are considered:

1. What are the seeds that are excreted intact by wild orangutans? This is baseline data that is crucial to gather in order to begin to consider wider questions of seed dispersal.
2. Do orangutans influence the time to germination? Is there an advantage to a seed in travelling through an orangutan gut?
3. What is the largest size of seed that travels intact through an orangutan gut? Is this a seed that that is likely to be excreted intact by other frugivore guilds? I.e. Do orangutans occupy a niche in transporting large seeds, compared to smaller bodied frugivores? Some of this question, is by its nature, only assumption, as other species were not included in the current study. However logical suppositions can be made when comparing gape-sizes of different animals and access (for non-aboreal frugivores in the same location). This question does illustrate the need for further avenues of research.

In **Chapter 5** I assess ranging of male and female orangutans in the different seasons (wet and dry) and apply a temporally-informed local convex hull model (T-LoCoH) to project movement patterns of the study animals through space and time.

From this I aim to not only extend the current knowledge of orangutan biology in the tropical peat-swamp forests of southeast-Asia, but also to demonstrate a proof of concept for the integration of ecophysiology and movement ecology. The broad research aims of this chapter are:

1. To create a physiologically-informed home range model to understand where and when orangutans deposit seeds in the study site at Sabangau Forest, Central Kalimantan, Indonesia
2. For the models created to be truly mechanistic i.e. independent of time and space, and able to be applicable therefore to other study sites. This would allow my model to be able make predictions about the dispersal of seeds by orangutans, or and the potential for environmental change (plant hetogenity) depending on orangutan population numbers and structure.

1.6.1 Chapter 2 summary

There have been a number of recent reviews on endozoochory (Traveset et al., 2007b, Côrtes and Uriarte, 2013) and future directions for its study (Cousens et al., 2010, Ruxton and Schaefer, 2012). For example, Ruxton and Schaefer (2012) in particular concentrated on the conservation physiology involved in endozoochorous as a key ecosystem service. To this end, I broadened the scope of my literature review to conservation physiology and examined what I believe to be a highly under-researched area, physiology in conservation translocation. This chapter is presented in its published form for the online journal, Conservation Physiology (Tarszisz et al., 2014) and is reproduced in PDF form, along with supplementary material in Appendix B. A statement confirming that I was the primary contributor to this work is included in Appendix C. This is an open source journal and as part of my copyright agreement with Oxford University Press I have retained the right, after publication, to use all or part of the article and abstract, in the preparation of derivative works, extension of the article into a booklength work, in a thesis/dissertation, or in another works collection, provided that a full acknowledgement is made to the original publication in the journal.

Translocations of animals are used commonly to restore species to their former ranges and increase their numbers, and are particularly important for the conservation and management of rare and threatened species. Despite laudable efforts, however, translocations have variable success: too little information is often available about the wellbeing of individuals to determine their likelihood of survival either before or after they are released. Conservation physiology provides a novel approach that could significantly improve this situation; it has been overlooked until recently, perhaps because of the invasive nature of some physiological techniques such as the sampling of body fluids or the use of surgical implants.

Here, I evaluated the potential for physiology to inform and improve conservation translocation protocols by reviewing 232 publications that deal with animal translocations, and examined factors that promoted translocation success. I redefined the most commonly used definition of translocation success—that success occurs when a target population becomes self-sustaining—because it is difficult to achieve in practice, and instead propose specific criteria that characterised project success as low or high. I confirm that it is important to consider different aspects of species' genetics, behaviour and ecology to achieve successful outcomes, and show also that physiological evaluation of animals before and after their release into the wild could improve the success of translocation projects still further. I propose a suite of physiological and animal health measures that may be useful in enhancing translocation success, and suggest also that monitoring should continue for long enough in the post-release period to ensure animal wellbeing and population persistence. The use of physiological assessments should have additional ethical benefits in helping to minimise the numbers of animals used in conservation translocation projects. With climate change likely to have global effects on habitats and environmental conditions, it will also become increasingly important to understand the physiological tolerances of threatened species to identify whether they have the capability to persist at reintroduction sites in future.

1.6.2 Chapter 3 Summary

This chapter is presented in the format suitable for the journal the Australian Journal of Zoology, and plans to submit following submission of this thesis. I wrote the entire paper, with editorial and stylistic inputs from my principal supervisor, Dr Adam Munn who is co-author on this paper and a statement to this effect is included in Appendix C.

Orangutans, both Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*), have a diet largely consisting of plant matter and are colon hindgut fermenters relying on assistance of symbiotic gut bacteria. Passage time can be measured in terms of transit time which is the time from ingestion to elimination. Indigestible portions of feed, such as seeds, are also measurable and useful for determining gut throughput. Here seed mimics were fed to six adult orangutans fed a zoo diet that consisted largely of plant matter. This study presents a representation of how seeds are dispersed in a natural environment, illustrating elimination of seeds in time-dependent pulses. We propose that evaluation of transit time, and elimination patterns are relevant for seed deposition studies in field studies of *in-situ* wildlife.

Transit time was found to be, on average 76 hours, with no significant differences between the different seed mimic sizes: 2, 4 and 6mm.

Seed mimics were excreted in large pulse doses, with small peaks surrounding the one or two larger peaks, with single defecations often having the majority of the seed mimics present. This has important implications for seed dispersal when applied to an in-situ location.

1.6.3 Chapter 4 summary

This chapter has been written in a format to present to the Journal of Austral Ecology for publication. I wrote the paper in its entirety, with either field assistance and/or editorial and stylistic inputs from authors 2-4, as per my research agreement with OuTrop and Dr Adam Munn, my primary supervisor, as the final author. A statement that I conducted the research and wrote this paper can be seen in Appendix C.

The passage of seeds through an animals gut can confer an improved change of germination onto the seed. Here I followed Bornean orangutans (*Pongo pygmaeus wurmbii*) in the Sabangau Forest, Central Kalimantan and collected faecal samples. Thirteen seed species were found in the faecal samples, which ranged from small to large sizes of seeds (length in cm 0.61 ±-0.10 – 2.16 ± 0.24). These formed part of the experiment for germination along with manually extracted seeds and whole fruits. Manually extracted seeds were found to germinate more then either gut passed seeds or whole fruits. No seed interspecies differences in germination were found. From these experiments I concluded that while orangutans may not confer enhanced germination ability to seeds, they are still functional dispersers for many plant species (moving them away from the parent plant), and for some plant species they may be more important than others. Seed spitting, although not quantified, is also discussed and may contribute to movement of seeds, as well as enhanced germination by the orangutans "manually extracting" the seeds from the fruit before moving them.

1.6.4 Chapter 5 summary

This chapter has been written as a thesis chapter rather than a journal article. However, it follows a format similar to a journal article, but requires altering once once the journal for submission is determined. I have written this chapter, with advice from Drs Mark Harrison and Helen Morrogh-Bernard in the field and in orangutan database use. Dr Sean Tomlinson assisted me in learning and subsequently using the R statistical software and T-LoCoH package. Editorial inputs were received from both Dr Tomlinson and my primary supervisor Dr Adam Munn. A statement certifying that I wrote this chapter is included in Appendix C.

In this chapter I describe the orangutan movements between September 2012 to December 2013. I explore a new mode of home range analysis, that of Time Local Convex Hull (T-LoCoH) which allows evaluation of movement through both space and time, in order to evaluate how orangutans move and utilise in their environment. Furthermore, employing the information gleaned in Chapter 3 about transit time of indigestible seed mimics, I applied this data to the T-LoCoH method to predict where a primary endozoochorus deposition of seeds could occur. This was then analysed against the location where orangutans defecated that I had noted during field studies and found to be an accurate predictor i.e. there was no significant difference between where I predicted that the orangutans would defecate and where they actually did (Pearson's $X^2_5 = 8.09$, $p = 0.151$) of orangutan defecation location. Other metrics such as step-length, revisitation rate and duration of visit per location was analysed for sex, season and sex*season. The results are presented in full in Chapter 5.

2 PHYSIOLOGY IN CONSERVATION TRANSLOCATION

Published in Conservation Physiology

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2.1 INTRODUCTION

The translocation, reintroduction and introduction of species to areas within their former range (or to areas considered appropriate or amenable to their survival and persistence) are entrenched and popular methods in conservation biology (Osborne and Seddon, 2012). These methods serve to improve the conservation status of focal species or restore ecosystem functions and processes (IUCN/SSC, 2013). Such deliberate transfers to promote conservation outcomes are collectively termed Conservation Translocations, and include any movement of animals (or plants) for conservation purposes (Osborne and Seddon, 2012, Seddon et al., 2012, IUCN/SSC, 2013). These transfers can be further classified into population restorations and conservation introductions (Seddon et al., 2012, IUCN/SSC, 2013); see Table 2.1. Population restorations involve either reinforcement of existing populations by movement and release of conspecifics, or reintroduction of extirpated animals into their indigenous range (IUCN/SSC, 2013). Conservation introductions involve moving organisms outside of their indigenous ranges either to avoid extinctions (i.e. assisted colonisation (Thomas, 2011, Seddon et al., 2012, IUCN/SSC, 2013), or because the organisms perform a specific function within the ecosystem, i.e. ecological replacement (Armstrong and Seddon, 2008, Seddon et al., 2012, IUCN/SSC, 2013, Seddon and van Heezik, 2013); examples of the latter species include ecosystem engineers and apex predators (Letnic et al., 2012, Ritchie et al., 2012, Seddon and van Heezik, 2013).

In recent years there has been an exponential increase in the number of conservation translocation projects worldwide (Seddon et al., 2007), and there have been several excellent reviews of reintroduction/translocation success in particular taxa e.g. (Griffiths and Pavajeau, 2008, Finlayson et al., 2010) and of directions in the field more generally (Ewen *et al*., 2012a). However, despite this increase in conservation translocation research, much of this work has focused on more easily assessable aspects of translocation protocols, such as release techniques, or on readily measured demographic aspects such as short-term survival rates. Consequently, less tractable but potentially critical aspects of the translocation process remain uncertain. One key factor that could significantly affect the success of translocations, and improve protocols, concerns the biology of individual animals, and specifically their physiological state, both pre- and post-release. Without doubt, the well being of individual animals in translocations is well considered by practitioners, but within the published literature it apparent that animal physiology is often under represented as a feature of direct concern. Deeper consideration of the physiology of individuals and populations from a conservation perspective falls within the domain of the emerging discipline of conservation physiology (Wikelski and Cooke, 2006, Chown and Gaston, 2008, Cooke and O'Connor, 2010).

To evaluate the potential for physiology to inform and enhance conservation and translocation science, we aim here to consider the factors that promote success in conservation translocations, and to focus on the role that conservation physiology might play. Thus, our review builds on concepts addressed by Fischer & Lindenmayer (2000) and Seddon *et al*. (2007), but adds new dimensions that have been hitherto little addressed in the published literature. To focus the review, we consider only studies of terrestrial vertebrates and aquatic mammals; these groups dominate in translocation studies, and therefore offer most opportunity to explore the role of conservation physiology in improving translocation success. We note that comprehensive translocation planning typically incorporates aspects of species' natural history (Pereira and Wajntal, 1999, Ottewell et al., 2014), resource and environmental requirements (Rittenhouse *et al*., 2008), as well as economic, social and cultural needs, e.g. (Williams et al., 2002). Here, we emphasise the evaluation of species' biological requirements as being imperative for the success of translocation programs, with particular focus on physiology.

2.1.1 Review Aims

Our specific aims are to:

(i) review conservation translocation papers for the presence/absence of quantitatively assessed physiological parameters,

(ii) assess the outcomes of conservation translocation studies,,

(iii) identify future directions for conservation translocation biology, with an emphasis on the role of conservation physiology

2.2 PHYSIOLOGY CONSERVATION TRANSLOCATIONS

Definitions of conservation physiology vary among practitioners, but most agree that the discipline investigates the physiological responses of organisms to anthropogenic threats and stressors that may contribute to declines in their populations (Wikelski and Cooke, 2006, Franklin, 2009, Seebacher and Franklin, 2012, Cooke et al., 2013), and that it provides a link between ecological patterns and environmental change (Seebacher and Franklin, 2012, Cooke et al., 2013). Much as the definitions of conservation translocation have evolved to their current state, conservation physiology also has broadened in scope to identify and resolve problems that exist in populations, with increased inclusiveness of all taxa. The discipline also seeks to expand to identify problems at levels of still broader interest to conservation practitioners, including species, communities and ecosystems (Cooke *et al*., 2013).

Physiology, when applied to conservation management of populations, provides vital data on the causal mechanisms that underlie current population problems (Carey, 2005, Wikelski and Cooke, 2006, Franklin, 2009), and also has the potential to illuminate previously neglected or concealed conservation issues (Chown and Gaston, 2008). Multiple factors influence conservation translocations, with interconnections between behaviour, physiology and ecology that can determine population survival (Tracy et al., 2006). This complexity is well illustrated in trials on resource acquisition by desert tortoises, which show how physiological processes interact with animal ecology and behaviour and are integral to the assessment of conservation status (Tracy et al., 2006, Drake et al., 2012, Cooke et al., 2013). In other examples, physiological approaches are being increasingly used to identify and reduce the effects of disease in population declines (Blaustein et al., 2012), to increase the sustainability of fisheries management (Cooke et al., 2012), to enhance understanding of seed dispersal by animals (Ruxton and Schaefer, 2012), and even to improve conservation policy (Cooke and O'Connor, 2010). The call for use of physiology in restoration ecology was given significant evaluation in a review (Cooke and Suski, 2008) largely in relation to plant taxa and restoration of degraded habitats. However mention of vertebrate taxa and incorporation of physiological assessment tools such as bio-monitoring; use of stable isotopes and doubly labelled water was called for with a note of the increased convenience of these tools (Cooke and Suski, 2008).

In terms of conservation science more generally, interest in conservation physiology arises because it offers opportunity to predict the responses of organisms to environmental change (Carey, 2005, Wikelski and Cooke, 2006, Cooke and Suski, 2008, Franklin, 2009, Kearney et al., 2010, Seebacher and Franklin, 2012), thereby informing actions and policies that might improve conservation outcomes. With the current challenge of climate change and its potentially catastrophic impacts on biodiversity in many regions, the playing field for reintroduction biology has moved. As emphasised by leading texts and articles, e.g. (Thomas, 2011, Osborne and Seddon, 2012, Bekoff, 2013), climate change has altered the context of conservation translocations because conditions often cannot be restored to "the way they were"; the original conditions simply no longer exist. Therefore, it is increasingly important to understand the physiological tolerances of vulnerable and endangered species to identify whether they have the physiological capability to adapt to changing climates or to respond to other anthropogenic modifications to the environment (Kearney and Porter, 2009b, Smith, 2011).

It is apparent from these and other considerations that physiological data are important in developing conservation protocols to improve rates of success in conservation translocations. This is particularly so with respect to understanding species' demographic performance and predicting the possible impacts of climate change and other environmental disturbances. Thus we introduce the term "Translocation Physiology" to describe the explicit evaluation of physiological parameters throughout the translocation process. This includes, but is not limited to, pre-release, the translocation event, and post-release monitoring.

2.2.1 Translocation Physiology

The adoption of physiology generally into conservation is an implicit acknowledgement of a previous deficit in conservation practice, especially—as we contend here—in reintroduction biology. Translocations are generally acknowledged as unavoidably stressful events (Dickens et al., 2010a, Parker et al., 2012, Seddon et al., 2012). The translocation itself is likely to be highly distressing, from capture and handling to transport to release (Dickens et al., 2010a, Parker et al., 2012). In an elegant example of this, Waas et al. (1999) used simulated translocation events for red deer (*Cervus elaphus*) (including catching/herding, pre- and post-transport confinement, loading on and off vehicles, road travel), and made detailed physiological evaluations of heart rate, haematocrit, cortisol and biochemical parameters such as blood sodium, lactate, glucose and magnesium. Even after habituation of animals to the simulated translocation, the actual event remained stressful. Animals showed consistently increased heart rate and levels of blood lactate and cortisol (Waas et al., 1999); elevated cortisol, or corticosterone, depending on species, is a typical response to physiological stress (Romero, 2004, Romero and Butler, 2007). Immediate post-release mortality can have significant impacts on the success of population establishment (Armstrong and Seddon, 2008, Armstrong and Reynolds, 2012, Parker et al., 2012).

Understanding and minimising animal stress in translocations is clearly important (Dickens et al., 2010a, Parker et al., 2012), and current literature rightly recommends that appropriate husbandry and release techniques be considered alongside knowledge of the biology and ecology (abiotic and biotic requirements) of any individuals that are to be translocated (Parker et al., 2012, IUCN/SSC, 2013). This is a key recommendation of the IUCN guidelines for translocations, and emphasises further that understanding the physiological status of both individuals and populations is a necessary and vital component of the translocation process.

Physiology enables a more in-depth understanding of individuals, populations and communities, and can assist in discerning potential responses of organisms to environmental change (Cooke et al., 2013). As knowledge of physiology elucidates cause-and-effect relationships (Cooke et al., 2013), its usefulness in pre- and post-translocation planning cannot be overstated. Translocation physiology can assist in all stages of the translocation process by: assessing the consequences of outbreeding and inbreeding depression; improving understanding of immune responses to captivity and release stressors and their consequences (e.g. fitness, disease expression); testing the suitability of habitats for populations; identifying threats that might cause success/failure; identifying optimal habitats; linking fitness of organisms to environmental conditions; and providing credibility and greater certainty about the process (Cooke et al., 2013).

2.3 REVIEW OF LITERATURE

For our review of conservation translocations we separated research papers into four distinct categories: *Pre-release*; *Conservation translocation*; *Post-release* and *Reviews*. *Pre-release* denoted any study dealing only with preparation for a reintroduction and not the act of the reintroduction itself. *Conservation translocation* denoted any study detailing the process and execution of one or more conservation translocation projects. *Post-release* denoted any study that dealt with the events following a translocation, but not the event itself. *Reviews* are self-explanatory. Conservation translocation papers alone were evaluated for their inclusion of physiological evaluation because neither the pre-release nor post-release papers covered the actual translocation event; these were noted but not used in our attempt to review the physiological factors that were considered in primary works. Occasionally, a paper covered more than one category. For example a paper described a number of releases of red wolves (*Canis rufus*) as well as pre-release preparation and post-release information in what was almost a review of the subject (Van Manen et al., 2000). In these cases, if translocation events were presented with other information, the paper was considered a *conservation translocation* study and not placed in other categories. To meet the first aim of our review, we then scored papers that had used physiology as part of their protocol as well as other factors such as genetics, behaviour, habitat, and whether key threatening processes had been considered in the translocation process (Table 2.1). A full list of papers evaluated is available in Appendix B supplementary material.

Table 2.1: Definitions of terms used in reintroduction projects (based on IUCN/SSC 2013).

Conservation translocation: The intentional movement and release of a living organism where the primary objective is a conservation benefit

Population restoration: Any conservation translocation within indigenous range. Comprises two activities

(i) ***Reinforcement:*** The intentional movement and release of an organism into an existing population of conspecifics

(ii) ***Reintroduction:*** The intentional movement and release of an organism inside its indigenous range from which it has disappeared

Conservation introduction: The intentional movement and release of an organism outside its indigenous range. Two types are recognised

(i) ***Assisted colonisation:*** The intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species

(ii) **Ecological replacement**: The intentional movement and release of an organism outside its indigenous range to perform a specific ecological function

Our intention was not to obtain an exhaustive summary of every translocation publication in the last decade, but rather to collate papers that would provide an indication of general trends in the field. Due to the marked influence of the Fischer & Lindenmayer (2000) review, we carried out a detailed search for relevant studies in the same 12 international journals that were used in this earlier work. We focused on the years 2000-2010. These 12 journals, as well as *Trends in Ecology and Evolution*, were searched issue-by-issue for articles containing the words translocation, reintroduction, or augmentation, and all papers concerning mammals, birds, reptiles and amphibians were considered (fish and invertebrates were beyond our scope). Using Google Scholar, we entered the same search terms as for our target journals and collated studies published in the ten years up to 2010. We did not include studies that had not been peer-reviewed, nor did we search for studies that had been cited in published papers but had been overlooked in Google Scholar. We assumed that our search methods were unbiased or at least not biased in any systematic way, and that the years we reviewed provide a reasonable sample of recent reintroduction studies.

Rehabilitation does not fall under the definition of conservation translocation according to the current IUCN/SSC guidelines (2013) as the release is considered to be for the welfare of individual animals rather than for organisations at higher levels, such as populations. We did, nonetheless, include three exceptional rehabilitation studies that were population-based and thereby fulfilled our criteria for adequate and quantitative reporting of reintroduction results (Goldsworthy et al., 2000, Manire et al., 2003, Molony et al., 2006)

We acknowledge that published papers that are designed to answer specific questions may not be representative of entire translocation projects, as opposed to translocation proposals and reports that are submitted to conservation agencies, and thus there may be inherent difficulties in subjecting these to meta-analysis or other forms of quantitative review (D. Armstrong *pers. comm.*). However, as peer-reviewed published literature is often the most readily accessible and primary source of background information on new translocation projects, we view the papers we examined as being broadly representative of the practices used currently by scientists involved in conservation translocations. To ensure the robustness of our approach and conclusions, we also consulted two influential recent works synthesising current trends and past and present data on reintroduction and translocation biology (Ewen et al., 2012a, Bekoff, 2013). We also consulted the most recent reintroduction guidelines provided by the IUCN (IUCN/SSC, 2013).

2.3.1 Evaluating success

With regards to assessment of the outcomes of conservation translocation studies (Aim ii), as each project evaluated had its own definition of success and was carried out over different time scales, we attempted to create specific criteria to determine the success of individual translocation projects in a repeatable and rigorous manner. We considered each study on its own merits. In the first instance we evaluated success, or otherwise, of a translocation project based on each study's self-evaluation. However, some studies, while considering their project a success, failed to meet their stated aims or, in our reading of the results, failed to state reasonable reasons for considering the project a success. Therefore, in addition to self-reported success and failure, we introduce a binary category for projects deemed successful, this being to denote ‘high’ or ‘low’ success.

a) High success was determined if:
    i. The translocation confirmed that a stable and/or increasing population was established during the study period; or
    ii. The project achieved its specified aims. For example, a project evaluating the effects of pre-release experience of elk (*Cervus elaphus*) with wolves (*Canis lupus*) and human hunters showed that experienced animals survived longer post-release, which was the specified aim (Frair et al., 2007); or
    iii. The project initially showed poor results, but improved them by altering protocols over time using information gleaned in earlier years (if releases took place over multiple years); i.e. there was some degree of adaptive management.

b) Low success was determined if:
    i. The study reported high success but failed to show conclusive results. For example, in a black bear (*Ursus americanus*) translocation that measured two different release techniques, >50% of study animals died or were unable to be included in the analyses due to lack of knowledge of their whereabouts (Eastridge and Clark, 2001);
    ii. A potentially threatening problem was present and could not be resolved, such as low genetic diversity due to small founder numbers or the presence of a key threatening process;

iii. Catastrophic events occurred and significantly affected the project's results. For example, during the Iraq war the flight of Bedouins from Kuwait and Iraq to Jordan led to a doubling of the livestock population in the host country. This led to overgrazing, reduced water supplies and higher prevalence of disease and parasites in Jordanian habitats, compromising the translocation of oryx (*Oryx leucoryx*) as a result (Harding et al., 2007);

iv. The sample size was too limited to have resulted in a self-sustaining population as, for example, in the translocation of a single orang-utan (*Pongo abelii*) to Sumatra (Cocks and Bullo, 2008);

v. There was limited scope for population expansion and persistence. For example, despite the establishment of a reproducing population of lions (*Panthera leo*) in Phinda private game reserve, the population remained small and isolated, with little scope for connection to other isolated populations and for addressing the long-term conservation problems of the species (Hunter et al., 2007); or

vi. The time of monitoring was too short to span even one breeding season. For example, a release of Pere David's deer (*Elaphurus davidianus*) in China spanned less than six months of monitoring (Hu and Jiang, 2002).

2.4 REVIEW

2.4.1 Literature review

We reviewed 232 publications, of which 44 described pre-release protocols, 68 described post-release protocols, and 120 reported conservation translocations, which are our primary focus below. These describe the translocation process in full including pre-release factors, the translocation event itself and post-release monitoring. There were also 40 reviews. Traditional physiological factors were noted in 9% of the translocation studies. By comparison, 33% of the translocation studies considered genetics, 78% described behaviour and >80% considered habitat factors or key threatening processes associated with the translocation attempt (Table 2.2).

Table 2.2: Detailed breakdown of biological and environmental factors considered in 120 reintroductions of terrestrial vertebrates and aquatic mammals, showing numbers of projects rated as failures, successes and, in the latter category, high and low success. See text for definitions of ‘high’ and ‘low’ success. KTP = key threatening process (see Appendix B)

Biological or environmental factor	**Total studies**	**Failures**	**Successes**	**Low success**	**High success**
Genetics	39	3	36	15	21
Behavioural	93	12	81	32	49
Physiology					
Traditional physiology					
Stress physiology	3	1	2	1	1
Water, micronutrients	3	0	3	1	2
Thermoregulation	3	1	2	0	2
Immunoecology	2	1	1	1	0
Condition					
Distress	26	5	21	8	13
Body condition	46	5	41	13	28
Nutrition					
Wild food	12	0	12	5	7
Commercial food	11	5	6	2	4
Combination	19	1	18	5	13
Supplementary feeding	27	5	22	5	17
Other/unknown	18	1	17	8	9
Health					
Vet/health check	37	5	32	14	18
Vaccinations	7	1	6	5	1
Parasite management	15	3	12	6	6
Quarantine/disease screen	26	1	25	9	16
Unknown	2	1	1	0	1

Habitat					
Edge of former range	6	3	3	2	1
Core of former range	50	5	45	14	31
Combination edge and core	1	0	1	0	1
Not reported	53	10	43	19	24
Predator proof fence	9	0	9	3	6
Substitution	4	0	4	0	4
KTP					
Absent	49	3	46	14	32
Present	49	9	40	17	23
Unknown	22	5	17	7	10

2.4.2 Physiology in conservation translocations

Detailed review of the 120 studies reporting conservation translocations suggested that physiological considerations could be broken down into four broad categories: condition, nutrition, health and ‘traditional’ physiology, each with two or more subcategories (Table 2.2). In total, 60% of studies (*n* = 72) reported the condition of animals that were being translocated and, of these, 86% were rated as successful (Table 2.2). Twenty-six studies (22%) noted whether animals showed distress reactions; 81% of these demonstrated success, with 62% of this subset rated as having highly successful outcomes (Table 2.2). Different approaches to assessing distress tended to be used on different vertebrate groups. For example, distress caused by handling and transportation was often considered in avian translocations such as those involving the black-faced honeycreeper *Melamprosops phaeosoma* (Groombridge et al., 2004) and sharp-tailed grouse *Tymphanchus phasianellus columbianus* (Coates et al., 2006), and also in some involving mammals (e.g. red howler monkey *Alouatta seniculus*, (Richard-Hansen et al., 2000). In these studies researchers generally attempted to minimise the time that animals spent in transit, met their resource needs while they were being transported, and ensured that benign weather conditions prevailed post-release. In contrast, while reactions to handling were mentioned in some projects that translocated reptiles, these ectotherms generally were considered to be most vulnerable to thermoregulatory distress. As such, housing during transit was usually the dominant factor that was considered as, for example, in a translocation study of the three-toed box turtle *Terrapene carolina triunguis* (Rittenhouse et al., 2008).

Body condition was used as an indicator of physiological state in 46 studies (38%), more frequently than any other physiological parameter. Although body condition may not be a direct measure of organism function, it is often assumed to correlate with individual ‘fitness’ (Marshall et al., 1996), at least with regard to an animal’s ability to withstand potential stressors such as immunological, nutritional or thermoregulatory challenges. Conservation translocation studies that considered body condition generally had high success; most used either qualitative indices of condition such as visual appearance, or more invasive but direct estimates of body fat content e.g. (Woolnough et al., 1997). Some studies also employed simple but quantitative indices based on regressions of body mass on linear measures of body size e.g. body, limb or foot length; (Krebs and Singleton, 1993, Schulte-Hostedde et al., 2005). Here, relatively massive individuals lying above the regression line (i.e. with positive residuals) are considered to be in good condition, and those below the line to be in poor condition. These residual-based indices of body condition need to be interpreted cautiously because body mass can fluctuate markedly over short periods, may not correlate well with other measures of body condition such as body fat (Krebs and Singleton, 1993), and may vary as animals grow (Peig and Green, 2010). However, provided that these limitations are borne in mind, the high success of conservation translocation studies using residual-based indices (Table 2.2) suggests that this approach to judging condition has considerable utility.

Food and nutrition were evaluated in many translocation protocols (Table 2.2), with researchers providing food during the reintroduction process or as supplementary fare after animals had been released. All projects that fed animals natural or wild-type foods as part of their translocation (10%) were considered successful, with 58% of these deemed highly successful (Table 2). Studies where reintroduced animals were fed a combination of wild and commercial-type food (16%) had a similarly high success rate of 95%, with 72% of these deemed highly successful, whereas those using only commercial-type food (9%) had a more mixed success rate of 54% (Table 2.2). Supplementary food after release was provided in 27 studies, generally as part of 'soft' release protocols that attempted to ensure that animals would not go hungry as they made the transition to eating naturally available foods e.g.(Richards and Short, 2003, Britt et al., 2004, Brightsmith et al., 2005). It is of note that 18 reintroduction studies provided food during the transfer or release stages, but failed to specify the type of food offered or how it was provided. Despite these deficiencies in reporting, the overall results suggest that appropriate food is important during and after animals have been released, and that success may be increased if natural foods are available to translocated animals before their release to the wild.

Using healthy animals would seem an obvious prerequisite for conservation translocation success (Stevenson and Woods, 2006), but health was mentioned in only half the studies we examined. Several studies advocated the need to make general heath checks prior to animals being released, both to maximise the survival chances of individuals and to minimise the potential for disease transfer to extant, resident populations of conspecific or congeneric species (Leighton, 2002, Mathews et al., 2006).

‘Traditional’ physiological factors were considered in only 11 (9%) of the translocation studies reviewed (Table 2.2), and included assessments of stress using glucocorticoid hormone assays (Manire et al., 2003, Pinter-Wollman et al., 2009, Zidon et al., 2009), as well as more direct evaluations of water use (Mathews et al., 2006, Field et al., 2007), micronutrient balance (Lapidge, 2005), and thermoregulation (Hardman and Moro, 2006, Rittenhouse et al., 2008, Santos et al., 2009). These studies were largely successful. Despite their emergence in other areas of wildlife ecology, such as in life history studies (Martin et al., 2006a, Martin et al., 2006b), immunoecological approaches were used in only two of the translocation projects we evaluated. One considered immunoecology tangentially by using hematophil-lymphocyte white blood cells as an indicator of stress (Groombridge et al., 2004), and the other used lymphocyte proliferation to evaluate immune function (Manire et al., 2003). Haematological parameters were measured in a translocation study of the water vole (*Arvicola amphibius*, formerly *A. terrestris*) (Mathews et al., 2006), but only erythrocytes were used to assess vole condition.

2.5 DISCUSSION

Conservation translocations and reintroduction biology are proceeding on a range of fronts, with varied protocols and different biological and environmental factors contributing to project success. In the section below, we review some of the biases and weaknesses of conservation translocation projects, focussing particularly on physiology, and we identify some of the key design and methodological issues that influence the likelihood that a project will succeed.

2.5.1 Translocation Physiology: what can it offer?

The disciplines of behaviour, genetics and ecology are well recognised elements in animal conservation biology and conservation translocation programs, and their importance is clearly appreciated (Griffith et al., 1989, Fischer and Lindenmayer, 2000, Letty et al., 2007, Seddon et al., 2007, Groombridge et al., 2012, Jamieson and Lacy, 2012, Keller et al., 2012). However, a key discipline area that has received less attention in conservation translocation projects is that of physiology, especially those aspects of the discipline that can be considered relatively 'traditional' (Table 2.2). In this section we focus on animal physiology in the pre-release and post-release design of conservation translocation projects, and highlight how it can offer important insights to improve both initial and ongoing translocation success.

2.5.2 Pre-release planning

Setting *a priori* hypotheses provides opportunities to answer targeted questions concerning the species of interest, to test the importance of predefined factors that may influence translocation success, and to distinguish the relative merits of different translocation protocols (Dickman, 1996, Armstrong and Seddon, 2008).

Recent literature on reintroduction and translocation biology (Ewen et al., 2012a, Bekoff, 2013) emphasises the need for more quantitative and rigorously assessable monitoring including during the planning or "risk assessment" phases. For example, when considering habitat suitability for a reintroduction it is easy to assume that historical locations indicate suitable habitat, but in fact this can be an erroneous and quite misleading indicator of habitat preferences (Osborne and Seddon, 2012). Furthermore, habitat does not encompass only vegetation, but should include all the biotic factors associated with it (Osborne and Seddon, 2012). Physiology has the ability to define cause-and-effect relationships and thereby is used to adapt conservation management (Cooke et al. 2013). In terms of habitat, for example, physiological stress and condition parameters demonstrate how landscape patterns affect species persistence (Ellis et al., 2012). Osborne and Seddon (2012) recognise that process-based species distribution modelling requires knowledge of physiological limits, but the authors also point out that "they are often not available". As suites of physiological monitoring tools become more sophisticated, understanding of physiological limits should increase and in turn greatly enhance the conservation translocation process.

2.5.3 Release

The release phase of the translocation process has received the greatest physiological focus in peer reviewed papers and in the current reintroduction literature (Parker et al., 2012, Seddon and van Heezik, 2013). We feel that acknowledgement of the stress of translocation is crucial, but thus far only stress hormones have been widely examined. Quantitative analysis of other physiological factors may give a more robust picture of the effects of translocation on animals (see below). The importance of understanding an animal's basic ecology and biology is well recognised (IUCN/SSC, 2013), but the need for physiological indices is less well established. If the aim is to reduce potential stressors then it follows that first we must fully understand the extent of stress on translocated individuals by collecting physiological indices both as baselines before, during and after the translocation process.

2.5.4 Post-release monitoring – establishment and persistence

To gauge outcomes of reintroductions, post-release monitoring is required. It therefore follows that the duration of post-release monitoring should be an important factor when considering success. The establishment of persistent and self-sustaining populations is one of the ultimate aims of conservation translocations (Parker et al., 2012), and as such it is necessary to determine if translocated animals can (a) establish initially, (b) reproduce successfully, and (c) persist long-term at the translocation site (or at the least persist independently following release, even if they disperse to different locations). Despite this, much of the work we reviewed focused on assessing outcomes (a) and (b), with few projects sustaining monitoring for long enough to judge long-term establishment under outcome (c). For example, most projects (72%) sustained monitoring for between < 1 month and five years (see Appendix B). This period is unlikely to cover more than a few generations for any vertebrate species, and perhaps reflects other imperatives such as the period over which interest or funding are available (e.g. many national and international funding schemes, such as the Australian Research Council, US National Science Foundation, provide grant funds for 2-5 years). Consequently, most projects that putatively demonstrated outcomes (a), (b) and (c), and thus self-evaluated as successful, were somewhat limited in their post-monitoring scope.

Current reintroduction literature (Ewen et al., 2012a, Seddon and van Heezik, 2013) and the IUCN/SSC (2013) guidelines advise the following: pre-release baseline ecological data; demographic performance; behavioural monitoring; ecological monitoring; genetic monitoring; health and mortality monitoring; and social, cultural and economic monitoring. This is a comprehensive list, but we argue that the use of physiological indices to gauge both individual and population level performance should be introduced explicitly. For example, acknowledgement that physiological differences and tolerances in and between individuals can affect population diversity (Cooke et al. 2013) has broad implications for long-term translocation success. Notably, health monitoring and conservation medicine are well-established and fundamental to reintroduction biology (Aguirre, 2002), but we suggest that non-clinical, pre-clinical and peri-clinical physiological aspects of individuals' biology could further advance the field of conservation translocations

2.5.5 Translocation Physiology: promoting two of the three Rs of animal welfare

The three Rs of animal welfare and ethics in research are well-established doctrines that promote the replacement (R1), reduction (R2) and refinement (R3) of animals used for research. These are highlighted as key considerations for any activity relating to animal research, and necessarily extend to conservation and reintroduction biology. However, despite tremendous advances in the science of reintroduction biology (Ewen et al., 2012a, Seddon and van Heezik, 2013), there remains a 'more animals' approach to reintroductions/translocations, at least tacitly by some conservation practitioners, in the hope some animals will survive and establish self-sustaining populations. This is not to suggest that the 'more animals' approach reflects active intentions or a lack of consideration for animal welfare and well-being, nor the view that 'more animals' is the best option for success, but it probably reflects the simple consequence of having the opportunity to release large numbers of animals, combined with low expectation for survival, presumably because information about how the animals will be impacted by release is necessarily limited. Nonetheless, we argue that this approach contravenes R2 and R3 of the codes of practice and recommendations from national and international animal ethics and welfare bodies.

Obviously, replacing animals (R1) for reintroduction is not possible, but the incorporation of physiology and physiological measures into the translocation paradigm could markedly improve the survival chances of released animals, as well as improve understanding of the reintroduction/translocation process generally. Physiological parameters could be used to determine which are the most robust animals for release, which would benefit from either health intervention and/or soft-release techniques prior to release, as just one example. These outcomes directly assist the principles of reducing the total number of animals (R2) and the refinement of methods (R3) to promote successful reintroductions and translocations. By extension, this also serves to achieve R1 (replacement of animals) by ultimately obviating the need to reintroduce further animals once a population has become self-sustaining. This last point is not trivial in that once a self-sustaining population is established, further monitoring of animals and their habitat and ecosystem more generally should then become a key aim of management, with the aim of eliminating further need for captive rearing and release or translocation.

From a practical perspective the ‘more animals’ approach can also be fiscally irresponsible, because of the generally high costs associated with rearing and releasing large numbers of animals. Many conservation and reintroduction organisations rely heavily on public support as charity, in addition to the financial support of government and non-government research organisations. As such, it is imperative that animals are used only when the chances of translocation success can be demonstrated as being high, and that every action has been examined and evaluated with the view to maximising the likelihood of success of establishing self-sustaining populations.

The genetic consequences of inbreeding and homozygosity inherent in small founder population sizes is a flip side that is relevant to the above points – reintroduced populations need to be large enough to have genetic heterozyosity and vigour, but small enough to be financially viable for release and post-release monitoring. Physiological evaluation in conjunction with suitable potential mates (from a genetic point of view) have the potential for greater success, again maximising the chances for self-sustaining population formation.

Given the inherent invasiveness of reintroductions generally, we argue that it is necessary to consider whether invasive and non-invasive physiological procedures should be given more consideration than has occurred to date. Translocations should be not only cost-effective, but also ethical undertakings in that only the minimum numbers of animals needed to ensure success are used. The idea of releasing large numbers of animals in the hope of having a few survive is, in our view, unacceptable, particularly given recent advances in conservation physiology that can help to improve the efficiency of breeding and reintroduction programs. We consider some of the most relevant advances below.

2.6 PHYSIOLOGY AND CONSERVATION TRANSLOCATION

2.6.1 'Stress' in conservation translocations

'Stress' consists of three interrelated components: stressors, the environmental stimuli that lead to a stress response; acute stress; and chronic stress (Romero and Butler, 2007). Translocations often involve multiple stressors, each of which can activate acute and longer lasting responses (Dickens et al., 2010a, Parker et al., 2012). Typically, a stress response begins with an immediate adreno-corticoid (fight-or-flight) cascade, characterised by the production of glucocorticoids or 'stress hormones' (Romero, 2004; see also Romero & Butler, 2007, Dickens et al., 2010 and Parker et al. 2012 for detailed descriptions of the endocrinological processes involved in stress). Therefore, the easiest and most common indicator of animal stress that could be monitored in translocation is the glucocorticoid response (Manire et al., 2003, Hartup et al., 2005, Pinter-Wollman et al., 2009, Zidon et al., 2009). The main glucocorticoids used in wildlife studies are cortisol (many mammals) and corticosterone (rodents, birds, amphibians and reptiles); their role in stress, and as measures of stress, have been reviewed extensively (Romero, 2004, Romero and Butler, 2007, Dickens et al., 2010b, Parker et al., 2012). Glucocorticoid production can persist as part of a longer term response to stressors (Romero and Butler, 2007), and its major effects include behaviour modification, increased blood glucose levels, inhibition of normal growth and reproduction, and depression of immune function (Romero & Butler, 2007). Additionally, for translocated animals, stress hormones may have unique and unforeseen impacts.

It is well known that glucocorticoids can affect almost all cell types and tissues (Dhabhar, 2009), and the changes they induce can be critically important for aiding survival and ameliorating recovery following distress. However, for naïve animals released into unfamiliar environments, as occurs during translocations, unusual or novel stressors may be particularly disruptive because naïve animals may have no behavioural or physiological frame of reference for displaying appropriate responses (Waas et al., 1999, Romero, 2004, Dickens et al., 2010a, Rensel and Schoech, 2011). Consequently, the impact of novel stressors on translocated animals may be more severe and persistent than expected, with implications for the development and assessment of conservation translocation protocols.

Despite the benefits of acute or immediate responses to stressors, persistent or chronic exposure to stressors (or the perception of stressors) can have a range of deleterious effects (Millspaugh and Washburn, 2004, Dhabhar, 2009). Persistent distress, for example, can impair feeding behaviours, thereby compromising daily energy and nutrient acquisition; it can also increase energy requirements (Dickens et al., 2010), thus presenting animals with conflicting challenges. Additionally, persistent endocrinological responses to stressors can dampen the immune systems of animals, depressing their abilities to respond to immune challenges (Dhabhar et al., 1996) such as injury or exposure to pathogens or parasites (Bortolotti et al., 2009). Such challenges can further stimulate stress responses, leading to synergistic cascades that may increase risks from further immune challenges (Woodford, 2002). These compounding problems are likely to be important for translocated animals because new environments may also expose them to new or different strains of pathogens and parasites, and may be particularly problematic for captive-born and reared animals that have had limited or no prior pathogenic-exposure. In this regard, captive-born and raised animals present a particular conundrum with regards to innate immunity and host-parasite interactions, simply because they may lack the acquired immunity associated with prior exposure (Mathews et al., 2006, Ewen et al., 2012). Thus, at the very least, pre-release health checks and vaccinations for appropriate diseases should be considered highly desirable, but we suggest also that breeding and release projects consider ‘training’ animal immune systems through direct challenges during the rearing process.

As the main components of translocation – capture, captivity, transport, and release into a novel area – are all individually stressful events (Parker et al., 2012), translocated animals will inevitably experience some degree of acute and /or chronic stress . This can lead to changes in both stress response physiology (fight-or-flight responsiveness, sympathetic nervous system (SNS) drivers, hypothalamic-pituitary–adrenal (HPA) axis function, and overall glucocorticoid (GC) secretion) and in the function of the immune system and behavioural coping strategies (Dickens et al., 2010b).

Stress may not be a frequent or direct cause of translocation failures, but it can certainly jeopardise the principal objective of most release projects, that being to establish self-sustaining populations. In this regard, chronic or persistent exposure to stressors is important because it can disrupt animal reproduction, both endocrinologically (Sapolsky et al., 2000, Berga, 2008) and behaviourally (Romero & Butler, 2007). Persistent stress responses by translocated animals can be potentially disastrous for the relevant species and for the specific release project (which may also jeopardise future funding prospects). Consequently, given the potential for translocations to perpetuate cycles of persistent stress, immune compromise, and reproductive failure, we argue that ongoing monitoring for indications of stress should be explicitly incorporated into conservation translocation protocols. Techniques for such monitoring may involve the invasive sampling of tissue or body fluids, such as blood or saliva, or the non-invasive collection of waste or shed material such as hair or feathers (Table 2.3), and thus may be selected as appropriate to the species that is being translocated. There is scope for baseline research in *ex-situ* situations on normal physiological values (for species that these values are unknown) situations to be undertaken in species where translocations are planned.

2.6.2 Beyond ‘stress’ – other useful physiological indicators

2.6.2.1 Health indices

Several field-based measurements can be used as indicators of the general health and well-being of individual animals or populations (Table 2.2 and Table 2.3). It is important to identify which measures and methods – especially invasive *versus* non-invasive methods (see Table 2.3) – will be most appropriate for particular species. Selection will depend on a range of factors including the target animal’s body size and life history, the degree of association that individuals have had with people, and ease of sample collection and storage. Other factors also may need to be considered for specific translocations, such as whether animals will be most effectively translocated while conscious or immobilised and, if the latter, whether appropriate anaesthetic drugs and personnel trained to administer these will be available.

Health and immunocompetence underpin the survival of individual animals, but may also provide insights into the health of populations more broadly. Poor health, for example, increases the risk of depredation (Krumm et al., 2010), and can lower reproductive success (Cook et al., 2004); each of these deficits is especially important in the context of conservation translocations because of the often small number of founder animals released, and because even small losses or reproductive impairments are likely to have major deleterious effects on project success. Basic pre-translocation evaluations of individual health have contributed to the success of captive-bred chimpanzees released into the Conkouati Reserve (Tutin et al., 2001), and also to translocations of water voles (Mathews et al., 2006) and bighorn sheep (Ostermann et al., 2001), but health assessments rarely extend beyond the release period.

The potential to transfer pathogens and parasites endemic in one location to a new location is another health-related concern relevant for animal translocations and to a lesser extent for captive-bred releases (Ewen et al., 2012). Importantly, when considered solely from a veterinary or health-evaluation perspective, the fact that an organism is non-pathogenic in one area may overlook the risks that pathogens or parasites could become problematic for animals moved to a new site (Armstrong & Seddon, 2008; also see Mathews *et al*., 2006 for a detailed discussion on the health of translocated water voles and captive dibblers, *Parantechinus apicalis*). Conversely, transmission of a disease from a hitherto unknown reservoir at a release-site can also occur. For example, reintroduced African wild dogs (*Lycaon pictus*) contracted rabies after ingesting infected jackal carcasses, despite the wild dogs being vaccinated for rabies pre-release (Woodroffe and Ginsberg, 1999). Such vulnerabilities may be particularly important for captive-bred animals, which have vastly different life-experiences as compared with wild-caught animals used for translocation. Overall, efforts to establish health status and the immunocompetence of animals to be translocated could have profound benefits for conservation translocations. As such, key indicators of animal health-status that are easy to access and track pre- and post-release could prove exceptionally useful in the translocation biologist's 'tool box'. We suggest below that thyroid hormones are good candidates for such health-tracking markers, and may offer tangible benefits for translocation projects generally.

Table 2.3 Physiology in the field: invasive and non-invasive measurements that can be taken to help facilitate success in conservation-based reintroductions of animals.

Physiological measurement	Biological material or method	Invasive (I) or Non-Invasive (NI)	Examples
Glucocorticoid ‘stress’ hormones	Blood	I	McKenzie, Deane & Burnett (2004)
	Saliva	I	Pearson, Judge & Reeder (2008)
	Faeces	I	Hartup, Olsen & Czekala (2005)
	Urine	NI	Sheriff *et al.* (2011)
	Hair, feathers	NI	Bortolotti *et al.* (2009)
Thyroid hormones	Blood	I	Yochem *et al.* (2008)
	Faeces	NI	Wasser *et al.* (2010)
Reproductive hormones	Blood	I	Brown (2000)
	Faeces	NI	Wasser & Hunt (2005)
	Urine	NI	Graham (2004)
Trace elements	Blood	I	Lapidge (2005)
Stable Isotopes	Blood	I	Janssen *et al*. (2011)
	Faeces	NI	Varo & Amat (2008)
	Hair & feathers	NI	Cerling *et al*. (2006)
Bio-monitoring (e.g. heart rate, temperature)	Implants	I	Waas *et al*.(1999)
	Remote sensing	NI	Lavers *et al.* (2009)
Metabolic rate and water turnover	Labelled water	I	Lapidge and Munn (2012)

2.6.2.2 *Thyroid hormones*

Thyroid hormones (T4, thyroxine and T3, triiodothyronine) convey important information about overall health and disease status in animals (Yochem et al., 2008), and they can also provide insight into an animal's underlying metabolic state (Rolland, 2000, Wasser et al., 2010) and thermoregulatory capacity. Additionally, thyroid hormones convey information about growth and development, including brain development (Silva, 2006, Wasser et al., 2010). Thus, characterising the thyroid status of individuals or groups of animals could contribute substantially to our understanding of their general health and well-being. Perhaps more importantly, measures of animal thyroid status could also identify sub-clinical (or undiagnosed clinical) diseases or other maladies (Mönig et al., 1999, Mooney et al., 2008) that may not be evident from cursory observations of animals. Maintenance of peak health is likely to be vital during all stages of a reintroduction procedure, from animal release to survival post-release, and to successful reproduction and population establishment. Hence, the assessment of animals' thyroid hormone status, accessed invasively or non-invasively (see Table 2.3), can offer an important indicator of health and survival prospects as well as overall population viability. We suggest also that ongoing or even *ad hoc* evaluations of the thyroid status of translocated animals may highlight hitherto unknown or unforeseen interactions between animal health, survival and ecology, thereby improving the science, and the success, of animal translocations more broadly.

2.6.2.3 *Nutritional physiology*

Many studies in our review evaluated habitat characteristics with the view to ensuring that adequate food resources would be available to animals post-release.

However, most studies also assumed that habitat equated to food resources, and overlooked important interactions between animal physiology and nutrition (but see (Lapidge and Munn, 2012). That critical food items are apparently available is not necessarily a reliable indication of how well an animal can access or utilise the resources appropriately. For example, there may be physical, behavioural or ecological constraints (e.g. the presence of other species) that preclude individuals from accessing food e.g.(Dickman, 1991). The role of nutritional physiology is perhaps the most neglected aspect of translocation biology, perhaps because it is not easily assessed. However, some methods are tractable and also readily accessible for conservation translocation programs.

Nutritional physiology encompasses more than a simple accounting of the foodstuffs that are available at a release site, and potentially considers a wide range of factors that are relevant to translocations. These include the phenotypic plasticity of the gastrointestinal system (Starck, 1999a, Starck, 1999b, Millán et al., 2003, O'Regan and Kitchener, 2005, Starck, 2005, Starck and Wang, 2005, Munn et al., 2006, Munn et al., 2009), the impacts of gut pathogens (Everest, 2007), microbes or other intestinal symbionts that are needed for healthy digestion (Hooper and Gordon, 2001, Kohl and Dearing, 2012), and microbial ‘seeding’ of captive-reared animals, particularly herbivores, to aid digestion following release, and even foraging behaviours; all of these factors can ultimately affect survival and breeding success.

Ensuring nutritional and digestive wellbeing may be critically important for captive-bred animals, especially if they have been reared on highly processed or commercial foods. Often, captive-bred animals do not have to ‘work’ for their food, at least not as intensively as their wild counterparts. As such, there are likely to be significant interactions between the nutritional experience of captive-reared animals and how they fare following release. Specific studies of these interactions are rare, but they could be investigated empirically using soft- and hard-release methods where animal condition can be observed. For example, in a study of released Peninsular bighorn sheep (*Ovis canadensis*), all released animals were fed on high-quality food (alfalfa pellets, plus salt and mineral blocks) in addition to having access to native vegetation in pre-release enclosures (Ostermann *et al.* 2001). The animals were then released into the wild without immediate acclimitisation to a diet consisting solely of native vegetation. The project failed to establish a self-sustaining population (Ostermann *et al.*, 2001) and, although numerous explanations were offered to account for the poor success, we contend that nutritional physiology was likely to have been relevant; indeed, the authors themselves suggested that higher success in certain releases was related to the availability of good quality forage and water (Ostermann *et al.*, 2001).

It is apparent that abrupt dietary changes can generate negative outcomes for animals through increasing stress and depriving them of key nutrients, both of which may lead to compromised immunity immediately post-release. The gastrointestinal tract is keenly influenced by the immune system, where the immune cells and resident microbes form a complex ecosystem (McCracken and Lorenz, 2001). This intestinal ecosystem can be altered by changes in diet (Liukkonen-Anttila et al., 2000, McCracken and Lorenz, 2001), and can further influence other physiological features, particularly when animal stress-hormones are elevated (Everest, 2007). Recent studies of wild versus captive wood grouse (*Tetrao urogallus*) (Wienemann et al., 2011), for example, have revealed major differences between the gastrointestinal microbiota of wild and captive birds. In the context of translocation biology, mismatch between the appropriate intestinal environment and that established in the released animals could adversely affect the survival of translocated animals. In another study, marbled teal (*Marmaronetta angustirostris*) maintained for a longer captive period before release showed lower survival rates compared to those released soon after fledging, and this was attributed to the longer-held animals being fed a commercial diet (Green et al., 2005). Therefore, dietary adjustments should be thoroughly considered in translocation protocols, and given that gut flexibility (both in terms of morphology and microbial composition) takes time to adjust e.g. (Moore and Battley, 2006), a gradual reduction of high-quality foodstuffs prior to release may improve survival post-release.

Assessment of micronutrients and trace elements is another component of nutritional physiology that holds potential value to translocation physiology. This is especially the case with respect to releases of captive animals, as demonstrated by Lapidge (2005). In that study, plasma vitamin E concentration (PVEC) was evaluated in yellow footed rock wallabies (*Petrogale xanthopus celeris*), due to prevalence of deficiencies in captive but not wild animals (Lapidge, 2005). This study aimed to assess welfare implications of releasing captive wallabies and demonstrated how the captive animals adjusted to the wild environment by rapidly increasing PVEC levels post-release to levels similar to their wild counterparts, thus indicating that there were no appreciable welfare implications.

Overall, nutrition is one of the more easily manipulated aspects of the translocation process and potentially also one of the most important. Nutrition can be manipulated non-invasively and with little expense, and the benefits of incorporating nutritional aspects of physiology should have flow-on effects for improved immune status, reproductive success and general animal health and wellbeing. For these reasons, we argue that more focus should be placed on priming the gastrointestinal tract of captive-reared animals before release, and that additional factors such as seasonal or diet-related plasticity of the gastrointestinal tract (Piersma and Lindström, 1997) should be incorporated into release protocols.

2.6.2.4 Other physiological factors

There are a collection of other physiological factors that could be of use to translocation physiology. Immunoecology (or ecological immunology) investigates underlying causes of immune system function between individuals and populations (Hawley and Altizer, 2011) and as such has close ties with health indices, disease and stress. Groombridge et al. (2004) demonstrated this via quantative evaluation of white blood cell counts to measure stress levels in Po'ouli (*Melamprosops phaeosoma*). Integration of immunoecological aspects of animal biology, and techniques used to evaluate immune status in the wild, may be particularly useful for understanding the cause-and-effect nature of translocations successes and failures.

Understanding a species' reproductive biology is also important for predicting viability of wildlife populations, as well as for developing best practice captive breeding programs (Brown, 2000, Graham, 2004, Wasser and Hunt, 2005, Asa, 2010). Details of the reproductive physiology and associated needs (e.g. specific resources) have scope for further inclusion in managing translocated populations.

Stable isotopes can be used to study diverse factors affecting wildlife, all of which are relevant to conservation translocations. These can range from identifying factors that affect growth (Janssen et al., 2011); determining migration patterns and diet changes (Cerling et al., 2006); and teasing out species differences in dietary assimilation to determine why species with similar ecologies were displaying different survivabilities in the same habitats (Varo and Amat, 2008) and range from invasive to non-invasive techniques (Table 2.3)

Stable and radioactive isotopes biology can also inform translocation science. Analysis of metabolic rate and water turnover can be used to measure how translocated animals, particularly those that are captive bred, adjust to wild conditions post release, and can be a particularly sensitive measure of success as demonstrated in Lapidge and Munn (2012).

2.6.3 Translocation Physiology – methods

Perhaps the most important aspect to consider prior to a translocation is whether invasive methods for monitoring physiology are appropriate, acceptable and practicable for the given situation. The level of information generated from physiological investigations should be expected to justify their use, or to rank whether relatively less-invasive methods would be better suited to the species in question.

Non-invasive methods for monitoring animal physiology have two main benefits for conservation translocation biologists. Firstly, they minimise direct contact with animals, and secondly, they can minimise direct or remote exposure of animals to humans (Table 2.3). However, it is important to remember that translocation is by its nature an invasive procedure. Animals are captured (whether free-living or captive) and transported to usually new and unfamiliar environments. The potentially profound impacts of translocation are highlighted by the often high mortalities that are seen for newly released animals. In a study of reintroduced European mink (*Mustela lutreola*), for example, mortality exceeded 40% in the first 30 days post-release (Maran et al., 2009). In a translocation of radio-collared elk (*Cervus elephas*), 15% of deaths occurred in the six weeks following release and were related to stresses associated with capture/release (Larkin et al., 2003). Consequently, careful attention to physiological measures indicating animal distress or compromised health and well-being should be explicitly included in translocation protocols. For example, identification of key trigger-points to initiate intervention during capture, transport and post-release could be crucial for ameliorating the apparently widely accepted high levels of post-release mortality in translocations. In particular, we suggest that a "more animals" approach to combating the high rates of post-release mortality in conservation translocations may be less successful than a "fewer animals – more invasive" approach.

The "more animals" approach is problematic for several reasons, not the least because it contravenes codes of practice and recommendations from national and international animal ethics and welfare bodies, which strive to reduce the numbers of animals used for science and research, and to refine the methods used to maximise the success of animal-based projects. In addition, a "more animals" approach is not fiscally responsible because of the generally high costs associated with rearing and releasing large numbers of animals. Therefore, given the inherent invasiveness of translocations, it is prudent to consider whether invasive procedures should be considered more often than has occurred previously, especially if this results in improved conservation translocation outcomes.

There are several invasive procedures that would probably benefit conservation translocation projects (Table 2.3) and that are appropriate for a range of taxa, including reptiles, mammals and birds. Of note, most of these procedures are well established in veterinary and physiology practice, making their inclusion in conservation translocation protocols relatively straightforward—especially if relevant experts are consulted. In this context, we suggest that several aspects of research could prove valuable for understanding and evaluating the entire translocation process, along with the mechanisms and factors that affect survival post-release. In particular, field metabolism (Lapidge and Munn, 2012), water use, heart rates and body temperature (Waas et al., 1999) could be used to determine how well animals are acclimating or adapting to their new environments, whether they are maintaining condition, are foraging successfully, and are they able to meet the energetic and nutritional demands needed for reproduction. These are important questions for which we have very limited data.

Radio- or GPS-tracking devices represent one semi-invasive method for evaluating animals post-release that has great potential for improving reintroduction success. Tracking devices can be considered invasive in that they require animals to wear electronic tags, either externally (e.g. as neck or leg collars) or as internal implants. Such devices could interfere with animals' daily activities, but may also provide unprecedented information about how individuals adapt to release. For example, tracking can provide information on daily ranging patterns (Campioni et al., 2013), insight into immediate post-release behaviours (Dennis and Shah, 2012), and otherwise cryptic, but critically important information about movements, habitats or nutrients that are essential for animal survival, e.g. (Gurarie et al., 2011). The ability to locate animals can assist with regular visual contact of subjects, thus allowing intensive behavioural monitoring, and can also present opportunities to collect additional physiological and behavioural information via collection of scats (providing information on, for example, diet and stress hormones) and urine (providing information on diet, stress hormones and water turnover). At the outset, placement of collars may require animals to be sedated, particularly for large mammals e.g. (Wear et al., 2005), but this also provides opportunities for collection of a wide array of baseline physiological data and indicators of animal health before release. Moreover, depending on the species and the situation, animals may be recaptured to replace the collar batteries or to retrieve GPS-data, providing further opportunity to collect more invasive data such as blood samples.

2.7 CONCLUSIONS AND RECOMMENDATIONS

The weight heretofore given to genetic (Groombridge et al., 2012, Jamieson and Lacy, 2012, Keller et al., 2012), disease (Sainsbury et al., 2012) and behavioural factors e.g.(Armstrong et al., 1999, Ostro et al., 1999, Munkwitz et al., 2005) in translocation planning needs to be extended to include physiological processes and mechanisms as a recognised complementary discipline. Some resistance might be expected in promoting physiology as a critical tool for use in translocation biology. The view that physiological methods may cause distress, particularly for invasive methods like surgical implantation of heart rate monitors, has likely impeded the advancement of physiology in conservation science generally. Obviously, the potential use of physiological tools, their invasiveness and possible impacts must be weighed against the potential benefits to the survival of a given species or population, with the rarity of a species probably dictating the outcomes of these evaluations. Nonetheless, we argue that the role of physiology in reintroduction and translocation science should be given greater consideration. The most recent IUCN Guidelines for conservation translocations recognise that physiology should be assessed, and we echo that recommendation. In fact, we would go further, and argue that physiology is the principal unifier that describes the basic ecological and behavioural features of organisms relevant for evaluating any reintroduction proposal. To this end, we propose the following recommendations for developing and evaluating reintroduction projects:

1. Reintroduction programs should consider the range of interactions between released animals and the environment, including potential interactions with other species that may be present at the release site and that can be illustrated by invasive or non-invasive physiological indices. This should include, for example, the potential physiological responses to predators, competitors, parasites and pathogens. The potential for such interactions must be considered pre- and post-release and in follow-up monitoring studies, and mitigated if required.

2. Databases of the physiology of reintroduced animals should be created prior to release, and they should include—at a minimum—information on genetic, behavioural, nutritional and health/disease aspects of the individuals being used.

3. Greater use and consideration of physiological assessments of animal wellbeing pre- and post-release must be incorporated into monitoring protocols. This should assist in ensuring the suitability of animals for release and their performance thereafter. It will also become increasingly important to understand the physiological tolerances of reintroduced animals and species to predict their ability to adapt to changing conditions.

4. Post-release monitoring should continue over longer periods than has been the case in most studies to date, particularly as conditions at many reintroduction sites are likely to change rapidly in future as the climate changes (Parmesan, 2006). Long-term

monitoring is often not possible because typical funding cycles run for just 3-5 years. Nonetheless, we urge that due consideration be given to defining and prescribing appropriate monitoring periods for specific reintroductions, partly to improve successes, but also to provide more realistic and rigorous evaluations of success. Moreover, monitoring of animal health and physiology should be considered at both early and later stages of reintroductions, either during or following acclimation in ‘soft-release’ studies, and also over longer periods.

In conclusion, we note that substantive advances have been made in improving the success of animal reintroductions in recent years (Ewen et al., 2012a). These advances have been assisted and supported by increased use of behavioural observations and ecological and genetic monitoring of released animals. However, from our review we argue that further advances in the field, and in the success of individual reintroductions and translocations, could be gained by broadening routine data collection to include relevant physiological measures. Such measures can inform researchers of the wellbeing of individuals and their chances of reproductive success and, thereby, the likelihood of a reintroduced population persisting post-release. As a starting point, we recommend that key indicators of animal health, such as cortisol and thyroid status, and of physiological state (e.g. condition, diet) be incorporated into routine pre- and post-release monitoring protocols. This is not to say that translocations or reintroductions should apply each of these recommendations unnecessarily, but they ought to be considered during planning for species-specific protocols, with the view to incorporating procedures strategically and in a manner most likely to benefit the success of the releaser. Nonetheless, given the persistent variability in the success rates of translocation, the collection of as much data as possible may assist future practitioners by accumulating a knowledge base of physiological indicators relevant to animal survival. Such indicators will help to identify potential problems that may not be apparent through *ad hoc* observations, and offer opportunity to improve translocations generally by focusing evaluations of ‘success’ on physiological wellbeing.

3 GUT THROUGHPUT OF SEED MIMICS IN THE ORANGUTAN (*PONGO ABELII AND HYBRID P. ALBELII X P. PYGMAEUS*)

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3.1 INTRODUCTION

Orangutans (Sumatran: *Pongo abelii* and Bornean: *Pongo pygmaeus.*) are the world's largest arboreal mammal (Ancrenaz et al., 2008), Asia's only great ape (Wich et al., 2008b) and are currently found only on the islands of Borneo and Sumatra (Wich et al., 2008b, Husson et al., 2009). Their main habitat distribution is across dipterocarp, peat-swamp, freshwater swamp and alluvial forests (Husson et al., 2009). Orangutans are largely arboreal, travelling through forest canopies (Rijksen, 1978, Delgado and van Schaik, 2000, Thorpe and Crompton, 2009). The orangutan consists of two species: Bornean (*Pongo pygmaeus*) and Sumatran (*Pongo abelii*) (Brandon-Jones et al., 2004), with further classification of Bornean orangutans into three genetically distinct subspecies: *P.p., wurmbii* in southwest and central Kalimantan; Western Bornean, *P.p. pygmaeus* from north-west Kalimantan to Sarawak; and *P.p. morio* from north-west Kalimantan to Sabah (Singleton et al., 2004) as well as hybrid forms found in some zoological collections. Different species are no longer inter-bred in zoos and relate to a time before the 1980's when Bornean and Sumatran orangutans were not recognized as distinct species but as sub-species that were difficult to differentiate (Mackinnon, 1975).

Orangutans have a diet largely consisting of plant matter (Chivers and Hladik, 1980, Caton et al., 1999a) and includes fruit, flowers, leaves and bark, pith and other vegetation (Rijksen, 1978, Galdikas, 1988, Harrison, 2009b, Russon et al., 2009), as well invertebrates, vertebrates and other non-animal, non-plant material such as fungi, honey, soil and water (Galdikas, 1988, Russon et al., 2009). Although the amounts and frequencies of foods eaten by orangutans vary across different geographical sites, with corresponding differences in life history stages, dietary intake and behaviour, (Harrison, 2009b, Russon et al., 2009), the general dietary components are similar.

The orangutan gastrointestinal morphology is similar to other mammalian herbivores that use colon-fermentation (Chivers and Hladik, 1980, Stevens and Hume, 1995, Caton et al., 1999a). This consists of a comparatively simple stomach, a relatively long small intestine, where digestive products are absorbed, and a capacious colon which is haustrated and is the principal site of fermentation of structural polysaccharides, i.e. pectins, cellulose and hemicellulose (Chivers and Hladik, 1980, Stevens and Hume, 1995, Caton et al., 1999a). Due to this morphology the orangutan colon possesses considerable versatility, especially when only poor quality foodstuffs are available (e.g. bark); the large size of the colon enabling more thorough digestion of poor quality foodstuffs via longer term retention (Stevens and Hume, 1995, Harrison, 2009b). Orangutans rely on the assistance of symbiotic gut bacteria that ferment plant fibres (Stevens and Hume, 1998), which requires both space and time. In this regard, the passage time of foodstuffs through the gut of these herbivorous animals is particularly important and is a major factor determining digestive efficiency (Bjorndal et al., 1990, Stevens and Hume, 1995)

Passage time of food through an animal's gastrointestinal tract is commonly measured as the mean retention time (MRT), which is the time food is available for digestion and absorption within the gut (Stevens and Hume, 1998). There is however another measure, transit time (TT), which is defined as the time between ingestion and first elimination in faeces and maximum time until last bead excretion (TT_{MAX}) (Robbins, 1993, Barboza et al., 2008), the time between ingestion to last detected elimination in faeces (Childs-Sanford and Angel, 2006, de Oliveira and Duarte, 2006, Clauss et al., 2007, Clauss et al., 2008).

Passage of discrete indigestible passages, like intact seeds (as opposed to seeds that are destroyed and eaten for nutritional value), has been used to determine gut throughput time in numerous studies and species e.g. in binturongs, *Arctictis binturong*, (Colon and Campos-Arceiz, 2013); various bird species (Traveset et al., 2001), and part of the wider area of seed dispersal research, an important component of forest ecology (Howe and Smallwood, 1982a, Willson and Traveset, 2001, Bascompte and Jordano, 2007). Experimental studies have evaluated MRT and TT using liquid and solid phase markers e.g. (Caton et al., 1999a, Clauss et al., 2005); with these sometimes then extrapolated to field studies. Previously results have been then utilised to determine seed dispersal effects of different frugivores e.g. Caton et al.'s (1999) data on MRTs in captive orangutans were cited by Nielsen et al. (2011) when assessing the potential role of slow digesta passage in a small scale germination study of orangutan defecated seeds in our study site. We feel that markers that mimic seeds could yield results more comparable to a wild situation where orangutans are ingesting seeds from plants in their environments. In this regard, gut throughput was of most interest to us, as this is part of a larger study of orangutan seed dispersal in the Sabangau Forest, Central Kalimantan, Indonesia. Thus, in our case, we wanted not only to ascertain the transit time (TT) and time until last elimination (TT_{MAX}) of seed-mimics in orangutans (i.e. time to appearance of the food markers until the markers were fully eliminated), but also the distribution of the excretion of seed mimics over time, rather than an average retention time, and to apply the findings to understand how seed elimination patterns may impact seed dispersal by orangutans more broadly.

In order to assess TT, TT_{MAX}, and elimination patterns that simulate the passage of indigestible seeds through the orangutan gut, six orangutans at two different Australian zoos were fed indigestible seed-mimic markers (beads). To the best of our knowledge, the only other study to investigate feed passage rates in orangutans was by Caton et al. (1999). However, Caton et al.'s (1999) study examined the gut passage of chemical markers and digestion, thus we felt that our study had merit as we are primarily interested in the passage of indigestible seed markers in order to extrapolate reliable information on seed passage relevant for broader-scale seed dispersal studies. Zoo diets have in the past featured these types of relatively homogenous foodstuffs, but modern captive diets ideally aim to meet nutrient requirements while considering natural foraging and feeding behaviour (Committee on Animal, 2003). Although our study contained a zoo formulated diet, current feeding habits in our study locations provided a majority proportion of plant-based unprocessed foodstuffs. While our diet was not analogous to a wild diet, the diet contents presented to the captive orangutans in our study received a majority of whole fruit and vegetables and limited processed material.

This study forms a part of a larger investigation into seed dispersal by orangutans in tropical peat swamp forest in the Sabangau Forest, Central Kalimantan, Indonesia. Data from wild orangutan observations has been utilised, with details on data collection methods in chapters 1 and 5.

3.1.1 Aims

1. To determine the time from mouth to first and last elimination, transit time (TT) and maximum time (TT_{MAX}) respectively, of indigestible seed-mimics
2. To determine the pattern of seed-mimic elimination of indigestible seed-mimics
3. To determine if transit time affected significantly by seed-mimic size.

3.2 MATERIALS AND METHODS

3.2.1 Taronga Zoo

Two adult hybrid Sumatran-Bornean orangutans at Taronga Zoo (AEC #4a/11/11) formed this part of the study, one male (27 years old, 115.5kg) and one female (29 years old, 66kg). Both animals were fed their regular diet and maintained in their regular enclosures, which consisted of three concrete pens and two separate outdoor areas. Additional banana was added to the regular diet to hide the seed mimics used (below).

Orangutan diet at Taronga Zoo (TZ) was made up to a pre-approved formula that changed for each day of the week but always largely consisted of plant-based material. Food intake could not be quantitatively assessed in this study, however, because all foodstuffs were shared between the two orangutans. The leaf component of the diet offered consisted of whole leaves from the following plants: Celtis (*Celtis australis*); The Weeping Fig (*Ficus benjamina*); Black Mulberry (*Morus nigra*) African Olive (*Olea europaea*) and Banana (*Musa spp.*). The vegetables included daily staples of: Sweet potato; spinach; celery; carrot; turnip, lettuce, capsicum and cucumber and a changing roster of fruits that included tomato, kiwi, pear, and apple. Only very small amounts of processed foods were fed, mainly to assist in training and enrichment through a daily "activity feed" of 3 x unshelled peanuts, sultana (10g) and 150g of primate cubes. Water was freely available at all times. Diets were made up and weighed by dedicated zoo staff, although it could not be distinguished the amounts each orangutan ate of each foodstuff as they shared an exhibit.

On Day 1 of each study, the orangutans were each fed differently coloured spherical seed mimics, of 2, 4 and 6 mm diameter polyethylene non-toxic beads (see Table 3.1). A normal diet was fed on every day with the addition of bananas to hide the seed mimics in on day 1. Each animal was fed the seed mimics at separate ends of the enclosure, while the other animal was distracted so as to ensure that there was no sharing of the different coloured beads. The male was fed green coloured beads and the female red coloured as per numerous other studies [see (Fuller et al., 2011)]. Attempts to disguise seed mimics greater than 6 mm diameter (i.e. 8 mm and 10 mm) in soft food were unsuccessful on repeated attempts despite orangutans ingesting seeds of with a width and length greater than 10 mm and 20 mm respectively (Chapter 4, Table 4.3)

Faeces were collected once daily over 10 days, with a minimum of seven days between the end of one experiment and the start of another. As faeces could not be evaluated straight away, a collection time period of 168 hours of collection (from T=0, ingestion to T=168) was deemed sufficient. This was based on the work of Caton et al. (1999) where the maximum time to elimination of was 99.9 hours, with the additional 68.1 additional hours allowing for differences in study animals and marker type. Due to poor initial compliance by the study animals, some experiments were repeated, by re-feeding the TZ male and female 2- and 4-mm seed mimics.

Throughout the entire experiment the orangutans were observed during daylight hours between 0530 and 1730 h. The enclosure design did not allow for camera placement to observe animals overnight, however, faeces could be distinguished by presence of different coloured seed mimics during unobserved times. If faeces could not be collected straight away, the location of faeces was noted and recorded on a map of the enclosures (photos were not allowed by the zoo administration). Night samples were considered to have occurred at the midpoint of the sampling interval. Corprohagy was not observed. Faecal elimination in the orangutan is noted as occurring mostly in the morning, with reduced production by afternoon and none overnight (Caton et al., 1999a). Preliminary observation of faecal production in wild orangutans agrees with this (see Table 3.3a,b) and the majority of defecations were observed by the primary investigator here (E. Tarszisz). Faeces were frozen immediately after collection before later thawing to extract eliminated beads.

3.2.2 Perth Zoo

Four orangutans at Perth Zoo (PZ) were part of this study (AR&E ZA/4991-4 #59404), three adult females with infants of varying ages [Female 1: 22 years old, 50.4 kg; Female 2: 24 years old, 40.95 kg; Female 3; 44 years old 42.5 kg] and one adult flanged male (27 years old, 119.6 kg). On Day 1 of this part of the study the orangutans were fed seed mimics as above (polyethylene non-toxic beads of 2mm, 4 mm and 6 mm diameter). The amounts fed differed per animal (Table 3.1). Some seed mimics were hidden in banana and some in cordial drink. The PZ individuals were all habituated to a daily ration of diet cordial (to facilitate administration of oral supplements and medications) and this assisted administration of the larger 4 and 6 mm seed mimics in our study. The total number of seed mimics swallowed varied per animal because there were inter-animal variations of acceptance, with some animals more prone to destroying the seed mimics. Some beads were crushed despite being hidden inside soft foodstuffs such as banana, and some were further ejected by spitting. These rejected beads were collected from the floor of the enclosures on day 1 to prevent confounding TT, TT_{MAX} and elimination curves. Broken beads that were found in the faeces were not included in the results and it was not possible to count how many of these were chewed; they were usually too severely fragmented to reform for bead counting.

Diets at PZ were made up the day before by the primary investigator (E. Tarszisz) according to veterinary instructions. The diet changed daily so each foodstuff was recorded, weighed to the closest gram. These diets again consisted of a majority of plant material. Browse leaves were provided daily in varying amounts with the most common species being: Accia species e.g. Mulga (*Acacia aneura*), Bamboo species e.g Common bamboo (*Bambusa vulgaris*), Ficus species e.g. Benjamins fig (*Ficus benjamina*), Kikuyu (*Pennisetum clandestinum*), Umbrella tree (*Schefflera actinophylla*) and Giant Strelizia (*Strelitzia nicolai*).

The diet largely consisted of vegetable matter including sweet potato; taro; cabbage; broccoli, cucumber, herbs (parsley, coriander, lemongrass), capsicum, lettuce, pak choi and green beans. Fruits were varied and included rambutan, coconut, apple, banana, watermelon, *Monstera deliciosa* (commonly known as Fruit Salad plant), and honeydew melon All female orangutans in this study were housed separately from other orangutans, with their infants, so total fecal output was able to be reliably measured for each female. The infant feces were easily identified by their small size and were ignored.

Faeces were collected twice daily between 0530 h and 1730 h on a regular basis for 11 days, the frequency of collection was dependent on the individual orangutans allowing access to their outdoor and indoor enclosures. The location of faeces was noted and recorded on a map of the enclosures (photos were not allowed by the zoo administration). Faeces voided between 1730 h and 0530 h were collected in the mornings. It is unlikely that orangutans defecated overnight (see above) but as video monitoring was logistically unviable, samples were considered to have occurred at the midpoint of the sampling interval. Although this may have introduced a degree of bias into the data, it was logistically the only option for collection. Once collected faeces were weighed and examined for seed mimics within 2-24 hours of collection. The female orangutans were not subjected to any stressful or unusual events as a result of this study. However the male at Perth Zoo had some social changes on days 1 and days 9-11 of this study. On these days he was introduced to a female and her almost independent juvenile (neither which were included in this study) whereas previously (and on days 2-8) he was alone in an enclosure. Faeces could be collected in entirety until day 9, after which faeces could only be collected from his night den but not his outdoor enclosure. Therefore for this individual, TT_{MAX} could not be calculated reliably. Faecal output was measurable for the days he was housed individually.

Faeces were washed through mesh sieves of decreasing diameter (down to 1mm) until all faeces had been examined and all seed mimics collected. Number of (if any) seed mimics was noted for each size class (2, 4 and 6mm) in each faecal sample (see totals in Table 3.1).

3.2.3 Calculation and plotting elimination patterns of seed mimics

The transit time (TT) and maximum time (TT_{MAX}) were quantified using Microsoft Excel (Redmond, Washington: Microsoft 2013) and graphically represented using GraphPad Prism version 6.00 for Windows (GrahPad Software, La Jolla California USA, www.graphpad.com). Elimination patterns were visualized by firstly plotting seed mimics as percentage of total quantity of intact beads fed over time since ingestion. Secondarily they were plotted as a percentage of the peak quantity, which was the single elimination with the highest number of defecated beads, in order to normalize the different absolute amounts. A one-way multivariate analysis of variance (MANOVA) was conducted to test the hypothesis that there would be one or more mean differences between the transit times for 2 mm, 4 mm and 6 mm seed mimic sizes. Plotting of percentage of peak patterns was only conducted where more than 5 seed mimics in a category (2, 4 or 6 mm) were ingested by an individual (Table 3.1, Fig 3.2).

3.2.4 Frequency of faecal production – Zoo vs. Wild

Feaces production from all 6 animals from four consecutive days (days 2-5) of each the zoo projects was recorded, with the first day of feeding excluded from consideration. For comparison, four days of faeces production frequency from six orangutan of similar age class/cohort (2 adult flanged males, 4 adult females with juveniles) were noted from data collected by the senior author (E. Tarszisz) at the Natural Laboratory of Peat-swamp Forest, Sabangau, Central Kalimantan, Indonesia (in a project conducted in partnership with the Orangutan Tropical Peatland Project (OuTrop) and their Indonesian partners The Centre for the International Cooperation in Management of Tropical Peatlands). The days were chosen, where possible, from four consecutive focal animal full-day (nest-nest) follows conducted in the more fruit abundant wet season (October/November-May/June) in 2013, with the view that this would more closely resemble food abundance in our zoo setting. The data from the current study of zoo animals was then compared to the data collected on wild orangutans in Central Kalimantan (unpublished) and un-paired t-test was performed to determine if frequency of defecation of zoo animals corresponded to that of their wild counterparts.

3.3 RESULTS

Transit time was quite long in our animals, with the average TT in our study being 70.6 ± 7.1, 72.5 ± 6.8 and 86.2 ± 16.6 hours for the 2, 4 and 6mm seed mimics, respectively (Table 3.1). TT_{MAX} were accordingly long, with an average of 159.3 $\underline{+}$ 14.2, 126.2 $\underline{+}$ 20.2 and 112.8 $\underline{+}$ 23.1 hours for 2,4 and 6mm seed mimics respectively (Table 3.2).

The orangutans showed a consistent pulse elimination pattern of seed mimics, when expressed as a percentage of total quantity (Fig 3.1). When elimination was presented as a percentage of total quantity, in order to normalise the distribution, the pulse elimination was still evident (Fig 3.2).

A MANOVA test was conducted to test the differences between seed mimic sizes, with no significant difference found between them (F = 0.36, d.f. = 2, 4 P = 0.54). The shortest TT was for the 6mm seed mimics in the TZ female and the longest TT for the 6mm seed mimics in PZ female 3 (Table 3.2). Potential reasons for this are discussed below.

We also found that there were no significant differences in defecation frequency between wild orangutans and their zoo-based counterparts (p>0.45, Table 3.3a,b).

Table 3.1: Total numbers of seed mimics consumed by orangutans. TZ = Taronga Zoo, PZ = Perth Zoo.

Values in parentheses indicate repeated experiments for Taronga zoo animals

Animal	**2mm**	**4mm**	**6mm**
TZ Male	29	9 (9)	6
PZ Male	45	14	4
TZ Female	135 (37)	4 (16)	6
PZ Female 1	15	4	3
PZ Female 2	19	2	2
PZ Female 3	21	12	5

Table 3.2: Transit times (TT), maximum transit time (TT_{MAX}) for 2, 4, and 6mm seed mimics in 6 orangutans, hours from T=0 (ingestion)

ANIMAL	**2MM TT**	**4MM TT**	**6MM TT**	**2MM TT_{MAX}**	**4MM TT_{MAX}**	**6MM TT_{MAX}**
TZ MALE	79.0	79.0[+]	91.0	150.0	114.0[+]	186.0
TZ FEMALE[+]	58.5[+]	41.0[+]	19.0	119.5[+]	67.0[+]	43.0
PZ MALE	42.0	71.0	71.0	173.0	138.0	125.0
PZ FEMALE1	77.0	77.0	96.0	168.0	120.0	96.0
PZ FEMALE 2	77.0	77.0	96.0	129.0	*77.0*	114.0
PZ FEMALE 3*	90.0	90.0	144.0	216.0	192.0	*144*.0
MEAN ± S.E.M.	70.6 ± 7.1	72.5 ± 6.8	86.2 ± 16.6	159.3 ± 14.22	126.2 ± 20.2	112.8 ± 23.1

[+] Averaged values for repeat experiments.

* PZ female who had chronic intermittent constipation and was fed diluted prune juice daily to ameliorate this.

Italicized values indicate where a single bead was swallowed for the size class and thus the TT= TT_{MAX}. These values were excluded from the mean.

Table 3.3a: Zoo orangutan defecation frequencies per 24 hours

Day	TZ Male	PZ Male	TZ Female 1	PZ Female 1	PZ Female 2	PZ Female 3
2	2	2	4	1	4	2
3	3	3	3	1	3	2
4	2	2	3	3	3	2
5	1	3	5	2	2	4
Mean±S.D.	2 ± 0.82	3 ± 0.58	4 ± 0.96	2 ± 0.96	3 ± 0.82	3 ± 1.00

Table 3.3b: Wild animal defecation frequencies per 24 hours

Day	TPSF Male1	TPSF Male2	TPSF Female 1	TPSF Female 2	TPSF Female 3 [¥]	TPSF Female 4 [+]
1	3	4	6	2	1	2
2	2	2	8	2	4	2
3	3	4	2	1	2	1
4	2	2	1	3	3	1
Mean ± S.D.	3 ± 0.58	3 ± 1.15	4 ± 3.30	2 ± 0.82	3 ± 1.29	2 ± 0.58

[¥] Days 1-2 were from consecutive nest-nest follows and Days 3-4 were consecutive nest-nest follows at a separate date

[+] Days 1-3 were taken from consecutive nest-nest follows, day 4 was from a separate follow

3.4 DISCUSSION

This study presents insight into the distribution of the elimination of seed mimics (plastic beads) in the orangutan when fed a heavily plant based diet with minimal processed foodstuffs. In this study the orangutans showed a consistent pulse elimination pattern of seed mimics, when expressed as a percentage of total quantity (Fig 3.1). The total quantity differed per animal due to difficulty in having each animal swallow the seed-mimics (totals given in Table 3.1). To normalize the distribution we presented elimination of seed mimics as a percentage of peak quantity (Matsuda et al., 2015). Although this did smooth some of the peaks for the Perth Zoo animals, they still had a single large peak and the Taronga Zoo animals showed several large peaks in elimination of beads. Our animals also demonstrated particularly long transit times (both TT and TT_{MAX}, Table 3.2), in comparison to Caton et al. (1999), where a particle marker (Cr-CWC) of 600-1200 µm had an average TT of just 24.2 ± 0.8 hours compared to our bead TTs of 76.4 ± 8.5 hours and a $TT_{MAX} = 81.4 \pm 13$ hours compared to ours of $TT_{MAX} = 132 \pm 23.9$ hours. This change is likely due to marker size (as well as different study aims), however differences in marker density and dry matter intake could be contributing factors and further research would clarify this. Nonetheless, the finding that the bead marker passage is slower than fine particle passage is consistent with previous studies gut of endozoochory (Traveset and Verdú, 2002).

3.4.1 Limitations of this study

There were several constrains on this study which should be acknowledged before examining the data further. Firstly as a study on captive animals the study subjects are exposed to unnatural conditions such as the housing together of male and female orangutans at Taronga Zoo, they are normally a semi-solitary species (Goossens et al., 2009), and placing flanged adult male and female together under artificial conditions, as was the case at Perth Zoo. The former is not expected to have altered defecation rate as they individuals have been housed together since 2009. The individuals at Taronga Zoo represent past breeding practices of hybridizing Bornean and Sumatran animals that are no longer in place with the male vasectomized (or female undergoing tubal ligation) to prevent further breeding (Porton, 2013). Of note, placing the male and female together at Perth Zoo limited our opportunity to collect faeces, created a potentially stressful situation, and prevented the introduced female from being part of this study because she refused to allow access to her areas where she was defecating, although she was fed seed mimics on Day 1.

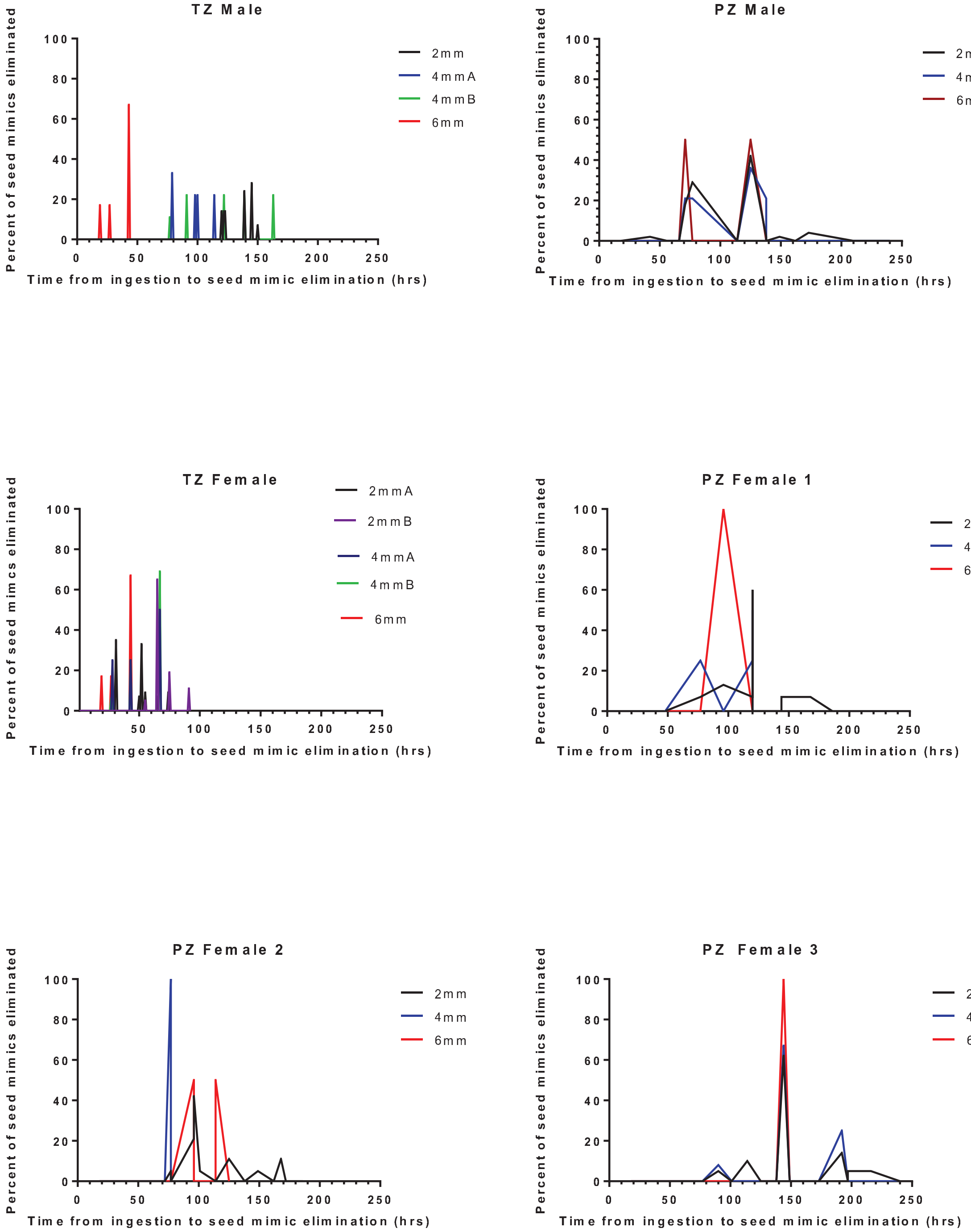

Fig 3.1: Elimination patterns of 2, 4 and 6mm seed mimics from ingestion to elimination (hours)

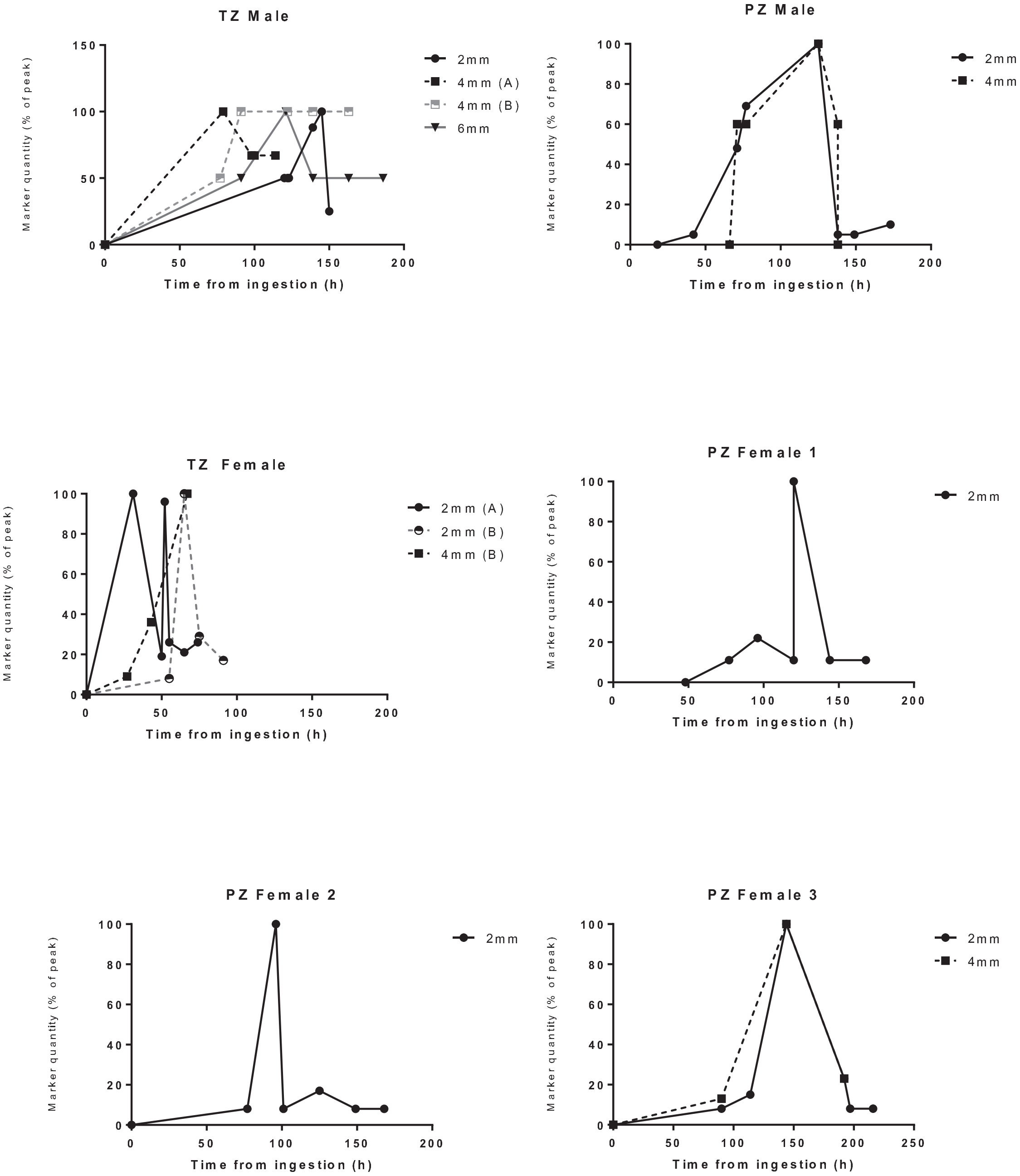

Fig 3.2: Time to seed mimic elimination (hours) presented as percentage (%) of the peak elimination

The diets used in captivity in our study are also quite different from those of wild animals. The zoo diet comprises vegetation grown largely for human consumption and differs from wild diets in type, quantity, digestibility (e.g. starchy vegetables), as well as fruits not found in tropical environments, legumes, protein sources (e.g. salmon, or lambs heart given in small quantities twice weekly in Perth Zoo) and pelleted feed (although these were given in minimal quantities). Despite this, the orangutan's diet in both Taronga and Perth Zoo's largely consisted of plant matter, which makes up the bulk of their wild diet (Chivers and Hladik, 1980, Caton et al., 1999a).

Activity levels are also quite different to those found in the wild, with wild orangutans travelling large distances with day ranges of 750m (585-1098,) and 908m (731-954m), adult flanged males and non-sexually active females respectively (Morrogh-Bernard, 2009). However, a study on resting metabolic rate in captive orangutans showed that this species, compared to its body size, has a very low basal metabolic rate even when estimated conservatively in captive animals (Pontzer et al., 2010) so energy expenditure differences between captive orangutans and their counterparts are unlikely to impact on our results.

In order to make this study more robust, measurement of dry matter intake and dried faecal weight would have made mean retention times calculable. Although mean retention time wasn't considered as important as the elimination pattern and transit times, it would have added another layer of complexity to this study. Unfortunately this wasn't logistically possible at the time of our study.

In our studies on seed dispersal on seed dispersal in wild Bornean orangutans (*Pongo pygmaeus wurmbii*), orangutans were found to swallow and eliminate intact seeds of up to 21 mm in length and 10 mm diameter (Chapter 4). In this study, however, the largest sized bead that the orangutans would consume was 6mm in diameter. Even when disguised in fruit or cordial the orangutans would not consume larger seed mimics, nor would they consume a set number of each of the different size of seed mimic. Therefore we were limited by what each individual would swallow.

3.4.2 Transit and elimination patterns

We found that transit time (TT) to be quite long (average when 2, 4, and 6mm were pooled, 76.42 ± 26.62 hours) when compared to the only other marker elimination study in orangutans, where TT = 24.2 ± 0.8 hours in orangutans (Caton et al., 1999). There are several possible explanations for these differences. Firstly there were considerable differences in the diets fed to the orangutans; our animals were fed diets more plant matter and a minimal amount of processed food, unlike the primate cake fed to the three orangutans in Caton et al. (1999), and secondly the types of markers used were different (as the aims of our experiments were different). In Caton et al.'s (1999) they used traditional fluid and small particle markers, as opposed to the large seed mimics we used. In many digesta passage studies, standard markers of cobalt-ethylenediaminetraccetic acid (Co-EDTA) for fluids and chromium mordanted fibers for particles <2mm e.g. (Udén et al., 1980, Caton et al., 1999a, Clauss et al., 2011) are used. Our study was designed to mimic the passage of intact indigestible seeds whereas the particulate markers in other studies were significantly smaller than those used here, with 2-6mm to be considered "large" particles compared to the particulate matter of other studies using Co-EDTA mordanted fibres of e.g. 600-1200 µm (Caton et al., 1999a) in orangutans and 500-1000 µm (Munn et al., 2012) in tammar wallabies (*Macropus eugenii)*.. It was not possible on this occasion to also examine the fluid and particle passage as did Caton et al. (1999) because the animals were unavailable for longer training and interventions. Nonetheless, the TTs of seed mimics, rather than a mean retention times, were deemed more suitable for further work in our seed dispersal studies. How seed mimics are eliminated is, we feel, a more appropriate representation of how seeds are dispersed in the orangutans' natural environment.

When our study animals are compared to other arboreal frugivores in similar tropical environments, the times are similarly disparate. For example, in the hoorlock gibbon (*Hylobates hoolock*), rates for different seed species ranged from 11.4 ± 4.9 hours to 24.2 ± 11.9 hours (Ahsan, 1994, McConkey, 2000) and Barito Ulu gibbons (*Hylobates mulleri x agilis*) where the mean transit time was 27.8 ± 10.7 hours (McConkey, 2000). While these are smaller bodied animals, the differences in TT are substantially disparate, and points to a need for further work to fully characterise the role of these different frugivores to overall forest seed dynamics.

Our experiment has demonstrated that seed mimics were not eliminated in an even pattern, but were time-dependently deposited in blocks, with a peak distribution between 50-150 hours. Visual representation of bead elimination when presented as percentage of total dose (Fig 3.1) differed markedly from that of the smaller markers of Caton et al. (1999), whose results were also displayed as percentage of dose. As described, our data showed numerous pulse elimination peaks, with smaller pulses before and after the major peak (Fig 3.1). In Caton et al. (1999) marker elimination demonstrated steady increase in quantity of markers with a high peak and then a steady decline for 2 of the study animals and a sharp peak and sharp decline for Male 1. We were unable to compare the results of percentage of peak marker quantities, as these have not been shown in the previous study. Regardless, the steady pattern of fluid and smaller particle elimination is typical of food marker passage generally e.g.

see (Stevens and Hume, 1998). Perhaps most importantly, we have demonstrated that the larger seed-mimic markers did not follow the general food-marker passage patterns typically considered in animal digestion studies. Our results indicate that seeds and seed-mimics do not flow through the gut in the same fashion as more processed digesta. This has implications for seed dispersal predictions for fruit eating animals such as the orangutan.

Digesta throughput is dependent on a number of factors on both the plant and animal side in herbivores. On the plant side, ingesta passage is related to the accessibility of nutrients (i.e. digestibility or refractory nature of the feed), method of digestion required to access those nutrients and any time dependent factors relevant to that access (Clauss et al., 2007, Clauss et al., 2008). On the animal side, gut structure and function are the first consideration, but there are also numerous factors present that can alter digestion. These include, but are not limited to, satiety, physiological drivers e.g. birth, lactation, growth, and animal behaviour, e.g. interaction with conspecifics, mating, fighting (Cousens et al., 2010). While we can account for the animal factors in that animals in both this study and in Caton et al. (1999) were all zoo-based animals, the bulk of the dietary matter diverged enough to create doubts as to the utility of Caton et al.'s (1999) data for a wild-type setting. Although not comparable to a wild-type diet, which consists of invertebrates and more refractory (difficult to digest) foodstuffs, including bark (Galdikas, 1988, Wich et al., 2006, Harrison, 2009b, Morrogh-Bernard et al., 2009, Harrison and Marshall, 2011), the diets fed to the orangutans in our studies were a closer approximation to a wild-type diet than any previous study. We did however, demonstrate a similarity in defecation frequency between wild orangutans and their zoo counterparts, a comparison (to the best of our knowledge) hitherto un-performed (Table 3.3).

One often quoted conclusion regarding endozoochorus seed passage is that small seeds are retained longer than large seeds (Traveset and Verdú, 2002) with small seeds from this meta-analysis being considered <5mm, medium seeds 5-10mm and large seeds >10mm (Traveset 1998, Traveset and Verdu, 2002). However, even though we found no significant differences in the passage of small and larger beads in our study, we cannot confirm the idea that small seeds are retained longer than larger seeds. Rather, our result likely reflects a minimal difference between 2-6mm seed mimics as orangutans have been observed, in other parts of this study, to consume and defecate seeds greater than 21mm in length and 10mm in diameter (see Table 4.3).

The females in our study displayed the widest variation in TTs, which may be a function of small sample size. However, the female with the longest TT (female 3, PZ) was known to suffer occasionally from constipation, and so she received a daily ration of prune juice. The reasons for the TZ female having the shortest TT are less clear but the pattern of elimination is still comparable with the other animals

Orangutans have been shown to repeatedly display extremely low daily energy expenditure, (Pontzer et al., 2010) even when accounting for body size, which may be a further factor in what appear to be extremely long TT and maximum times (TT_{MAX}). Orangutans generally live in environments with unreliable fruit availability, more so on Borneo than Sumatra (Wich et al., 2009) and this is reflected in their low energy use and reproduction rates (Wich et al., 2009, Pontzer et al., 2010, Russon, 2010). Demonstration in the orangutan of a physiological adaptation for decreasing energy throughput, rather than alteration of energy allocation (Pontzer et al. 2010), even when accounting for likely differences in activity between zoo and wild animals, is further supported here by extremely long TTs. It is worth considering that the long TTs of orangutans may relate to their slow life histories and their natural environments being subject to high levels of stochastic food availability (Pontzer et al., 2010). While this isn’t relevant for zoo animals that don’t face periods of low food availability, it has important implications in wild populations. The potential relationship of our work to wild orangutans is further substantiated by measurement of frequency of defecation frequencies similar to that of wild orangutans. Moreover, a deeper consideration of the interactions between orangutan physiology and their role in ecological processes, such as seed dispersal, is warranted. For example, in a preliminary seed dispersal study on orangutans in Central Kalimantan, Indonesia (the first of its kind in peat swamp), researchers relied on the mean retention time data from Caton et al. (1999) as a guide for predicting the dispersal of seeds (Nielsen et al., 2011). We propose that, because of the above reasons, Caton et al. (1999) may not accurately predict orangutan gut throughput relevant for wild orangutan seed dispersal studies.

3.5 CONCLUSIONS

1. Transit time of indigestible seed mimics for orangutans is much longer than has been previously shown in marker studies.
2. Seed mimics were eliminated in a pulse pattern, rather than evenly distributed.
3. Orangutans have the potential to provide longer long distance dispersal from the parent plant than other arboreal mammalian frugivores, particularly with regards to large seeds, due to their very long retention times.

4 GARDENERS OF THE FOREST? THE INFLUENCE OF SEED HANDLING AND INGESTION BY ORANGUTANS ON GERMINATION SUCCESS

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4.1 INTRODUCTION

Forty to ninety percent of tropical plant species rely on animals to disperse their seeds (Jordano, 2001, Bascompte and Jordano, 2007, Côrtes and Uriarte, 2013). The disproportionate influence of large bodied frugivores for seed dispersal has been well documented in tropical forests, as has the influence of their extirpation on forest structure (Corlett, 1998, Wright et al., 2000, Beckman and Muller-Landau, 2007, Corlett, 2007, Muller-Landau, 2007, Nuñez-Iturri and Howe, 2007, Peres and Palacios, 2007, Wang et al., 2007, Wright et al., 2007, Effiom et al., 2013). Although many vertebrate species disperse small and medium sized seeds, large seeds are generally only swallowed intact by large frugivores (Peres and van Roosmalen, 2002, Peres and Palacios, 2007, Stoner et al., 2007a, Wotton et al., 2012, Vidal et al., 2013), such as chimpanzees (*Pan troglodytes*) (Wrangham et al., 1994) and western lowland gorillas (*Gorilla gorilla gorilla*) (Petre et al., 2013), which also tend to have longer gut passage times and move greater distances (e.g (Ruxton and Schaefer, 2012, Wotton et al., 2012), Chapter 3). Some plant species depend particularly heavily on large frugivores e.g. *Balanites wilsoniana* (a upper canopy tree) dispersed by elephants (*Loxodonta africana*) (Chapman et al., 1992, Cochrane, 2003), and *Diospyros egrettarum* a critically endangered endemic ebone tree in Mauritius, which was dispersed by an extinct giant tortoise (*Cylindraspis*) (Griffiths et al., 2011, Ruxton and Schaefer, 2012). Unsurprisingly, therefore, the extirpation of large bodied frugivores in many tropical forests has led to a corresponding decrease in large-seeded tree species (Peres, 2000, Peres and van Roosmalen, 2002, Nuñez-Iturri and Howe, 2007, Peres and Palacios, 2007, Stoner et al., 2007a, Terborgh et al., 2008, Bass et al., 2010, Harrison et al., 2013, Fuzessy et al., 2015) and general plant diversity (Corlett, 2007, Muller-Landau, 2007, Wang et al., 2007, Fuzessy et al., 2015).

Passage of seeds through the guts of animals potentially confers three major advantages for the seeds. Firstly there is a functional movement of the seeds from the parent plants to more distant sites (Traveset, 1998, Howe and Miriti, 2000, Samuels and Levey, 2005, Traveset et al., 2007b, Herrera, 2009, Schupp et al., 2010, Fuzessy et al., 2015) with the potential to avoid competition from the parent plant and thus density-dependent mortality, and/or deposit them in microsites more favourable to establishment (Traveset, 1998, Howe and Miriti, 2000, Nathan and Muller-Landau, 2000, Santamaría et al., 2007, Herrera, 2009). Secondly there is the potential to enhance germination via the removal of the fruit pulp, which can contain germination inhibitors (Traveset, 1998, Samuels and Levey, 2005, Robertson et al., 2006, Traveset et al., 2007b). This is achieved through the mechanical and/or chemical effects of digestion on seed coat or endocarp (Traveset and Verdú, 2002, Samuels and Levey, 2005). Finally, faeces may act as a fertilizer for the deposited seed (Traveset and Verdú, 2002, Robertson et al., 2006, Traveset et al., 2007b, Fuzessy et al., 2015).

To isolate the effect of gut passage on germination of seeds, it is recommended that studies should include three components: (i) manually extracted i.e. removed from whole fruits and washed; (ii) gut passed; and (iii) intact un-ingested and un-manipulated fruits (Samuels and Levey, 2005, Robertson et al., 2006). Out of 99 studies that tested the effect of gut passage on seed germination (as reviewed by Samuels and Levy 2005), only 18% evaluated all three outcomes, with the majority (77%) comparing manually extracted and gut-passed seeds but omitting intact fruits (Samuels and Levey, 2005, Robertson et al., 2006). Without the presence of intact fruits as a control, one cannot separate the action of gut-processing versus pulp removal on germination (Samuels and Levey, 2005, Robertson et al., 2006). By including intact fruits we can begin to tease out the role of an animal in seed germination ascertaining whether their gut enhances, inhibits or exerts no influence on germination. We looked at this interaction *in situ* in a known seed dispersing primate, the orangutan (*Pongo pygmaeus wurmbii*), with an aim to determine what, if any, affect their guts have on seed germination.

Orangutans were chosen as a study subject because they are the world's largest arboreal frugivore (Ancrenaz et al., 2008) that is known to disperse seeds (Rijksen, 1978, Nielsen et al., 2011). They eat a wide variety of foodstuffs but are considered primarily frugivorous (Morrogh-Bernard et al., 2009, Russon et al., 2009), with a gut adapted to process plant material via hindgut microbial fermentation ((Stevens and Hume, 1995, Caton et al., 1999b); Chapter 3).

Although previous orangutan studies had documented the presence of intact seeds in orangutan faeces (Rijksen, 1978, Galdikas, 1982), only one previous study has investigated germination of seeds found in orangutan faeces (Nielsen et al. 2011). Data from this study, which was conducted over just a six-week period in the Sabangau Forest in Borneo found 71.4% of faecal sample had at least one intact seed and germinated three out of five species studied, and highlighted the need for further work in this area (Nielsen et al. 2011), hence this longer 7 month study.

In addition to the high year-round proportion of fruit in the peat-swamp orangutan diet (Morrogh-Bernard et al., 2009), a variety of characteristics in orangutans suggests that they are likely to be good/important seed dispersers. Seed deposition in both time and space is affected by the passage rate of food through an animal's gut. This in turn depends on the proportion of digestible versus indigestible food that is in the gastrointestinal tract (GIT), digestion rate, liquid/solid digesta ratio, particle size of masticated food and GIT structure (van Soest, 1994, Traveset et al., 2008, Cousens et al., 2010). Orangutans have been demonstrated to have very long particle transit and mean retention times ((Caton et al., 1999a); Chapter 3). This infers a functional ability to move seeds comparatively long distances away from the parent tree. This is known as a long distance dispersal (LDD) event which is largely purported to confer a survival advantage on the seed due to reduction of: competition from the parent plant and seedlings with deposition at potentially favourable microsites; reduced secondary seed predation; and reduced pathogen attack (Janzen 1970; Connell 1971; (Howe and Smallwood, 1982a, Traveset, 1998, Cain et al., 2000, Nathan et al., 2002, Jordano et al., 2007, Nathan et al., 2008b, Schupp et al., 2010). Considering this, and the orangutan's widespread popular reputation as a "gardener of the forest", and rapid declines in both forest cover and orangutan populations in Borneo and Sumatra, it is therefore surprising that so little empirical information is available on seed dispersal by orangutans.

Thus, building on an earlier study on the role of orangutans in processing seeds in Sabangau (Nielsen et al., 2011), we aimed to determine the effect of both orangutan handling and gut processing on seed germination. We propose that orangutans have the potential to confer both a functional advantage on seeds through LDD and a chemical and/or mechanical advantage via action of the gut on seeds. To test these hypotheses, we aimed to ascertain the answers to the following:

1. Which species and size of seeds do orangutans disperse intact through their gut?
2. To what extent do orangutans act as seed predators vs. seed dispersers?
3. Does seed extraction by orangutans affect germination? I.e. do intact fruits and extracted seeds differ in terms of germination success?
4. Does passage through the orangutan gut affect seed germination either positively or negatively?

4.2 MATERIALS AND METHODS

4.2.1 Study site

We carried out field research as part of the OuTrop-CIMTROP multi-disciplinary research project within the 500 km^2 Natural Laboratory of Peat-Swamp Forest (NLPSF), which is and part of the wider 9,200 km^2 of peat-swamp forest in the Sabangau ecosystem, Central Kalimantan, Indonesia (Morrogh-Bernard *et al.*, 2003); Page et al., 1999). The Sabangau ecosystem contains the largest remaining contiguous population of Bornean orangutans (6900 individuals) (Wich et al., 2008). The area is a truly ombrogenous (water and nutrient supplied entirely aerially) peat-forming wetland with an organic matter depth greater than 50 cm (Page et al., 1999).

The NLPSF Field Station is situated 20 km southwest of Palangka Raya in the upper reaches of the Sabangau River. It was subject to concession logging until 1997 and illegal logging until 2004, which has had an influence on tree species composition.

4.2.2 Data collection

In total 13 individual orangutans (4 adult females, 5 flanged males, 2 sub-adult females and 2 unflanged males) were followed using standardised protocols (Martin and Bateson, 1986, Morrogh-Bernard et al., 2002, Harrison, 2009b, Morrogh-Bernard, 2009, Harrison et al., 2010) and faeces collected between March – September 2013. Faeces were collected from the specific individual being followed, but if multiple orangutans were present, faeces were opportunistically collected from others as well. A note was made about if complete or partial faeces samples were collected as due to the arboreal nature of orangutans sometimes faeces splattered and it was impossible to locate the entire faeces, and faeces frequently fell partially in water pools during the wet season.

Collected faeces were stored in a plastic box and transported back to the research camp at the end of the day, where they were weighed and washed through sieves of decreasing diameter – down to 1.5mm. Seeds $\leq$2mm were not evaluated because they could not be reliably distinguished from other ground foodstuffs. Furthermore, seeds < 2mm are usually fig species and these are not considered a particularly important fruit for orangutans in Sabangau (Harrison 2009, Harrison et al. 2010).

Total seed weight was calculated for each faecal sample. Seeds were then separated into intact and depredated (i.e. damaged by the masticatory/digestive process) seeds and identified to species level where possible. Species identifications were performed by skilled local botanists and follow Harrison et al. (2010). Intact seeds were separated into species, total seed weight/species in each faeces was calculated, and number of seeds for each species per sample was quantified.

It was often not possible to determine the number of depredated seeds present within a faecal sample, as many were ground through mastication. A species was only included as depredated if there was enough of the seed left to reliably recognize the plant species.

Controls for germination testing of each fruit species were fresh fallen fruits (for washed seeds and intact fruit categories) collected from observed orangutan feeding trees, or where that was not possible from nearby trees of the same species. Seeds and fruits were collected at the same stage of ripeness as the seeds/fruits eaten by the observed orangutans. For whole fruits, each seed within the fruit was considered as a separate unit if there were greater than one seed per fruit. For example, *Diospyros bantamensis* has 8 seeds/fruit, so germination of four seeds from a one whole fruit would be considered as 50% germination success.

Germination was tested under ambient outdoor conditions in the Sabangau Seedling nursery (SSN). Environmental conditions within the nursery were similar to those within the forest and local peat was used as the growth medium, which is also comparable to peat in the forest (Graham et al. 2008).

Trays were prepared with approximately 4 cm of peat as the growth medium following Graham *et al*. (2008) and seeds were sown on the surface. The rain and temperature gauges are situated in easily accessible locations, with the rain gauge in the open and temperature gauges in the shade (Harrison et al., 2015). Rainfall was measured twice daily at 0600 and 1800 hrs; the temperature gauge was checked for minimum and maximum temperatures in the mornings (see Fig 1.2, 1.3). Study seeds were checked and recorded for 60 days, following which experiments were discontinued if seeds had not yet germinated. Germination was considered to have occurred at the first emergence of the radicle (Matthews and Powell, 2012).

Rate of germination (ROG) was defined as per Traveset (1998) as the time elapsed until the first germination.

We concentrated on seeds greater than 2mm in this study, because in TPSF, unlike the lowland dipterocarp forests, figs and other smaller-seeded fruits do not constitute a major or even ‘fall-back’ food for orangutans (Harrison 2009, with fall-back foods being defined as food whose utilization is inverse to the presence of preferred foods). In fact, orangutans in the Sabangau Forest have been found to not use fall-back fruits (Harrison 2009), likely because of the asynchronous fruiting nature of TPSF and the more consistent year round availability of varied food types (Morrogh-Bernard, 2009), with only leaves and bark being identified as fall-back foods in this environment (Harrison, 2009b, Morrogh-Bernard et al., 2009, Harrison and Marshall, 2011). Fruits with much smaller seeds such as figs, do constitute important components of the diet in other orangutan habitats, especially in Sumatra (Wich et al., 2006, Harrison et al., 2010, Harrison and Marshall, 2011), and thus should potentially be considered in germination studies in other forest types.

4.2.3 Statistical analysis

Results were analysed in the R Studio platform version 0.99.489 (R Studio Team, 2015) which utilises the R statistical environment R version 3.2.2 (R Core

Team, 2015) for full factorial one-way ANOVA test and Minitab® (version 17.1.0.0, 2013) for homogeneity of variances, normality and non-parametric tests.

The test for equal variances for the rate of germination (ROG) were compared between the three different treatment groups and Levene's test performed. A full factorial analysis of variance (ANOVA) was performed. Additionally a Kruskal-Wallis rank sum test was run to compare to the ANOVA results.

Percentage of total seeds germinated by end of each experiment (60 days) was calculated for each seed. To produce homogeneity of variances the data were first log transformed (Bland and Altman, 1996) and further arcsine transformed to normalize the distribution. A one-way ANOVA test was conducted and post-hoc tests, Student-Newman-Keuls (SNK) and Tukey's tests were used to identify if there were any differences of germination percentage between treatment groups of defecated, washed and intact fruits.

Time to first germination was also evaluated and an ANOVA run to test if there was any effect of either the plant species and/or the treatment group on this. Post-hoc Tukey's tests were used to identify which species differed from each other in time to first germination.

4.3 RESULTS

4.3.1 Food eaten

During our study period, the orangutans ate 51 species of fruit (43 tree species and 8 liana species, table 4.1).

Table 4.1: Plant species eaten by orangutans during period March 2012-December 2013

	Local name	Scientific name
Trees	Dawat	*Antidesma coriaceum*
	Kenari	*Blumeodendron elateriospermum/kurzii*
	Kenyem burung	*Buchanania cf. arborescens*
	Terantang	*Campnosperma coriaceum*
	Bintan red hair (Kayu Cahang)	*Ctenolophon parvifolius*
◉	Malam malam	*Diospyros bantamensis*
	Arang	*Diospyros confertiflora*
⊼	Ehang	*Disopyros siamang*
	Jelutong	*Dyera lowii*
◉	Mangkinang	*Elaeocarpus mastersii*
	Lunuk spp	*Ficus sp*
	Manggis	*Garcinia bancana*
⊼	Pissang pisang kecil	*Garcinia sp. 1*
	Nyatoh palanduk	*Isonandra lanceolta*
	Kempas	*Koompassia malaccensis*
	Bintan peter peter	*Licania splendens*
	Pampining Bitik	*Lithocarpus cf. dasystachys*
	Pampaning Bayang Besar	*Lithocarpus conocarpus*
	Tampang	*Litsea cf. rufo-fusca*
	Tabaras akar tingi	*Mesua sp.1*
⊼	Pisang pisang besar	*Mezzettia letopoda /parviflora*
⊼	Aci	*Mezzettia umbellata*
	Mahadarah hitam	*Myristica lowiana*
◉	Rambutan hutan	*Nephellium lappaceum*
	Kelumin bhuis	*Nephellium maingayi*
	Nyatoh burung	*Palaquium cf. xanthochymum*
	Nyatoh gagas	*Palaquium cochlearifolium*
	Hangkang	*Palaquium leiocarpum*
	Nyatoh babi	*Palaquium pseudorostratum*
	Nyatoh burung	*Palaquium ridleyii / xanthochymum*

	Pandan	*Pandanus sp.1*
	Papong	*Sandoricum beccanarium*
	Teras Bamban - Santiria	*Santiria cf. griffithi*
⦿	Tabaras no roots (pasir pasir)	*Stemonorus scorpiodes/ secundiflorus*
	Loting	*Sterculia rhoiidifolia*
	Jambu Jambu	*Syzgium garcinfolia*
	Jambu burung	*Syzgium garcinfolia*
⦿	Kayu lalas dan besar	*Syzygium cf. valevenosum*
	Tatumbu	*Syzygium havilandii*
†	Ponak	*Tetarmerista glabra*
	Tagula	*Xylopia cf. malayana*
⊼	Jankang khuning	*Xylopia fusca*
Lianas		
	Kelanis	*Alyxia sp. 1*
	Kalawit hitam	*Atrobotrys cf. roseus*
	Khuning	*Fibraurea tinctoria*
⦿	Bajakah luah	*Gnetum sp 1*
	Oto oto	*Gnetum sp 2*
	Willhubia	*Willughbeia sp. 1*

⦿ *Seeds excreted intact*
⊼ *Seeds depredated*
Seeds both excreted intact and depredated

4.3.2 Seeds discovered in faeces

A total of 247 faecal samples were collected. Of these, 154 were complete samples and 93 partial. The number of animals and weights for complete faecal samples divided into age/sex cohort can be seen in Table 4.2. Overall, 181 samples (73% of all faecal samples) contained seeds; of these 116 complete faecal samples had seeds and 65 partial samples had seeds. The number of seed species found in complete faecal samples at any one time ranged from 0 to 5, with a mean of 1.71 ± 0.95

species/faeces.

Table 4.2: Number of defecation samples in age/sex class

Age/Sex Cohort	Partial	Complete	Average weight S.D. (complete samples only)	# of animals
Flanged males	21	58	132.00 ± 110.40	5
Adult females	54	82	83.12 ± 51.69	4
Sub adult females	17	9	64.80 ± 27.50	2
Unflanged males	2	4	43.13 ± 13.66	2
TOTAL	94	153	247	13

We identified 13 species of seed in orangutan faeces, of which 92% were from trees and 8% from lianas. Although 51 species of fruits were eaten, the orangutans only defecated seeds of 13 of these intact, and depredated 5 other species. Of the remaining 18 species, the seed was entirely ignored for the pulp and/or skin.

The maximum number of seeds found in any samples was 828 (all *Elaeocarpus masteresii*). The average number of each seed species found in faeces from orangutans in our study is listed in Table 4.3.

The size of seeds found in faeces ranged between 6 mm for *Campnosperma coriaceum* and *Palaquium ridleyii* to greater than 25 mm for *Diospyros bantamensis* (Table 4.3, largest measured seed 26mm). These were the largest seeds orangutans were observed to have eaten and then defecated intact out of more than 600 hours of observation.

4.3.3 Predation versus dispersal

Seeds depredated by orangutans are identified in Table 4.1. For some tree species orangutans were both seed dispersers and seed predators. Despite some of the seeds from some tree species being eliminated from the orangutan intact rather than destroyed (i.e. chewed), when both states of seed were present in faeces, intact seeds generally far outnumbered depredated or damaged seeds by a magnitude of 10 to 100.

4.3.4 Germination of seed samples

Germination percentages were different for each species so it was not possible to make any generalized statements about orangutan gut-passed seeds versus manually extracted seeds and whole fruits. Some species e.g. *Nephellium maingayi, Diospyros bantamensis,* and *Sandoricum beccanarium*, showed a clearly improved germination with gut passed and manually extracted seeds over whole fruits; whereas others such as *Elaeocarpus masteresii and Campnosperma coriaceum* showed poorer results of gut passed fruits to whole fruits (Table 4.4). All species except *Campnosperma coriaceum* displayed increased germination for manually extracted seeds over either gut-passed or whole fruits.

The test for equal variances for the rate of germination (ROG) (Traveset, 1998) were not statistically significant between the three different treatment groups

Table 4.3: Properties of seeds that were excreted intact through the orangutan gut

Species	Frequency of occurrence in samples	Average no of seeds/defecation*	Months eaten	Seed weight ± S.D	Seed length ± S.D	Seed width ± S.D	Seeds /fruit
Elaeocarpus mastersii	89	142	October-December	0.13 ± 0.08	0.83 ± .08	0.41 ± 0.13	1
Tetramerista glabra	87	8	May-Sept, December	0.14 ± 0.29	1.19 ± 0.47	0.47 ± 0.12	4
Sandoricum beccanarium	38	18	August-October	0.69 ± 1.59	1.28 ± 0.19	0.88 ± 0.15	2
Nephellium maingayi	20	39	October	0.49 ± 0.38	1.06 ± 0.07	0.63 ± 0.06	1
Nephellium lappaceum	16	5	July-August, December	1.06 ± 0.78	1.84 ± 0.20	1.13 ± 0.14	1
Campnosperma coriaceum	13	10	September	0.08 ± 0.01	0.67 ± 0.09	0.39 ± .03	1
Palaquium ridleyii	12	2	October	0.11 ± 0.03 ^{o}	0.61 ± 0.10 ^{o}	0.32 ± .04 ^{o}	1
Diospyros bantamensis	11	4	November	3.67 ± 0.19	2.16 ± 0.24	1.04 ± 0.17	8
Palaquium cochlearifolium	6	1	October-November	0.05 ± 0.01 ^{o}	1.67 ± 0.17 ^{o}	0.77 ± 0.05 ^{o}	4
Gentum sp. 1	5	4	June	1.36 ± 0.16	1.02 ± .09	0.89 ± 0.1	1
Stemonorus cf. scorpiodes	2	1	October	0.75 ł	ISS	ISS	2^{Ω}
Syzgium cf. valvenosum	1	1	June	0.1 ł	ISS	ISS	1

** where present in defecation*

ł from Graham et al (2008)

Ω from Chenyne and Harrison, unpublished data

^{o} *small sample size*

ISS Insufficient sample size

on both multiple comparisons (P = 0.47) and Levene's Test (P=0.36). Similarly the assumption of normality was met for ROG (P=0.06, Mean 7.71; StDev 7.51). A full factorial analysis of variance (ANOVA) was performed and no significance results were found between the species (P=0.22), treatment group (P=0.17) or interaction of the species versus treatment group (P=0.29).

Table 4.4: Germination percentage for plant species within treatment groups

Group	1. Gut passed (%) ± S.D.	2. Manually extracted (%) ± S.D.	3. Whole fruit (%) ± S.D.
Nephellium maingayi	44.27 ± 41.51 (96)	100.00 ± 0 (34)	0.00 (11)
Diospyros bantamensis ǂ	96.00 (24)	86.00 (6)	0.00 (8)
Elaeocarpus mastersii	4.20 ± 5.06 (181)	63.63 ± 49.95 (63)	29.37 ± 27.08 (47)
Sandoricum beccanarium	58.71 ± 32.23 (134)	95.00 ± 7.07 (31)	0.00 (21)
Campnosperma coriaceum	48.75 ± 54.80 (58)	42.19 ± 59.67 (49)	70.00 ± 0 (20)

ǂ *Only 1 set of experiments obtained for this so no stdev able to be applied*
Sample sizes are in brackets ()

Homogeneity of variances was achieved for both multiple comparisons (α=0.05, P=0.35) and Leven's Test (α=0.05, P=0.28). However normality of distribution was not (P<0.01) and this was assumed to be because there were a number of 0 values where no seeds in a treatment group and species germinated, thus skewing the data. Regardless of this, we conducted ANOVA tests on these data, as ANOVA is not considered to be very sensitive to moderate deviations from normal variation (Lix et al., 1996).

Despite the above points, we additionally ran a non-parametric test to make sure we did not get spurious results from the ANOVA (as the distribution was not normal). The results confirmed that there were statistically significant differences between treatment groups (Kruskal-Wallis $X^2 = 9.683$, df = 2, p-value = 0.008).

One-way ANOVA results revealed statistically significant results in germination between treatment groups ($F_{2,20} = 6.486$, p=0.007), but not between plant species ($F_{4,20} = 1.001$, p=0.430) or any interactions between plant species and treatment groups ($F_{8,20} = 1.601$, p=0.185). Therefore a further ANOVA test was run where species were excluded from the analysis and instead treatment groups were focused on, with significant results (P = 0.007, F = 5.73 df = 2,20). Post-hoc tests were used to identify differences between treatment groups. Student-Newman-Keuls (SNK) illuminated significant results between treatment group 1, gut passed seeds and group 2, manually extracted (P=0.03) and group 2, manually extracted seeds, and group 3 (P = 0.006), but NS (P=0.14) between groups 1 and 3. Tukey's test (table 4.5) revealed similar results with almost significant differences between groups 1 and 2 (P=0.07), significant results between groups 2 and 3 (P=0.006) and NS between groups 1 and 3 (P=0.30).

Table 4.5: Tukey's multiple comparisons of means (95% family-wise confidence level). GP = gut-passed; ME = manually extracted, WF = whole fruit

Treatment group	Diff	Lwr	Upper	p
ME – GP	0.128	-0.008	0.264	0.068
WF – GP	-0.090	-0.237	0.056	0.295
WF - ME	-0.219	-0.381	-0.057	0.006

No effect was found of treatment group ($F_{2, 20} = 0.153$, p=0.859) or species*treatment group ($F_{8,20} = 0.633$, 0.741) on days to first germination. While not statistically significant ($p>0.050$), there was a weak interaction between species and days to first germination ($F_{4,20}$= 2.643, $p=0.063$). Post-hoc Tukey's revealed a significant interaction between species ($F_{4,30}$ = 3.126, $p=0.029$) although only one species, *Sandoricum beccanarium*, germinating significantly faster ($p=0.039$) than another, *Elaeocarpus mastersii*.

4.4 DISCUSSION

Ingestion and defecation of seeds by orangutans has been shown here to confer some advantage on germination, when compared to seeds from manually extracted fruits. Although this advantage was not as pronounced as we expected, the combination of some germination advantage conferred by orangutans combined with their large mean day range of 834m (Morrogh-Bernard 2009), tendency to long distance travel (Morrogh-Bernarnd 2003, Singleton et al 2009) and long transit times of indigestible seed mimics (i.e. 24.2 ± 0.8 hours for both solute and particle markers (Caton et al 1999) and 70.6 ± 7.1, 72.5 ± 6.8 and 86.2 ± 16.6 hours for 2, 4 and 6mm seed mimics, respectively (Chapter 3) supports the assertion that orangutans contribute considerably to the dispersal and germination of seeds in Sabangau and, we expect, in other forest areas where they occur. Only one species, *Diospyros bantamensis*, germinated more for gut-passed seeds than manually extracted seeds. This could lead to the conclusion that handling by orangutan's does damage a percentage of seeds either through mechanical (e.g. chewing, action of gut) and/or chemical gut processes (Samuels and Levy 2005). Despite this, based on our results, orangutan ingested seeds conferred greater survival on seeds than if fruit remained intact (Table 4.4).

Carrying and then spitting of seeds might play a particularly important role for dispersal of some seed species, due to the significantly higher proportion of germination success for manually extracted seeds over both gut-passed and whole fruits for the majority (80%) of species considered here. There was a high germination in the manually extracted i.e. washed seeds. We contend therefore that it is likely that when orangutans "wash" seeds by removing the pulp and then spitting them (E. Tarszisz, per sobs), the germination rate of these seeds will be high. While we weren't able to quantify this in the field, it is worth considering as a future avenue of research.

Our data show that handling by orangutans plays an important role in seed dispersal of several plant species. While there was a significant difference between germination in orangutan gut-passed seeds and manually extracted seeds, as well as manually extracted seeds versus whole fruits, there was no significant difference between the germination success of gut-passed seeds and those from whole fruits. This was unexpected from an observational point of view as several of the species found in faeces, notably *Nephellium maingayi, Sandoricum beccanarium* and *Diospyros bantamensis* failed to germinate at all in their whole fruit form (Table 4.4). Grossly there seemed to be obvious differences between whole fruits and gut-passed seeds. For example, 96% of gut-passed and 86% of manually extracted *Diospyros bantamensis* germinated while none (0%) of whole fruit germinated. Similarly no *Sandoricum beccanarium* whole fruits germinated despite an average (across several repeat experiments) of 58.71% of gut-passed and 95.00% of manually extracted seeds germinating for this species (Table 4.4). It was surprising, based on raw observations that the ANOVA or Kruskal-Wallis analyses showed no significant effects of plant species versus treatment group. There are a number of different possible explanations for this. It may be that because the gut-passed seeds were removed from faeces, they lacked access to the potential of faeces to enhance germination (Traveset, 1998, Traveset et al., 2007b), and therefore their germination potential wasn't fully realised when compared to the other treatment group. Alternatively, the statistical methodology employed here may have not been ideal, and a different analysis of the same data may yield different results. In a meta-analysis of the effects of different primate guts on germination times, primates that ate insects, like our study subjects here, did not reduce the germination time either, and in some cases, increased it (Fuzssey et al., 2015).

A previous short term study conducted at this study site revealed a lower germination rate of spat-out and controls (seeds from fruits of the same ripeness as those eaten by orangutans) for *Elaeocarpus mastersii* (Nielsen et al., 2011) which is at odds with our findings here. Regardless of this, the orangutans are still facilitating the long distance dispersal (LDD) of these plant species, by functionally moving them away from the parent plant, even if ingestion isn't directly conferring a significant advantage on the seed.

Orangutans are assumed to be disproportionally important for animal-mediated seed dispersal for several reasons. Firstly they have a very large home ranges; for example, in Sabangau the mean for adult females is 250-300 ha, (Morrogh-Bernard et al., 2003, Singleton et al., 2009). Flanged males were thought to have ranges >560 ha (Utami et al., 2009), but a recent more intensive study of males revealed flanged males have a mean home range of 1900 ha and unflanged males 2000 ha (Buckley, 2014). In contrast, southern Bornean gibbon (*Hylobates albibarbis*) home ranges in Sabangau are approximately 47ha (Cheyne, 2010). Secondly, orangutans have a large gape size with the corresponding ability to ingest large, as well as small and medium sized seeds, without damaging them (Vidal et al., 2013). We were not able to ascertain the level of scarification on seeds passing though the orangutan gut as advised by Fuzessy et al. (2015) but that is also an avenue of future research.

Recent studies have elegantly demonstrated that different types of vertebrates often interact with the same seeds in different ways, playing complementary, rather than redundant roles (McConkey and Brockelman, 2011). As the largest arboreal frugivore in this assemblage, with associated large home ranges, orangutans, who have been shown here to affect removal of several seed species, can be expected to not only play a complementary role in seed dispersal but also contribute to LDD events in an inordinately high proportion, for all sizes of seeds, but particularly for large seeded species.

Some plant species failed to germinate under any treatment in our study i.e. *Tetramerista glabra* and *Gnetum* sp. Similar results were also found for the same species in a previous 6-week study at the same site (Nielsen et al., 2011), and a study conducted in West Kalimantan in a similar peat swamp environment recorded only 17 out of 774 (2%) *Tetramerista glabra* seeds germinating in 5 months (Gavin and Peart, 1997). Thus we suspect this species either has a very poor germination rate or requires highly specific conditions that we were unable to simulate in order to stimulate germination.

The action of spitting also potentially plays an important role in seed dispersal via removal of pulp containing germination inhibitors (Traveset, 1998, Traveset and Verdú, 2002, Robertson et al., 2006). This is an often overlooked component of animal-mediated seed dispersal that can play an influential role in the primary seed shadow ((Kleyheeg and van Leeuwen, 2015), McConkey pers. comms.). Spitting can even influence establishment. For example seed handling by two different primate species demonstrated that spit seeds, while deposited much closer to their parent trees than defecated seeds, experienced establishment rates of seeds that were much higher (Gross-Camp and Kaplin, 2011). Seed spitting and germination of these seeds was not quantified here, due to the difficulty of measuring distance of seeds while also following a moving orangutan in an already challenging habitat. However, some spat seeds were observed to fall between 1-10m from under the parent crown and for *Sandoricum beccanarium* orangutans were directly observed spitting clumps of seeds at a distance of 200m away from the feeding tree while travelling (E. Tarsizsz, pers. obs.). In doing this the seeds gain the advantage of LDD as well as the deinhibition effect from removal of pulp (Traveset, 1998, Traveset and Verdú, 2002, Robertson et al., 2006).

This also highlights the phenomenon of post-primary dispersal and how movement of seeds through the gut is not the entire picture in the seed dispersal cycle (Wang and Smith, 2002). Different researchers have assessed other points in this cycle. A project to ascertain the role of terrestrial animals in secondary seed predation was conducted in this study site to assess secondary seed dispersal by terrestrial seed predators across the forest floor, finding very little movement of seeds that had fallen from trees and rare removal from the shadow of the parent tree (D’Arcy and Graham, 2008). The reduced roll of secondary seed dispersers in this habitat therefore makes the role of primary seed dispersers such as orangutans (and gibbons) potentially even more important in comparison to other types of forests (D’Arcy and Graham, 2008).

4.5 CONCLUSIONS

1. Seed travel through the orangutan gut was not the most significant factor in germination as manually extracted seeds showed the highest rates of germination over both orangutan “gut-treated” seeds and whole fruits.
2. Orangutans might play a more important role in germination when seeds are moved, by spitting whole seeds out.
3. Despite 1., seeds passed intact via orangutan faeces still germinated and contributed to the primary seed shadow of many plant species.
4. Orangutans move seeds from the parent plant by ingesting and later defecating these seeds. Some of these seeds germinate, resulting in long distance dispersal events. These include very large seeds (>25mm), which are unlikely to be moved intact by other arboreal frugivore guilds, although further study of secondary seed dispersers is warranted.
5. As there is a relative lack of secondary seed removal in this particular environment (a peat-swamp forest), orangutans can be expected to play a disproportionate role in seed dispersal, although further evaluation is required.

5 PEAT SWAMP FOREST SEED DISPERSAL: THE IMPORTANCE OF ORANGUTAN MOVEMENTS

5.1 INTRODUCTION

Movement ecology, the study of animals' use of, and movement through, the environment, incorporates both intrinsic and extrinsic factors of species biology (Nathan et al., 2008a, Jachowski and Singh, 2015). Technological advances in remote animal monitoring (radiotelemetry equipment, GPS tagging), and spatial information (remote sensing, digital elevation data, GIS analysis software) have facilitated the consolidation of the fields of animal movements and ecology, such that movement ecology now aims to understand the underlying processes and systems that govern the movements of animals in their natural habitats, and even to predict ecological consequences of those movement patterns, and changes to those movement patterns (Nathan et al., 2008a, Cagnacci et al., 2010, Hebblewhite and Haydon, 2010, Kie et al., 2010, Morales et al., 2010). The key element required to understanding the interaction between the individual and its environment (and by extension the species and its environments) is the spatio-temporal pattern over which interactions take place. Patterns through time and space involve a complex set of possible parameters that define an animal's home range.

5.1.1 Home range analysis

The formal definition of a home range continues to evolve, as does the methodology employed to quantify it e.g. (Börger et al., 2006, Laver and Kelly, 2008). One of the most widespread methods employed to ascertain animal home ranges is the construction of minimum convex polygons (MCP) which uses straight lines between peripheral data points to create the smallest possible polygon around them e.g. (Quin et al., 1992, Burgman and Fox, 2003, Bradshaw et al., 2007). The advantages of employing MCP estimates are the relative simplicity of this method and its suitability for presence-only data (Burgman and Fox, 2003). Despite its widespread use e.g. (Quin et al., 1992, Jetz et al., 2004, Bradshaw et al., 2007), its application is of limited value when an animal's home range or population's distribution is non-convex (Burgman and Fox, 2003, Getz and Wilmers, 2004, Börger et al., 2006, Fieberg and Börger, 2012, Munn et al., 2013). Furthermore, minimum convex polygons are biased by multiple factors including (but not limited to): sampling strategy and duration; outlier treatment; survey effort and number of location estimates (Quin et al., 1992, Burgman and Fox, 2003, Börger et al., 2006, Laver and Kelly, 2008). These problems arise largely because the polygons are created from the peripheral points and therefore assume the same intensity of use at the edge of the polygon as in the centre. This assumption is inconsistent with the movement patterns of most animals, which are dictated by a myriad of internal and external motivators, such as forage availability, reproduction and the presence/absence of conspecifics e.g. (Nathan et al., 2008a, Cousens et al., 2010, Jachowski and Singh, 2015). As a result of the assumed homogeneity of area use, differences in area use intensity cannot be identified with this method (Getz and Wilmers, 2004).

Kernel density estimation (KDE) constituted a paradigm shift in spatial mathematics that resolved many of the possible biases of home range estimation using the MCP method. KDE directly produces a density estimate from the data and it is more flexible in assessing the densities of different shapes (Seaman and Powell, 1996). Kernel density estimation first constructs a probability density or "kernel" over each sampled point, places a rectangular grid onto the data, and then estimates density at each intersection of the grid (Seaman and Powell, 1996, Burgman and Fox, 2003). At these intersections, the average of the densities of all the overlapping kernels is taken. These averages contribute to the overall home range estimate, with high densities in areas with more observations and lower densities in areas with fewer observations (Seaman and Powell, 1996, Burgman and Fox, 2003), rather than just the edge as with MCP estimation. Although an improvement on MCP, the accuracy of KDE depends heavily on how it is implemented described as the "bandwidth" or "smoothing" of the kernel (Worton, 1995, Seaman and Powell, 1996, Burgman and Fox, 2003, Börger et al., 2006, Laver and Kelly, 2008). This parameter, which is chosen by the operator, places a weighting factor on the contributions of each point to the density estimates (Seaman and Powell, 1996). The same training data can result in highly variable estimates of home range, depending on the "bandwidth" at which the data are interrogated (Worton, 1995, Seaman and Powell, 1996, Burgman and Fox, 2003, Laver and Kelly, 2008).

Due to the great variability of KDE estimates, dependence on chosen parameters and relative complexity compared to MCP estimation e.g.(Burgman and Fox, 2003) alpha-hull construction became one of the next iterations in home range analysis. Alpha-hulls are generated by modifying Delauney triangulations. This is achieved by connecting all the points, so that no lines intersect between points, averaging the length of all the lines and then removing all sides that are "α" times longer than the median of the original sides (Burgman and Fox, 2003, Getz and Wilmers, 2004). Habitat area is then calculated by adding the area of the remaining triangles i.e. after the longer lines/sides have been excluded (Burgman and Fox, 2003). This excludes some points which can lead to inaccurately small home range estimations (a Type I error) and, like MCP doesn't reveal areas of high and low use or clustering of point fixes (Getz and Wilmers, 2004).

Two recent alternative developments in spatial statistics aiming to quantify home range (HR) centre around the construction of local convex hulls (LoCoH; (Getz and Wilmers, 2004, Getz et al., 2007, Lyons et al., 2013), and Outlier-restricted edge polygons (OREP; (Kenward et al., 2008, Munn et al., 2013). The two are essentially the same, in that they construct reiterative kernel analyses on the basis of prescribed numbers of nearest neighbour points (Kenward et al., 2008, Munn et al., 2013), and I shall use the term LoCoH from herein.

LoCoH produces a set of non-parametric kernels constructed by aggregating local mean convex polygons and computing a density estimate distribution for all locations based on nearest neighbour linkages (Getz and Wilmers, 2004, Getz et al., 2007, Getz and Saltz, 2008, Lyons et al., 2013, Lyons et al., 2015), the union of which estimates the HR (Getz and Wilmers, 2004, Getz et al., 2007). As LoCoH utilizes a non-parametric approach to HR estimation it avoids assumptions about the distribution form that is inherent in parametric kernel methods (Getz and Wilmers, 2004, Getz et al., 2007). LoCoH is particularly good at creating home ranges from areas with "idiosyncratic geometries", avoiding inclusion of geographical boundaries such as rivers or mountains (Getz and Wilmers, 2004, Getz et al., 2007, Getz and Saltz, 2008, Lyons et al., 2013). This reduces Type II errors (overestimates including an invalid area) when compared to parametric kernel methods (Getz and Wilmers, 2004, Getz et al., 2007, Getz and Saltz, 2008). As a result of these refinements LoCoH has increased accuracy over many of the commonly employed methods for home range estimation discussed previously (Getz and Wilmers, 2004, Getz et al., 2007, Lyons et al., 2013).

Spatial movement patterns are, however, often complicated by temporal behavioural patterns (daily movement routines, seasonal effects, migration), which have substantial impacts on home range estimation. Continued development has incorporated time into the LoCoH model, which (Lyons et al., 2013) refer to as a Time Local Convex Hull (T-LoCoH) method. T-LoCoH is a modification of LoCoH which incorporates timestamps of each point in both nearest neighbour selection and sorting of hulls (Lyons et al., 2013). Inclusion of time allows points that are close together in space but distant in time to be teased apart, and thereby separates revisitation of the same locations, as well as exploring the time spent in different locations. The "distance" between points is calculated in T-LoCoH by a parameter called the Time Scaled Distance (TSD) which is "a hybrid space-time metric" (Lyons et al., 2013). This method allows a greater array of space use models to be constructed to investigate space and time use patterns and generate maps based on behaviour (Lyons et al., 2013). While traditional home ranges will include revisitation to the same area as a "dense blob" (Lyons et al., 2013) typifying a 'core area', temporal partitioning facilitates the evaluation of behaviour by characterising the core home range as a highly revisited area and provides potential insight into the reasons for which an animal is utilising this area, such as water sources, food, access to mates, or if this is a travel throughway between resources.

Although T-LoCoH is only one amongst a number of methods for home range analysis which incorporate space and time, including Brownian bridge movement models (BBMM) and movement-based KDE (MKDE), T-LoCoH is the most intuitive and best integrated approach (Lyons et al. 2013). Therefore, in this chapter I am focusing only on the kernel based approaches for spatial modelling.

5.1.2 Ecophysiological Interpretation of Movement Ecology: Ecological Service Provision of Seed dispersal

The increasing sophistication of spatial statistics that contribute to home range analysis has facilitated an expansion from descriptive to predictive forms of movement ecology, providing insight into not just where animals go, but how they use space and resources within their home range (Börger et al., 2008, Morales et al., 2010, Jachowski and Singh, 2015). This has often been used to understand the effects of changing ecological context (e.g. habitat loss and fragmentation, landscape degradation, climate change) on the spatial requirements of animal populations, range shifts and local carrying capacity e.g. (McRae et al., 2008, Huey et al., 2012, Hetem et al., 2014, Jachowski and Singh, 2015). What has been far less well explored are the downstream ecological effects of changing animal movement patterns on fauna-mediated ecosystem service provision (Tomlinson et al., 2014).

While the majority of attention has focused upon the role of movement ecology in understanding pollination patterns e.g. (Ellstrand, 1992, Sork et al., 1999, Krauss et al., 2009, Menz et al., 2011, Rosas et al., 2011), animal-mediated seed dispersal (zoochory) is a crucial component of plant population dynamics, influencing plant populations and communities through both short and long distance dispersal e.g.(Howe and Miriti, 2000, Nathan and Muller-Landau, 2000, Wang and Smith, 2002, Russo et al., 2006, Cousens et al., 2010, McConkey et al., 2012). The influence of zoochory, and disruptions to zoochory, have recently been powerfully inferred on the basis of population genetic structures of plant populations, even though their dependence upon zoochory is, in some cases, otherwise poorly substantiated (Nathan and Muller-Landau, 2000, Wang and Smith, 2002, He et al., 2009, Krauss et al., 2009, Hamrick and Trapnell, 2011, Pascov et al., 2015). As discussed in Chapters 1 and 4, large-bodied frugivores are critically important for long distance seed dispersal and, in many cases, the extirpation of large bodied frugivores throughout the tropics has seen a decline in plant species diversity e.g.(Chapman and Onderdonk, 1998, Peres, 2000, Peres and van Roosmalen, 2002, Corlett, 2007, Muller-Landau, 2007, Peres and Palacios, 2007, Stoner et al., 2007b, Wang et al., 2007, Bass et al., 2010, McConkey et al., 2012, Ruxton and Schaefer, 2012, Harrison et al., 2013).

Zoochory is an important limiting factor for a seed in several respects. It can determine the location where plants have a potential to establish (Schupp et al., 2010), removes the seeds from competition with the parent plant (Howe and Miriti, 2000, Levin et al., 2003, Muller-Landau, 2007, Nathan et al., 2008b, Schupp et al., 2010, Ruxton and Schaefer, 2012), can protect the seeds from pathogens and predators (Levin et al., 2003, Nathan et al., 2008b, Schupp et al., 2010, Ruxton and Schaefer, 2012) and has the potential to deposit the seeds in favoured microsites (Nathan and Muller-Landau, 2000, Schupp et al., 2010, Ruxton and Schaefer, 2012). The spatial arrangement of seed deposition also contributes to at least half the gene-flow of plants, and their population genetic structure may be highly dependent on fauna-mediated seed dispersal (Manel et al., 2003, Manel and Holderegger, 2013), particularly in tropical forests (Jordano, 2001, Bascompte and Jordano, 2007, Côrtes and Uriarte, 2013). A decline or extirpation of seed dispersers can potentiate a flow-on effect for plant community diversity e.g. (Muller-Landau, 2007, Peres and Palacios, 2007, Stoner et al., 2007a, Stoner et al., 2007b, Wright et al., 2007, Brodie et al., 2009, Effiom et al., 2013) and genetic diversity (Manel et al., 2003, Manel and Holderegger, 2013) although due to the generally slower growth of plants relative to animal dispersal agents, there can be a time lag in floral diversity reduction e.g. (Muller-Landau, 2007, Brodie et al., 2009, McConkey et al., 2012).

Animal-mediated seed dispersal is intricately bound with movement ecology (Nathan and Muller-Landau, 2000), as the habitat through which an animal moves comprises the areas where they will deposit seeds, whether near or far from the parent tree. Barriers to fauna-mediated seed dispersal may be a hidden driver of biodiversity loss and genetic fragmentation (Manel et al., 2003, Bradford and Westcott, 2010, Manel and Holderegger, 2013). Recent discussion, however has examined the role of animal physiology in constraining many of the processes structuring ecosystems and populations, particularly those that are dependent upon animal-plant interactions (such as pollination or seed dispersal (Abrol, 2005, McCallum et al., 2013, Tomlinson et al., 2014)). While Tomlinson et al. (2014) focused heavily upon the importance of animal energetics, other aspects of animal physiology, as well as energetics could influence endozoochory (the movement of ingested seeds), where the capacity of an animal to disperse a seed is not just mediated by where the animal moves, but also the timing of elimination events. Such interactions may also have a role in epizoochory (Will et al., 2007, Will and Tackenberg, 2008, Cousens et al., 2010), but the causal effects are not so obvious, and not intuitive in our study system, where orangutans eat seeds encased in fleshy fruits. The capacity to disperse seed by endozoochory is an interaction between animal movements, and seed movement from ingestion to elimination, necessitating an ecophysiologically-informed spatial model.

In the climatically important and ecologically diverse peat-swamp forests of Borneo (see section 1.3), slash-and-burn agricultural practices, commercial palm oil plantations and large-scale clearance of landscape for agricultural developments, such as the Mega-Rice project, have destroyed and fragmented habitat and reduced habitat quality to a globally-significant extent (Rieley et al., 1997, Page et al., 2002, Page et al., 2008, Hergoualc'h and Verchot, 2011, Page et al., 2011). I studied the movement ecology and seed dispersal capacity of the largest bodied arboreal frugivore in this environment, the orangutan (*Pongo pygmaeus wurmbii*; (Ancrenaz et al., 2008)), which has been found to defecate seeds of varying sizes (table 4.3) (Rijksen, 1978, Galdikas, 1982, Nielsen et al., 2011). Large bodied frugivores, such as the orangutan, are likely to be critically important seed dispersers as there are typically few animals that can effectively disperse large-seeded species, which has often lead to co-evolution of the plant-animal interaction (Chapman and Onderdonk, 1998, Barlow and Martin, 2002, Brodie et al., 2009, Effiom et al., 2013, Hall and Walter, 2013)). Furthermore, orangutans have a slow life history with a long interbirth interval (Knott et al., 2009, van Shaik et al., 2009) and are subject to increased human disturbance, mostly from habitat destruction and encroachment as well as from direct targeting through hunting (Morrogh-Bernard et al., 2003, Marshall et al., 2006, van Shaik et al., 2009). Despite its charisma and its ecological importance, little is understood of the seed dispersal agency associated with orangutan movement, let alone the potential impacts of drastic landscape modifications on this ecological service provision.

5.1.3 Aims

I aimed in this chapter of my thesis to determine how orangutans move around their environment and develop mechanistic model expectations of how they disperse seeds as a result. I began by developing utilization distribution maps that evaluated the space used by my study animals. I aimed to ascertain if there were any interactions between animals, sexes and seasons in these space-use allocations. A combination of GPS technology and vigorous on-the-ground monitoring has enabled us to map the details of orangutan movement through the challenging environment of tropical peat-swamp forest (TPSF), monitor their behaviour through instantaneous sampling (Morrogh-Bernard et al., 2002, Morrogh-Bernard, 2009), including records of primary and secondary activities, feeding habits and locations of faecal deposition (Appendix B) with subsequent analysis of faeces for seed identification and germination trials (Chapter 4).

5.2 MATERIALS AND METHODS

5.2.1 Study site

I carried out field research as part of the multidisciplinary research partnership of Orangutan Tropical Peatland Project (OuTrop) and their Indonesian counterparts, the Centre for the International Cooperation in Sustainable Management of Tropical Peatlands (CIMTROP). The field program was conducted within the Natural Laboratory of Peat-Swamp Forest (NLPSF) which is a 500 km^2 subset of the wider 9,200 km^2 of peat-swamp forest in the Sabangau ecosystem between the Katingan River to the west and the Kahayan River to the east, Central Kalimantan, Indonesia (Morrogh-Bernard *et al.*, 2003, Page et al., 1999).

The Sabangau climate is a tropical system with high annual rainfall, e.g. 3108 mm in October 2012- November 2013, fig 1.3). Rain falls throughout the year however there are distinct wet and dry seasons that last from October to May (305.06 mL per month on average October 2012- May 2013, and see Fig 1.3) and June to September (149.73 mL per month on average in June 2013- September 2013 and see Fig 1.3) respectively. This is a non-masting forest, which produces fruit relatively consistently throughout the year, although there are temporal variations in fruit (and flower) availability. Peak fruit (and flower) availability occurs during the dry period between June-October (Harrison, 2009b) when rainfall is negligible (2353.90 mL, 2012-13, Fig 1.3) compared to the wet season (598.90 mL). The relative homogeneity of this environment (Singleton et al., 2009), as well as limited secondary seed dispersers and seed predators (D'Arcy and Graham, 2008) makes this an ideal location for modelling primary seed dispersal in TPSF by the largest bodied arboreal frugivore (Ancrenaz et al., 2008).

The NLPSF Field Station is situated just inside the edge of the forest on a former logging concession (Fig 1.1b). Here, there is an abrupt edge between the forest and the sedge swamp that borders the river. The area that is now sedge swamp was once covered in riverine forest, but this has all been felled and is now considered to likely be extinct ((Page et al 1997, Harrison 2009), Figs 1.1b, 1.4a,b). A trail grid system, ca. 900 ha has been cut into mixed swamp forest in the NLPSF (fig 1.4a,b).

Previous home range estimates for orangutans at this site applied both MCP and KDE. Using MCP the average home range was >560 ha for adult (flanged) male and 250-300 ha for adult females (Morrogh-Bernard et al., 2003, Utami et al., 2009). A recently concluded study on males at the OuTrop study site estimated home ranges for flanged males using KDE with the least square-cross validation method and found a mean of 1,900 ha for males followed outside the research grid (Buckley, 2014). The modelling approaches available at the time did not allow for any substantial interrogation of time-space usage or seed dispersal capacity. My first aim was to extend these previous findings using T-LoCoH to estimate HR for the orangutans in such a way as to model space and time use, and the seasonal changes in these spatio-temporal patterns.

Secondly, I aimed to tease out the role of orangutans as primary seed dispersers by the modification of T-LoCoH models with physiological information. While several reviews have described other potential methods for prediction of seed dispersal e.g. (Nathan and Muller-Landau, 2000, Nathan et al., 2008b, Côrtes and

Uriarte, 2013), as far as I am aware, mine are the first ecophysiologically-informed kernel models that predict the spatial consequences of animal-plant interactions *via* seed dispersal. The spatial models constructed on the basis of animal movements were modified on the basis of previous studies on gut transit time of captive orangutans ((Caton et al., 1999a), Chapter 4). By modelling the ecological cascade of endozoochory mechanistically I aimed to make this methodology potentially applicable to the continued study of orangutans at this study site, with the ability to model and predict seed movements with changing orangutan populations.

5.2.2 Data collection

Orangutan "follows" were conducted according to a standardized orangutan data collection protocol (Martin and Bateson, 1986, Morrogh-Bernard et al., 2002, Morrogh-Bernard, 2009). In summary, once orangutans were located on the research grid (fig 1.4a,b) they were followed for a maximum of six consecutive days by two-person teams until they nested at night. One member of the team recorded the location of the orangutan at five-minute intervals, identified and tagged feeding trees as well as collecting faecal samples for seed germination trials. The second person observed the orangutan behaviour, including feeding activity.

Nocturnal nests were marked by trailing a spool of cotton to the nearest transect, enabling observers to return to the nest with relative ease the next day before dawn and make full day, nest-to-nest observations. During diurnal orangutan follows feeding data were recorded continuously, including start and finish of feeding bouts, food item eaten and what part of this was ingested i.e. fruit (whole, skin, pulp, seed and combinations thereof), leaf (young or mature), bark or pith. If an orangutan ceased feeding for one or more minutes on a particular foodstuff then recommenced, this was considered as a second feeding bout. A complete set of activities, primary and secondary is included in Appendix A.

5.2.3 Data Handling

Only full day (nest-nest) data contributed to this study. Prior to kernel analysis all location data were checked for internal consistency and points resulting from accidental GPS fixes were removed. This occurred for two females who had outliers, which represented 0.22% of all GPS fixes for female 2 and 0.42% of all GPS fixes for female 3. All subsequent point locations were standardised from longitude and latitude into UTM zone 49M coordinates using Earth Point (Clark, 2016). As all data were initially recorded in local time, they were time stamped with the appropriate code “tz=Asia/Magadan, MAGT” using R Studio (R Core Team, 2015, R Studio Team, 2015) before being transformed into Coordinated Universal Time (UTC).

I used the T-LoCoH package (Lyons et al., 2015) in the R Studio statistical environment to construct two temporally-rectified hull models based upon the filtered subset of known point locations for each orangutan. One model aimed to estimate the likely utilisation patterns and movements of the orangutans themselves, while the second model was informed by known gut passage times for orangutans (Chapter 3) to estimate likelihood kernels for the dispersal of seeds eaten by orangutans. While greater detail can be found elsewhere (Lyons et al., 2013), T-LoCoH constructs movement hulls by first identifying a range of nearest neighbours, then simplifies a series of minimum convex polygons based upon a time series specifically set by the user to represent a consensus model of probabilistic kernels. At each level of the process there are a number of ways to proceed, largely dependent upon the objective of the overall exercise (Lyons et al 2013).

Three methods can be employed in the T-LoCoH program to find nearest neighbours, the “k”, “r” and “a” methods. In all three methods the nearest neighbours are selected based on the TSD, separating points that may be close in space but are distant in time (Lyons et al. 2013). The *k*-LoCoH method “finds the *k*th nearest neighbours around each point”, which is determined by the TSD (Getz and Wilmers, 2004, Getz et al., 2007, Lyons et al., 2013). This is an egalitarian method where hulls are constructed such that every hull contains the same number of nearest neighbours (Getz and Wilmers, 2004, Getz et al., 2007). However, the results are not always ideal if there is substantial spatial heterogeneity in the data (i.e. sparse and dense areas of data collection (Getz and Wilmers, 2004, Getz et al., 2007, Lyons et al., 2013)). The *a*-LoCoH method aims to reduce the number of nearest neighbours in areas with thin, scattered points, to better homogenise potential sampling bias. The *a* method adds cumulative distance from the parent point up to an ‘*a*’ value (Lyons et al., 2013, Lyons et al., 2015) and determines nearest neighbours whose aggregate distance is $\leq a$ (Lyons et al., 2013, Lyons et al., 2015). *A*-LoCoH was found to be the most robust method as it is both “the most insensitive to suboptimal value choices for its kernel parameters” (Getz et al., 2007) and can be superior to *k*-LoCoH for reducing the minimum spurious hole covering (Getz et al., 2007, Lyons et al., 2013), and thus that was the method that I employed throughout this chapter.

Since time is a critical factor contributing to space usage in T-LoCoH, the first step in implementing T-LoCoH is to determine an appropriate value by which to scale the maximum theoretical velocity, V_{max}, which (Lyons et al., 2013) denote as the dimensionless scaling factor *s*. When s=0, the effect of time on distance becomes null, and the model becomes space selected only (Lyons et al., 2013). With an increasing value of *s,* the importance of time increases, leading to nearest neighbour selection based on a time window, creating a link of time to space-use (Lyons et al., 2013). To construct the home range kernels of the orangutans I chose 24 hour intervals because orangutans are largely diurnally active, sleeping from dusk to dawn (Mitra Setia et al., 2009). When modelling seed dispersal hullsets, *s* was chosen based on the average transit time for seed mimics in orangutans fed a largely plant-based diet (Chapter 3). As there was no significant difference in gut passage times between the seed mimic sizes (see section 3.3), an average passage time of all sizes was used (76hrs).

Kernel Model Refinement

In applying the *a*-LoCoH approach, the most appropriate value of *a* was established by examining the differing density of isopleths, overlaid on GIS data to reduce both Type I (including areas that aren't part of the home range) and Type II (overlooking areas that are part of the home range) errors. I checked the validity of the initial value of *a* by visually assessing whether the "a^{th}" isopleth encompassed 95-% of the data, which is often considered as comprising the home range (Laver and Kelly, 2008, Lyons et al., 2013). Secondly I refined this estimate by plotting the isopleth area curve and the isopleth edge area ratio for the different values of *a* (Fig 5.2).

The isopleth area plot displays the area of each isopleth for the different values of *a*. Sharp jumps in the isopleth area curve between slight increases in *a* indicate a likely Type I error (Fig 5.2a,b) signalling that a big area of new habitat was included, and the value of *a* needed to be reduced to below this jump. The next step was for me to created hullsets for individual levels of *a* between the initial chosen value and the "below-jump" level and evaluate theseindividually before making a final selection of *a*, thereby refining my space use model.

The isopleth edge:area curves are used to avoid making Type II errors and refine the model further. They describe the total perimeter ratio to the area for each isopleth level (Lyons et al. 2015). Very high values indicate lots of small holes and indicate a too small value of *a*. The chosen *a* based on these graphs (and refined further by checking the hullsets) should match those chosen for the isopleth area plot. As each animal had a different V_{max}, and different movement patterns, the *a* value differed between each animal.

5.2.3.1 Temporal Effects

Within the T-LoCoH kernel models, I computed revisitation rate and duration of use by first specifying an intervisit gap (IVG) of 24 hours. This means that observations were only recognised by the T-LoCoH model as separate visits if 24 hours had elapsed between them.

Secondly, an IVG of 76 hours, the average time for a transit of an undigested seed was specified, creating metrics for revisitation and duration of use over this larger time scale. In effect, for each individual we modelled two “animals” separately: the orangutan which moved in “real time” and the average seed in their gut, which was approximately three times “slower”. Seed dispersal was therefore explored by interrogating the differences of revisitation, duration of stay and space use for this second “animal”. Spatially-explicit figures were generated by exporting the probability kernels as shapefiles and displaying them using the freeware GIS package qGIS v2.4.0-Chugiak (Fig 5.1a-f). The home range estimates resulting from the T-LoCoH approach were compared against MCP estimates made using the “convex hulls” command in qGIS that is consistent with previous studies of home range at NLPSF (Morrogh-Bernard et al., 2003, Utami et al., 2009).

5.2.4 Statistical analyses

In order to test the capacity of the kernel models to predict defecation, known locations of defecation were recorded in the field and not used to train the model. These locations were intersected with the kernel models of defecation/seed dispersal in qGIS. The expected proportions of defecation points falling into each kernel were tested against the observed proportion falling into each kernel using Pearson's chi-squared test for all animals, and also for males and females seperately.

I explored the effect of sex and season on orangutan movements and seed dispersal capability by constructing generalised linear models (GLMs) of several modelled elements of orangutan movement, including step length, 75% kernel area, residency (revisitation rate) and duration of stay. Initial tests were constructed using a fully factorial design of sex and season, but where significant interactions of sex×season were found, I combined these into a concatenate factor with four levels (i.e. males in the dry season, males in the wet season, females in the dry season and females in the wet season). The effect of the concatenate factor was then analysed by ANOVA, and a post-hoc Tukey's test applied to resolve points of difference. All analyses were conducted using R v3.2.2 (R Core Team, 2015) in the R studio shell v0.99.48 (R Studio Team, 2015), and all data are reported as means ± 1SEM unless stated otherwise.

Individuals can exert potential bias on the data structure, and in order to counteract this and place each individual on an equal footing (Vonesh and Chinchilli, 1996), I ran a repeated measures ANOVA on residency and duration of stay variables.

5.3 RESULTS

The kernel models that I constructed show that, with the exception of two related females, orangutans are solitary, with very little overlap between kernel models of the same sex (Fig 5.1). Males tended to have much more disjunct movement patterns than females, and also tended to overlap several females' home ranges within their own. Home ranges were characterised by higher revisitation rates for females (4.01±0.02 visits per day for females compared to 1.24±0.01 visits per day for males, see table 5.1) in the core range, but also had long loops of short duration and low revisitation around the edges of their home ranges. Predicted defecation models followed the same spatial patterns as orangutan movement, but with lesser revisitation rates. The core range was initially defined by examining the distribution of hulls in time-use space, choosing a value of a which filled core areas and minimised spurious cross-overs (Lyons et al. 2013) and is defined here as the 20% likelihood kernel. This describes locations that are the most heavily used, which encompass a small proportion of known locations. A counter-intuitively smaller likelihood results, as the core area is more tightly resolved. Hence, a lower likelihood represents a more finely resolved home range. The average home range size estimated for an orangutan at NLPSF by T-LoCoH was 55.2±12.00 ha, with an average step-length of 8.89±0.11 m, a revisitation rate (number of visits to the same location within 24hrs) of 3.43±0.02 visits each day, and an average visit duration of 41.00±20.18 minutes. The T-LoCoH home range estimated for females in the dry and wet seasons were 55.31±6.97 ha and 52.38±8.35 ha respectively. The minimum convex polygons for females in the dry and wet seasons were 149.00 ha and 160.84 ha respectively.

I found differences in most of the movement parameters of the orangutans based on sex, season and sex×season interaction (Table 5.1). There were significant effects of the sex×season concatenate factor for revisitation rate ($F_{11,19413}$ = 9.16; p = 0.002) and visit duration ($F_{1,19413}$ =4.13; p = 0.042), although there was no significant difference in step length based on sex×season interactions ($F_{1,\ 19328}$ = 0.07, p=0.792. For the 75% kernel area, sex was significant ($F_{1,\ 5}$ = 16.78 P=0.009), although season didn't significantly influence the home range area of females ($F_{2,5}$ = 0.70, p=0.540). Male orangutan movements were not different in either season (Table 5.1a), but revisitation was higher and intervisit duration shorter for females than males in either season (Table 5.1a). Female orangutans had higher revisitation rates and shorter intervisit durations during the dry season than the wet season.

I found differences in all the seed dispersal parameters based on sex of orangutan dispersal vectors, season and sex×season interactions (Table 5.1b). There were significant influences of the sex×season concatenate factor, for revisitation rate ($F_{1,19414}$ = 40.19; p = 2.358 X 10^{-16}) and intervisit duration ($F_{1,19414}$ = 7.47; p = 0.006). Seeds were less likely to be dispersed differently by males in either season, but revisitation was higher and intervisit duration shorter for seeds dispersed by females than for those dispersed by males in either season. Seeds dispersed by females were more likely to have higher revisitation rates and shorter intervisit durations during the dry season than the wet season (Table 5.2a,b).

There was no significant difference between the proportion of defecation events observed in each seed dispersal kernel and the expected rate of seed dispersal (Pearson's X^2_5= 8.09, p = 0.151). The mean average percent error (MA%E) of model predictions was 3.86±0.97%, ranging from 1.05% to 7.89%. The model fit was stronger for females only (X^2_5 = 0.229, p = 0.999), but marginally less so for males, although they were still not statistically significant (X^2_5 = 8.28, p = 0.141)

Table 5.1: a) Effects of season and sex on the measures of orangutan movement, intervist gap (IVG) = 24 hrs at NLPSF extracted from T-LoCoH kernel modelling. **b)** Effects of sex and season on movement when intervisit gap is modified for seed dispersal using T-LoCoH kernel modelling (*IVG* = 76hrs). Revisitation rate here is the number of visits to the same location per 24 hours and the duration of visit gives the average number of minutes spent at each location. Note: Step lengths were not directly calculable for seed dispersal estimates at *IVG* = 76hrs

		Step length (m)			**Revisitation rate**			**Duration of visit**		
a)		Mean (S.E.M.)	$F_{1,\ 19329}$	p	Mean (S.E.M.)	$F_{1,19413}$	p	Mean (S.E.M.)	$F_{1,19413}$	p
Season	Dry	8.61 (0.15)	41.88	**9.95×10^{-11}**	3.37 (0.02)	93.74	**2.20×10^{-16}**	43.06 (0.30)	249.78	**2.00×10^{-16}**
	Wet	9.12 (0.16)			3.48 (0.02)			39.29 (0.21)		
Sex	M	7.28 (0.26)	55.66	**9.00×10^{-14}**	1.24 (0.01)	7550.57	**2.20×10^{-16}**	61.69 (0.40)	4412.03	**2.00×10^{-16}**
	F	9.32 (0.12)			4.01 (0.02)			35.50 (0.18)		
season×sex	DM	6.34 (0.39)	0.07	0.79	1.18 (0.01)	9.16	**0.002**	65.57 (0.68)	4.13	**0.042**
	WM	7.90 (0.35)			1.27 (0.01)			59.16 (0.47)		
	DF	8.57 (0.17)			3.85 (0.02)			38.03 (0.30)		
	WF	9.98 (0.18)			2.05 (0.02)			33.26 (0.19)		

b)										
Season	Dry	-			3.02 (0.02)	243.19	**2.200×10^{-16}**	47.60 (0.31)	416.00	**2.200×10^{-16}**
	Wet	-			3.24 (0.02)			41.86 (0.22)		
Sex	M	-			1.20 (0.01)	7217.79	**2.200×10^{-16}**	62.60 (0.20)	2933.97	**2.200×10^{-16}**
	F	-			3.65 (0.01)			36.69 (0.01)		
season×sex	DM	-			1.16 (0.01)	40.19	**2.358×10^{-10}**	65.73 (0.68)	7.47	**0.006**
	WM	-			1.23 (0.01)			60.47 (0.47)		
	DF	-			3.42 (0.02)			43.63 (0.33)		

Table 5.2: Effects of sex-season concentate on revisitation rate for **a)** IVG = 24hrs and **b)** IVG = 76hrs. WF = female wet season, DF = female dry season, WM = male wet season, DM = male dry season

A	**Group 1 mean**	**Group 2 mean**	**Diff**	**P adjust**
WF – DF	2.05±0.02	3.05±0.02	0.293	**<0.01**
DM – DF	1.18±0.01	3.05±0.02	-2.268	**<0.01**
WM – DF	1.27±0.01	3.05±0.02	-2.58	**<0.01**
DM – WF	1.18±0.01	2.05±0.02	-2.97	**<0.01**
WM – WF	1.27±0.01	2.05±0.02	-2.873	**<0.01**
WM - DM	1.27±0.01	1.18±0.01	0.096	0.344
B				
WF – DF	3.87 ± 0.02	3.42 ± 0.02	0.444	**<0.01**
DM – DF	1.16 ± 0.01	3.42 ± 0.02	-2.261	**<0.01**
WM – DF	1.23 ± 0.01	3.42 ± 0.02	-2.19	**<0.01**
DM – WF	1.16 ± 0.01	3.87 ± 0.02	-2.705	**<0.01**
WM – WF	1.23 ± 0.01	3.87 ± 0.02	-2.633	**<0.01**
WM - DM	1.23 ± 0.01	1.16 ± 0.01	0.071	0.522

The repeated measures ANOVA confirmed significant difference of movement patterns when the factors of sex, season and sex*season were taken into account. When IVG = 24hours, for residency there was significance for all three values measured: i) sex ($F_{1,19409} = 170.8$, p= 2×10^{-16}), ii) season ($F_{1,19409} = 433.5$, p= 2×10^{-16}) and iii) sex*season ($F_{1,19409} = 730.5$ p= 2×10^{-16}). Similarly, for intervisit duration all ($F_{1,19409} = 348.4$, p= 2×10^{-16}); season ($F_{1,19409} = 114.9$, p= 2×10^{-16}) and sex*season ($F_{1,19409} = 420.1$, p= 2×10^{-16}). The results for a repeated measures on the seed model, where intervisit gap = 76 hours were also all significant for residency with regards to all factors: sex ($F_{1,19409} = 2694.7$, p= 2×10^{-16}); season ($F_{1,19409} = 201.7$, p= 2×10^{-16}) and sex*season ($F_{1,19409} = 414.4$, p= 2×10^{-16}). All factors were significant for duration of stay: sex ($F_{1,19409} = 291.8$, p= 2×10^{-16}); season ($F_{1,19409} = 17.05$, p= $3.7 x 10^{-5}$) and sex*season ($F_{1,19409} = 414.4$, p= 2×10^{-16}).

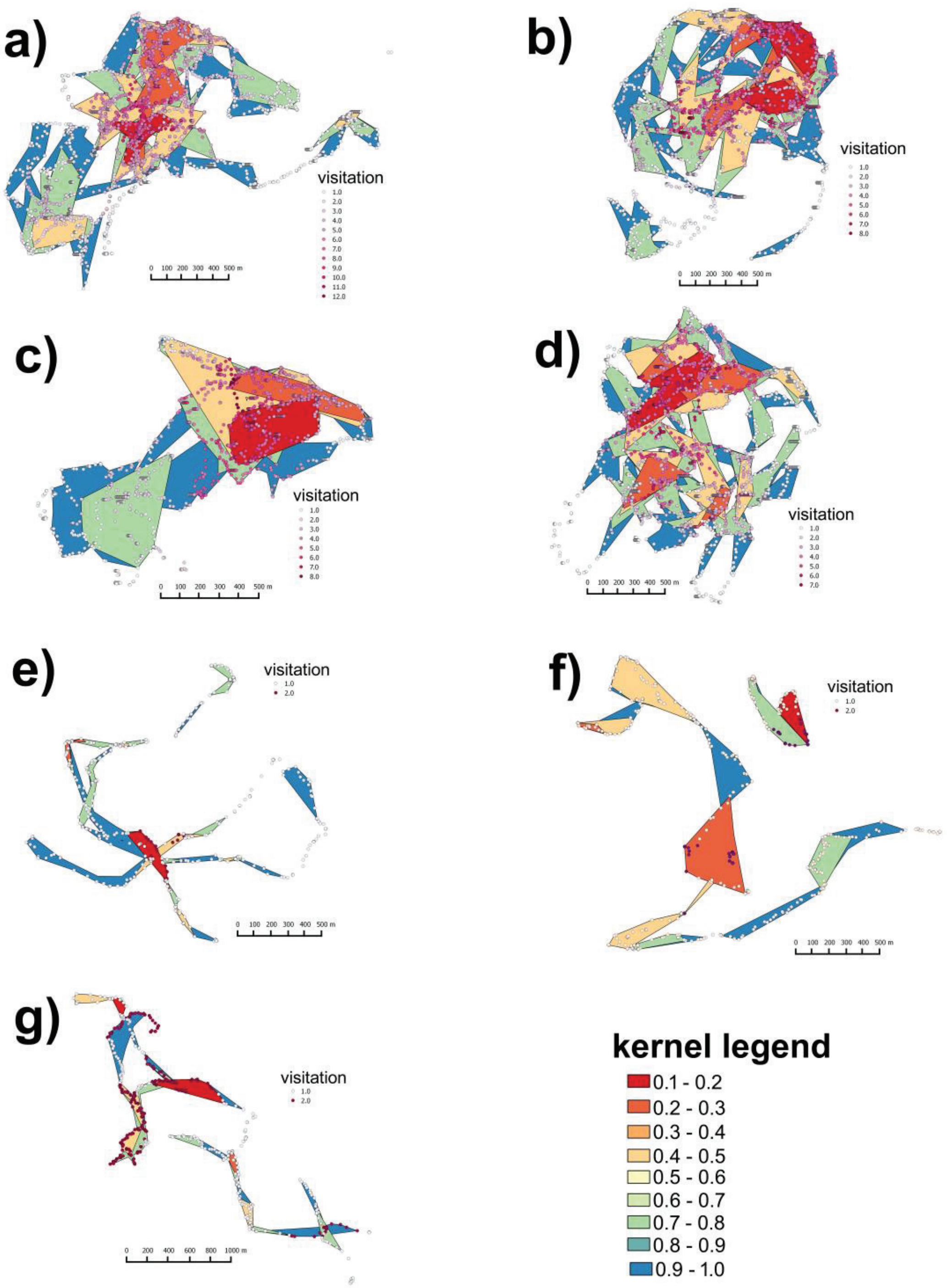

Fig 5.1: Likelihood distribution kernels and revisitation points as determined by T-LoCoH analysis period = 24hrs with revisitation points for a) female 1; b) female 2; c) female 3; d) female 4, e) male 1, f) male 2, g) male 3

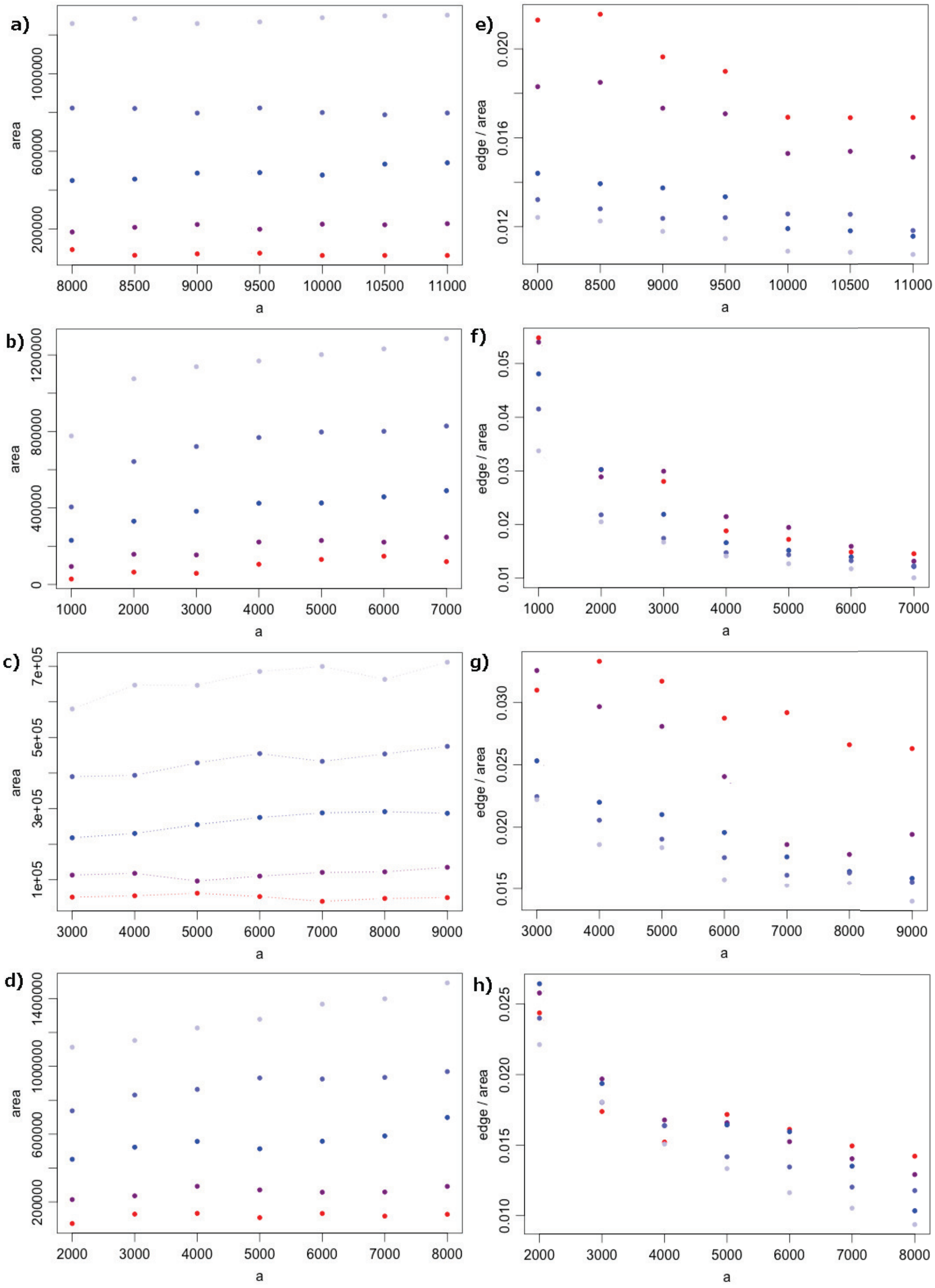

Fig 5.2a: Female isopleth area curves a)-d) and isopleth edge:area ratio curves e-h). Isopleth area curves show the area for different values of "*a*" and assist in determining a value that avoids type II errors. Where 'a' is the cumulative distance from the parent point up to an '*a*' value, as determine by Lyons et al. (2015) Isopleth

edge:area ratio curves are the ratio of the total perimeter to the area for each isopleth levels and are used to avoid type I errors and conform to the minimum spurious hole covering (MSHC) rule.

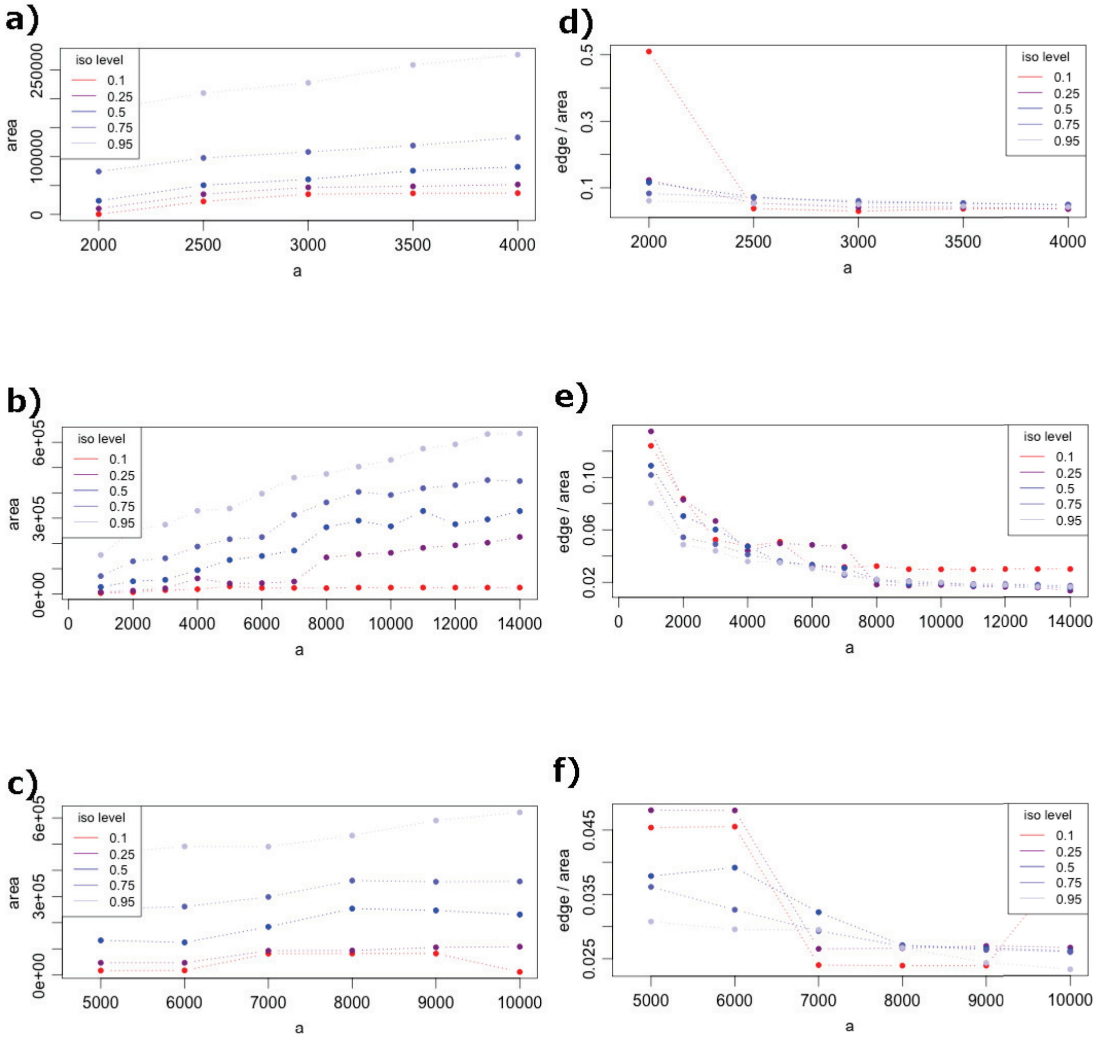

Fig 5.2b: Male isopleth area curves a)-c) and isopleth edge:area ratio curves

5.4 DISCUSSION

Development of ever newer methodologies of estimating home range and space use is a critical component of the burgeoning field of movement ecology. The existence of a multitude of different methodologies illustrates that there isn't a one-size-fits-all solution to gauging an individual animal's or species' distribution (Cagnacci et al., 2010, Frair et al., 2010, Hebblewhite and Haydon, 2010, Kie et al., 2010, Morales et al., 2010, Tomkiewicz et al., 2010). However, I believe that by the employment of T-LoCoH, a relatively new, non-parametric home range analysis tool that incorporates time (Lyons et al., 2013), I have resolved estimates of space use that account for errors most completely and are also flexible to future data. Furthermore, the models are applicable to broad ecological questions, and I have employed them here to look at seed dispersal by orangutans.

Evaluating orangutan mediated seed dispersal was the objective for this chapter, which I achieved through several steps. Firstly I created probability kernels of utilisation distribution, which described movement over time, for males and females (Fig 5.1), and found that both sex and season influenced most of the measures of orangutan movement at NLPSF. Males tended to move further than females, but my data for males were less consistent than for females, reducing my confidence in their analysis. Females tended to move more in the dry season than in the wet, ranging over larger home ranges. Secondly, I modified the kernel models of orangutan movements by incorporating aspects of their digestive physiology to produce a plausible model for predicting the primary deposition of seeds by the orangutans in peat-swamp forest habitat. The longer time interval, implying a "slower" rate of movement for seeds than for their orangutan dispersal vectors, meant that the plausible dispersal kernels were a smaller spatial subset of the orangutan home ranges, and tended to cluster most tightly within the core feeding areas of female orangutans. Male orangutans appear to be less effective seed dispersers, but may be responsible for long-distance dispersals; however my data are sparse, and not strongly indicative of the role of male orangutans in seed dispersal.

5.4.1 Orangutan movement, sexes and seasons

The use of T-LoCoH generated several informative parameters describing the movement ecology of orangutans at NLPSF: kernel area, revisitation rate, step length and duration of stay. I believe the kernel areas I have described (Fig 5.1) give a time-space-integrated view of orangutan home range use for females, as opposed to previous kernel areas based on space alone (Morrogh-Bernard, 2009, Singleton et al., 2009). Previous models have evaluated space-use, but used parametric approaches that did not incorporate space and time explicitly together. The estimates that I made using T-LoCoH produced home ranges that were, on average, 10% of the previous estimates of home range. Large discrepancies between LoCoH methods and more traditional methods (MCP, KDE and alpha-hull) have been reported in other studies (Getz and Wilmers, 2004, Getz et al., 2007).

The MCP estimates of home range that I made for females in each season (150 ha in the dry and 160 ha in the wet) are consistent with previous reports (Morrogh-Bernard, 2009, Singleton et al., 2009). MCP estimates for males were even greater due to their greater and more erratic movement patterns. Compared to previous findings at NLPSF and my MCP estimates, my T-LoCoH kernels are a lot smaller. LoCoH approaches tend to produce smaller, more refined estimates than MCP or KDE with fewer Type I and II errors (Getz and Wilmers, 2004, Getz et al., 2007), and my data further confirmed that traditional home range methods, such as MCP can substantially over-estimate home-range and space use. My MCP home range estimates more closely approximated previous findings, and my T-LoCoH estimates are approximately 36% of my MCP projections for females across both seasons.

Refining models of space use to understand temporal patterns gives much greater insight into the ecology component of movement ecology – not only can I estimate where the orangutans are most likely to be, and most likely moving to, but also where they are going during different seasons and the duration of time they stay in particular areas in different seasons. Revisitation indices, as well as duration of stay can illustrate the importance of different regions in different seasons. Considering time, as I have done here, typifies a different way of examining and considering "core area" based on when, rather than just where an area is used. Core home range is often taken to be 50% of observed locations (Singleton et al., 2009, Lyons et al., 2013). Integration of time has shown significant interactions between both how and where space is used in different seasons (Table 5.1), and suggests that definitions of home range need to evolve again to accommodate this.

The flexibility inherent in a T-LoCoH model provides avenues to make ecological inferences of movement patterns. My analyses demonstrate powerful univariate effects of both season and sex on both the residency and duration models (Tables 5.1-5.2). The movement parameters generated by T-LoCoH (step length, revisitation rate and duration of stay) for orangutans at the NLPSF are all influenced by sex and season and all suggest that males range over greater areas than females, but are resident for less time, and visit each location less often than females. There aren't any evident seasonal patterns in the movements of males, suggesting that they move nomadically within home ranges that don't fluctuate in accordance to patterns of fruiting at NLPSF. The lack of seasonal patterns for males is in stark contrast to the seasonal differences between the movement patterns of females, where females move more often, over greater distances and areas in the dry season. This is consistent with the known fruiting patterns at NLPSF, because there is less food available in the wet season (Harrison, 2009b), and the females are likely moving around in order to meet their requirements. In the dry season they can afford to monopolise fruiting trees for longer periods before moving on. While females are probably foraging in accordance with fruiting patterns, males are apparently moving in relation to another powerful imperative – that of mating and/or avoiding (or aggressing) other conspecifics, which is consistent with other studies where flanged males have been found to have much larger and less stable home ranges in order to increase access to females (Utami et al., 2009). My interpretations of flanged males must be tempered due to the sparse data that contributed to my models of male movements. While male ranges are more labile than those of females, this also makes collecting robust data on their movements difficult, and it is likely that the scarcity of data undermines their reliability, as I believe happened with my data. While these home range models are partially indicative of male orangutan movements, they do not give as complete or refined a picture as emerges for the females. It is entirely possible that with more data for males, I would have found some stability and connectivity of male home ranges, and probably seasonal differences that were not evident in this study, although the consistency of my results with previous research suggests that this problem has yet to be overcome in the literature (Morrogh-Bernard, 2009, Utami et al., 2009).

The accuracy of modelling is always contingent upon the refinement of the data contributing to it. In this case I had a trade-off to make between a reduced temporal span over which I could collect data, and a greater amount of information that I could collect by following the orangutans on foot. Remote sensing (GPS tags) would have facilitated a greater number of individuals, followed constantly and consistently without any risk of the presence of human observers disturbing the orangutans and altering their movements more often than in natural conditions. A prime example is the difficulty in collecting contiguous data on unflanged (immature) males due to their larger home ranges compared to all other age/sex classes, including flanged males (Buckley, 2014) which contributes directly to the lack of habituated study subjects. The study subjects that informed the data in this chapter were habituated and ignored the presence of researchers, but without remote sensing I am unable to determine if the presence of humans affected their movement patterns.

Remote sensing would also guarantee consistent survey effort, regardless of the constraints of manpower and inclement conditions (Kie et al., 2010, Tomkiewicz et al., 2010, Lyons et al., 2013). A cost does come with high human resource use, in comparison with remote sensing, although each pose their own set of challenges (Frair et al., 2010, Hebblewhite and Haydon, 2010). Gathering contiguous data by on-ground follows became difficult if not impossible, during inclement weather, and it can make scaling up to population inferences somewhat questionable ((Cagnacci et al., 2010, Frair et al., 2010, Hebblewhite and Haydon, 2010, Kie et al., 2010, Morales et al., 2010, Smouse et al., 2010) and see section 5.4.3).

Mitigating the trade-off of between continual movement data is the facilitation of on-the ground analysis of behaviour concurrently with GPS data. In this way I have bypassed one of the problems of remote GPS sensing: the incongruity between animal movements and what is happening on the ground (Moorcroft et al., 2006, Cagnacci et al., 2010, Hebblewhite and Haydon, 2010, Kie et al., 2010, Morales et al., 2010, Smouse et al., 2010). I have, therefore, been able to collect more information on the orangutan behavioural ecology that remote sensing cannot impart. For example, without daily follows I would have been unable to collect the independent defecation data that facilitated my testing the goodness of fit of my model. However, some authors have used fine scale movements to upscale animal movements from individuals to population levels when these are modelled mechanistically. For example a project in Yellowstone National Park, USA, utilised a mechanistic home range model to tease out the underlying processes - prey distribution and avoidance of conspecific packs - influencing movements of coyotes (*Canis latrans*), and then demonstrated how this could be used in a predictive fashion (Moorcroft et al., 2006, Moorcroft and Barnett, 2008).

The movement of each animal in this study has been modelled in detail through the T-LoCoH package, incorporating different time and space-use metrics to estimate behaviour patterns i.e. residency and duration of stay of females and males (although see section 5.4.3 for discussion on males). I believe that with use of the T-LoCoH model I have presented a viable alternative to currently employed methods of orangutan home range estimation in tropical peat swamp forest. These models are replicable for other individuals, and can be readily remodelled as additional future data is gathered. Furthermore, due to the malleability of this model, I have been able to extend this to the prediction of downstream ecological patterns resulting from orangutan movement. Specifically in this case, I have used the T-LoCoH program to model seed dispersal.

5.4.2 Implications for predicting seed dispersal

I found that, when altered for gut transit of seeds, the dispersal kernels created were similar to the 24-hour movement kernels, but the "seed kernels" had lower visitation and residency rates of seeds being deposited by defecation. Primary endozoochorous seed dispersal can be effectively predicted on the basis of where an animal, in this case an orangutan, will defecate (Wang and Smith, 2002, Cousens et al., 2010). My model predictions of defecation patterns were well supported by the X^2 test of actual defecation data, with only a small (<10%) error, suggesting that physiologically-informed T-LoCoH models should provide accurate estimates of primary seed dispersal.

Seed dispersal is a critical component of plant dispersal and ultimately plant population structure. The movement of seeds can powerfully contribute to colonisation, succession, post-disturbance recovery, and ecological restoration and management (Wang and Smith, 2002, Bascompte and Jordano, 2007, Schupp et al., 2010, Ruxton and Schaefer, 2012, Côrtes and Uriarte, 2013). Seed dispersal represents half of the gene flow pattern of plant populations (the other half being pollination, e.g. (Abrol, 2005, Krauss et al., 2009, Menz et al., 2011, McCallum et al., 2013), which is a powerful contributor to population genetic structure. As a critical element of ecological and evolutionary processes, the mechanistic estimation of passive seed dispersal has made considerable strides (Nathan et al., 2002, Wright et al., 2008, Nathan et al., 2011). The modelling of plant-animal interactions in a mechanistic fashion has, however, remained somewhat elusive, with most zoochory studies applicable only to the time and place of their training (Cousens et al., 2010, Schupp et al., 2010, Côrtes and Uriarte, 2013). This is largely due to the plethora of stochastic influences such as sex, season, reproductive patterns and ecological energetics (Nathan et al., 2008a), all of which make predication of animal movements difficult, even in a hypothetically stable ecological system (Guisan and Zimmermann, 2000, Guisan and Thuiller, 2005). In novel ecological “hyperspace” represented by areas of changing land-use and/or climate, the changing patterns of ecological cascades that influence spatial population structure are rendered unpredictable (Dormann et al., 2012, Mesgaran et al., 2014). This doesn’t make the task of creating a process based seed-dispersal model impossible, but does hinder a straightforward creation of a model that incorporates biological complexity (Cousens et al., 2010, Côrtes and Uriarte, 2013). Considering my physiologically-informed kernel models in this light suggests a few more obvious limitations.

5.5 Limitations of this study

Most pervasive amongst the limitations on my data is its internal consistency. Time and logistical constraints made continuous monitoring of the same animals difficult. In particular there is a paucity of data on adult males, compared to adult females, due to their increased space use requirements (Utami et al., 2009, Buckley, 2014), their fast movement on the ground, causing increased “loss” of males during follows compared to females, and their more labile home ranges, based on competing males, both mature (flanged) and immature (unflanged). Lack of data on unflanged males was also regrettable. This was both the most difficult age/sex cohort to locate and to follow through inaccessible environments (see 1.3 for description). As previously discussed, there are modifications to the methodology that could overcome this, such as remote animal monitoring, but application of different technology must be considered in the light of other data that would be lost in remote sensing, such as defecation locations and feeding observations.

Similarly I collected data on sub-adult females, and although the analysis of faecal samples was included in my germination studies (Chapter 4), it was not contributed to the physiologically-informed kernel modelling because there have not been any studies of gut throughput for juvenile orangutans and the two sub-adult females followed during the study period spent a portion of each day that they were followed within visible range of their mothers (who were also followed and had faeces collected) and largely nested nearby. As such my data for juvenile females are not easily distinguished as contributing independent seed shadows from their mothers. This raises interesting questions as to whether T-LoCoH could be used to unpick spatial patterns of relatedness in seed dispersal kernels, given that my two related females had substantial home range overlap, and juvenile females follow their mothers for much of the time, even when they are nominally independent. It is plausible that patterns of relatedness in plants may reflect patterns of relatedness in their dispersal vector, at least as far as orangutan-mediated dispersal is concerned.

The theoretical underpinnings of this approach should be generalizable to novel locations, as the orangutan gut doesn't differ morphologically between species and sub-species, all being large hind-gut fermenters, the gut of which is designed to process polysaccharides *via* microbial fermentation (Stevens and Hume, 1995, Caton et al., 1999b), and the T-LoCoH program allows for different space use patterns to be analysed from sets of GPS points that are date and time stamped. The nature of kernel and hullset models is that they are highly data-referential, however, and as such do not interact well with environmental data to facilitate *a priori* expectations.

5.6 CONCLUSIONS

1. Spatial movements are fundamental to how animals interact with their ecosystem and tie animal ecology to ecosystem processes, particularly to animal mediated seed dispersal, with which I was intimately concerned here.

2. My data here link animal movements with the provision of endozoochory. The approach offers a powerful tool to reliably begin predicting the primary deposition of seeds by a large, charismatic, species such as the orangutan in contiguous TPSF. This is the first objective tool of its kind in orangutan ecological research in TPSF, and the first application of T-LoCoH to ecological service provision anywhere.

3. Given the complexity of unravelling the contributory factors of this ecological service, and the potential applications of this understanding to ecological and evolutionary cascades this study represents an important step forward. I believe that this process is basal to establishing a training region for mechanistic models to make *a priori* projections of seed dispersal dynamics in novel ecosystems.

6 CONCLUSIONS AND RECOMMENDATIONS

6.1 INTRODUCTION

More than 40 years have passed since the Janzen-Connell hypothesis first made waves on the seed dispersal ‘scene’ (Janzen, 1970, Connell, 1971). Since then investigation into this theory, and others that were generated in response (Chapter 1), has brought increasing recognition to the study of seed dispersal and it’s importance. The departure of a seed from its parent and its subsequent journey towards (eventual) germination and establishment has formed the basis of a vast number of studies. Both past and present literature have examined this journey through a top-down lens by examining the dispersal agent (abiotic and biotic mechanism, see section 1.1), and also through a bottom-up viewpoint by examining the dispersal unit/seed or through a combination thereof (see section 1.1). A large part of this work has focused on the action of the agent, the animal, in seed dispersing, i.e. zoochory. However, one principal area of research that has been rare or absent has been to focus on the animal physiology, and not just its action of moving a seed, i.e. the animal physiology of endozoochory (Cousens et al., 2010, Ruxton and Schaefer, 2012, Côrtes and Uriarte, 2013).

When examining zoochory, specifically endozoochory whereby animals moves seed following ingestion, the disproportionate role of large bodied frugivores in moving seeds than smaller frugivores has been highlighted in numerous studies (Chapters 4 and 5). This holds a particularly stark relevance in landscapes where the large-bodied frugivores have been extirpated for long enough to cause reduction in plant heterogeneity e.g. (Effiom et al., 2013, Vidal et al., 2013). Data on transit time and seed germination, while basic, was heretofore quite sparse in relation to the orangutan. I have, to some extent, rectified this and collected important baseline data on seed passage and endozoochorus effects on germination for this charismatic, flagship species. This work is critical for understanding peat swamps where seeds may have only a limited time to germinate before the landscape becomes flooded (see section 1.3). Moreover, the extent of the role of tropical peat swamp forests (TPSFs) in carbon storage has only begun to be realised in recent times (Page et al., 2002, Page et al., 2011). Due to the difficult terrain and access into TPSFs, study of orangutans and their ecology was fairly recent in this habitat type, for example see (Singleton and van Schaik, 2001, Morrogh-Bernard et al., 2003, Morrogh-Bernard, 2009). There was a major knowledge gap of the ecosystem service of seed dispersal provided by the orangutan, that I have sought to rectify here. In particular, I used data from a series of gut passage experiments along with animal movement tracking to further explore the complexity of seed dispersal by orangutans in TPSF in one of the worlds largest contiguous orangutan populations (Morrogh-Bernard et al., 2003, Wich et al., 2008a).

The use of spatio-temporally informed models of animal movement and its relationship to the ecosystem service-provision of seed dispersal has not previously been attempted as far as I am aware. This work is also of chief importance in current times because it presents an example of the confluence of ecology and conservation physiology (Chapter 2; (Tarszisz et al., 2014)). Broadly, ecology is the study of the interrelationships of organisms and their environments, and conservation physiology investigates the physiological responses of organisms to anthropogenic threats and stressors that may contribute to declines in their populations (Wikelski and Cooke 2006, Franklin 2009, Seebacher and Franklin 2012, Cooke et al. 2013, Tarszisz et al. 2014). In order to even begin to assess the responses of animals, such as orangutans, to anthropogenic stressors, their ecological role in ecosystem provision, such as in seed dispersal, first needed to be established. My data, presented in Chapter 5, created an objective tool using T-LoCoH animal-range modelling to link orangutan movement in a TPSF with endozoochory provision. This tool provided a basis to overlay mechanistic niche envelope estimates over the T-LoCoH models I have created and therefore to make *a priori* predictions of seed dispersal dynamics in novel ecosystems. To that end, this study on orangutan seed dispersal provides a leap in teasing out the impact of orangutans on their environment, which in turn gets us one step closer to understanding the possible consequences of the extermination of this charismatic primate from a region of global ecological importance.

6.2 SUMMARY OF MAIN RESULTS

The main aims of this study were to devise a method of predicting the primary deposition of seeds by orangutans by endozoochory. To this end, I first studied the transit time of indigestible seed mimics though the orangutan gut in a controlled zoo setting (Chapter 3), and then followed orangutans *in-situ* in the Sabangau forest, Central Kalimantan, Indonesia, collecting faeces for germination studies (Chapter 4) and collecting detailed GPS movement data, behavioural and feeding data (Chapter 5).

6.2.1 Translocation physiology

On the surface, this chapter may not explicitly appear to fit with the synthesis of the remainder of the thesis (for reasons outlined in section 1.6). However, this chapter and subsequent publication (Tarszisz et al., 2014) are of importance and are relevant to the topic of seed dispersal for two reasons. First, this review necessarily covered a much broader subject of physiology in conservation and explored numerous aspects of animal ecophysiology (as opposed to the single aspect of endozoochory) to highlight the role that animal physiology may play in conservation science generally. Secondly, the work provides important examples of how individual animal physiology can be used not only in conservation translocations, but also in understanding the role of endangered animals for exploring translocations or other interventions necessary to support the species management, and thereby the management of the ecosystems which may depend on them. The conclusions of this project are outlined in detail in section 2.7.

6.2.2 Gut transit

I found gut transit to be considerably longer than has been previously found for the orangutan, although there was only one study for me to make a comparison from (Caton et al., 1999b). A variety of factors could have influenced this, including my study design and factors beyond my control (e.g inability to remove faeces from zoo grounds to a site with suitable equiptment to facilitate calculation of mean retention time, difficulty measuring feed intake in Taronga Zoo animals which were housed together, and other reasons which are fully documented in section 3.4.1). However, despite these limitations, when these data from my *ex-situ* studies was used to train the model created in Chapter 5, there were no significant differences between where I predicted the study animals would defecate and the actual locations of defecation (p=0.15), lending much weight to the accuracy of my measurements of seed mimic transit times (Chapter 3) as relevant to similarly sized seeds ingested by wild orangutans..

My study highlighted the potential of orangutans to provide longer long-distance dispersal from the parent plant than other mammalian frugivores, such as southern Bornean gibbons which have smaller home ranges (Section 4.4(Cheyne, 2010)) and especially with regards to large seeds, due to their very long retention times in the orangutan gut (Chapter 3). When this was combined with home range data, as in Chapter 5, the extent of the orangutans' long-distance dispersal capacity can be realised. How significant this may be to the long-term structuring of their habitat in the Sabagua TPSF requires further investigation, but the data I have provided will be central to developing these ideas and studies.

My work advanced our understanding of seed dispersal in fecaes of orangutangs by descrbing the pattern of seed mimic deposition, which differed somewhat from that seen in non-seed mimics food passage studies. Specifically, the interesting finding was that the elimination of seed mimics occurred distinct pulses, than in an evenly distributed fashion throughout every faeces. This has wider reaching implications for *in situ* situations, such as those explored in Chapters 4 and 5. Typically, for mixed-feeding herbiovres especially and also ominvores, i.e. species that have greater meal mixing, there is a spread of transit time (and mean retention time). However, I found that pulses were important. Thus much more work is needed to fully appreciate how seeds, especially larger seeds, are handled by animal guts e.g. are they selectively retained or pushed through?; are they eliminated in small, even pulses, or do they have one or two big pulse releases, followed by smaller ones, as I found (Chapter 3). We can't simply use the exisiting transit time or mean retention time for animals because these typically look at particles and fluids transport, but larger seeds and seed mimics may move through very differently. Put simply explicit species- and seed-specific studies are needed.

6.2.3 Seed germination

I had originally expected that seed travel through the orangutan gut would have been the most significant factor affecting germination, when compared to manually extracted seeds, but this was not the case. Manually extracted seeds showed the highest rates of germination over both orangutan “gut-treated” seeds and whole fruits. However, gut-passed seeds were still more successful in germinating than whole fruits, with orangutans conferring an increased survival on the plants than if they just fall from the tree, independent of the location they fall in. Thus, although it wasn’t quantitated, based on gross observation and the evidence of higher germination rate for manual extraction, orangutans might play a more important role in germination when seeds are moved by spitting whole seeds out, in addition to those passed through the gut following ingestion. Moreover, as previously stated, orangutans are the largest arboreal frugivore in TPSF. I found very large seeds (>25mm) were defecated. Seed sizes of this magnitude are unlikely to be moved intact by other arboreal frugivore guilds, representing further importance of the orangutan in this location.

6.2.4 Movement physiology

I have constructed models of orangutan movement, and then modified these on the basis of physiological processes to estimate drivers of ecological patterns. These models, being data-referential, provide limited projective capacity for novel locations or ecosystems. Hence my models represent downstream estimations from the ‘midpoint’ of an ecological cascade. My model wasn’t completely static, and thus extrapolation to other peat-swamp areas is possible, if not also to other orangutan environments. The next step towards a truly predictive model would be to use my model as the basis for training models, overlaying T-LoCoH models with mechanistic niche envelope estimates (Austin, 2007, Kearney and Porter, 2009a, Kearney et al., 2010, Kearney et al., 2012, Mesgaran et al., 2014). Such a process would make it possible to project orangutan movements and seed dispersal without *a priori* expectations in novel habitats, but would simply require details of seed passage times and orangutan movements. Nonetheless, I have shown here how successful a model of overlaying animal physiology (gut passage) and ecology (movement) can inform our understanding of plant dispersal (esp. large seeded plants) in the TPSF regions.

The TPSF is an important orangutan habitat that is considerably less studied than the dipterocarp forests of Borneo (and Sumatra) (Harrison, 2009b), and this has begun to be redressed in recent years e.g. (Rieley et al., 1997, Page et al., 1999, Jauhiainen et al., 2005, Hooijer et al., 2010, Page et al., 2011). Ecological processes differ considerably between the pet swamp and other forest habitats (Cannon et al., 2007, Harrison, 2009b). I believe that T-LoCoH provides a method to accurately predict movement, at least within TPSF, and it is therefore likely that seed dispersal cascades are going to be the same in other TPSF landscapes both within the Sabangau forest and outside of it.

It is important to recognise that I have studied only one step in the seed dispersal cycle (Wang and Smith, 2002), with secondary dispersal and/or destruction by seed predators (vertebrate and invertebrate) and scatter hording rodents having the potential to greatly alter final seed deposition (Wang and Smith, 2002, McConkey, 2005a, McConkey, 2005b). However, one of the reasons our study site was considered ideal for evaluation of primary seed dispersal was because secondary seed predation has been evaluated for several fruit trees and was found to be minimal.

Thus, unlike other forest habitats, secondary seed dispersers do not contribute greatly to seed dispersal at the NLPSF (D'Arcy and Graham, 2008). Thus our model may not represent the most powerful rate-limiting step to seed dispersal in other ecosystems, but it provides a necessary foundation from which other studies could advance these ideas, following adjustment for other study sites where secondary seeds disperse may play a greater role in altering seed shadows.

6.3 IMPLICATIONS FOR FUTURE RESEARCH

The location of the wild orangutans studied here presents unique opportunity to further develop ecophysiology-based studies of large frugivorous on ecosystem dynamics. Notably, OuTrop began began data collection at this site in 1999, at a time when the forest structure and orangutan population was quite different due to the combination of logging and forest fires (which are interconnected as outlined in section 1.3.4). Using this extensive dataset future researchers would have the opportunity to make *a priori* predictions on how forest structure might look based on my application of T-LoCoH (Chapter 5) to recorded orang movements. This could then be compared to years of data on forest phenology monitoring to evaluate its accuracy with a much larger dataset. Perhaps more importantly, by the simple act of recording where organutans defecate during ongoing data collection on daily follows, the application of my model could be tested for robustness, in addition to presenting opportunity to further train the model to provide greater accuracy. This could then be applied in a forward-manner to making predictions about forest structure, at least for tree species that orangutans ingest and defecate intact.

By training the models I developed via using larger data sets and for more animals, not only are the above appications possible, but the increased accuracy of said modelling could be make predictions about degraded TPSF habitats such as the Mega-Rice Project (mentioned briefly section 5.1.2). Application of my ecophysiologically-informed model, in combination with recorded observations of orangutans population density in degraded habitats (Cattau et al., 2015) and current population numbers, could make predictions concerning the role of orangutans in reforestatrion projects. For example, the model could, in theory, predict the minimum number of orangutans and sex-ratio required to repopulate an area with endozoochorusly dispersed trees. Alternatively, if the models predict that a given organutan population size is unable to adequatly foster reforestation, the model/s could be used to determine which plant species should become the focus of anthropogenic reforestation efforts, or other interventions promoting reforestation..

By providing proof of concept for my eco-physiologically informed model for endozoochory by orangutans, the foundation has been layed for a host of other projects concerning other seed dispersing animals. For example, my project could provide a springboard for evaluation of seed dispersal in peat swamp forest by investigationg traits of transit time, movement patterns, faecal presence and germination species (and success) of other mammalian frugivores, such as the southern Bornean gibbon and sun bears, which could lead to greater appreciation of primary seed shadows within TPSF.

It would also be worth trialling similar work in diepterocarp forests and comparing to the data gleaned in this project, with the caveat that secondary sead dispersal would likely be more prevalent and add complexity to the current picture. There is already a significant body of work of dietary intake by orangutans in dipterocarp forests, so I believe future researchers could make reasonable predictions about what will come out in the stool. A caveat to this is that germination characteristics likely to be different in non-flooded forests.

A major criticism of modelling-focused research programs is that the model represents a set of evidence-based hypotheses that are rarely tested (Tomlinson et al 2014). My internal statistical tests notwithstanding, it must be noted that I haven't provided empirical tests of my model hypotheses. The modelling of seed dispersal, whilst being a process that contributes to the population structures of the plants dispersed (McConkey, 2000, Wang and Smith, 2002, Jordano et al., 2007, Cousens et al., 2010, Côrtes and Uriarte, 2013), and the community that results (Howe and Miriti, 2000, Wang and Smith, 2002, Bascompte and Jordano, 2007, McConkey et al., 2012), is also a model prediction of maternal gene flow (Wang and Smith, 2002, Jordano et al., 2007, Hamrick and Trapnell, 2011). This also implies that measurements of maternal gene flow could be used to test these models. These could be carried out using parentage assignment of seeds collected from orangutan defecation within the bounds of the models that I have constructed, using an array of emerging next-generation technology (Pritchard et al., 2000, Chen et al., 2007, Poland et al., 2012, Grabowski et al., 2014).

6.4 FINAL CONCLUSIONS

The TPSF represents a regionally important habitat for Sabangau orangutans, but also for local human populations. Ultimately, pressures from conservation and development both impact of the TPSF and its inhabitants. However, on-going management and conservation of this and other Asian peat forests requires a deep understanding of the ecological processes that sustain these regions. One critical feature of the forests is seed dispersal by frugivores. Currently there is limited data on the relationship between these frugivores and seed dispersal beyond simple accounting of the fruits that different animals eat. Here I have sought to expand this information vase by clarifying the role of the orangutan, the largest local frugivore, in seed dissemination. I have done this using basic experimental approaches using captive orangutans (Chapter 3) and used this information to extrapolate to wild situation (Chapters 4 and 5) to develop a mechanistic, physiologically-informed model of seed movement from modern animal-range models. From this synthesis of traditional and new approaches my thesis has generated three general conclusion relevant to the field of conservation physiology, seed dispersal biology and animal movement studies:

1. Animal physiology is relevant to *in-situ* and *ex-situ* conservation, either through translocations or re-introductions, and more broadly for endangered species managemnmt to better understand their role in the ecosystem. Specific example then followed using orangs and seed dispersal.

2. Specific physiology of digestion is important for knowing which seeds are eaten and can germinate, and how they move through the animal (TTs).

3. How transit time of seeds can be overlaid on animal movement models to produce reliable predictions of seed deposition. Explicitly, I have provided a tool that is species and location specific but time independent. This is relevant for orangutans in TPSF, which although limited to a few locales, is of global importance. My work has potential application to other orangutan sites in TPSF. Furthermore, refinement and modification of my methodology has the potential to apply it to other species in TPSF, other orangutan locations, other endozoochorus species in different habitats

This work highlights the growing recognition of linking physiological features of animal to ecological phenomena and conservation. I have shown that there is a tight pattern between the animal, it’s foraging and movement decisions, consequent seed dispersal and thus germination and ecosystem servicing that feeds back into plant community structure. In this there are implications for conservation of whole communities not just species.

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APPENDIX A: DATASHEETS FROM SABANGAU FOREST ORANGUTAN FOLLOWS

Order of Activities: 1= *Feed*, 2 = *Nest* 3 = *Social / Play / Groom / Interact with Mother / Infant / Interact with Observer*, 4 = *Travel*, 5 = *Rest*

1. **FEEDING** / ***Makan***	**F**
CO-FEEDING / ***Makan bersama***	**CF**
FOOD SEARCH / ***Mencari makanan***	**FS**
Fruit:	
Fruit ripe	FR
Fruit unripe	FUM
Pulp	/ P
Seeds	/ S
Skin	/ SK
whole fruit	/ WH
unknown part	/ U
Other Foods:	
Flowers	FL
Flower bud	FLB
Mature leaves / other green vegetative matter	L
Leaf shoots	LS
Epiphytes (orchids, ferns etc.)	E
Pith of Rattan Stem	PR
Pith of Pandan	PPN

2. **NEST BUILDING** / ***Buat Sarang***	**N**
Day nest	DN
Night nest	NN
New Nest	/ NEN
Rebuilt nest	/ RB

Reused nest	/ RU

A - Branch
B - Trunk
C - Tied trees
D - top of tree
E - ground

3.7 **AGGRESSION TO OBSERVER**	**ATO**
AGGRESSION TO OTHER PERSON	**AOP**
Kiss squeak towards observer / other person	KSTO
Threatening observer / other person (shake/throw branch,etc)	THTO
Watch Observer	OOP

Pith of Liana Stem	PLS
Pith of Branch	PBR
Other Pith (suli / grasses etc.)	PI
Bark (cambium)	B
Roots	RT
Invertebrates (termites, ants, caterpillars etc.)	IV
Honey	HY
Fungi	FG
Meat (vertebrates)	M
Soil	SL
Rotten wood (no termites)	RW
Sap	SAP
Water	W
Mothers Milk	SUSU
Unknown Food	UF

6. OTHER PRIMARY ACTIVITIES	
Medication	**ME**
Fur-rubbing	/ FUR
Manipulate Object (notes: type, purpose)	**MO**
Giving Birth	**GB**
Defecate / Urinate	**DU**
Other (Take notes)	**O**

4. TRAVELLING / *Bergerak*	**T**
Treesway	TT
Clambering	CLA
Climbing / Descending	CLI
Brachiating	BR
Quadrupedal Walking	QW
Bipedal Walking	BI

5. RESTING / *Beristirahat*	**R**
Clinging ventrally (infant)	CLV
Clinging dorsally (infant)	CLD
Sitting	SI
Standing	ST
Lying Down	LD
Hanging	HA
Quadrupedal	Q
Tree / branch	/ TR
Liana	/ LI
Ground	/ G
Nest / sarang	/ N

Unknown	**U**
Lost	**L**

Order of Activities: 1= ***Feed*, 2 = *Nest* 3 = *Social / Play / Groom / Interact with Mother / Infant / Interact with Observer*, 4 = *Travel*, 5 = *Rest***

3.1 **PLAY / *Bermain***	**P**
Independent Play - Repetitive movement such as swinging around	IPS
Independent Play - Non-functional play with object	IPO
Play with other Individual	PL
with mother	/ M
with offspring	/ O
with other adult	/ A
with other infant	/ IN
with other adolescent	/ AJ

3.2 **GROOM / *Mengutui***	**G**
Self-Groom / Allogroom	SG
Groom another Individual	GA
Grooming Recipient	GR
with mother	/ M
with offspring	/ O
with other adult	/ A
with other infant	/ IN
with other adolescent	/ AJ

3.3. **SOCIAL BEHAVIOURS / *Aktifitas Sosial***	**S**
Aggressive - Dominance (use social sheet)	
Aggressive chase / charge	ACH
Aggressive contact / fighting	ACT
Aggressive kiss squeak	AKS
Aggressive snag crashing	ASC
Aggressive branch breaking / shaking / display	ABB
Submissive	SB
Ignore display	IG
Flee	FE
Mating behaviours (use social sheet)	
Male pursue female (non-aggressive chase)	NACH
Sex Investigate	SV
Mating Invitation (erect/present)	MI

3.4 **MOTHERING ACTIVITIES / *Aktifitas khusus induk***	**AKI**
Retrieve Infant	RI
Make Bridge (during travel, either using body or pulling trees together)	BD
Food-share (to infant, requested)	FSH
Give Food (not requested)	GF

3.5 **INFANT ACTIVITIES / *Aktifitas khusus anak***	**AKA**
Observe mother	OM
Observe other orangutan	OOU
Observe observer or other person	OOP
Infant Tantrum / cry	IT
Imitate Mother (not if ingesting food)	IM
Try Food (try / taste without really eating)	FT
Beg for food	BEG

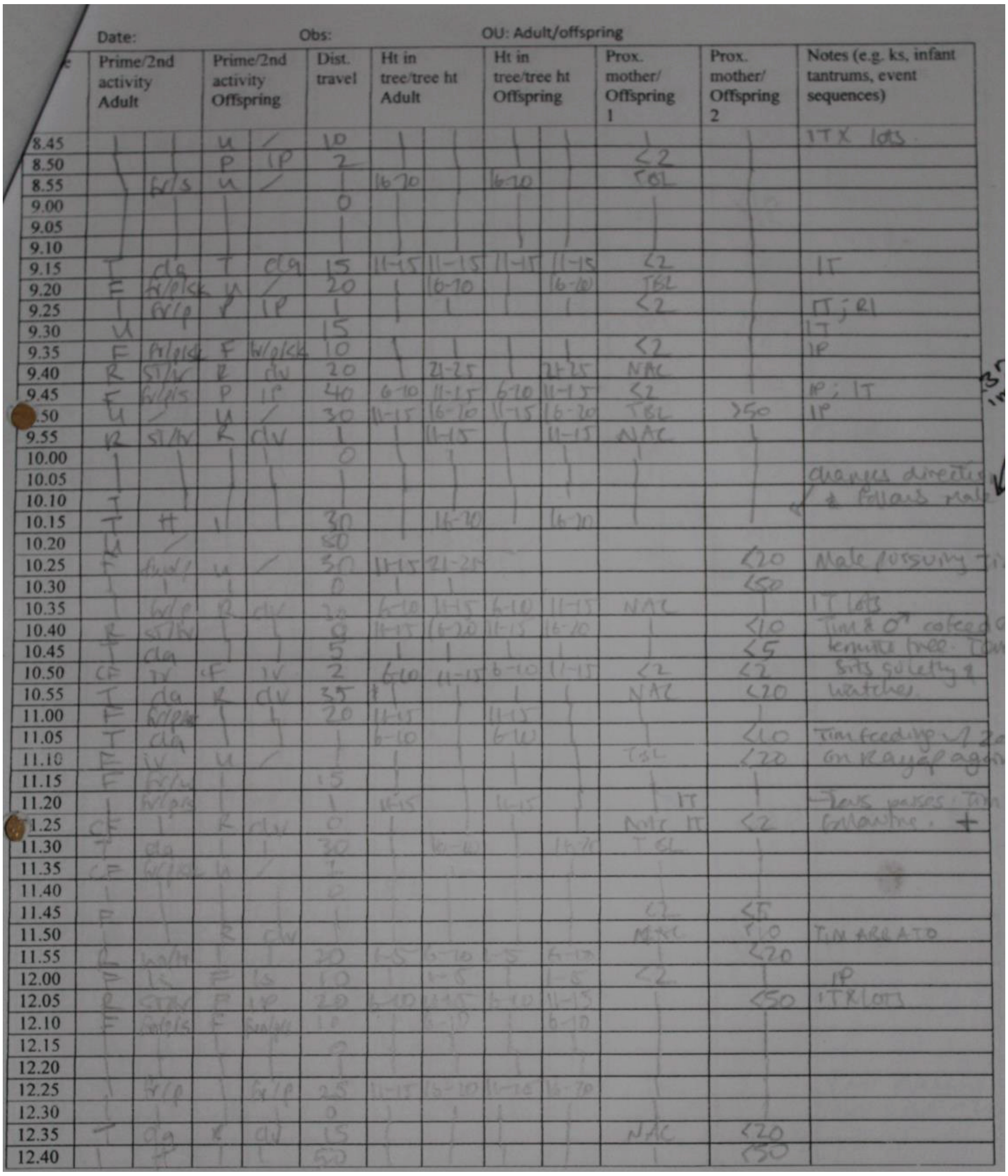
Female resist mating	FRS
Copulation attempt (primarily males)	CAT
Mating / Copulation	MA
Other Social (use social sheet)	
Touch (Non-aggressive contact)	TC
Watch (Close attention to the activities of another)	WC
Food share	FSH
Beg for food	BEG

3.6 VOCALISATION	**V**
Long-call	LC
Kiss Squeak (not to observer or AKS)	KS
Cry (not infant tantrum)	CY
Gorkum	GORK
Grumble	GRBL
Grumph	GRPH
Grunt (pig-grunt)	GRNT
Lork (female long call)	LK
Other (describe)	VO

Tolerated Food Theft (from mother or other OU)	TFT
Non-tolerated Food Theft (from mother or other OU)	NTFT
Receive Food (from mother or other individual)	RF

Proximity	
Proximity 0 (contact)	0
Proximity <2m (no contact)	<2
Proximity 2-5m	<5
Proximity 6-10m	<10
Proximity 11-20m	<20
Proximity 21-50m	<50
Proximity >50m (out of sight)	>50

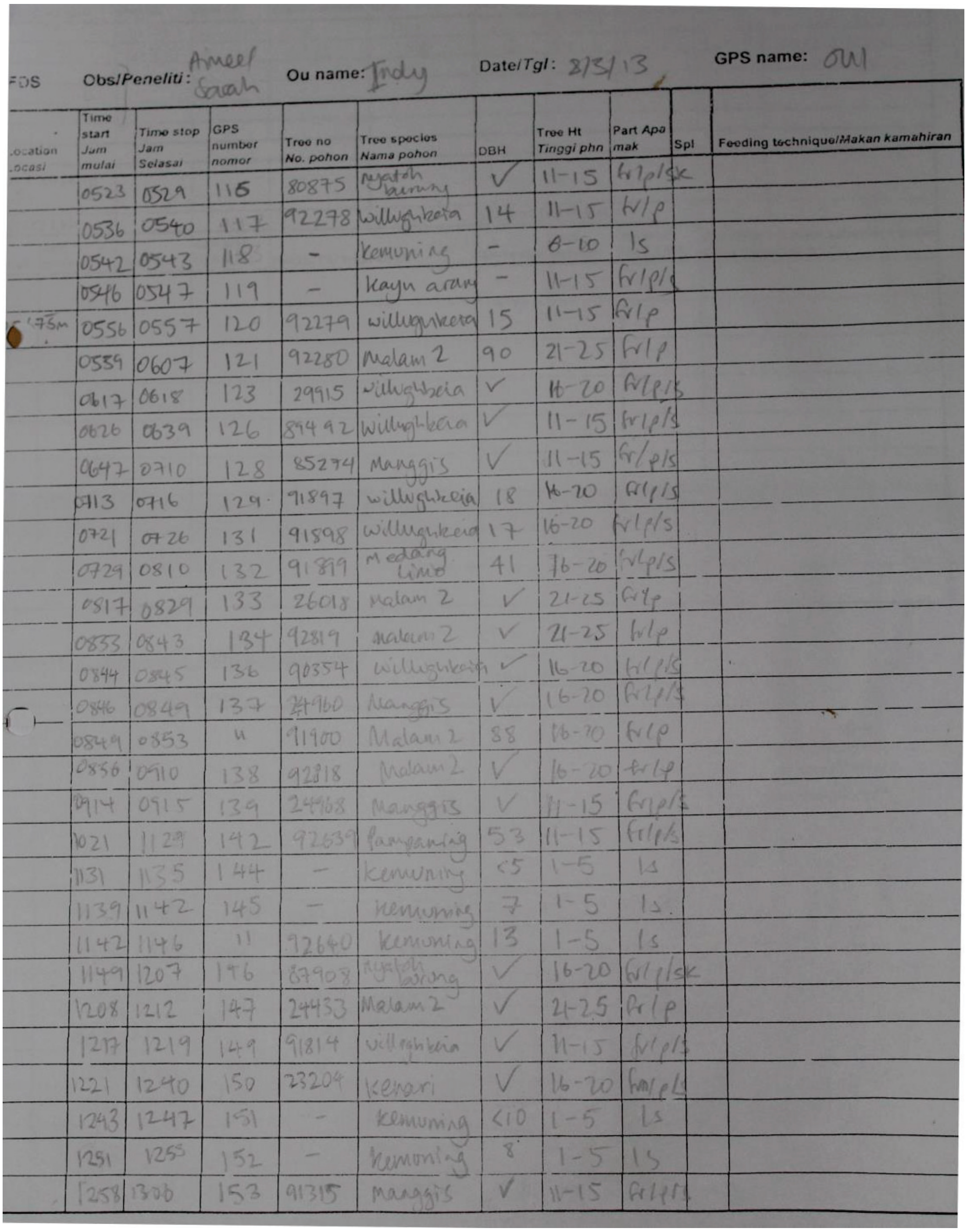
Fig A1: Behaviour ethiogram for orangutan follows



Date: Obs: OU: Adult/offspring

e	Prime/2nd activity Adult		Prime/2nd activity Offspring		Dist. travel	Ht in tree/tree ht Adult		Ht in tree/tree ht Offspring		Prox. mother/ Offspring 1	Prox. mother/ Offspring 2	Notes (e.g. ks, infant tantrums, event sequences)
8.45			u	/	10							ITX lots
8.50			P	IP	2					<2		
8.55		Gr/s	u	/		16-20		16-20		TBL		
9.00					0							
9.05												
9.10												
9.15	T	da	T	da	15	11-15	11-15	11-15	11-15	<2		IT
9.20	F	Fr/p/ck	u	/	20		16-20		16-20	TBL		
9.25	T	Gr/p	P	IP						<2		IT; RI
9.30	U				15							IT
9.35	F	Fr/p/ck	F	W/p/ck	10					<2		IP
9.40	R	ST/IV	R	dv	20		21-25		21-25	NAC		
9.45	F	Gr/p/s	P	IP	40	6-10	11-15	6-10	11-15	<2		IP; IT
9.50	U	/	U	/	30	11-15	16-20	11-15	16-20	TBL	>50	IP
9.55	R	ST/IV	R	dv			11-15		11-15	NAC		
10.00					0							
10.05												changes directi
10.10	T											& follows mal
10.15	T	H			30		16-20		16-20			
10.20	U	/			80							
10.25	F	Fr/w/l	u	/	30	11-15	21-25				<20	Male pursuing Ti
10.30					0						<50	
10.35		Gr/p	R	dv	20	6-10	11-15	6-10	11-15	NAC		IT lots
10.40	R	ST/IV			0	11-15	16-20	11-15	16-20		<10	Tim & ♂ cofeed o
10.45	T	da			5						<5	termite tree. Tim
10.50	CF	IV	CF	IV	2	6-10	11-15	6-10	11-15	<2	<2	sits quietly &
10.55	T	da	R	dv	35					NAC	<20	watches
11.00	F	Gr/p/k			20	11-15		11-15				
11.05	T	da				6-10		6-10			<10	Tim feeding w/ 2
11.10	F	iv	u	/						TSL	<20	on Rayap agai
11.15	F	Fr/w			15							
11.20		Gr/p/k				11-15		11-15		IT		Tews passes: Tim
11.25	CF		R	dv	0					NAC IT	<2	follows him. +
11.30	T	da			30		16-20		16-20	TSL		
11.35	CF	Gr/p/ck	u	/	1							
11.40					0							
11.45	F									<2	<5	
11.50			R	dv						NAC	<10	TIM ARRATO
11.55	R	w/h			20	1-5	6-10	1-5	6-10		<20	
12.00	F	ls	F	ls	10		1-5		1-5	<2		IP
12.05	R	ST/IV	P	IP	20	6-10	11-15	6-10	11-15		<50	ITX lots
12.10	F	Gr/p/s	F	Gr/p/k	10		6-10		6-10			
12.15					0							
12.20												
12.25		Fr/p		Gr/p	25	11-15	16-20	11-15	16-20			
12.30					0							
12.35	T	da	R	dv	15					NAC	<20	
12.40		H			50						<50	

Fig A2: Example of follow data sheet 08:45-12:40 (sheets run from 04:00-20:00)



FDS Obs/*Peneliti*: Amee/ Sarah Ou name: Indy Date/*Tgl*: 8/3/13 GPS name: OW

Location *Locasi*	Time start *Jam mulai*	Time stop *Jam Selasai*	GPS number *nomor*	Tree no *No. pohon*	Tree species *Nama pohon*	DBH	Tree Ht *Tinggi phn*	Part *Apa mak*	Spl	Feeding technique/*Makan kamahiran*
	0523	0529	115	80875	nyatoh burung	✓	11-15	fr/p/s	k	
	0536	0540	117	92278	willughbeia	14	11-15	fr/p		
	0542	0543	118	-	kemuning	-	6-10	ls		
	0546	0547	119	-	kayu arang	-	11-15	fr/p/s		
.75m	0556	0557	120	92279	willughbeia	15	11-15	fr/p		
	0559	0607	121	92280	Malam 2	90	21-25	fr/p		
	0617	0618	123	29915	willughbeia	✓	16-20	fr/p/s		
	0626	0639	126	89492	willughbeia	✓	11-15	fr/p/s		
	0647	0710	128	85274	Manggis	✓	11-15	fr/p/s		
	0713	0716	129	91897	willughbeia	18	16-20	fr/p/s		
	0721	0726	131	91898	willughbeia	17	16-20	fr/p/s		
	0729	0810	132	91899	medang limo	41	16-20	fr/p/s		
	0817	0829	133	26018	malam 2	✓	21-25	fr/p		
	0833	0843	134	92819	malam 2	✓	21-25	fr/p		
	0844	0845	136	90354	willughbeia	✓	16-20	fr/p/s		
	0846	0849	137	24960	Manggis	✓	16-20	fr/p/s		
	0849	0853	"	91900	Malam 2	88	16-20	fr/p		
	0856	0910	138	92818	Malam 2	✓	16-20	fr/p		
	0914	0915	139	24968	Manggis	✓	11-15	fr/p/s		
	1021	1129	142	92639	pampaning	53	11-15	fr/p/s		
	1131	1135	144	-	kemuning	<5	1-5	ls		
	1139	1142	145	-	kemuning	7	1-5	ls		
	1142	1146	"	92640	kemuning	13	1-5	ls		
	1149	1207	146	87908	nyatoh burung	✓	16-20	fr/p/s	k	
	1208	1212	147	24433	Malam 2	✓	21-25	fr/p		
	1217	1219	149	91814	willughbeia	✓	11-15	fr/p/s		
	1221	1240	150	23204	kenari	✓	16-20	fr/p/s		
	1243	1247	151	-	kemuning	<10	1-5	ls		
	1251	1255	152	-	kemuning	8	1-5	ls		
	1258	1306	153	91315	manggis	✓	11-15	fr/p/s		

Fig A3: Example of feeding data sheet

GPS Lembar 3

Date:_____________

Observer/peneliti:______________ Nama GPS__________________ Ou nama: ________________

Seed collection table

Seed event key

K = kotoran (defecation)

S = ________ (spit)

F = _______ (fallen)

Lokasi key

HU = Hummock [A hillock, knoll, or mound]

HL = Hollow

Time (Jam)	**GPS co-ordinate**	**Seed event (K, S, F)**	**Lokasi (hummock, hollow)**	**Canopy closure (%)**	**Total or partial kotoran collected ? (T/P)**	**Weight (g)**

Food carrying

Time (Jam)	**Tree species (of initial tree/seeds)**	**GPS co-ordinates (from-to)**	**Lokasai seeds dropped (hummock or hollow)**	**Canopy cover % (where dropped)**

Fig A4: Example of defecation collection sheet

APPENDIX B: (I) PUBLISHED VERSION OF CHAPTER 2 AND (II) SUPPLEMENTARY MATERIAL FOR CHAPTER 2

(I) PUBLISHED PAPER

Conservation Physiology
Volume 2 • 2014
10.1093/conphys/cou054
SEB Society for Experimental Biology

Review

Physiology in conservation translocations

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Conservation translocations aim to restore species to their indigenous ranges, protect populations from threats and/or reinstate ecosystem functions. They are particularly important for the conservation and management of rare and threatened species. Despite tremendous efforts and advancement in recent years, animal conservation translocations generally have variable success, and the reasons for this are often uncertain. We suggest that when little is known about the physiology and wellbeing of individuals either before or after release, it will be difficult to determine their likelihood of survival, and this could limit advancements in the science of translocations for conservation. In this regard, we argue that physiology offers novel approaches that could substantially improve translocations and associated practices. As a discipline, it is apparent that physiology may be undervalued, perhaps because of the invasive nature of some physiological measurement techniques (e.g. sampling body fluids, surgical implantation). We examined 232 publications that dealt with translocations of terrestrial vertebrates and aquatic mammals and, defining 'success' as high or low, determined how many of these studies explicitly incorporated physiological aspects into their protocols and monitoring. From this review, it is apparent that physiological evaluation before and after animal releases could progress and improve translocation/reintroduction successes. We propose a suite of physiological measures, in addition to animal health indices, for assisting conservation translocations over the short term and also for longer term post-release monitoring. Perhaps most importantly, we argue that the incorporation of physiological assessments of animals at all stages of translocation can have important welfare implications by helping to reduce the total number of animals used. Physiological indicators can also help to refine conservation translocation methods. These approaches fall under a new paradigm that we term 'translocation physiology' and represent an important sub-discipline within conservation physiology generally.

Key words: Conservation physiology, conservation translocation, monitoring, vertebrate

Editor: Steven Cooke

Received 10 March 2014; Revised 23 October 2014; accepted 30 October 2014

Cite as: Tarszisz E, Dickman CR, Munn AJ (2014) Physiology in conservation translocations. *Conserv Physiol* 2: doi:10.1093/conphys/cou054.

Introduction

The translocation, reintroduction and introduction of species to areas within their former range (or to areas considered appropriate or amenable to their survival and persistence) are entrenched and popular methods in conservation biology (Osborne and Seddon, 2012). These methods serve to improve the conservation status of focal species or restore ecosystem functions and processes (IUCN/SSC, 2013). Such deliberate transfers to promote conservation outcomes are collectively termed 'conservation translocations', and include any movement of animals (or plants) for conservation purposes (Osborne and Seddon, 2012; Seddon *et al.*, 2012; IUCN/SSC, 2013). These transfers can be classified further into population restorations and conservation introductions (Seddon, *et al.*, 2012; IUCN/SSC, 2013); see Table 1. Population restorations involve either reinforcement of existing populations by movement and release of conspecifics or reintroduction of extirpated animals into their indigenous range (IUCN/SSC, 2013). Conservation introductions involve moving organisms outside of their indigenous ranges either to avoid extinctions (i.e. assisted colonization; Thomas, 2011; Seddon *et al.*, 2012; IUCN/SSC, 2013) or because the organisms perform a specific function within the ecosystem, i.e. ecological replacement (Armstrong and Seddon, 2008; Seddon, *et al.*, 2012; Seddon and van Heezik, 2013; IUCN/SSC, 2013); examples of the latter species include ecosystem engineers and apex predators (Letnic *et al.*, 2012; Ritchie *et al.*, 2012; Seddon and van Heezik, 2013).

In recent years, there has been an exponential increase in the number of conservation translocation projects worldwide (Seddon *et al.*, 2007), and there have been several excellent reviews of reintroduction/translocation success in particular taxa (e.g. Griffiths and Pavajeau, 2008; Finlayson *et al.*, 2010) and of directions in the field more generally (Ewen *et al.*, 2012a). However, despite this increase in conservation translocation research, much of this work has focused on more easily assessable aspects of translocation protocols, such as release techniques, or on readily measured demographic aspects, such as short-term survival rates. Consequently, less tractable but potentially critical aspects of the translocation process remain uncertain. One key factor that could significantly affect the success of translocations and improve protocols concerns the biology of individual animals, and specifically, their physiological state, both pre- and post-release. Without doubt, the wellbeing of individual animals in translocations is well considered by practitioners, but within the published literature it is apparent that animal physiology is often under-represented as a feature of direct concern. Deeper consideration of the physiology of individuals and populations from a conservation perspective falls within the domain of the emerging discipline of conservation physiology (Wikelski and Cooke, 2006; Chown and Gaston, 2008; Cooke and O'Connor, 2010).

To evaluate the potential for physiology to inform and enhance conservation and translocation science, we aim here to consider the factors that promote success in conservation translocations and to focus on the role that conservation physiology might play. Thus, our review builds on concepts addressed by Fischer and Lindenmayer (2000) and Seddon *et al.* (2007), but adds new dimensions that have been little addressed hitherto in the published literature. To focus the review, we consider only studies of terrestrial vertebrates and aquatic mammals; these groups dominate in translocation studies and therefore offer the greatest opportunity to explore the role of conservation physiology in improving translocation success. We note that comprehensive translocation planning typically incorporates aspects of species' natural history (Pereira and Wajntal, 1999; Ottewell *et al.*, 2014), resource and environmental requirements (Rittenhouse *et al.*, 2008), as well as economic, social and cultural needs (e.g. Williams *et al.*, 2002). Here, we emphasize the evaluation of species' biological requirements as being imperative for the success of translocation programmes, with particular focus on physiology.

Aims of the review

Our specific aims are as follows: (i) to review conservation translocation papers for the presence or absence of quantitatively assessed physiological parameters; (ii) to assess the outcomes of conservation translocation studies; and (iii) to identify future directions for conservation translocation biology, with an emphasis on the role of conservation physiology.

Physiology in conservation translocations

Definitions of conservation physiology vary among practitioners, but most agree that the discipline investigates the physiological responses of organisms to anthropogenic threats and stressors that may contribute to declines in their populations (Wikelski and Cooke, 2006; Franklin, 2009; Seebacher and Franklin, 2012; Cooke *et al.*, 2013) and that it provides a link between ecological patterns and environmental change (Seebacher and Franklin, 2012; Cooke *et al.*, 2013). Much as the definitions of conservation translocation have evolved to their current state, conservation physiology also has broadened in scope to identify and resolve problems that exist in populations, with increased inclusiveness of all taxa. The discipline also seeks to expand to identify problems at levels of still broader interest to conservation practitioners, including species, communities and ecosystems (Cooke *et al.*, 2013).

Physiology, when applied to conservation management of populations, provides vital data on the causal mechanisms that underlie current population problems (Carey, 2005; Wikelski and Cooke, 2006; Franklin, 2009) and also has the potential to illuminate previously neglected or concealed conservation issues (Chown and Gaston, 2008). Multiple factors influence conservation translocations, with interconnections between behaviour, physiology and ecology that can determine population survival (Tracy *et al.*, 2006). This complexity is well illustrated in trials on resource acquisition by desert tortoises, which show how physiological processes interact with animal ecology and behaviour and are integral to the assessment of conservation status (Tracy *et al.*, 2006; Drake *et al.*, 2012; Cooke *et al.*, 2013). In other examples, physiological approaches are being increasingly used to identify and reduce the effects of disease in population declines (Blaustein *et al.*, 2012), to increase the sustainability of fisheries management (Cooke *et al.*, 2012), to enhance understanding of seed dispersal by animals (Ruxton and Schaefer, 2012) and even to improve conservation policy (Cooke and O'Connor, 2010). The call for use of physiology in restoration ecology was given significant evaluation in a review (Cooke and Suski, 2008) largely in relationship to plant taxa and restoration of degraded habitats; however, mention of vertebrate taxa and incorporation of physiological assessment tools such as bio-monitoring, use of stable isotopes and doubly labelled water was called for, with a note of the increased convenience of these tools.

In terms of conservation science more generally, interest in conservation physiology arises because it offers an opportunity to predict the responses of organisms to environmental change (Carey, 2005; Wikelski and Cooke, 2006; Franklin, 2009; Kearney *et al.*, 2010; Seebacher and Franklin, 2012), thereby informing actions and policies that might improve conservation outcomes. With the current challenge of climate change and its potentially catastrophic impacts on biodiversity in many regions, the playing field for reintroduction biology has moved. As emphasized by leading texts and articles (e.g. Thomas, 2011; Osborne and Seddon, 2012; Bekoff, 2013), climate change has altered the context of conservation translocations because conditions often cannot be restored to 'the way they were'; the original conditions simply no longer exist. Therefore, it is increasingly important to understand the physiological tolerances of vulnerable and endangered species in order to identify whether they have the physiological capability to adapt to changing climates or to respond to other anthropogenic modifications to the environment (Kearney and Porter, 2009; Smith, 2011).

It is apparent from these and other considerations that physiological data are important in the development of conservation protocols to improve rates of success in conservation translocations. This is particularly relevant with respect to understanding species' demographic performance and predicting the possible impacts of climate change and other environmental disturbances. Thus, we introduce the term 'translocation physiology' to describe the explicit evaluation of physiological parameters throughout the translocation process. This includes, but is not limited to, pre-release, the translocation event and post-release monitoring.

Translocation physiology

The adoption of physiology generally into conservation is an implicit acknowledgement of a previous deficit in conservation practice, especially—as we contend here—in reintroduction biology. Translocations are generally acknowledged as unavoidably stressful events (Dickens *et al.*, 2010; Parker *et al.*, 2012; Seddon, *et al.*, 2012). The translocation itself is likely to be highly distressing, from capture and handling to transport to release (Dickens *et al.*, 2010; Parker *et al.*, 2012). In an elegant example of this, Waas *et al.* (1999) used simulated translocation events for red deer (*Cervus elaphus*; including catching/herding, pre- and post-transport confinement, loading on and off vehicles and road travel) and made detailed physiological evaluations of heart rate, haematocrit, cortisol and biochemical parameters, such as blood sodium, lactate, glucose and magnesium. Even after habituation of animals to the simulated translocation, the real event remained stressful. Animals showed consistently increased heart rates and concentrations of blood lactate and cortisol (Waas *et al.*, 1999); elevated cortisol or corticosterone, depending on species, is a typical response to physiological stress (Romero, 2004, Romero and Butler, 2007). Immediate post-release mortality can have significant impacts on the success of population establishment (Armstrong and Seddon, 2008; Armstrong and Reynolds, 2012; Parker *et al.*, 2012).

Understanding and minimizing animal stress in translocations is clearly important (Dickens *et al.*, 2010; Parker *et al.*, 2012), and current literature rightly recommends that appropriate husbandry and release techniques be considered alongside knowledge of the biology and ecology (abiotic and biotic requirements) of any individuals that are to be translocated (Parker *et al.*, 2012; IUCN/SSC, 2013). This is a key recommendation of the IUCN guidelines for translocations, and emphasizes further that understanding the physiological status of both individuals and populations is a necessary and vital component of the translocation process.

Physiology enables a more in-depth understanding of individuals, populations and communities and can assist in discerning potential responses of organisms to environmental change (Cooke *et al.*, 2013). As knowledge of physiology elucidates cause-and-effect relationships (Cooke *et al.*, 2013), its usefulness in pre- and post-translocation planning cannot be overstated. Translocation physiology can assist in all stages of the translocation process in the following ways: assessing the consequences of outbreeding and inbreeding depression; improving understanding of immune responses to captivity and release stressors and their consequences (e.g. fitness, disease expression); testing the suitability of habitats for populations; identifying threats that might cause success or failure; identifying optimal habitats; linking fitness of organisms to environmental conditions; and providing credibility and greater certainty about the process (Cooke *et al.*, 2013).

Review of literature

For our review of conservation translocations, we separated research papers into four distinct categories: pre-release; conservation translocation; post-release; and reviews. 'Pre-release' denoted any study dealing only with preparation for a reintroduction and not the act of the reintroduction itself. 'Conservation translocation' denoted any study detailing the process and execution of one or more conservation translocation projects. 'Post-release' denoted any study that dealt with the events following a translocation, but not the event itself. 'Reviews' are self-explanatory. Conservation translocation papers alone were evaluated for their inclusion of physiological evaluation because neither the pre-release nor the post-release papers covered the translocation event; these were noted but not used in our attempt to review the physiological factors that were considered in primary works. Occasionally, a paper covered more than one category. For example, Van Manen *et al.* (2000) described a number of releases of red wolves (*Canis rufus*), as well as pre-release preparation and post-release information in what was almost a review of the subject. In these cases, if translocation events were presented with other information, the paper was considered a 'conservation translocation' study and not placed in other categories. To meet the first aim of our review, we then scored papers that had used physiology as part of their protocol as well as other factors, such as genetics, behaviour, habitat and whether key threatening processes had been considered in the translocation process (Table 1). A full list of papers evaluated is available online as supplementary material.

Our intention was not to obtain an exhaustive summary of every translocation publication in the last decade, but rather to collate papers that would provide an indication of general trends in the field. Due to the marked influence of the review by Fischer and Lindenmayer (2000), we carried out a detailed search for relevant studies in the same 12 international journals that were used in this earlier work. We focused on the years 2000–2010. These 12 journals, as well as *Trends in Ecology and Evolution*, were searched issue by issue for articles containing the words translocation, reintroduction or augmentation, and all papers concerning mammals, birds, reptiles and amphibians were considered (fish and invertebrates were beyond our scope). Using Google Scholar, we entered the same search terms as for our target journals and collated studies published in the 10 years up to 2010. We did not include studies that had not been peer reviewed, nor did we search for studies that had been cited in published papers but had been overlooked in Google Scholar. We assumed that our search methods were unbiased or at least not biased in any systematic way and that the years we reviewed provide a reasonable sample of recent reintroduction studies.

Rehabilitation does not fall under the definition of conservation translocation according to the current IUCN/SSC guidelines (IUCN/SSC, 2013) because the release is considered to be for the welfare of individual animals rather than for organizations at higher levels, such as populations. We did, nonetheless, include three exceptional rehabilitation studies that were population based and thereby fulfilled our criteria for adequate and quantitative reporting of reintroduction results (Goldsworthy *et al.*, 2000; Manire *et al.*, 2003; Molony *et al.*, 2006).

We acknowledge that published papers designed to answer specific questions may not be representative of entire translocation projects, as opposed to translocation proposals and reports that are submitted to conservation agencies, and thus there may be inherent difficulties in subjecting these to meta-analysis or other forms of quantitative review (D. Armstrong, personal communication). However, as peer-reviewed published literature is often the most readily accessible and primary source of background information on new translocation projects, we view the papers we examined as being broadly representative of the practices used currently by scientists involved in conservation translocations. To ensure the robustness of our approach and conclusions, we also consulted two influential recent works synthesizing current trends and past and present data on reintroduction and translocation biology (Ewen *et al.*, 2012a; Bekoff, 2013). We also consulted the most recent reintroduction guidelines provided by the IUCN (IUCN/SSC, 2013).

Evaluation of success

With regard to assessment of the outcomes of conservation translocation studies (Aim ii), given that each project evaluated had its own definition of success and was carried out over a different time scale, we attempted to create specific criteria to determine the success of individual translocation projects in a repeatable and rigorous manner. We considered each study on its own merits. In the first instance, we evaluated success or otherwise of a translocation project based on each study's self-evaluation. However, some studies, while considering their project a success, failed to meet their stated aims or, in our reading of the results, failed to state reasonable reasons for considering the project a success. Therefore, in addition to self-reported success and failure, we introduced a binary category for projects deemed successful, this being to denote 'high' or 'low' success.

High success was determined if at least one of the following criteria was met.

(i) The translocation confirmed that a stable and/or increasing population was established during the study period.

(ii) The project achieved its specified aims. For example, a project evaluating the effects of pre-release experience of elk (*Cervus elaphus*) with wolves (*Canis lupus*) and

Table 1: Definitions of terms used in reintroduction projects (based on IUCN/SSC, 2013)

Conservation translocation: the intentional movement and release of a living organism where the primary objective is a conservation benefit
Population restoration: any conservation translocation within indigenous range. This comprises the following two activities:
(i) **reinforcement:** the intentional movement and release of an organism into an existing population of conspecifics; and
(ii) **reintroduction:** the intentional movement and relase of an organism inside its indigenous range, from which it has disappeared
Conservation introduction: the intentional movement and release of an organism outside its indigenous range. The following two types are recognized:
(i) **assisted colonization:** the intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species; and
(ii) **ecological replacement**: the intentional movement and release of an organism outside its indigenous range to perform a specific ecological function

human hunters showed that experienced animals survived longer post-release, which was the specified aim (Frair *et al.*, 2007).

(iii) The project initially showed poor results, but improved them by altering protocols over time using information gleaned in earlier years (if releases took place over multiple years), i.e. there was some degree of adaptive management.

Low success was determined if at least one of the following criteria was met.

(i) The study reported high success but failed to show conclusive results. For example, in a black bear (*Ursus americanus*) translocation that measured two different release techniques, >50% of study animals died or were unable to be included in the analyses due to lack of knowledge of their whereabouts (Eastridge and Clark, 2001).

(ii) A potentially threatening problem was present and could not be resolved, such as low genetic diversity due to small founder numbers or the presence of a key threatening process.

(iii) Catastrophic events occurred and significantly affected the project's results. For example, during the Iraq war the flight of Bedouins from Kuwait and Iraq to Jordan led to a doubling of the livestock population in the host country. This led to overgrazing, reduced water supplies and higher prevalence of disease and parasites in Jordanian habitats, compromising the translocation of oryx (*Oryx leucoryx*) as a result (Harding *et al.*, 2007).

(iv) The sample size was too limited to have resulted in a self-sustaining population as, for example, in the translocation of a single orang-utan (*Pongo abelii*) to Sumatra (Cocks and Bullo, 2008).

(v) There was limited scope for population expansion and persistence. For example, despite the establishment of a reproducing population of lions (*Panthera leo*) in Phinda private game reserve, the population remained small and isolated, with little scope for connection to other isolated populations and for addressing the long-term conservation problems of the species (Hunter *et al.*, 2007).

(vi) The time of monitoring was too short to span even one breeding season. For example, a release of Pere David's deer (*Elaphurus davidianus*) in China spanned <6 months of monitoring (Hu and Jiang, 2002).

Results

Literature review

We reviewed 232 publications, of which 44 described pre-release protocols, 68 described post-release protocols and 120 reported conservation translocations, which are our primary focus below. The conservation translocation studies describe the translocation process in full, including pre-release factors, the translocation event itself and post-release monitoring. There were also 40 reviews. Traditional physiological factors were noted in 9% of the translocation studies. In comparison, 33% of the translocation studies considered genetics, 78% described behaviour and >80% considered habitat factors or key threatening processes associated with the translocation attempt (Table 2).

Physiology in conservation translocations

Detailed review of the 120 studies reporting conservation translocations suggested that physiological considerations could be broken down into four broad categories, i.e. condition, nutrition, health and 'traditional' physiology, each with two or more subcategories (Table 2). In total, 60% of studies (n=72) reported the condition of animals that were being translocated and, of these, 86% were rated as successful (Table 2). Twenty-six studies (22%) noted whether animals showed distress reactions; 81% of these demonstrated success, with 62% of this subset rated as having highly successful outcomes (Table 2). Different approaches to assessing distress tended to be used on different vertebrate groups. For example, distress caused by handling and transportation was often considered in avian translocations, such as those involving the black-faced honeycreeper (*Melamprosops phaeosoma*; Groombridge *et al.*, 2004) and sharp-tailed grouse (*Tymphanchus phasianellus columbianus*; Coates *et al.*, 2006), and also in some involving mammals (e.g. red howler monkey, *Alouatta seniculus*; Richard-Hansen *et al.*, 2000). In these studies, researchers generally attempted to minimize the time that animals spent in transit, met their resource needs while they were being transported and ensured that benign weather conditions prevailed post-release. In contrast, while reactions to handling were mentioned in some projects that translocated reptiles, these ectotherms generally were considered to be most vulnerable to thermoregulatory distress. As such, housing during transit was usually the dominant factor that was considered as, for example, in a translocation study of the three-toed box turtle (*Terrapene carolina triunguis*; Rittenhouse *et al.*, 2008).

Body condition was used as an indicator of physiological state in 46 studies (38%), more frequently than any other physiological parameter. Although body condition may not be a direct measure of organism function, it is often assumed to correlate with individual 'fitness' (Marshall *et al.*, 1996), at least with regard to the ability of an animal to withstand potential stressors, such as immunological, nutritional or thermoregulatory challenges. Conservation translocation studies that considered body condition generally had high success; most used either qualitative indices of condition, such as visual appearance, or more invasive but direct estimates of body fat content (e.g. Woolnough *et al.*, 1997). Some studies also employed simple but quantitative indices based on regressions of body mass on linear measures of body size (e.g. body, limb or foot length; Krebs and Singleton, 1993; Schulte-Hostedde *et al.*, 2005). Here, relatively

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Table 2: Detailed breakdown of biological and environmental factors considered in 120 reintroductions of terrestrial vertebrates and aquatic mammals, showing numbers of projects rated as failures, successes and, in the latter category, high and low success

Biological or environmental factor	Total studies	Failures	Successes	Low success	High success
Genetics	39	3	36	15	21
Behaviour	93	12	81	32	49
Physiology					
Traditional physiology					
Stress physiology	3	1	2	1	1
Water, micronutrients	3	0	3	1	2
Thermoregulation	3	1	2	0	2
Immunoecology	2	1	1	1	0
Condition					
Distress	26	5	21	8	13
Body condition	46	5	41	13	28
Nutrition					
Wild food	12	0	12	5	7
Commercial food	11	5	6	2	4
Combination	19	1	18	5	13
Supplementary feeding	27	5	22	5	17
Other/unknown	18	1	17	8	9
Health					
Veterinary/health check	37	5	32	14	18
Vaccinations	7	1	6	5	1
Parasite management	15	3	12	6	6
Quarantine/disease screen	26	1	25	9	16
Unknown	2	1	1	0	1
Habitat					
Edge of former range	6	3	3	2	1
Core of former range	50	5	45	14	31
Combination of edge and core	1	0	1	0	1
Not reported	53	10	43	19	24
Predator-proof fence	9	0	9	3	6
Substitution	4	0	4	0	4
KTP					
Absent	49	3	46	14	32
Present	49	9	40	17	23
Unknown	22	5	17	7	10

See main text for definitions of 'high' and 'low' success.

massive individuals lying above the regression line (i.e. with positive residuals) are considered to be in good condition and those below the line to be in poor condition. These residual-based indices of body condition need to be interpreted cautiously because body mass can fluctuate markedly over short periods, may not correlate well with other measures of body condition, such as body fat (Krebs and Singleton, 1993) and may vary as animals grow (Peig and

Green, 2010). However, provided that these limitations are borne in mind, the high success of conservation translocation studies using residual-based indices (Table 2) suggests that this approach to judging condition has considerable utility.

Food and nutrition were evaluated in many translocation protocols (Table 2), with researchers providing food during the reintroduction process or as supplementary fare after animals had been released. All projects that fed animals natural or wild-type foods as part of their translocation (10%) were considered successful, with 58% of these deemed highly successful (Table 2). Studies where reintroduced animals were fed a combination of wild and commercial-type food (16%) had a similar high success rate of 95%, with 72% of these deemed highly successful, whereas those using only commercial-type food (9%) had a more mixed success rate of 54% (Table 2). Supplementary food after release was provided in 27 studies, generally as part of 'soft' release protocols that attempted to ensure that animals would not go hungry as they made the transition to eating naturally available foods (e.g. Richards and Short, 2003; Britt *et al.*, 2004; Brightsmith *et al.*, 2005). It is of note that 18 reintroduction studies provided food during the transfer or release stages but failed to specify the type of food offered or how it was provided. Despite these deficiencies in reporting, the overall results suggest that appropriate food is important during and after animals have been released and that success may be increased if natural foods are available to translocated animals before their release to the wild.

Using healthy animals would seem an obvious prerequisite for conservation translocation success (Stevenson and Woods, 2006), but health was mentioned in only half the studies we examined. Several studies advocated the need to make general heath checks prior to animals being released, both to maximize the survival chances of individuals and to minimize the potential for disease transfer to extant, resident populations of conspecific or congeneric species (Leighton, 2002; Mathews *et al.*, 2006).

'Traditional' physiological factors were considered in only 11 (9%) of the translocation studies reviewed (Table 2) and included assessments of stress using glucocorticoid hormone assays (Manire *et al.*, 2003; Pinter-Wollman *et al.*, 2009; Zidon *et al.*, 2009), as well as more direct evaluations of water use (Mathews *et al.*, 2006; Field *et al.*, 2007), micronutrient balance (Lapidge, 2005) and thermoregulation (Hardman and Moro, 2006; Rittenhouse *et al.*, 2008; Santos *et al.*, 2009). These studies were largely successful. Despite their emergence in other areas of wildlife ecology, such as in life-history studies (Martin *et al.*, 2006a, b), immunoecological approaches were used in only two of the translocation projects we evaluated. One study considered immunoecology tangentially by using the haematophil/lymphocyte ratio (see also heterophil/lymphocyte ratios) as an indicator of stress (Groombridge *et al.*, 2004), while the other used lymphocyte proliferation to evaluate immune function (Manire *et al.*, 2003). Haematological parameters were measured in a translocation study of the water vole (*Arvicola amphibius*, formerly *Arvicola terrestris*; Mathews *et al.*, 2006), but only erythrocytes were used to assess vole condition.

Discussion

Conservation translocations and reintroduction biology are proceeding on a range of fronts, with varied protocols and different biological and environmental factors contributing to project success. In the sections below, we review some of the biases and weaknesses of conservation translocation projects, focusing particularly on physiology, and we identify some of the key design and methodological issues that influence the likelihood that a project will succeed.

Translocation physiology: what can it offer?

The disciplines of behaviour, genetics and ecology are well-recognized elements in animal conservation biology and conservation translocation programmes, and their importance is clearly appreciated (Griffith *et al.*, 1989; Fischer and Lindenmayer, 2000; Letty *et al.*, 2007; Seddon, *et al.*, 2007; Groombridge *et al.*, 2012; Jamieson and Lacy, 2012; Keller *et al.*, 2012). However, a key disciplinary area that has received less attention in conservation translocation projects is that of physiology, especially those aspects of the discipline that can be considered relatively 'traditional' (Table 2). In this section, we focus on animal physiology in the pre-release and post-release design of conservation translocation projects and highlight how it can offer important insights to improve both initial and ongoing translocation success.

Pre-release planning

Setting *a priori* hypotheses provides opportunities to answer targeted questions concerning the species of interest, to test the importance of predefined factors that may influence translocation success and to distinguish the relative merits of different translocation protocols (Dickman, 1996; Armstrong and Seddon, 2008).

Recent literature on reintroduction and translocation biology (Ewen *et al.*, 2012a; Bekoff, 2013) emphasizes the need for more quantitative and rigorously assessable monitoring, which includes the planning or 'risk-assessment' phases. For example, when considering habitat suitability for a reintroduction it is easy to assume that historical locations indicate suitable habitat, but in fact this can be an erroneous and misleading indicator of habitat preferences (Osborne and Seddon, 2012). Furthermore, habitat does not encompass only vegetation, but should include all the biotic factors associated with it (Osborne and Seddon, 2012). Physiology has the ability to define cause-and-effect relationships and can therefore be used to adapt conservation management (Cooke *et al.*, 2013). In terms of habitat, for example, physiological stress and condition parameters demonstrate how landscape patterns affect species persistence (Ellis *et al.*, 2012). Osborne and Seddon (2012) recognize that process-based species distribution modelling requires knowledge of physiological limits, but the authors also point out that 'they are often not available'. As suites of physiological monitoring tools become more sophisticated, understanding of physiological limits should increase and, in turn, greatly enhance the conservation translocation process.

Release

The release phase of the translocation process has received the greatest physiological focus in peer-reviewed papers and in the current reintroduction literature (Parker *et al.*, 2012; Seddon and van Heezik, 2013). We feel that acknowledgement of the stress of translocation is crucial, but thus far only stress hormones have been examined widely. Quantitative analysis post-release of other physiological factors may give a more robust picture of the effects of translocation on animals. The importance of understanding an animal's basic ecology and biology is well recognized (IUCN/SSC, 2013), but the need for physiological indices is less well established. If the aim is to reduce potential stressors then it follows that first we must fully understand the extent of stress on translocated individuals by collecting physiological indices as baselines before, during and after the translocation process.

Post-release monitoring: establishment and persistence

In order to gauge outcomes of reintroductions, post-release monitoring is required. It therefore follows that the duration of post-release monitoring should be an important factor when considering success. The establishment of persistent and self-sustaining populations is one of the ultimate aims of conservation translocations (Parker *et al.*, 2012) and, as such, it is necessary to determine whether translocated animals can carry out the following: (i) establish initially; (ii) reproduce successfully; and (iii) persist long term at the translocation site (or at the least persist independently following release, even if they disperse to different locations). Despite this, much of the work we reviewed focused on assessing outcomes (i) and (ii), with few projects continuing to monitor for long enough to judge long-term establishment under outcome (iii). For example, most projects (72%) sustained monitoring for between 1 month and 5 years (see online supplementary material). This period is unlikely to cover more than a few generations for any vertebrate species and perhaps reflects other imperatives, such as the period over which interest or funding is available (e.g. many national and international funding schemes, such as the Australian Research Council, US National Science Foundation, provide grant funds for 2–5 years). Consequently, most projects that putatively demonstrated outcomes (i), (ii) and (iii), and thus self-evaluated as successful, were somewhat limited in their post-monitoring scope.

Current reintroduction literature (Ewen *et al.*, 2012a; Seddon and van Heezik, 2013) and the IUCN/SSC (2013) guidelines advise the following: pre-release baseline ecological data; demographic performance; behavioural monitoring; ecological monitoring; genetic monitoring; health and mortality monitoring; and social, cultural and economic monitoring. This is a comprehensive list, but we argue that the use of physiological indices to gauge both individual and population-level performance should be introduced explicitly. For example, acknowledgement that physiological differences and tolerances in and between individuals can affect population diversity (Cooke *et al.*, 2013) has broad implications for long-term translocation success. Notably, health monitoring and conservation medicine are well established and fundamental to reintroduction biology (Aguirre, 2002), but we suggest that non-clinical, pre-clinical and peri-clinical physiological aspects of individuals' biology could further advance the field of conservation translocations

Translocation physiology: promoting two of the three Rs of animal welfare

The three Rs of animal welfare and ethics in research are well-established doctrines that promote the replacement (R1), reduction (R2) and refinement (R3) of animals used for research. These are highlighted as key considerations for any activity relating to animal research and necessarily extend to conservation and reintroduction biology. However, despite tremendous advances in the science of reintroduction biology (Ewen *et al.*, 2012a; Seddon and van Heezik, 2013), there remains a 'more animals' approach to reintroductions/translocations, at least tacitly by some conservation practitioners, in the hope that some animals will survive and establish self-sustaining populations. This is not to suggest that the 'more animals' approach reflects active intentions or a lack of consideration for animal welfare and wellbeing, nor the view that 'more animals' is the best option for success, but it probably reflects the simple consequence of having the opportunity to release large numbers of animals, combined with low expectation for survival, presumably because information about how the animals will be impacted by release is necessarily limited. Nonetheless, we argue that this approach contravenes R2 and R3 of the codes of practice and recommendations from national and international animal ethics and welfare bodies.

Obviously, replacing animals (R1) for reintroduction is not possible, but the incorporation of physiology and physiological measures into the translocation paradigm could markedly improve the survival chances of released animals, as well as improving our understanding of the reintroduction/translocation process generally. These outcomes directly assist the principles of reducing the total number of animals (R2) and the refinement of methods (R3) to promote successful reintroductions and translocations. By extension, this also serves to achieve R1 (replacement of animals) by ultimately obviating the need to reintroduce further animals once a population has become self-sustaining. This last point is not trivial, in that once a self-sustaining population is established, further monitoring of animals and their habitat and ecosystem more generally should then become a key aim of management, with the aim of eliminating further need for captive rearing and release or translocation.

From a practical perspective, the 'more animals' approach can also be fiscally irresponsible, because of the generally high costs associated with rearing and releasing large numbers of animals. Many conservation and reintroduction organizations rely heavily on public support as charity, in addition to the financial support of government and non-government research organizations. As such, it is imperative that animals are used only when the chances of translocation success can be demonstrated to be high and that every action has been examined and evaluated with a view to maximizing the likelihood of success of establishment of self-sustaining populations.

Given the inherent invasiveness of reintroductions generally, we argue that it is necessary to consider whether invasive and non-invasive physiological procedures should be given more consideration than has occurred to date. Translocations should be not only cost-effective, but also ethical undertakings, in that only the minimal numbers of animals needed to ensure success are used. The idea of releasing large numbers of animals in the hope of having a few survive is, in our view, unacceptable, particularly given recent advances in conservation physiology that can help to improve the efficiency of breeding and reintroduction programmes. We consider some of the most relevant advances below.

Physiology and conservation translocation

'Stress' in conservation translocations

'Stress' consists of three interrelated components: stressors, which are the environmental stimuli that lead to a stress response; acute stress; and chronic stress (Romero and Butler, 2007). Translocations often involve multiple stressors, each of which can activate acute and longer lasting responses (Dickens *et al.*, 2010; Parker, *et al.*, 2012). Typically, a stress response begins with an immediate adrenocorticoid (fight-or-flight) cascade, characterized by the production of glucocorticoids or 'stress hormones' (Romero, 2004; for detailed descriptions of the endocrinological processes involved in stress see also: Romero and Butler, 2007; Dickens *et al.*, 2010; Parker *et al.*, 2012). Therefore, the easiest and most common indicator of animal stress that could be monitored in translocation is the glucocorticoid response (Manire *et al.*, 2003; Hartup *et al.*, 2005; Pinter-Wollman *et al.*, 2009; Zidon *et al.*, 2009). The main glucocorticoids used in wildlife studies are cortisol (many mammals) and corticosterone (rodents, birds, amphibians and reptiles); their roles in stress and as measures of stress have been reviewed extensively (Romero, 2004; Romero and Butler, 2007; Dickens *et al.*, 2010; Parker *et al.*, 2012). Glucocorticoid production can persist as part of a longer term response to stressors (Romero and Butler, 2007), and its major effects include behaviour modification, increased blood glucose levels, inhibition of normal growth and reproduction, and depression of immune function (Romero and Butler, 2007). Additionally, for translocated animals, stress hormones may have unique and unforeseen impacts.

It is well known that glucocorticoids can affect almost all cell types and tissues (Dhabhar, 2009), and the changes they induce can be critically important for aiding survival and ameliorating recovery following distress. However, for naïve animals released into unfamiliar environments, as occurs during translocations, unusual or novel stressors may be particularly disruptive because naïve animals may have no behavioural or physiological frame of reference for displaying appropriate responses (Waas *et al.*, 1999; Romero, 2004; Dickens *et al.*, 2010; Rensel and Schoech, 2011). Consequently, the impact of novel stressors on translocated animals may be more severe and persistent than expected, with implications for the development and assessment of conservation translocation protocols.

Despite the benefits of acute or immediate responses to stressors, persistent or chronic exposure to stressors (or the perception of stressors) can have a range of deleterious effects (Millspaugh and Washburn, 2004; Dhabhar, 2009). Persistent distress, for example, can impair feeding behaviours, thereby compromising daily energy and nutrient acquisition; it can also increase energy requirements (Dickens *et al.*, 2010), thus presenting animals with conflicting challenges. Additionally, persistent endocrinological responses to stressors can dampen the immune systems of animals, depressing their abilities to respond to immune challenges (Dhabhar *et al.*, 1996), such as injury or exposure to pathogens or parasites (Bortolotti *et al.*, 2009). Such challenges can further stimulate stress responses, leading to synergistic cascades that may increase risks from further immune challenges (Woodford, 2002). These compounding problems are likely to be important for translocated animals because new environments may also expose them to new or different strains of pathogens and parasites and may be particularly problematic for captive-born and-reared animals that have had limited or no prior pathogenic exposure. In this regard, captive-born and-raised animals present a particular conundrum with regard to innate immunity and host–parasite interactions, simply because they may lack the acquired immunity associated with prior exposure (Mathews *et al.*, 2006; Ewen *et al.*, 2012b). Thus, at the very least, pre-release health checks and vaccinations for appropriate diseases should be considered highly desirable, but we suggest also that breeding and release projects consider 'training' animal immune systems through direct challenges during the rearing process.

As the main components of translocation—capture, captivity, transport and release into a novel area—are all individually stressful events (Parker *et al.*, 2012), translocated animals will inevitably experience some degree of acute and/or chronic stress. This can lead to changes both in stress response physiology (fight-or-flight responsiveness, sympathetic nervous system drivers, hypothalamic–pituitary–adrenal axis function and overall glucocorticoid secretion) and in the function of the immune system and behavioural coping strategies (Dickens *et al.*, 2010).

Stress may not be a frequent or direct cause of translocation failures, but it can certainly jeopardize the principal objective of most release projects, that being to establish self-sustaining populations. In this regard, chronic or persistent exposure to stressors is important because it can disrupt animal reproduction, both endocrinologically (Sapolsky *et al.*, 2000; Berga, 2008) and behaviourally (Romero and Butler, 2007). Persistent stress responses by translocated animals can potentially be disastrous for the relevant species and for the specific release project (which may also jeopardize future funding prospects). Consequently, given the potential for translocations to perpetuate cycles of persistent stress, immune compromise and reproductive failure, we argue that ongoing monitoring for indications of stress should be incorporated explicitly into conservation translocation protocols. Techniques for such monitoring may involve the invasive sampling of tissue or body fluids, such as blood or saliva, or the non-invasive collection of waste or shed material, such as hair or feathers (Table 3), and thus may be selected as appropriate to the species that is being translocated.

Beyond 'stress': other useful physiological indicators

Health indices

Several field-based measurements can be used as indicators of the general health and wellbeing of individual animals or populations (Tables 2 and 3). It is important to identify which measures and methods (especially invasive *versus* non-invasive methods; see Table 3) will be most appropriate for particular species. Selection will depend on a range of factors, including the target animal's body size and life history, the degree of association that individuals have had with people and the ease of sample collection and storage. Other factors may also need to be considered for specific translocations, such as whether animals will be translocated most effectively while conscious or immobilized and, if the latter, whether appropriate anaesthetic drugs and personnel trained to administer these will be available.

Table 3: Physiology in the field: invasive and non-invasive measurements that can be made to help facilitate success in conservation-based reintroductions of animals

Physiological measurement	Biological material or method	Invasive or non-invasive	Examples
Glucocorticoid 'stress' hormones			
	Blood	I	McKenzie *et al.* (2004)
	Saliva	I	Pearson *et al.* (2008)
	Faeces	NI	Hartup *et al.* (2005)
	Urine	NI	Sheriff *et al.* (2011)
	Hair and feathers	NI	Bortolotti *et al.* (2009)
Thyroid hormones			
	Blood	I	Yochem *et al.* (2008)
	Faeces	NI	Wasser *et al.* (2010)
Reproductive hormones			
	Blood	I	Brown (2000)
	Faeces	NI	Wasser and Hunt (2005)
	Urine	NI	Graham (2004)
Trace elements			
	Blood	I	Lapidge (2005)
Stable isotopes			
	Blood	I	Janssen *et al.* (2011)
	Faeces	NI	Varo and Amat (2008)
	Hair and feathers	NI	Cerling *et al.* (2006)
Bio-monitoring (e.g. heart rate, temperature)			
	Implants	I	Waas *et al.* (1999)
	Remote sensing	NI	Lavers *et al.* (2009)
Metabolic rate and water turnover	Labelled water	I	Lapidge and Munn (2012)

Abbreviations: I, invasive; and NI, non-invasive.

Health and immunocompetence underpin the survival of individual animals but may also provide insights into the health of populations more broadly. Poor health, for example, increases the risk of depredation (Krumm *et al.*, 2010) and can lower reproductive success (Cook *et al.*, 2004); each of these deficits is especially important in the context of conservation translocations because of the often small number of founder animals released and because even small losses or reproductive impairments are likely to have major deleterious effects on project success. Basic pre-translocation evaluations of individual health have contributed to the success of captive-bred chimpanzees released into the Conkouati Reserve (Tutin *et al.*, 2001) and to translocations of water voles (Mathews *et al.*, 2006) and bighorn sheep (Ostermann *et al.*, 2001), but health assessments rarely extend beyond the release period.

The potential to transfer pathogens and parasites endemic in one location to a new location is another health-related concern relevant for animal translocations and, to a lesser extent, for captive-bred releases (Ewen *et al.*, 2012b). Importantly, when considered solely from a veterinary or health-evaluation perspective, the fact that an organism is non-pathogenic in one area may overlook the risks that pathogens or parasites could become problematic for animals moved to a new site (Armstrong and Seddon, 2008; also see Mathews *et al.*, 2006 for a detailed discussion on the health of translocated water voles and captive dibblers, *Parantechinus apicalis*). Conversely, transmission of a disease from a hitherto unknown reservoir at a release site can also occur. For example, reintroduced African wild dogs (*Lycaon pictus*) contracted rabies after ingesting infected jackal carcasses, despite the wild dogs being vaccinated for rabies pre-release (Woodroffe and Ginsberg, 1999). Such vulnerabilities may be particularly important for captive-bred animals, which have vastly different life experiences in comparison to wild-caught animals used for translocation. Overall, efforts to establish health status and the immunocompetence of animals to be translocated could have profound benefits for conservation translocations. As such, key indicators of animal health status that are easy to access and track pre- and post-release could prove exceptionally useful in the translocation biologist's 'tool box'. We suggest below that thyroid hormones are good candidates for such health-tracking markers and may offer tangible benefits for translocation projects generally.

Thyroid hormones

Thyroid hormones [thyroxine (T_4) and triiodothyronine (T_3)] convey important information about overall health and disease status in animals (Yochem *et al.*, 2008), and they can also provide insight into an animal's underlying metabolic state (Rolland, 2000; Wasser *et al.*, 2010) and thermoregulatory capacity. Additionally, thyroid hormones convey information about growth and development, including brain development (Silva, 2006; Wasser *et al.*, 2010). Thus, characterization of the thyroid status of individuals or groups of animals could contribute substantially to our understanding of their general health and wellbeing. Perhaps more importantly, measures of animal thyroid status could also identify sub-clinical (or undiagnosed clinical) diseases or other maladies (Mönig *et al.*, 1999; Mooney *et al.*, 2008) that may not be evident from cursory observations of animals. Maintenance of peak health is likely to be vital during all stages of a reintroduction procedure, from animal release to survival post-release, and to successful reproduction and population establishment. Hence, the assessment of animals' thyroid hormone status, accessed invasively or non-invasively (see Table 3), can offer an important indicator of health and survival prospects as well as overall population viability. We suggest also that ongoing or even *ad hoc* evaluations of the thyroid status of translocated animals may highlight hitherto unknown or unforeseen interactions between animal health, survival and ecology, thereby improving the science and the success of animal translocations more broadly.

Nutritional physiology

Many studies in our review evaluated habitat characteristics with a view to ensuring that adequate food resources would be available to animals post-release. However, most studies also assumed that habitat equated to food resources and overlooked important interactions between animal physiology and nutrition (but see Lapidge and Munn, 2012). The finding that critical food items are apparently available is not necessarily a reliable indication of how well an animal can access or use the resources appropriately. For example, there may be physical, behavioural or ecological constraints (e.g. the presence of other species) that preclude individuals from accessing food (e.g. Dickman, 1991). The role of nutritional physiology is perhaps the most neglected aspect of translocation biology, perhaps because it is not easily assessed. However, some methods are tractable and also readily accessible for conservation translocation programmes.

Nutritional physiology encompasses more than a simple accounting of the foodstuffs that are available at a release site, and potentially considers a wide range of factors that are relevant to translocations. These factors include the phenotypic plasticity of the gastrointestinal system (Starck, 1999a, b, 2005; Millán *et al.*, 2003; O'Regan and Kitchener, 2005; Starck and Wang, 2005; Munn *et al.*, 2006, 2009), the impacts of gut pathogens (Everest, 2007), microbes or other intestinal symbionts that are needed for healthy digestion (Hooper and Gordon, 2001; Kohl and Dearing, 2012), and microbial 'seeding' of captive-reared animals, particularly herbivores, to aid digestion following release, and even foraging behaviours; all of these factors can ultimately affect survival and breeding success.

Ensuring nutritional and digestive wellbeing may be critically important for captive-bred animals, especially if they have been reared on highly processed or commercial foods. Often, captive-bred animals do not have to 'work' for their food, at least not as intensively as their wild counterparts. As such, there are likely to be significant interactions between the nutritional experience of captive-reared animals and how they fare following release. Specific studies of these interactions are rare, but they could be investigated empirically using soft- and hard-release methods where animal condition can be observed. For example, in a study of released Peninsular bighorn sheep (*Ovis canadensis*), all released animals were fed on high-quality food (alfalfa pellets plus salt and mineral blocks) in addition to having access to native vegetation in pre-release enclosures (Ostermann *et al.*, 2001). The animals were then released into the wild without immediate acclimitization to a diet consisting solely of native vegetation. The project failed to establish a self-sustaining population (Ostermann *et al.*, 2001) and, although numerous explanations were offered to account for the poor success, we contend that nutritional physiology was likely to have been relevant; indeed, the authors themselves suggested that higher success in certain releases was related to the availability of good-quality forage and water (Ostermann *et al.*, 2001).

It is apparent that abrupt dietary changes can generate negative outcomes for animals by increasing stress and depriving them of key nutrients, both of which may lead to compromised immunity immediately post-release. The gastrointestinal tract is keenly influenced by the immune system, where the immune cells and resident microbes form a complex ecosystem (McCracken and Lorenz, 2001). This intestinal ecosystem can be altered by changes in diet (Liukkonen-Anttila *et al.*, 2000; McCracken and Lorenz, 2001) and can further influence other physiological features, particularly when animal stress hormones are elevated (Everest, 2007). Recent studies of wild vs. captive wood grouse (*Tetrao urogallus*; Wienemann *et al.*, 2011), for example, have revealed major differences between the gastrointestinal microbiota of wild and captive birds. In the context of translocation biology, mismatch between the appropriate intestinal environment and that established in the released animals could adversely affect the survival of translocated animals. In another study, marbled teal (*Marmaronetta angustirostris*) maintained for a longer captive period before release showed lower survival rates compared with those released soon after fledging, and this was attributed to the longer held animals being fed a commercial diet (Green *et al.*, 2005). Therefore, dietary adjustments should be considered thoroughly in translocation protocols and, given that gut flexibility (both in terms of morphology and microbial composition) takes time to adjust (e.g. Moore and Battley, 2006), a gradual reduction of high-quality foodstuffs prior to release may improve survival post-release.

Assessment of micronutrients and trace elements is another component of nutritional physiology that holds potential value to translocation physiology. This is especially the case with respect to releases of captive animals, as demonstrated by Lapidge (2005). In that study, plasma vitamin E concentration was evaluated in yellow-footed rock wallabies (*Petrogale xanthopus celeris*), due to prevalence of deficiencies in captive but not wild animals (Lapidge, 2005). The study aimed to assess the welfare implications of releasing captive wallabies and demonstrated how the captive animals adjusted to the wild environment by rapidly increasing plasma vitamin E concentrations post-release to levels similar to their wild counterparts, thus indicating that there were no appreciable welfare implications.

Overall, nutrition is one of the more easily manipulated aspects of the translocation process and potentially also one of the most important. Nutrition can be manipulated non-invasively and with little expense, and the benefits of incorporating nutritional aspects of physiology should have flow-on effects for improved immune status, reproductive success and general animal health and wellbeing. For these reasons, we argue that more focus should be placed on priming the gastrointestinal tract of captive-reared animals before release and that additional factors, such as seasonal or diet-related plasticity of the gastrointestinal tract (Piersma and Lindström, 1997), should be incorporated into release protocols.

Other physiological factors

There is a collection of other physiological factors that could be of use to translocation physiology. Immunoecology (or ecological immunology) investigates underlying causes of immune system function between individuals and populations (Hawley and Altizer, 2011) and, as such, has close ties with health indices, disease and stress. Groombridge *et al.* (2004) demonstrated this via quantative evaluation of white blood cell counts to measure stress levels in Po'ouli (*Melamprosops phaeosoma*). Integration of immunoecological aspects of animal biology and techniques used to evaluate immune status in the wild may be particularly useful for understanding the cause-and-effect nature of translocation successes and failures.

Understanding a species' reproductive biology is also important for predicting the viability of wildlife populations, as well as for developing best practice captive-breeding programmes (Brown, 2000; Graham, 2004; Wasser and Hunt, 2005; Asa, 2010). Details of the reproductive physiology and associated needs (e.g. specific resources) have scope for further inclusion in managing translocated populations.

Stable isotopes can be used to study diverse factors affecting wildlife, all of which are relevant to conservation translocations. These can range from, for example, identifying factors that affect growth (Janssen *et al.*, 2011), determining migration patterns and diet changes (Cerling *et al.*, 2006) and teasing out species differences in dietary assimilation to determining why species with similar ecologies are displaying different survivabilities in the same habitats (Varo and Amat, 2008) and range from invasive to non-invasive techniques (Table 3).

The biology of stable and radioactive isotopes can also inform translocation science. Analysis of metabolic rate and water turnover can be used to measure how translocated animals, particularly those that are captive bred, adjust to wild conditions post-release, and can be a particularly sensitive measure of success, as demonstrated by Lapidge and Munn (2012).

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Translocation physiology: methods

Perhaps the most important aspect to consider prior to a translocation is whether invasive methods for monitoring physiology are appropriate, acceptable and practicable for the given situation. The level of information generated from physiological investigations should be expected to justify their use or to rank whether relatively less-invasive methods would be better suited to the species in question.

Non-invasive methods for monitoring animal physiology have two main benefits for conservation translocation biologists. Firstly, they minimize direct contact with animals, and secondly, they can minimize direct or remote exposure of animals to humans (Table 3). However, it is important to remember that translocation is, by its nature, an invasive procedure. Animals are captured (whether free-living or captive) and transported, usually to new and unfamiliar environments. The potentially profound impacts of translocation are highlighted by the often high mortalities that are seen for newly released animals. In a study of reintroduced European mink (*Mustela lutreola*), for example, mortality exceeded 40% in the first 30 days post-release (Maran *et al.*, 2009). In a translocation of radio-collared elk (*Cervus elephas*), 15% of deaths occurred in the 6 weeks following release and were related to stresses associated with capture and/or release (Larkin *et al.*, 2003). Consequently, careful attention to physiological measures indicating animal distress or compromised health and wellbeing should be included explicitly in translocation protocols. For example, identification of key trigger points to initiate intervention during capture, transport and post-release could be crucial for ameliorating the apparently widely accepted high levels of post-release mortality in translocations. In particular, we suggest that a 'more animals' approach to combating the high rates of post-release mortality in conservation translocations may be less successful than a 'fewer animals–more invasive' approach.

The 'more animals' approach is problematic for several reasons, not least because it contravenes codes of practice and recommendations from national and international animal ethics and welfare bodies, which strive to reduce the numbers of animals used for science and research and to refine the methods used to maximize the success of animal-based projects. In addition, a 'more animals' approach is not fiscally responsible because of the generally high costs associated with rearing and releasing large numbers of animals. Therefore, given the inherent invasiveness of translocations, it is prudent to consider whether invasive procedures should be considered more often than has occurred previously, especially if this results in improved conservation translocation outcomes.

There are several invasive procedures that would probably benefit conservation translocation projects (Table 3) and that are appropriate for a range of taxa, including reptiles, mammals and birds. Of note, most of these procedures are well established in veterinary and physiological practice, making their inclusion in conservation translocation protocols relatively straightforward, especially if relevant experts are consulted. In this context, we suggest that several aspects of research could prove valuable for understanding and evaluating the entire translocation process, along with the mechanisms and factors that affect survival post-release. In particular, field metabolism (Lapidge and Munn, 2012), water use, heart rates and body temperature (Waas *et al.*, 1999) could be used to determine how well animals are acclimatizing or adapting to their new environments, whether they are maintaining condition, are foraging successfully and are able to meet the energetic and nutritional demands of reproduction. These are important questions, for which we have very limited data.

Radio- or GPS-tracking devices represent one semi-invasive method for evaluating animals post-release that has great potential for improving reintroduction success. Tracking devices can be considered invasive, in that they require animals to wear electronic tags, either externally (e.g. as neck or leg collars) or as internal implants. Such devices could interfere with animals' daily activities, but may also provide unprecedented information about how individuals adapt to release. For example, tracking can provide information on daily ranging patterns (Campioni *et al.*, 2013), insight into immediate post-release behaviours (Dennis and Shan, 2012) and otherwise cryptic, but critically important information about movements, habitats or nutrients that are essential for animal survival (e.g. Gurarie *et al.*, 2011). The ability to locate animals can assist with regular visual contact of subjects, thus allowing intensive behavioural monitoring, and can also present opportunities to collect additional physiological and behavioural information via collection of scats (providing information on, for example, diet and stress hormones) and urine (providing information on diet, stress hormones and water turnover). At the outset, placement of collars may require animals to be sedated, particularly for large mammals (e.g. Wear *et al.*, 2005), but this also provides an opportunity for collection of a wide array of baseline physiological data and indicators of animal health before release. Moreover, depending on the species and the situation, animals may be recaptured to replace the collar batteries or to retrieve GPS data, providing another opportunity to collect more invasive data, such as blood samples.

Conclusions and recommendations

The weight heretofore given to genetic (Groombridge *et al.*, 2012; Jamieson and Lacy, 2012; Keller *et al.*, 2012), disease (Sainsbury *et al.*, 2012) and behavioural factors (e.g. Armstrong *et al.*, 1999; Ostro *et al.*, 1999; Munkwitz *et al.*, 2005) in translocation planning needs to be extended to include physiological processes and mechanisms as a recognized complementary discipline. Some resistance might be expected in promoting physiology as a critical tool for use in translocation biology. The view that physiological methods may cause distress, particularly for invasive methods like surgical implantation of heart rate monitors, has probably impeded the advancement of physiology in conservation science generally. Obviously, the potential use of physiological tools, their invasiveness and possible impacts must be weighed against the potential benefits to the survival of a given species or population, with the rarity of a species probably dictating the outcomes of these evaluations. Nonetheless, we argue that the role of physiology in reintroduction and translocation science should be given greater consideration. The most recent IUCN Guidelines for conservation translocations recognize that physiology should be assessed, and we echo that recommendation. In fact, we would go further, and argue that physiology is the principal unifier that describes the basic ecological and behavioural features of organisms relevant for evaluating any reintroduction proposal. To this end, we propose the following recommendations for developing and evaluating reintroduction projects.

(i) Reintroduction programmes should consider the range of interactions between released animals and the environment, including potential interactions with other species that may be present at the release site and that can be illustrated by invasive or non-invasive physiological indices. This should include, for example, the potential physiological responses to predators, competitors, parasites and pathogens. The potential for such interactions must be considered pre- and post-release and in follow-up monitoring studies, and mitigated if required.

(ii) Databases of the physiology of reintroduced animals should be created prior to release, and they should include—at a minimum—information on genetic, behavioural, nutritional and health/disease aspects of the individuals being used.

(iii) Greater use and consideration of physiological assessments of animal wellbeing pre- and post-release must be incorporated into monitoring protocols. This should assist in ensuring the suitability of animals for release and their performance thereafter. It will also become increasingly important to understand the physiological tolerances of reintroduced animals and species in order to predict their ability to adapt to changing conditions.

(iv) Post-release monitoring should continue over longer periods than has been the case in most studies to date, particularly as conditions at many reintroduction sites are likely to change rapidly in future as the climate changes (Parmesan, 2006). Long-term monitoring is often not possible because typical funding cycles run for merely 3–5 years. Nonetheless, we urge that due consideration be given to defining and prescribing appropriate monitoring periods for specific reintroductions, partly to improve successes, but also to provide more realistic and rigorous evaluations of success. Moreover, monitoring of animal health and physiology should be considered at both early and later stages of reintroductions, either during or following acclimatization in 'soft-release' studies, and also over longer periods.

In conclusion, we note that substantive advances have been made in improving the success of animal reintroductions in recent years (Ewen *et al.*, 2012a). These advances have been assisted and supported by increased use of behavioural observations and ecological and genetic monitoring of released animals. However, from our review we argue that further advances in the field and in the success of individual reintroductions and translocations could be gained by broadening routine data collection to include relevant physiological measures. Such measures can inform researchers of the wellbeing of individuals and their chances of reproductive success and, thereby, the likelihood of a reintroduced population persisting post-release. As a starting point, we recommend that key indicators of animal health, such as cortisol and thyroid status, and of physiological state (e.g. condition, diet) be incorporated into routine pre- and post-release monitoring protocols. This is not to say that translocations or reintroductions should apply each of these recommendations unnecessarily, but they ought to be considered during planning for species-specific protocols, with a view to incorporating procedures strategically and in a manner most likely to benefit the success of the release. Nonetheless, given the persistent variability in the success rates of translocation, the collection of as many data as possible may assist future practitioners by accumulating a knowledge base of physiological indicators relevant to animal survival. Such indicators will help to identify potential problems that may not be apparent through *ad hoc* observations and offer the opportunity to improve translocations generally by focusing evaluations of 'success' on physiological wellbeing.

Supplementary material

Supplementary material is available at *Conservation Physiology* online.

Acknowledgements

Adam Munn and Chris Dickman thank the Australian Research Council for supporting their research over many years, and Chris Dickman thanks the Australian Research Council especially for providing a fellowship that has afforded time to write and think. Our sincere thanks go to an anonymous reviewer and especially to Doug Armstrong for providing insightful and constructive criticism and for supporting our underlying approach and encouragement to present these ideas to the field of conservation biology more generally.

Funding

No specific funding was awarded for this project. Esther Tarszisz is funded by the Australian Postgraduate Award (APA) scheme.

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(II) SUPPLEMENTARY MATERIAL

B1: Criteria for data inclusion summarised in Table 2.2

(1) Criteria for inclusion

Of the papers discovered in the literature search, only those with a conservation basis were considered. Studies without a conservation basis, such as those describing the relocation of nuisance urban animals (human-wildlife conflict), were excluded (see Massei *et al*., 2010 for a review of such studies), as were those that dealt with the translocation of wolves or other large predators as a non-lethal means of reducing predation on livestock (Bradley et al., 2005). Studies that concentrated only on the source population, rather than the reintroduced population, were also omitted, e.g. (Bain and French, 2009). Papers lacking sufficient information to be included in quantitative analyses were excluded, as were those that focused on specific aspects of the reintroduction process, such as how to improve the detection of the study species (Reindl-Thompson et al., 2006). Papers that focused solely on anthropogenic factors involved in translocations (particularly those concerning carnivores) also were excluded if they lacked quantitative information on the reintroduction subjects themselves. For example, (Williams et al., 2002) described community attitudes to wolf (*Canis lupus*) reintroductions; this study was not included because it provided little quantitative insight into how wolves were reintroduced.

(2) Analysis of the literature

The search process yielded 232 papers (not including reviews) that met our criteria for inclusion. A full list of these papers is available in supplementary material. To examine broad trends in reintroduction research, we first considered the geographical regions where studies had been carried out and the species and taxonomic groups that had been studied. We then focused on the papers that we had classified as *reintroduction* studies and examined these in more detail. The following questions were asked:

i. What was the stated purpose of the study?
ii. What period were releases carried out over?
iii. Was any pre-release preparation initiated and, if so, what was the focus of this preparation (e.g. population viability analysis, habitat surveys)?
iv. Was there any post-release monitoring and, if so, what was the nature of this (e.g. radio/GPS tracking, re-capturing, visual observation)?
v. How many animals were used?
vi. Was the reintroduction considered a success or failure and, if deemed to be successful, was it of high or limited success? We define levels of success in the following section.

In addition to these questions, we defined a number of key biological and environmental factors that appeared likely to influence reintroduction success and asked whether these had been considered in the protocols of each study. These were scored as 'yes' or 'no' depending on whether the studies had met specific criteria for each factor. The criteria were as follows:

(a) Genetics

To receive a 'yes' for this category the study needed to have considered one or more of the following:

i. Number of founders and the effects this might have on inbreeding and/or outbreeding depression; and
ii. Relatedness of individuals involved in the translocation (e.g. stock book, laboratory study of tissue samples for genetic analysis).

(b) Behaviour

To receive a 'yes' for this category the study needed to have considered one or more of the following:

i. Behavioural acclimation of animals to a new location (this was of particular importance for captive-born/raised animals);
ii. Interactions with conspecifics; and
iii. Predator/prey interactions (if relevant).

We considered the relative merits and disadvantages of soft- *versus* hard-release (i.e. releases, respectively, where supplementary food or shelter resources are, or are not, provided) to be part of pre-release preparation unless specific behavioural training was undertaken, the latter being a more directed and deliberate method typically aimed at improving success. Shier (2006) and Shier & Owings (2006), for example, assessed the effect of predator training on the behaviour and post-release survival of captive prairie dogs (*Cynomys ludovicianus*).

(c) Physiology

This was further divided into four subcategories. Three of these—condition, nutrition, and health—can, in a broad sense be considered as components of physiology at an individual and population level as all contribute significantly to an animal's physiological state. Our fourth subcategory includes studies that had adopted more 'traditional' physiological approaches.

i. Condition

To receive a 'yes' for this subcategory the study needed to have considered one or more of the following:

a) Degree of distress associated with the release process (reactions of animals assessed qualitatively by observation, with no endocrine monitoring); and
b) Body condition. Many studies scored condition using visual appraisals of physical appearance or as indices of body fat, but more-quantitative methods using residuals derived from regressions of body mass on body length or other linear measures were also included. Studies that considered body condition *post hoc* were excluded, as were those that used body condition to age the study subjects.

ii. Nutrition

To receive a 'yes' for this subcategory the study needed to have considered one or more of the following:

a) Pre-release diet; and
b) Post-release diet (if relevant, e.g. supplemental feeding).

iii. Health

To receive a ‘yes’ for this subcategory the study needed to have considered one or more of the following:

a) Health status of the source population;
b) Health check (generally by a veterinarian);
c) Vaccinations;
d) Parasite management;
e) Disease screening;
f) Quarantine; and
g) Presence of unfamiliar diseases/parasites at the release site.

iv. ‘Traditional’ physiology

To receive a ‘yes’ for this subcategory the study needed to have considered one or more of the following:

a) Stress associated with the release process (with monitoring of glucocorticoids or other ‘stress hormones’);
b) Water and micronutrient balance;
c) Thermoregulation; and
d) Immunoecology.

(d) Habitat

To receive a ‘yes’ for this category the study needed to have considered one or more of the following:

i. Suitability of habitat for the target species at the new location; this included, for example, considerations of habitat fragmentation, human/animal activities in the area, whether the area was protected or multi-use, whether adequate food, water and shelter were available, and whether the reintroduction was specified as taking place in the species' indigenous range; and

ii. Whether specific enemy-shelter such as a predator-proof fence was available or necessary.

(e) Key Threatening Processes (KTPs)

Populations of many species that have been extirpated or severely compromised in an area can be impacted by one or more key threatening processes (KTPs). For example, a release of brush-tailed bettongs (*Bettongia penicillata*) in Australia was managed by the control of one threat, the predatory red fox (*Vulpes vulpes*), but was compromised by inattention to another threat – predation from the feral cat (*Felis catus*) (Priddel and Wheeler, 2004). In this review we scored known or identified KTPs as present (P) or absent (A), but note that often there was minimal information on threatening processes. If some but not all known KTPs had been eliminated prior to a reintroduction, KTPs were considered to be present, but if all known KTPs had been eliminated they were considered absent.

(3) Quantifying reintroduction success

The most commonly used definition of 'success' in reintroduction programs is whether the programs result in self-sustaining populations of the target species (Griffith *et al*., 1989; Fischer & Lindenmayer, 2000). However, for several reasons this ostensibly simple definition can be difficult to meet.

Firstly, few studies specify how long a program should be monitored to confirm viability, although many acknowledge that years or decades may be required for success to become clear (Griffith *et al.,*1989, Fischer & Lindenmayer, 2000; Seddon *et al.,* 2007; Armstrong & Seddon, 2008). Post-release monitoring can necessarily continue only for a finite length of time in most projects; unless a target population becomes unambiguously self-sustaining in this time, success may be illusory and the true outcome of the project will remain unknown.

Secondly, as natural populations frequently decline to low numbers and become locally extinct, reintroduction success as measured by population persistence should also take account of the 'background' rate of population loss. For example, the 'average' species consists of 220 populations, of which about 8% are lost every decade (Hughes et al., 1997). From this we might expect a 92% chance for a reintroduced population to survive 10 years. Even this would be generous, however, given that most reintroduced populations are small and solitary and lack connectivity with other populations that could bolster them via dispersal or migration. Persistence times also are likely to be species-specific and perhaps less for already-threatened species than others. These considerations suggest that a 10-year background success rate for reintroduced populations could be set at 90% or less, but with considerable uncertainty due to the biology of the target species.

Thirdly, what appears to be a self-sustaining population at one point can decline rapidly, thereby reducing the chance of long-term persistence. For example, unexpected but catastrophic flooding greatly reduced the survival of reintroduced riparian brush rabbits (*Sylvilagus bachmani riparius*) in an otherwise successful program in California (Hamilton et al., 2010). Even without such stochastic events, researchers may remain uncertain whether they have established a viable and self-sustaining population if they do not create measurable objectives against which to test a project's performance (Sheean et al., 2012); the lack of clarity about the achievement of success also makes subsequent meta-analyses very difficult (Nakagawa and Cuthill, 2007).

To overcome these difficulties, we attempted to create specific criteria to determine the success of individual reintroduction projects in a repeatable and rigorous manner. As our review concerns reintroductions carried out over varying lengths of time, we considered each study on its own merits. In the first instance we evaluated success, or otherwise, of a reintroduction project based on each study's self-evaluation. However, some studies, while considering their project a success, failed to meet their stated aims or, in our reading of the results, failed to state reasonable reasons for considering the project a success. Therefore, in addition to self-reported success and failure, we introduce a binary category for projects deemed successful, this being to denote 'high' or 'low' success.

c) High success was determined if:
    i. The reintroduction confirmed that a stable and/or increasing population was established during the study period; or
    ii. The project achieved its specified aims. For example, a project evaluating the effects of pre-release experience of elk (*Cervus elaphus*) with wolves (*Canis lupus*) and human hunters showed that experienced animals survived longer post-release, which was the specified aim (Frair et al., 2007); or
    iii. The project initially showed poor results, but researchers improved them by altering protocols over time using information gleaned in earlier years (if releases took place over multiple years).

d) Low success was determined if:

   i. The study reported high success but failed to show conclusive results. For example, in a black bear (*Ursus americanus*) reintroduction that measured two different release techniques, >50% of study animals died or were unable to be included in the analyses due to lack of knowledge of their whereabouts (Eastridge and Clark, 2001);
   ii. A threatening problem was present and could not be resolved, such as low genetic diversity due to small founder numbers or the presence of a key threatening process;
   iii. Stochastic events occurred and significantly affected the project's results. For example, during the Iraq war the flight of Bedouins from Kuwait and Iraq to Jordan led to a doubling of the livestock population in the host country. This led to overgrazing, reduced water supplies and higher prevalence of disease and parasites in Jordanian habitats, compromising the reintroduction of oryx (*Oryx leucoryx*) as a result (Harding et al., 2007);
   iv. The sample size was too limited to have resulted in a self-sustaining population as, for example, in the reintroduction of a single orang-utan (*Pongo abelii*) to Sumatra (Cocks and Bullo, 2008);
   v. There was limited scope for population expansion and persistence. For example, despite the establishment of a reproducing population of lions (*Panthera leo*) in Phinda private game reserve, the population remained small and isolated, with little scope for connection to other isolated populations and for addressing the long-term conservation problems of the species (Hunter et al., 2007); or

vi. The time of monitoring was too short to span even one breeding season. For example, a release of Pere David's deer (*Elaphurus davidianus*) in China spanned less than six months of monitoring (Hu and Jiang, 2002)

Table B1: Length of post-release monitoring

Length of post-release monitoring	Total Number	Failure	Success
<1 month	3	2	1
1-6 months	15	1	14
6-12 months	11	5	6
1-2 years	23	3	20
2-5 years	34	3	31
5-10 years	20	2	18
10-20 years	10	2	8
20+ years	3	0	3

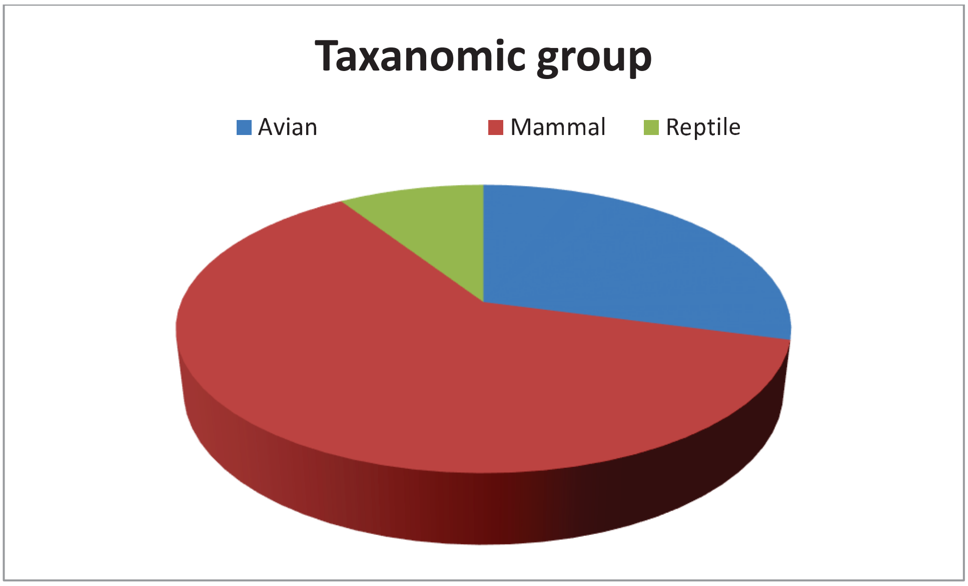

Fig B1: Translocation papers separated by taxa (see references below)

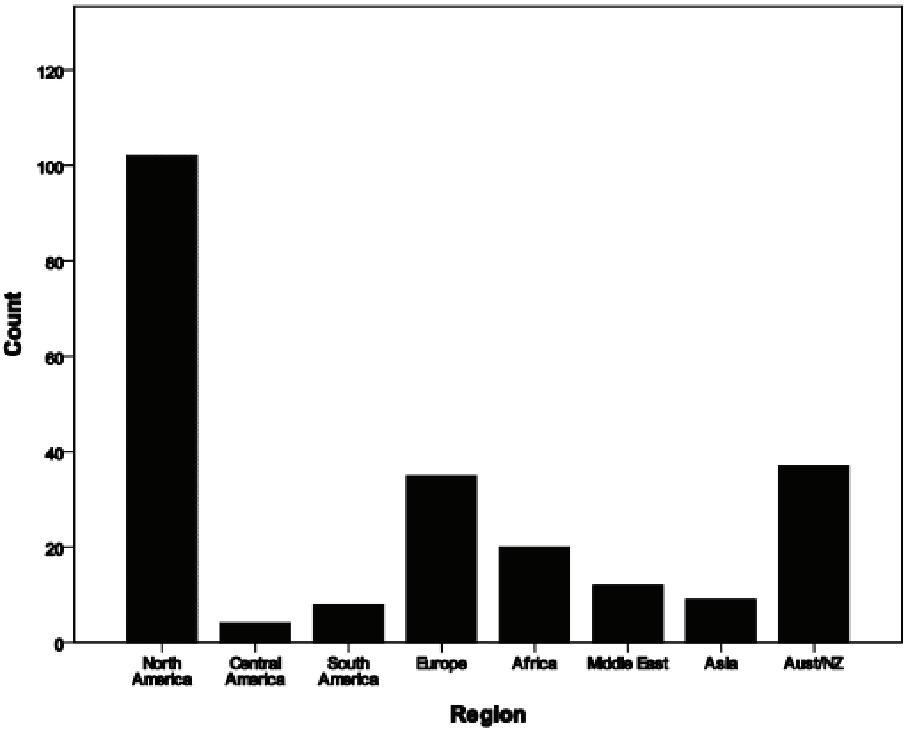

Fig B2: Region where studies were conducted (see references below): Evident is a disproportionate amount of studies were reported from Western/developed regions such as North America, Europe and Australia/New Zealand

Supplementary material: References for the 232 papers that were analysed

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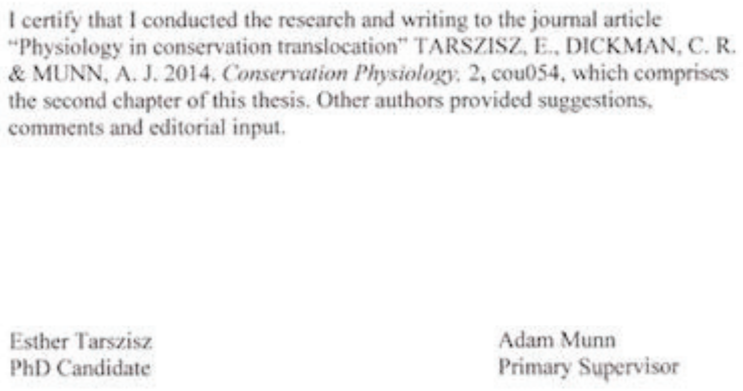
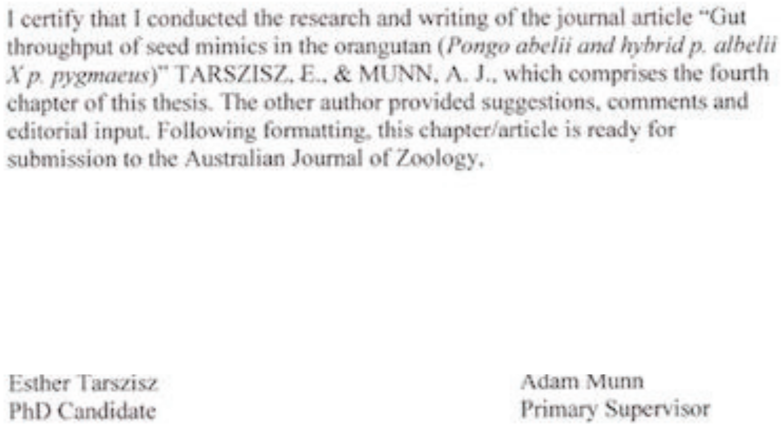
APPENDIX C: STATEMENTS CERTIFYING THESIS CHAPTERS WRITTEN AS JOURNAL ARTICLES AS MY OWN WORK (AS PER UNIVERSITY OF WOLLONGONG GUIDELINES FOR STYLE 2)



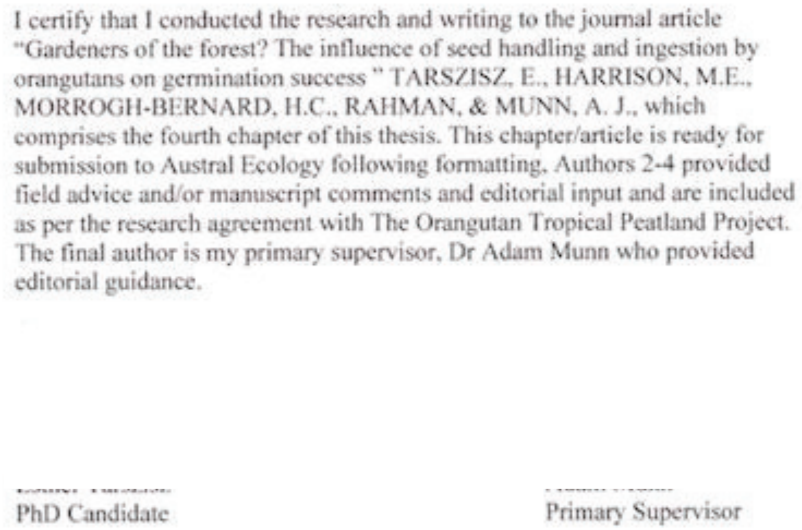
I certify that I conducted the research and writing to the journal article "Physiology in conservation translocation" TARSZISZ, E., DICKMAN, C. R. & MUNN, A. J. 2014. *Conservation Physiology*, 2, cou054, which comprises the second chapter of this thesis. Other authors provided suggestions, comments and editorial input.

Esther Tarszisz PhD Candidate	Adam Munn Primary Supervisor



I certify that I conducted the research and writing of the journal article "Gut throughput of seed mimics in the orangutan (*Pongo abelii and hybrid p. albelii X p. pygmaeus*)" TARSZISZ, E., & MUNN, A. J., which comprises the fourth chapter of this thesis. The other author provided suggestions, comments and editorial input. Following formatting, this chapter/article is ready for submission to the Australian Journal of Zoology.

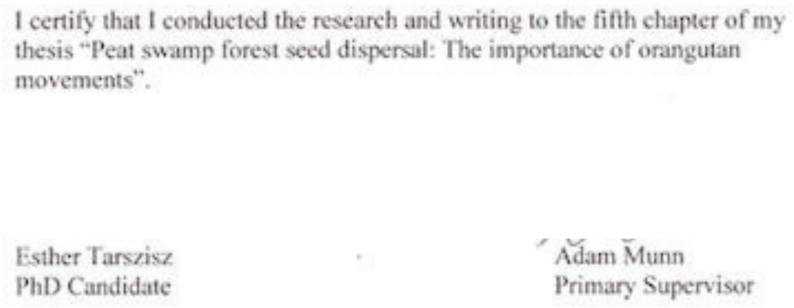
Esther Tarszisz PhD Candidate	Adam Munn Primary Supervisor



I certify that I conducted the research and writing to the journal article "Gardeners of the forest? The influence of seed handling and ingestion by orangutans on germination success " TARSZISZ, E., HARRISON, M.E., MORROGH-BERNARD, H.C., RAHMAN, & MUNN, A. J., which comprises the fourth chapter of this thesis. This chapter/article is ready for submission to Austral Ecology following formatting. Authors 2-4 provided field advice and/or manuscript comments and editorial input and are included as per the research agreement with The Orangutan Tropical Peatland Project. The final author is my primary supervisor, Dr Adam Munn who provided editorial guidance.

PhD Candidate

Primary Supervisor



I certify that I conducted the research and writing to the fifth chapter of my thesis "Peat swamp forest seed dispersal: The importance of orangutan movements".

Esther Tarszisz
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Adam Munn
Primary Supervisor