The Effects of Forest Fires on the Behaviour and Health of Bornean Orang-utans in Sebangau Peat-Swamp Forest

Submitted by Abigail Louise Gwynn to the University of Exeter

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

Signature: ……A. Gwyn………………………………………

Abstract

Forest fires are one of the greatest threats to endangered species in tropical peat-swamp forests. Over the last two decades, it has become evident that forest fires are increasing in frequency and severity at an alarming rate as a result of increasing anthropogenic land modification and climate change. Once considered a depauperate habitat type, peat-swamp forests have now been shown to contain considerable diversity and endemism. Of particular attention is the importance of peat-swamp forests for the critically endangered Bornean orang-utan (*Pongo pygmaeus*). Peat-swamp forests contain high densities and some of the last remaining strongholds of orang-utans in the world. The way in which fire affects orang-utans, in terms of their individual fitness, ability to survive and reproductive success may provide an early warning system and key insights into future fire-induced population trajectories. This study investigates variation in orang-utan activity budgets, physiological condition and gastrointestinal parasite infection before and after major fire events. I analysed 8056.8 hours of behavioural observations collected between 2011 and 2019 using generalised linear mixed models to assess if a major fire event in 2015 impacted the amount of time orang-utans allocate to daily activities. I revealed that orang-utans decrease their active period and allocate less time to resting over the long-term, four years post-fire, but increase their time allocation to resting in the short-term, up to nine months post-fire. I did not detect any decline in physiological condition after the 2015 fire event from analysis of ketones and specific gravity in 262 urine samples collected between 2009 and 2019. I employed the use of the Mini-FLOTAC faecal analysis technique to investigate changes in gastrointestinal parasite prevalence and load after a major fire event 2019. I collected 77 faecal samples between March and December 2019 from which I identified and counted the presence of gastrointestinal nematode eggs and larvae. Using zero-inflated negative binomial models and Fisher's exact tests, I revealed that overall nematode intensity was greater post-fire but detected no significant change in parasitic prevalence. From these findings, I suggest that orang-utans may have been employing energy conserving behavioural strategies to cope with fire disturbance, but this was unlikely due to a negative energy balance. The findings of a greater nematode intensity warrants further investigation into alternative

physiological markers and the impact of forest fires on wildlife health. Understanding how orang-utans are affected by forest fires will considerably improve the ability to manage and conserve remaining populations in forests prone to fire.

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1.1. Introduction

1.1.1. The Impacts of Fire in Tropical Peat-Swamp Forests

Anthropogenic land use change is the greatest threat to wildlife populations across the globe (Brooks *et al.* 2002; Maxwell *et al.* 2016). Between one third and one half of the Earth's land surface is now transformed by human action, which includes activities such as agriculture, deforestation, urbanisation, spreading of invasive species, release of pollutants, and resource extraction (Vitousek *et al.* 1997). As land modification continues and the global climate warms, fire damage to landscapes is becoming ever more frequent and severe. Although historically fires have been associated with grassland and shrubland ecosystems, over recent years, anthropogenic activity has made fire increasingly common in tropical forest ecosystems (Herawati and Santoso, 2011). Naturally, tropical forests are fire-resistant. On average, they receive more than 2000mm of rain annually, and the intact canopy creates a high humidity microclimate in the understorey (Malhi and Wright, 2004; Lauer, 1989). Plant and animal communities have adapted to life without significant fire disturbance, therefore making fire one of the most damaging threats to tropical forest communities (Harrison *et al.* 2009).

During the last 50 years, the above-mentioned human activities have made tropical forests prime sites for ignition. Logging and land clearance remove densely packed vegetation, reducing transpiration and opening up the canopy, which reduces the humidity understorey microclimate, making conditions drier and more susceptible to burning (Laurence and Williamson, 2001; McAlpine *et al.* 2018). Transpiration from tropical rainforests is important in influencing downwind precipitation and can contribute to over 25-35% of the annual rainfall in some tropical regions (Eltahir and Bras, 1996). A reduction in transpiration can also result in less rainfall in surrounding regions, making the effects of land use change on climate and fire susceptibility more widespread than just the directly damaged area (Spracklen, Arnold and Taylor, 2012). Changes in global climatic cycles can also increase the occurrence of fires in tropical regions. Warming of the climate due to rising greenhouse gas emissions is increasing the frequency and severity of El Nino Southern Oscillation (ENSO) events

(Cai *et al.* 2014). ENSO events are a reversal in the atmospheric trade winds which create warmer than average waters in the Eastern Pacific, and cooler than average waters in the Western Pacific. These cooler waters in the Western Pacific reduce rainfall over South-East (SE) Asia creating drought conditions (Philander, 1983). The areas over which drought occurs as a result of ENSO events contain some of the largest tropical forests in the world, making them more susceptible to fire. ENSO events naturally occur every 3-7 years, but climate change is increasing their frequency and severity, with dramatic fires in the tropics coinciding with ENSO events (Timmermann *et al.* 1999).

The influence of land use change and ENSO events on escalating fire risk is very severe in tropical peat-swamp ecosystems. Peat-swamp forests are rainforests with a naturally waterlogged, peat substrate and low to medium canopy. Peat-swamp forests occur where environmental conditions allow the formation of peat soils. These conditions include high precipitation, high humidity, topographic and geological conditions that favour water retention, acidic substrate pH and nutrient availability (Page *et al.* 2006). Peat can accumulate for thousands of years, forming peat deposits of up to 20m deep due to the production of organic matter exceeding its decomposition (Anderson, 1983). Geographically, tropical peat-swamp forests are located near the equator in the regions of South and Central America, the Caribbean, Africa, and SE Asia (Page *et al.* 1999). Once disturbed, peat-swamp forests are more vulnerable to destruction by fire than other types of tropical forest (Langner *et al.* 2007, Posa *et al.* 2011). The high volume and low density layers of peat makes it a highly flammable substrate once dried out, with fires able to burn below as well as above ground. As a result, there is no barrier to fire spread. Once ignited, fires can burn underground for months, even years, without being detected (e.g. Ellery *et al.* 1989). To exemplify the problem, in 2002 peat-swamp forests covered 23% of the forest area of Borneo. Yet 73% of the total fire-affected forest area was peat-swamps. In terms of fire hotspots, 81% were located on peat-swamp forests (Langner *et al.* 2007).

Peat-swamp forests are highly degraded and susceptible to fire primarily because of drainage for logging and crop plantations. Peat-swamps contain a number of valuable timber trees, such as meranti (*Shorea* spp.) and ramin (*Gonystylus* *bancanus*) (Morrogh-Bernard *et al.* 2003; Yule, 2010). As such, peat-swamps have been the site of legal, concession-based selective logging for 50 years, and more recently illegal logging. A common feature of logging activity in peat-swamps is the construction of canals in order to float out logs to sawmills. These canals, which can be up to 10 m wide and extend for tens of kilometres, drain the naturally high water table of the peat. The construction of canals also causes subsidence and oxidation of the peat, resulting in increased flammability and greater aerobic emissions of carbon dioxide into the atmosphere (Hooijer *et al.* 2006; Hooijer *et al.* 2012; Wosten *et al.* 2006; Wosten *et al.* 2008). Peat drainage also occurs as a result of plantation development. Waterlogged peat soils are not ideal growing conditions for crops such as oil palm or *Acacia.* These crops thrive when the water table is approximately 50 cm below the surface, whereas undisturbed peat-swamps usually experience flooding in the wet season and a water level of 20-40 cm below the surface in a normal dry season (Takahashi *et al.* 2002; Wosten *et al.* 2006). Therefore, plantation developers often drain the peat to create more ideal conditions for these crops. This dries out the peat severely, providing a large, flammable biomass fuel load. A powerful example is the Mega Rice Project in Central Kalimantan. In 1996, the Indonesian government attempted to transform 1 Mha of peat into rice paddies (Aldhous, 2004). Thousands of kilometres of canals were excavated to drain excess water in the wet season and provide water for irrigation in the dry season (Muhamad and Rieley, 2002). However, the project failed, and no rice was ever harvested. The Mega Rice Project area was left deforested, dry and thus a prime site for ignition (Jaenicke *et al.* 2010). Peat-swamp forest area in Block C, the western-most 450,000 ha of the Mega Rice Project, has decreased by 80% since monitoring began in 1973 with the primary cause being fire (Page *et al.* 2009). The area continues to burn every year, with larger reductions in forest seen in more severe ENSO years (Hoscilo *et al.* 2011).

As well as land modification for plantations and logging, areas are often cleared with the use of fire, known as the ‘slash-and-burn’ method. ‘Slash-and-burn’ has been common practice among small-scale farmers inhabiting tropical regions in order to prepare land for agriculture quickly and cost-effectively (Kleinman *et al.* 1995; Tomich *et al.* 1998; Ketterings *et al*. 2000). This method is prominent in Indonesia due to its easy and economical means of increasing access to agricultural fields

(Ketterings *et al.* 1999). In Indonesia, fire is also used by fishermen to create pools in the peat into which fish flow and become trapped (Borneo Nature Foundation, pers. comms.). Traditionally, the use of the slash-and-burn method in shifting cultivation of foodcrops was sustainable, provided population densities were low enough to allow long uncultivated periods during which land could recover (Tomich *et al.*1998). However, when population densities and land modification began to increase in the 1970's, slash-and-burn became more industrialised which resulted in environmental degradation, making areas less productive over the long-term and highly vulnerable to fires burning out of control and into bordering forests (Varma, 2003). Up until the 1990's, it was thought that small-scale shifting cultivators using slash-and-burn methods were responsible for widespread fires (Lennertz and Panzer, 1984). However, by the time of the devastating fires in 1997, it was more commonly acknowledged that fires were also started by industrial-scale land clearance for oil palm (*Elaeis guineensis*) and timber (Cattau *et al.* 2016). These two levels of activity are not mutually exclusive in responsibility for peat fires. Both small-scale and industrial-scale activities openly set fires as the cheapest and quickest way to clear land. The deliberate setting of fires in tropical regions, combined with other forms of forest clearance and ENSO events, is rapidly increasing fire occurrence in peat-swamp ecosystems, far beyond natural levels.

SE Asia is particularly affected by fire due to its extensive peat deposits. There are approximately 24.8 Mha of peat in SE Asia, which represents 41% of global tropical peatland area (Warren *et al.* 2017). During mega-fire events in 1982/83, 1997/98, and 2006, 0.55 Mha, 2.4 Mha, and 2 Mha of peat-swamp forest respectively were destroyed over SE Asia (Page *et al.* 2002; Langner *et al.* 2007; Page *et al.* 2009). Indonesia holds the majority of SE Asia's peat, 21 Mha, representing 36% of the global tropical peatlands area. It is estimated that Indonesia holds between 13.6 and 57.4 Gt of carbon in its peat, up to 65% of the tropical peat carbon stock (Page *et al.* 2011; Warren *et al.* 2017). As a result, Indonesia is one of the biggest emitters of carbon dioxide and has one of the highest rates of deforestation worldwide. During the 1997/98 fire event, 0.87-2.57 Gt of carbon was released from Indonesian peat-swamps into the atmosphere (8% of the total peat-swamp carbon store). This was equivalent to 13-40% of mean annual global carbon emissions from fossil fuels in 1997 (Page *et al.* 2002). The most recent severe fire event occurred in 2015, when

2.6 Mha of Indonesian land was burnt, of which 33% was peatland (Glauber *et al.* 2016). Air quality recorded near one of the most severely affected Indonesian cities (Palangka Raya) was hazardous, reaching a particulate matter (PM_{10}) concentration of 1,829 ug m^{-3} (Erb *et al.* 2018). According to the Clean Air Act, the US Environmental Protection Agency states that a PM_{10} concentration over 150 µg m^{-3} in a 24-hour period is harmful to public health and the environment. The increase in air pollutants resulted in a huge increase in respiratory illnesses such as bronchial asthma, bronchitis, and acute respiratory infection (Aditama, 2000), and it is estimated that there were 91,600 excess deaths across the country (Koplitz *et al.* 2016). Hence, mitigating forest fires in Indonesia is of global importance for climate regulation and to protect human health, before even considering the effects on the country's biota.

Indonesia is one of the most biodiverse countries in the world and continued forest loss due to fire could cause numerous species extinctions. Indonesia contains 10% of the world's flowering plants (25,000 species), 12% of the world's mammals (515 species), 16% of the world's reptiles (781 species), and 17% of the world's birds (1,592 species) (CBD Secretariat, 2016). Nearly one third of Indonesia's species are endemic and 10% threatened by extinction (UNEP-WCMC, 2004). Indonesia's peat-swamp forests are critical habitats to many of these species. Due to limited scientific research in peat-swamp forests until the 1990's, peat-swamps were previously considered a depauperate habitat type unable to sustain high biodiversity or large populations of species due to their harsh acidic and nutrient poor conditions (Janzen, 1974). However, peat-swamps are now acknowledged as highly important areas for the conservation of many threatened species (e.g. *Pongo* spp.: Morrogh-Bernard *et al.* 2003; Hylobatidae: Campbell *et al.* 2008; *Presbytis rubicunda*: Ehlers Smith and Ehlers Smith, 2013; *Neofelis diardi* and other felids: Cheyne *et al.* 2011, 2013; *Ciconia stormi*: Cheyne *et al.* 2014). An assessment of just one peat-swamp forest in Central Kalimantan identified 215 tree, 92 non-tree flora, 73 ant, 66 butterfly, 297 spider, 41 dragon/damselfly, 55 fish, 11 amphibian, 46 reptile, 172 bird and 65 mammal taxa (Husson *et al.* 2018). Unfortunately, Indonesia's peat-swamps are one of the most rapidly degrading habitats on Earth, yet only 9% are designated protected areas (Posa *et al.* 2011). Kalimantan, a region of Borneo which has a long history of logging and agricultural plantations as well as fire disturbance, has seen a reduction of pristine peat-swamp forest to just 7.4% of the prior total peatland area (Miettinen *et al.*, 2016). It is projected that by 2080, 30-49% of Bornean mammal species will lose more than 30% of their habitat (Struebig *et al.* 2015). The loss and fragmentation of peat-swamp habitat in SE Asia has resulted in 45% of mammals and 33% of birds being classified as Near Threatened, Vulnerable or Endangered by the IUCN Red List (Posa *et al.* 2011). What has also come to light in recent years is the importance of peat-swamp habitats for the Critically Endangered orang-utan (*Pongo* spp.) and how the continued reduction of this habitat pushes them closer to extinction.

1.1.2. Integrating fire ecology, animal behaviour and health to assess the impacts of fire on wildlife

Fire is likely to have many different effects on species based on its frequency, size, type, intensity, severity, and seasonality, collectively known as the 'fire regime' (Lyon *et al.* 2000), and the ecology and life history of the species in question. Many of these effects will not be immediately apparent, only appearing some months or years after a fire event, but are likely to affect more individuals than those immediately affected by fire (e.g. caught in the flames) and occur over a longer period of time through changes in habitat structure and quality, affecting long-term survival and reproduction. Fire can destroy extremely large areas of habitat in a relatively short period. During the 2015 Indonesian fires, nearly 10% of Sebangau National Park was burned (Alsop, 2016). Analysis of orang-utan populations and habitat loss suggests that orang-utans were displaced, showing local population increases in the mixed swamp interior habitat type and decreases in mixed swamp perimeter, with both habitat types losing forest cover (Mang, 2017). Populations experiencing these changes in individual distribution are vulnerable to the effects of 'refugee crowding' – when density increases and the carrying capacity of an area neighbouring disturbance is overshot due to an influx of displaced individuals (Rijksen and Meijaard, 1999; Husson and Morrogh-Bernard, 2015; Vallejos *et al.* 2019). This has a range of knock-on effects such as reduced resource availability, more intraspecific interactions, greater competition, and potential for increased disease transmission (Husson and Morrogh-Bernard, 2015).

Tree mortality and heat stress also reduces resource availability to primates. In Borneo, Leighton and Wirawan (1986) and Campbell (1992) found that up to 60% of primate fruit trees and 90% of large lianas and figs were killed. Canopy trees that are not killed by the fire and in surrounding areas can abort fruit crops and shed leaves as a result of traumatic heat and smoke stress, prolonging the period of potential food scarcity (Peres, 1999; Harrison *et al.* 2007). Consequently, many organisms will have to modify their behaviour in order to cope with fire damage to their habitat and these increased pressures to meet their energy requirements. In fire disturbed Dipterocarpaceae habitats, orang-utans have been documented shifting their diet to cope with lower food availability. During the large fires of 1982/83, mortality of primate fruit trees and lianas in Kutai National Park was 44% and 97% respectively (Leighton and Leighton, 1983). Five to 10 months after the fires, percentage of fruit in the diet had decreased by 43.8%, whereas leaves, bark and other food items increased (Rodman, 1977; Suzuki, 1984). Fruit is a much higher-energy and preferred food source, therefore, the reduction of fruit in the diet may have resulted in individuals having less energy available to maintain a good physiological condition, robust immune system, or to invest in reproduction (Milton, 1993). Animals may also alter activity patterns to meet their energy requirements, varying the amount of time allocated to feeding, resting, travelling, and social activity to conserve energy in lower quality habitats (Oates, 1977; Marsh *et al.* 1981; Menon and Poirier, 1996; Li and Rogers, 2003; Yang *et al.* 2007). After the 2015 Indonesian fires, orang-utans employed energy conserving strategies by increasing resting time during the smoke period (defined as visible presence of smoke in the air) and decreasing travelling time after the smoke period (Erb *et al.* 2018). Behaviour can also help to infer the effects of fire on wildlife health. Toxic smoke from the 2015 fires caused Bornean white bearded gibbons (*Hylobates albibarbis*) to sing on significantly fewer days and for shorter bouts than when there was no smoke (Harrison *et al.* 2007). It is likely that the smoke was irritating their respiratory system, similarly to how humans suffer from respiratory infections such as bronchitis and asthma. However, confirming this in wild individuals is unfeasible without immobilisation of the individual. Therefore, behaviour can provide a good initial measure of an animal’s physiological state when conditions do not allow quantitative health analyses.

Studying wildlife health in line with behavioural changes caused by fire is highly valuable but can be practically challenging. Assessing an animal's health commonly requires invasive techniques such as tranquilising, taking biopsies, or blood samples. These processes can cause high levels of stress and pose a high risk of injury, or even death, to wild animals. Therefore often, the information gained from such research does not warrant the risks to animals that researchers are ultimately trying to protect. Alternatively, some of the best, non-invasive techniques to assess health in wild animals are to investigate urinary biomarkers and faecal parasites. A component of urine that can be a useful indicator of physiological condition is ketones. Ketones are produced when an animal experiences a negative energy balance so must catabolise fat reserves to attempt to meet energy requirements (Robinson and Williamson, 1980). The production of ketones is usually associated with reduced food availability, when energy intake is reduced (Knott, 1998; 1999), but ketones may also be produced when energy intake is stable and energetic output is greater due to increased allostatic load. In a study by Erb *et al.* (2018), orang-utans employed energy conserving strategies but not because of reduced energy intake. This was highlighted by the presence of ketones in the post-smoke period but an increase in calorific intake. Fat catabolism was occurring most likely due to other factors such as increased stress hormone production or elevated immune response, resulting in more energy being expended than was ingested, or conserved by the behavioural strategies. Therefore, it is important to integrate behavioural ecology and physiology to understand the full effects of fire on wildlife.

Monitoring gastrointestinal parasitic infection using faecal samples is also a useful, non-invasive measure of physiological condition and stress in response to fire damage to habitat. Fire has been an under-recognised form of anthropogenic land-use change influencing parasitic infection and transmission (Scasta, 2015). Most of the research to date has focussed on the use of fire to reduce disease risk in domesticated animals declining populations. For example, fire reduced the free-living stages of gastrointestinal parasites of sheep in Australia and controlled burning of pastures has been suggested to reduce gastrointestinal nematodes and the susceptibility of sheep (Barger, 1978). Fire may decrease parasitic infection by killing those with free-living stages such as nematodes, but the habitat damage and subsequent behavioural change of animals in areas not directly burned may alter parasitic infection and transmission in other ways. For example, other forms of habitat disturbance, such as logging, increase the prevalence and richness of gastrointestinal parasites in red-tailed guenons (*Cercopithecus ascanius*) (Gillespie *et al.* 2005). Patterns of parasitism are influenced by many factors such as host density, ranging patterns intra- and interspecific contacts, and diet (Hudson *et al.* 2002; Nunn *et al.* 2003). Red-tailed guenons were found to have larger home ranges and longer day ranges in logged forests than unlogged forests, which increased their exposure to parasites (Gillespie *et al.* 2005). Epidemiological theory states that increasing host density should increase parasitic prevalence and species richness as it leads to more intensive use of the same habitat patches, increasing the levels of contamination of the environment with infective stages of parasites and increasing host contact rates (Mbora and McPeek, 2009). As fire can alter host density by displacing individuals, it may result in more parasitic infections in areas neighbouring burned areas experiencing inflated host densities. How fire influences parasitic infection in wildlife populations will depend highly on the characteristics of the host, life cycle of the parasite, host-parasite interactions, and fire regime. Many parasites that can be studied using non-invasive methods, i.e. gastrointestinal parasites from faecal samples, are not directly lethal (unless in extremely high burdens) and pose little significant risk to populations. But these parasites can increase the allostatic load of the host so that more energy is required by the immune system, diverting resources away from other physiological processes or behavioural activities which are necessary to optimise survival and reproduction.

It is clear that anthropogenic land modification is intensifying fire damage in Indonesia’s tropical peatland ecosystems. The burning peat-swamp forests has terrible consequences for the global climate and human health and is now considered one of the most significant threats to peat-swamp-dwelling species, contributing to many population declines. However, little is known on the mechanisms of how fire interacts with species’ ecology and life history traits in peat-swamps. Therefore, studies integrating behavioural ecology and wildlife health will help us to understand the factors influencing survival and reproduction of individuals and key drivers of population declines. This will aid in designing peatland restoration strategies to minimise further wildlife population declines and reduce future susceptibility to fire in degraded peat-swamps.

1.1.3. Study System

1.1.3.1. Orang-utan Life History

The orang-utan is Asia’s only great ape, found exclusively on the islands of Borneo and Sumatra. Historically, orang-utan distribution was widespread across south-east and mainland Asia, with fossils dating back to the Pleistocene found in regions between southern China, Vietnam and Java (Tshen, 2016). By the end of the Pleistocene, 12,500 years ago, post-glacial sea levels rose resulting in regular submergence of the Batam-Riau-Lingga land bridge connecting Sumatra to mainland Asia. This fragmented orang-utan populations, separating the mainland from Sundaland, and submergence of the Bangka-Bilitung-Karimata-Schwaner land bridge divided the islands of Borneo, Sumatra and Java (Rikjsen and Meijaard, 1999). Populations on the mainland experienced rapid encroachment of humans and subsequent hunting pressure which led to their extinction (Rikjsen and Meijaard, 1999). A similar story unfolded on Java and orang-utans were thought to be absent there by the end of the 17th century (Dobson, 1953). The populations that remained are those on the islands of Borneo and Sumatra.

The isolation of orang-utan populations on Borneo and Sumatra led to genetic divergence between them, which is estimated to have occurred between 0.6 and 6.4 million years ago (Goossens *et al.* 2009). It was only in 1996 that these distinct populations were recognised as separate species; the Bornean orang-utan (*Pongo pygmaeus*) and Sumatran orang-utan (*Pongo abelii*) (Xu and Arnason, 1996). In 2017, an isolated population from Batang Toru, at the southern-most range limit of Sumatran orang-utans, was shown to be distinct from both the Bornean and Sumatran species; designating a third species of orang-utan; the Tapanuli orang-utan (*Pongo tapanuliensis*) (Nater *et al.* 2017). The Bornean orang-utan is split into three sub-species, *Pongo pygmaeus morio* in Eastern Borneo, *Pongo pygmaeus pygmaeus* in Western Borneo, and *Pongo pygmaeus wurmbii* in Southern Borneo (Warren *et al.* 2001).

The Bornean orang-utan inhabits a wide range of forest types, including dry lowland and sub-montane forests dominated by the Dipterocarpaceae family, peat-swamp forests, freshwater swamp forests and alluvial forests (Husson *et al.* 2009). These are regarded as prime habitats as they produce sufficient amounts of food to sustain the orang-utan's frugivorous diet (Marshall *et al.* 2009a; Morrogh-Bernard *et al.* 2009; Russon *et al.* 2009a). Fruit comprises approximately 66% of their diet, leaves compose 17%, and bark, flowers, herbs and insects make up the remaining 17% of their diet (Morrogh Bernard *et al.* 2009). However, orang-utans can be highly flexible, shifting their diet according to spatial and temporal environmental conditions (Morrogh-Bernard *et al.* 2009). It is even thought that orang-utans inhabiting different forest types have different strategies to deal with low fruit availability. For example, Dipterocarpaceae forests exhibit mast fruiting events, occurring every 2-10 years, when trees synchronously produce large amount of fruit (Harrison *et al.* 2010a). Orang-utans deal with periods of low fruit availability in between these events by switching to fallback foods such as bark, leaves, and herbs which are much lower in energy content (Marshall *et al.* 2009b). Under these circumstances, orang-utans conserve their energy by travelling less and resting more, known as the 'low energy strategy'. On the other hand, peat-swamp forests exhibit a more regular, yet lower quality and less abundant, fruit supply. It is therefore more optimal to spend more time searching for fruit, rather than falling back on lower quality foods which are more locally abundant (the 'high energy strategy'). The regularity of fruit availability in peat-swamps means that if orang-utans continue searching for fruits, there is a higher likelihood they will find them compared to in masting forests (Marshall *et al.* 2009b, Morrogh-Bernard *et al.* 2009). Orang-utans can also inhabit heath forests, limestone-karst forest (Payne, 1987; Marshall *et al.* 2006, 2007), and have even been recorded in oil palm plantations and mangroves, although cannot persist there without more favourable forest nearby (Ancrenaz and Lackman-Ancrenaz, 2004).

Orang-utans require large areas to find enough food to sustain their metabolic needs as food is often scarce. Ranging is variable by sex, with females having a home range of approximately 850 ha and males 2500 ha (Singleton and van Schaik, 2001). Most females have a stable home range, utilising the same general area throughout their lives. Females are philopatric and adolescents often establish their home range adjacent to their mother's range (Galdikas, 1988). Male home range is less stable and more transient, as males need to actively seek out receptive females to mate with or avoid confrontation with other more dominant males (McConkey, 2005). This ranging behaviour (as a result of scarcity of resources) supports a semi-solitary social organisation (van Schaik, 1999). However, the need for large home ranges makes orang-utans highly vulnerable to population decline if forests are fragmented or destroyed.

Orang-utans can live up to 45 years in the wild and have the longest interbirth interval (7-9 years) of any non-human mammal (Rijksen and Meijaard, 1999; van Noordwijk and van Schaik, 2005). Female orang-utans do not have their first offspring until approximately 15 years old (Knott *et al.* 2009), therefore females will produce 3-4 offspring throughout their entire life, provided environmental conditions allow. This extremely slow rate of reproduction can be attributed to the orang-utan's semi-solitary lifestyle, driven by low resource availability (van Noordwijk and van Schaik, 2005). As recruitment is far slower than the time it takes to remove an individual from a population, orang-utans extremely vulnerable to population decline. Population viability analysis suggests that a female take-off rate of more than 1% would result in population decline (Marshall *et al.* 2009c). Therefore, many aspects of orang-utan life history make the species highly vulnerable to population decline.

1.1.3.2. Orang-utan Conservation

All three species of orang-utan are now classed as critically endangered by the IUCN (Ancrenaz *et al.* 2016; Singleton *et al.* 2017; Nowak *et al.* 2017). The most severe threat is habitat loss, which over the last 70 years has resulted in rapid population declines. Since 1950, the Bornean orang-utan population declined by over 60%, and it is projected that 80% of the Bornean population will have been lost by 2025 leaving 47,000 individuals remaining (Ancrenaz *et al.* 2016). Habitat loss became a severe threat to Bornean orang-utans in the 1950's, when mechanised logging intensified (Ancrenaz *et al.* 2016). Destruction was occurring at unprecedented rates by the 1970's when industrial-scale extractive logging and oil palm plantations were established. Between 1973 and 2010, Borneo's forest cover had declined by 30%, with logging and oil palm plantations accounting for 10% of Borneo's land area (Gaveau *et al.* 2014). In 2010, it was estimated that 61% of the suitable orang-utan habitat from 1973 remained. It is projected that just 39% will remain by 2025 (Wich *et al.* 2012).

A substantial amount of research has been conducted to assess the effects of logging and plantations on orang-utan populations, however hunting also poses a significant threat to populations. Orang-utans are hunted for food, in retaliation to crop raiding, to obtain infants for the pet trade, and for traditional medicine (Rijksen and Meijaard, 1999). There are few, if any, cultural taboos about hunting orang-utans, as there are with chimpanzees or other great apes in areas such as Equatorial Guinea (Sabater-Pi and Groves, 1972). Although reported hunting rates in Borneo are low (annual female take off rate estimated between 0.9 and 3.6%), orang-utan populations will experience decline even at a hunting rate of just 1% as populations have low intrinsic rates of increase due to long inter-birth intervals (Marshall *et al.* 2009c; Meijaard *et al.* 2011). Hunting is highly interlinked with habitat loss as activities such as logging, plantation establishment and fire destruction displace orang-utans and open up areas of forest which were previously difficult to access. This increases encounter rates with orang-utans and force them closer to settlements where conflict may occur (Meijaard *et al.* 2011).

As well as the ever-present threats of logging, oil palm plantations and hunting to orang-utan populations, fire has recently become one of the leading causes of decline in Borneo. Though, it is important to remember that land modifications (such as logging and plantations) often instigate fire, combined with ENSO events from which Borneo suffers extreme droughts. Since the large fires of 1997, there has been some preliminary analysis, albeit very little, on the impact of fire on orang-utan populations. The sparsity of information is mainly due to the difficultly of quantifying exactly how many orang-utans die with fire as a direct cause. It is estimated that 1,000 out of 40,000 orang-utans in Borneo (2.5%) died as a result of the 1997 fires, and there was a report of three orang-utans dying of disease due to food stress after 1972 fires (Marshall *et al.* 2009c). However, major problems are likely to come from the long-term changes to forest habitat, creating new challenges of surviving in a fire-altered landscape. The Bornean orang-utan population is especially vulnerable to fire as five of the eight largest orang-utan populations are found in the highly-flammable peat-swamp ecosystem (e.g. Sebangau National Park - 6,080, Tanjung Puting National Park – 4,180 and Gunung Palung National Park – 3,280; Utami-Atmoko *et al.* 2017). During the 2015 fire period, fire hotspots showed a 54% overlap with peatlands and 30% overlap with orang-utan range in Kalimantan (Harrison *et al.*

2016). Once considered poor habitats for orang-utans, peat-swamps are now recognised as one of the richest habitats (Russon *et al.* 2001). In Gunung Palung National Park, peat-swamp is the most densely populated orang-utan habitat, containing approximately 31% higher density of individuals than non-peat lowland forest (Johnson *et al.* 2005). Therefore, peat-swamp forests are critical, yet highly vulnerable, areas for orang-utan conservation.

Fire is now one of the greatest pressures on orang-utan survival. It is set to become an even more damaging threat as forests, in particular peat-swamps, become increasingly damaged by anthropogenic activity and droughts become more frequent due to ENSO events. Considering such a large proportion of the remaining orang-utan population is found in peat-swamps and that large areas are lost to fire every year, peat-swamps are critical areas to target in order to conserve the species. Borneo's peat-swamps currently have very little protection and research is needed imminently to assess the effects of fire on orang-utans to promote additional protection of these areas. Not only is this essential to preserve the biodiversity of peat-swamps, but it is also essential for protecting human health and slowing the rate of anthropogenically-induced climate change.

1.1.4. Study Aims

This thesis aims to understand how Bornean orang-utans are affected by peat-swamp forest fires, both behaviourally and physiologically. I will do this by investigating changes in orang-utan activity budgets, urinary biomarkers, and parasitic infection before and after the large forest fire events of 2015 and 2019 in Indonesia. Using a long-term dataset spanning over 16 years, I will assess changes to behaviour and physiology over both short- and long-term periods to identify immediate and delayed effects of fire damage to habitat on orang-utans. These aims will be addressed over two chapters, the first (Chapter 2 of this thesis) will investigate changes in activity budgets and urinary biomarkers of general health up to four years after the 2015 fire event. I predict that orang-utans will show energy conserving behavioural strategies and reduced general health in response to more challenging environmental conditions created by the fire disturbance, such as reduced food availability and smoke exposure. The second (Chapter 3 of this thesis) will introduce a new technique to study gastrointestinal parasites in great apes in the field and how this can be used to assess seasonal and fire-induced variation in parasitic infection. I predict that parasitic infection will increase during the dry season and after fire disturbance. This research aims to aid conservation planning for orang-utan populations which are vulnerable to decline due to fire in peat-swamp forests.

1.2. Research Methods

1.2.1. Study Area

The Laboratorium Alam Hutan Gambut (LAHG) is a 500km^2 protected research area within the Sebangau forest catchment, Central Kalimantan, Indonesia (Fig 1). The Sebangau forest catchment is located in the south of the island of Borneo, between the Katingan and Kahayan rivers (west and east, respectively). The catchment covers an area of approximately 8,750km^2 and is primarily covered in tropical peat-swamp forest. In 2004, the forested area between the Katingan and Sebangau rivers (*ca.* 5,780km^2) was designated as the Sebangau National Park. Sebangau National Park is thought to contain approximately 6,080 orang-utans, one of the largest remaining viable populations in the world (Utami-Atmoko *et al.* 2017).

The LAHG is located 20km south-west of the provincial capital of Central Kalimantan, Palangka Raya. Base camp is situated on the forest edge (2°19'S and 114°00'E), next to the Sebangau river where local settlements have been established on the opposing banks. The LAHG was designated for the purpose of scientific research in 1997 when the legal Setia Alam Jaya timber concession ended. Since then, it has been managed by the Centre for International Cooperation in Management of Tropical Peatlands (CIMTROP) and the University of Palangka Raya, in collaboration with Borneo Nature Foundation (BNF) who now run long-term biodiversity monitoring and restoration activities at the site.

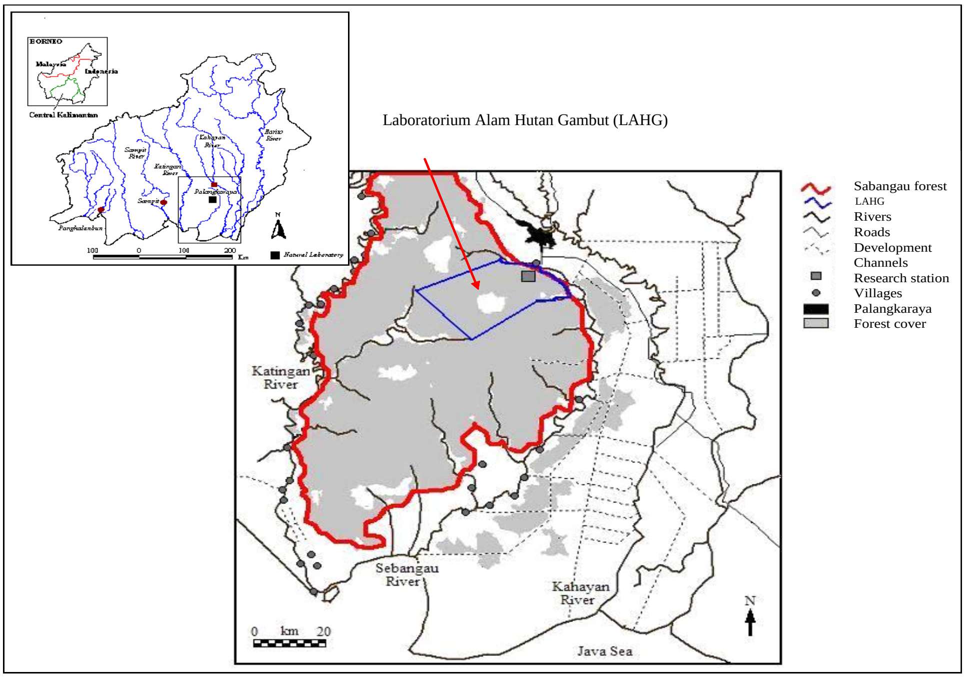


Figure 1. The location of the LAHG within the Sebangau forest, Central Kalimantan, Indonesia. Adapted from Morrogh-Bernard (2009).

1.2.2. Habitat and Fauna

The LAHG consists of three main peat-swamp forest sub-types. Mixed swamp forest is the dominant forest sub-type, extending up to approximately 6km beyond the limit of river flooding on peat 2-6m thick and with a maximum canopy height of 35m. Between 6 and 11km from the river is low-pole forest. Low-pole forest occurs on peat 7-10m thick, has a maximum canopy height of 20m and a permanently high water table. 12-25km from the river is the tall interior forest. This occupies the most elevated part of peat dome and the water table is below the surface all year round. It contains the tallest peat-swamp trees with a canopy at 45m. For this study, all surveys were undertaken in the mixed swamp forest type.

The Sebangau forest supports a vast array of biodiversity and significant populations of species designated high conservation priority. 65 mammals, 172 birds, 45 reptiles, 11 amphibians, 55 freshwater fish, 64 dragonflies/damselflies, and 307 tree and non-tree flora have been identified at the LAHG (Husson *et al.* 2018). It is estimated that Sebangau contains one of the largest orang-utan populations in the world; at 6,080 individuals (Utami-Atmoko *et al.* 2017). 210 of these inhabit the LAHG and approximately 20 of these have been habituated to human presence as a part of BNF’s long-term orang-utan research project.

1.2.3. Disturbance

The previous activity of legal and illegal logging means that the LAHG has been subject to human disturbance prior to designation for research. Legal, selective logging occurred from the 1970’s to 1997 which removed many of the large tropical hardwood trees that species such as orang-utans rely on for food and arboreal travel pathways. From 1997 to 2005, illegal logging occurred in the Sebangau forest which led to the construction of over 1,000 canals cut through the peat in order to float timber out of the forest to sawmills (Morrogh-Bernard, 2009).

The construction of canals has been the most damaging human modification to the Sebangau forest. The forest now dries out beyond pre-disturbance levels every dry season causing fires to occur annually. During the El Nino years of 1997, 2002, 2006, 2015 and 2019, major fire events occurred, burning large areas of the Sebangau forest. Fire is now considered the single greatest threat to the orang-utan population in Sebangau. Analysis of the 2015 fire event revealed that 510.3km^2 (~10%) of forest cover was lost (Mang, 2017). Within the LAHG, large areas burned to the south-east and south-west of the research camp (Fig 2).

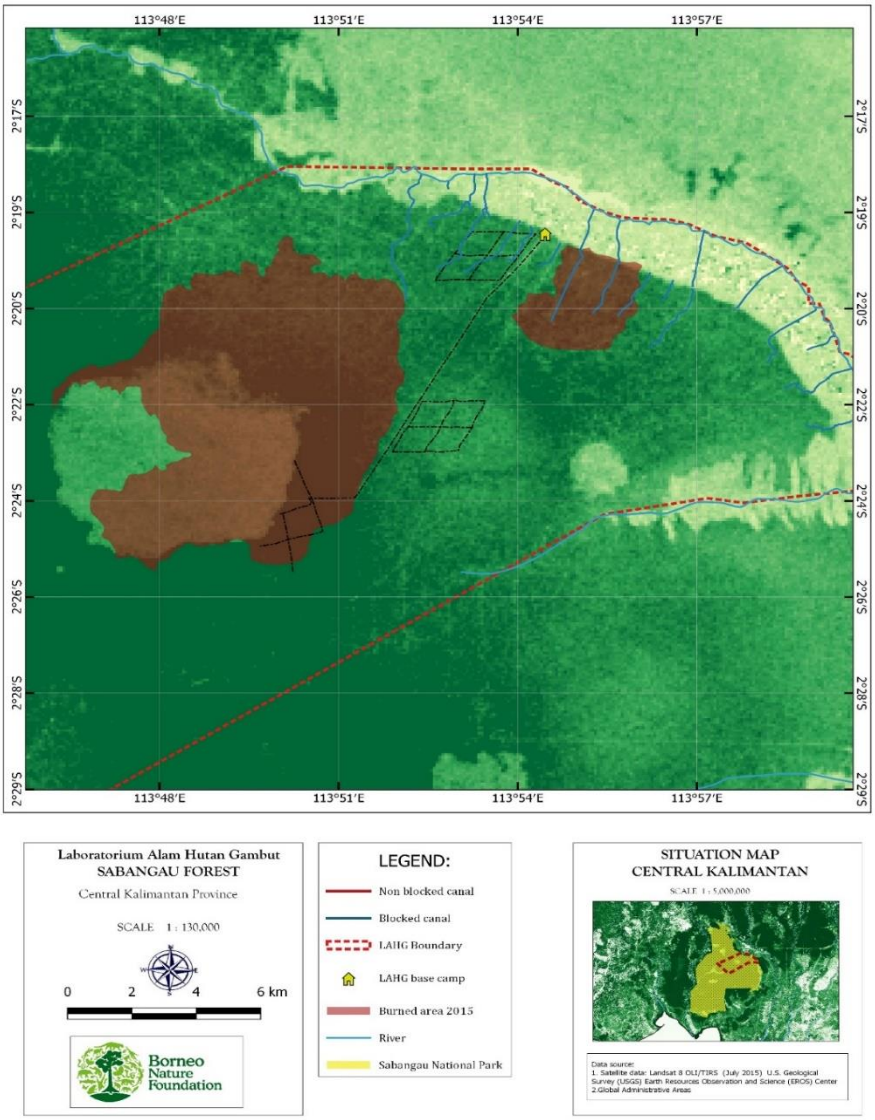


Figure 2. Burned areas of the Laboratorium Alam Hutan Gambut, Sebangau Forest (Ripoll Capilla, 2016).

1.2.4. Data Collection Procedure

BNF’s Orangutan Behaviour Project has been collecting data on orangutan behaviour and ecology since 2003. The project has followed over 100 individuals and collected over 20,000 focal follow hours. Fieldwork conducted as part of this thesis adds to BNF’s long-term dataset and my analysis utilises the previous data collected. Fieldwork took place between March 2019 and January 2020 in the LAHG using BNF’s Standard Operating Procedure for collecting data from wild, habituated orang-utans (Morrogh-Bernard *et al.* 2002). In order to locate orang-utans, I, along with members of the field team, conducted ‘search’ days. Two to five people would search systematically in targeted areas of the 3 km x 3 km research grid (Fig 3). Searching routes were pre-arranged on the morning of the search so that each person was searching as efficiently as possible. Team members would search alone to minimise noise and maximise search effort. Searching for orang-utans involved walking very slowly along the pre-decided route to find signs of orang-utans. Orang-utans were usually encountered by hearing movement in the trees, eating, or seeing fresh signs of food on the ground. Search days started at 08:30 and finished at 15:00 if no orang-utan was found. If an orang-utan was found, two members of the search team would follow until it built the night nest. Upon encountering an orang-utan, individuals were identified by experienced field staff and data collection began once both observers who were assigned to data collection for that day had arrived with the orang-utan.

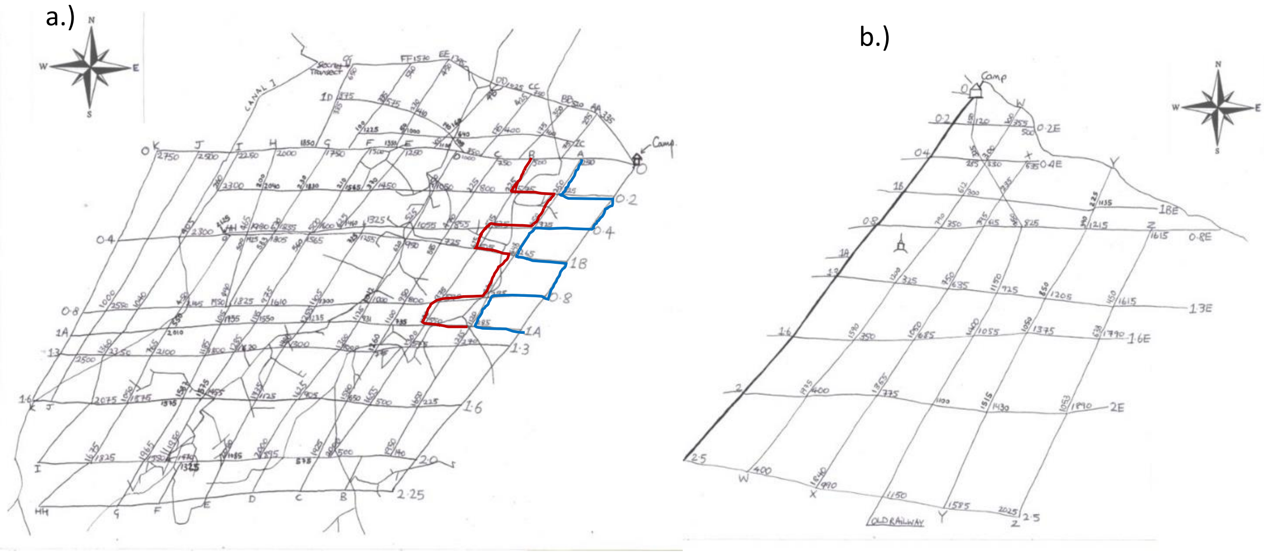


Figure 3. Maps of the a.) west and b.) east of the research grid. Red and blue lines indicate an example route for a 2-person search team.

The goal of orang-utan follows for this project were to obtain three types of data; behavioural, urine samples, and faecal samples. A three-person team would follow an orang-utan during their entire period of daily activity; known as nest-to-nest. Orang-utans were always followed nest-to-nest unless they were lost or became stressed as a result of observer presence. In such cases, follows were stopped. On average, 81% of follows end at the nest, with 51% being nest-to-nest follows. One person was responsible for recording behavioural data, one person was responsible for recording other data relevant for BNF's long-term monitoring (GPS points), and another person was responsible for collecting urine and faecal samples. The team would aim to arrive at the nest before the orang-utan woke up, at approximately 04:50, in order to start data collection as soon as the orang-utan began its daily activities.

Chapter 2: Impacts of the 2015 Forest Fires on the Behaviour and Health of Bornean Orang-utans

2.1. Abstract

Understanding how animals respond to anthropogenically-induced habitat disturbance is a key question in conservation biology. Behavioural and physiological changes act as an early warning system for subsequent population-level effects, allowing implementation of measures to prevent population declines. Anthropogenic disturbance causes reductions in food availability, fragments areas, and releases pollutants, generating additional stress on an animal's ability to meet its energy requirements and maintain a good physiological condition. The Bornean orang-utan is experiencing rapid population decline due to logging, oil palm plantations, hunting, and most recently, loss of habitat due to fire. Forest fires are now one of the greatest threats to orang-utan populations inhabiting peat-swamp forests yet are one of the least studied. I investigated the behavioural and physiological effects of a major fire event on orang-utans in Sebangau peat-swamp forest. Using over 8056.8 hours of observations on orang-utan activity patterns collected between 2011 and 2019, I showed that orang-utans decreased their active period and overall resting time over four years post-fire in comparison to pre-fire time allocations. In the short-term, orang-utans increased their resting time up to nine months after the fire. Orang-utans did not experience a negative energy balance, indicated by the extremely low presence of ketones in urine samples. Using 262 urine samples collected between 2009 and 2019, I showed that, on average, male orang-utans have lower hydration levels compared to female and young orang-utans. I found variation in hydration levels across the fire period however, further investigation of hydration levels over finer time increments and of alternative physiological markers are needed to be conclusive about the effects of fire on orang-utan physiology. Groundwater level, food availability, and age/sex class also affected orang-utan activity budgets and hydration status, hence seasonality, orang-utan age, and sex should be considered when investigating the impacts of anthropogenic change. As forest fires are becoming increasingly frequent and severe, these changes in activity budgets are likely to affect the energetic balance of orang-utans more severely, reducing

individual fitness and subsequently inducing population-level impacts upon birth and death rates.

2.2. Introduction

The way in which animals allocate time to different activities has important implications for their fitness. To meet energetic requirements and maintain a healthy physiological condition, animals must spend sufficient time carrying out behaviours such as feeding, travelling, resting, and socialising (McNamara and Houston, 1986). Such time allocations, termed ‘activity budgets’, are highly influenced by physical, ecological, and social factors. There is a growing understanding that anthropogenic activities cause animals to alter their behaviour to cope with associated changes in food availability, habitat connectivity, and population densities (McLennan *et al.* 2017). The effects of habitat disturbance on activity budgets are likely to differ between species and among individuals of the same species, due to differences in age/sex class traits, body size, dietary requirements, and the type and severity of habitat disturbance (Clutton-Brock, 1977; Strier, 1987; Li and Rogers, 2003). Such imposed changes in activity budgets may be detrimental to an animal’s energy balance, worsening their physiological condition and reducing survival and reproduction. Understanding how anthropogenic activity induces behavioural and physiological change in animals can provide an early warning system for future population-level effects and is therefore critical information for the conservation of endangered species (Wildermuth *et al.* 2012; Cooke *et al.* 2014).

Anthropogenically-induced habitat disturbance is the main threat to many primate species, with 61% of non-human primates now classed as vulnerable, endangered, or critically endangered (IUCN, 2020). Activity budgets of primates are well studied, with some studies comparing activity budgets of animals occupying habitats of varying degradation levels. For example, white-headed langurs (*Trachypithecus poliocephalus*) in a highly disturbed area spent more time feeding and young langurs spent less time playing (Li and Rogers, 2003). In contrast, lion tailed macaques (*Macaca silenus*), Tana River red colobus (*Piliocolobus rufomitratus*) and black and white colobus (*Colobus guereza*) fed for less time in highly disturbed habitats compared to less disturbed habitats (Menon and Poirier, 1996; Marsh *et al.* 1981; Oates, 1977). Some studies suggest an energy conserving strategy in response to reduced food availability in damaged habitat. Lar gibbons (*Hylobaetes lar*) and black-crested Sumatran langurs (*Presbytis melalophos*) spent more time resting and less time feeding and travelling after selective logging occurred in their habitat which was thought to be due to a reduction in their preferred foods (Johns, 1986). Here I investigate the impact of the most rapidly progressing type of anthropogenic habitat degradation in a peat-swamp forest, fire, on the activity budgets and physiological condition of one of the world's most iconic and critically endangered primates, the Bornean orang-utan (*Pongo pygmaeus*).

Forest fires are likely to be a significant driver of behavioural alteration in primates due to their rapid and drastic effects of food availability; yet have received little research attention as compared to other forms of habitat disturbance, such as logging and agriculture. Fire is indiscriminate and has the potential to remove all kinds of vegetation in its path. In addition to killing living vegetation, fire also limits the growth of secondary succession species and promotes the growth of pioneer species (Woods, 1989). Even in areas which have not been directly burned but are affected by smoke, trees can increase leaf shedding which may have detrimental effects on future investment in fruit production (Harrison *et al.* 2016). Leaf shedding and any consequential disruption in phenology alters the composition and distribution of food sources, and hence is likely to affect primate behaviour and survival in the long-term. One of the major issues for primates is loss of fruiting trees and fragmentation of areas. Changes in primate activity budgets have often been attributed to a reduction in fruit availability. Spider monkeys (*Ateles geoffroyi*) in Belize decreased their time spent feeding and increased inactivity after a fire and hurricane. They also increased their consumption of less favourable foods such as unripe fruit and leaves and decreased consumption of ripe fruit, most likely due to lack of availability (Champion, 2013 unpublished data). Hence, there is an indication that forest fires can result in reduced consumption of preferred foods, which will likely alter the energy balance of individuals and result in compensations in energy expenditure by adjusting time spent on activities other than feeding.

As well as food availability being a major driver of primate behavioural change, other conditions created by fire may also induce behavioural adjustments and changes in physiological condition. Smoke from peat fires is particularly hazardous and is known to have negative effects on human health, such as bronchial asthma, bronchitis, acute respiratory infection (Aditama, 2000), and cause death (Koplitz *et al.* 2018). Given the close similarities between human and primate physiology, the effects of smoke on bodily function in primates is likely to be the same (e.g. Black *et al.* 2017). Some studies have indicated the negative effects of smoke from forest fires on primate health. For instance, Erb *et al.* (2018) showed that orang-utans conserved energy after a smoke period by increasing resting time and decreasing travelling time. Erb *et al.* (2018) also found a greater production of ketones after the smoke period. Ketones are produced in the urine when an animal experiences a negative energy balance so must catabolise fat reserves to attempt to meet energy requirements and are a useful, non-invasive indicator of physiological condition. (Robinson and Williamson, 1980). This negative energy balance was unlikely due to low food availability as orang-utans increased their calorific intake after the smoke period. An increase in ketosis combined with greater calorie intake and energy conserving strategies suggests that an alternative physiological stressor such as smoke inhalation was resulting in orang-utans altering their activity patterns to conserve energy. Hence, it is important to consider physiological indicators of health in line with behavioural adjustments to fully understand the effects of fire on primates.

Another non-invasive measure of physiological condition is the specific gravity (SG) of urine. SG measures the concentration of excreted molecules in urine, with a higher value indicating lower hydration (Chadha *et al.* 2001). Ring-tailed lemurs (*Lemur catta*) living in a more degraded habitat showed higher specific gravity of urine, along with other measures of dehydration. This may be attributed to the associated effects of habitat degradation on food availability. It was suggested that the more arid plant community of the degraded habitat provided less dietary water than the undisturbed area (Singleton *et al.* 2015). As most primates typically obtain some water from their diet (Carter and Bradbury, 2016), a reduction in the availability of foods with a high water content (e.g. fruits; Sourd and Gautier-Hion, 1986; and leaves; Oates *et al.* 1980) may contribute to lower hydration levels (Singleton *et al.*

2015). These studies highlight the detrimental effects of fire and other forms of anthropogenic disturbance on primate health and emphasise the need to investigate behaviour and physiological condition concurrently. An impaired physiological condition may reduce survival and reproductive output, consequently causing population decline if sustained in many individuals over a long period.

Forest fires are occurring in peat-swamp forests with increasing frequency and severity over recent years (Langner and Siegert, 2009; Taylor, 2010; Hoscilo *et al.* 2011; Gaveau *et al.* 2014; Miettinen *et al.* 2016). Peat-swamp forests are rainforests with a naturally waterlogged, peat substrate, with low to medium canopy (Page *et al.* 2006). However, most peat-swamps have been subject to intense anthropogenic disturbance through logging and drainage for agriculture and many areas have become much drier, making them highly susceptible to fire. The high volume and low density layers of peat makes it a highly flammable substrate once dried out, with fires able to burn below as well as above ground for months or years. Indonesia contains some of the most extensive peat deposits in the world, and in 2015, experienced one of the worst fire events on record. 2.6 Mha of land was burnt, of which 33% was peatland (Glauber *et al.* 2016). It is estimated only 36% of the historical peat-swamp area remains, and disturbance is most extreme in Kalimantan (the Indonesian part of Borneo) where only 7.4% remains (Posa *et al.* 2011; Miettinen *et al.* 2016). Thus, fires poses a significant threat to wildlife in the form of peat-swamp habitat loss. This is particularly eminent for the Bornean orang-utan which is already classed as critically endangered. Peat-swamp forests are some of the last, large areas of viable orang-utan habitat and hold the largest remaining populations (Ancrenaz *et al.* 2016; Utami-Atmoko *et al.* 2017). Bornean orang-utans have experienced more than a 60% population decline since 1950 (Ancrenaz *et al.* 2016) and will have lost approximately 61% of their habitat by 2025 (Wich *et al.* 2012). Therefore, studying the effects of fire on orang-utans is imperative in understanding their ability, or lack of, to adapt behaviourally and cope physiologically. This will be important in determining consequences on survival and reproduction, and any potential population declines.

Based on the previous research discussed, I generate three hypotheses. Firstly, orang-utans will display energy conserving strategies in the initial months after the fire period in response to the unhealthy conditions created by smoke from peat fires.

Energy conserving strategies will be shown as reduced active period, increased feeding time, increased resting time, and decreased travelling time. Secondly, as time after the fire increases and smoke exposure decreases, orang-utans will reduce energy conserving strategies. Thirdly, orang-utans will show a reduction in physiological condition after the fire period, indicated by a greater presence of ketones and higher specific gravity in urine samples. This study builds upon previous research by investigating changes in orang-utan activity budgets and physiological condition up to four years after a fire event, as well as the period immediately following the fire event. I also build upon previous research by investigating specific gravity levels, as well as ketones, in orang-utan urine to assess changes in hydration as another biomarker of orang-utan health. Knowledge of how fire influences orang-utan activity budgets and physiological condition is important for understanding the ecological traits of fire affecting orang-utan survival, and thus how effects can be mitigated. A clearer picture of behavioural and physiological response could aid in forest restoration (e.g. planting important food trees), designing education programmes on the safe use of fire in local communities, and provide evidence for government legislation on the use of fire by large companies to clear land in order to conserve this species and others that inhabit peat-swamp forests.

2.3. Methods

2.3.1. Activity budget data collection

The study was conducted in the Laboratorium Alam Hutan Gambut (LAHG) research area which lies within the Sebangau forest catchment, Central Kalimantan, Indonesia (2°19'S and 113°54'E; Fig. 1). The LAHG has experienced substantial anthropogenic disturbance. Until 1997, it was a legal timber concession, but was subsequently designated for scientific research. From 1997 to 2005, illegal logging occurred leading to the construction of many canals cut through the peat to float timber out to sawmills (Morrogh-Bernard, 2009). This resulted in peat drainage and subsidence, altering the delicate hydrological balance and increasing the risk of fire in the dry season. Between the 5th August and 8th November 2015, Sebangau National Park lost 510.3km^2 of forest cover due to fires (Mang, 2017). Within the LAHG, two large patches of forest burned to the east and south-west of the research camp (Fig. 2).

Standardised field data collection procedures were used to collect data on orang-utan activity budgets from habituated individuals (see Morrogh-Bernard *et al.* 2002). To locate orang-utans, ‘search’ days were conducted by walking very slowly and quietly through the forest to look and listen for signs of orang-utans. Upon encountering a habituated individual, it was followed (no closer than 10m) and data were recorded on the primary behaviour being carried out using instantaneous sampling at five-minute intervals (see Appendix I for ethogram and datasheet). Primary behaviours (in order of notation priority) included feeding, nest building, special behaviours (e.g. self-medication or manipulating objects), mating, aggressive-dominance, social playing, social grooming, other social activities, aggression to another animal, aggression to observer, infant behaviours, travelling, self-grooming, and resting. If multiple activities occurred simultaneously, the behaviour with highest notation priority was recorded, i.e. if an orang-utan was eating whilst travelling, ‘feeding’ was recorded. Behaviours of particular interest were feeding, travelling and resting, with all other primary activities grouped into an ‘other’ category for analysis. The time the orang-utan woke up and finished building the night nest was recorded to calculate the length of the active period. With the exception of females with infants, orang-utans nest alone and very rarely change location during the night, therefore I could be sure of the identity of the individual.

2.3.2. Assessment of physiological condition

Physiological condition of orang-utans was assessed by examining ketones and the specific gravity (SG) of urine samples. Samples were collected in the early morning as the orang-utan left its night nest to begin daily activities. Samples were collected in one of two possible ways; by holding a long stick with a plastic bag on the end to catch the urine as it fell, or by pipetting from leaves on the ground. The former technique was preferred to reduce chance of contamination of the urine by groundwater. If urine was pipetted from the ground, samples were not taken if it had rained the previous night and effort was made to take samples from urine pools on leaves. If it had rained the previous night or there was a lot of water mixing with the urine, the sample was not collected as this would have made the reading inaccurate. For standardisation, only samples from the early morning were collected and tested, even if there was another opportunity to collect urine during the follow. This was to account for that fact that hydration levels may vary throughout the day with what orang-utans eat and how much they travel. Urine samples were tested for ketones with a Siemens Multistix 10SG reagent strip in the field as soon as possible after collecting. 40 seconds after administering the urine onto the test pad, the level of ketones in the urine was recorded (corresponding acetoacetate concentration in brackets): negative, trace (<0.5mmol/L), low (1.5mmol/L), medium (4mmol/L), high (8mmol/L), or very high (>16mmol/L). Urine was pipetted into a 2ml plastic vial for transportation back to the research station to test SG using a refractometer.

2.3.3. Data Analysis

All analyses were conducted in R version 3.6.3 (R Core Team, 2020). For activity budget analysis, the *glmmTMB* package (Brooks *et al.* 2017) was used to create generalized linear mixed models (GLMM). Separate models were fit for each response variable; length of active period, time spent feeding, time spent resting, time spent travelling. Predictors included in all global models were: fire time, age/sex class, food availability (FA), and groundwater level as fixed terms, and orang-utan ID as a random term. Fire time was split into pre-fire (46 months before September 2015) and post-fire (49 months including and after September 2015). Short-term effects of fire were investigated over a maximum of 12 months after the fire, and long-term encompassed the entire 49 months of the post-fire period. Orang-utans were classified into age/sex categories, in line with widely used classifications (Table 1; Morrogh-Bernard *et al.* 2009). FA was calculated from monthly surveys of six transects running east-west in the research grid, each divided into two sub-plots of size 300x5m (Plots 0) and 500x5m (Plots 1) (covering a total of 2.4 ha). Plots 0 were surveyed for trees 10-19.9 cm dbh and over the six transects, totalled a combined plot area of 0.9 ha. Plots 1 were surveyed for trees >20 cm dbh, lianas and figs, and totalled a plot area of 2.4 ha. In order to include all sampled trees in the FA calculation and to represent each size class in proportion to their availability, I used the following equation to calculate an estimated monthly FA:

$$FA = [\ F10 / N10 * P10\ ] + [\ F20 / N20 * P20\ ]$$

where: F = the number of trees in fruit for each size class (10 = 10-19.9 cm dbh; 20 = >20 cm dbh), N = the total number of trees sampled for each size class, and P = the proportion of trees that are in each size class (calculated from the 0.9 ha subset of the plots; P10 + P20 = 1) (from Morrogh-Bernard, 2009). Groundwater level was measured at five monitoring locations (excluding canal locations) per month. At each monitoring location, there is a permanent water pipe of which the height above ground is measured (a). A dry stick is inserted into the water pipe and after removal, the dry part of the stick is measured (b). The groundwater level is calculated from a – b, and was averaged across the five locations by month. If the water level was below ground, the value was negative.

Activity budget data were collected between October 2011 and October 2019 and only data from habituated individuals with more than 50 hours of data in total each were used. Analyses were restricted to using full day, nest-to-nest follows because the unit of measurement chosen was minutes, thus, if orang-utans distributed their time between different activities unevenly throughout the day, (e.g. feeding in the morning to replenish energy after the night, or travelling more in the afternoon to search for a suitable nesting tree), incomplete follows would have misrepresented the data. The data analysed consist of a total of 8056.8 hours of observations from 25 individuals, 20 of which were present in the pre-fire period, 17 in the post-fire period, and 12 in both periods. For analyses of time spent feeding, resting, and travelling, the daily active period was used as an offset. The dataset includes 4 age/sex classes: sexually active female (SAF), flanged male (FM), unflanged male (UFM), and adolescent (Table 1.). Data from the age/sex class nulliparous female (NLF) were removed from analysis as they consisted of only 7 full day follows from 1 individual. Sample size for each age/sex and fire period level is shown in Appendix II Table 1.

Between March 2009 and November 2019, 337 urine samples were collected. 159 of the samples were tested for ketones in the field straight after collection. Only samples tested for ketones in the field were used in analysis as the colour of the urine can change quickly and obscure the subtle differences in the Multistix test result colour. Two samples were excluded from analysis due to observer uncertainty in the Multistix test strip colour. Thus, the ketone analysis included 157 samples (from 31 orang-utans), 65 samples were obtained from 24 orang-utans in the pre-fire period and 92 samples were obtained from 14 orang-utans in the post-fire period. Naumenko *et al.* (2019) showed that the categories of 'negative' and 'small' cannot be statistically differentiated, therefore I pooled 'negative', 'trace' and 'small' into one 'negligible' category. It was not possible to analyse the ketone data statistically as 155 of the 157 samples were negligible therefore there was not sufficient variability in the data. The SG of 202 urine samples was measured using a refractometer. Only samples for which a SG value was obtained with a refractometer were used as the Multistix scale for SG is not a high enough resolution for meaningful analysis. 20 samples were excluded due to likely errors in the data entry. Thus, SG analysis included 182 samples (from 33 orang-utans), 101 samples were obtained from 27 orang-utans in the pre-fire period, and 81 samples were obtained from 13 orang-utans in the post-fire period. The *glmmTMB* package was used to create a generalized linear mixed model (GLMM) to analyse changes in urine SG. The SG dataset includes five age/sex classes (SAF, FM, UFM, Adolescent, Infant; Table 1.). Sample size for each age/sex and fire period level is shown in Appendix II Table 2 and Appendix II Fig. 1. Predictors included in the global model were fire period, FA, groundwater level, and age/sex class as fixed terms, and orang-utan ID as a random term.

For all analyses, the *dredge* function from the package *MuMIn* (Barton, 2019) was used to determine which of the models derived from the global model received the most support. Models were ranked using AICc. The top model sets were formed from application of the nesting rule and retention of models with delta < 6 (Richards *et al.* 2011; Harrison *et al.* 2018). Model fit was assessed using standard residual plots and Cook's distance to identify particularly influential datapoints. Model outputs were obtained using *tab_model* from *sjPlot* (Ludecke, 2020) of the best supported model and are reported as the estimate (with standard error), confidence intervals (CI) and p-value.

Table 1. Description of the age/sex classes.

Age/Sex Class	Description

Sexually active female (SAF)	Sexually mature adults able to produce offspring. Therefore, are either pregnant accompanied by an infant or without offspring because of juvenile independence.
Nulliparous female (NLF)	Sexually mature female with no accompanying offspring and not pregnant.
Flanged male (FM)	Fully developed sexually mature male with large cheek pads and throat sac.
Unflanged male (UFM)	Undeveloped sexually mature male with no cheek pads.
Adolescent	Sexually inactive and living independently of their mother.
Infant	Dependent on mother (suckling), travelling primarily on the mother’s body.

2.4. Results

2.4.1. Active Period

Mean (± SE) active period was 633 ± 2.5 minutes, after removal of the orang-utan ‘Indy’. Indy was identified to have high leverage over the data on the basis of Cook’s distance as she accounted for 20% of the datapoints and her mean active period was 15 minutes shorter than the mean excluding her records. The best supported model included the fixed effects: fire time, age/sex class, food availability (FA), and groundwater level, with interactions between age/sex and fire time, age/sex and FA, age/sex and groundwater level, and FA and groundwater level (Table 2 for summary of best supported model; see Appendix III Table 1 for a comparison of the models in the top model set). Orang-utan ID was included as a random term. Active period of sexually active females (SAF) was significantly shorter in the post-fire period compared to the pre-fire period (*b* ± s.e = -42.47 ± 7.11, CI = -64.09 - -20.85, p < 0.001; Fig 4). A significant interaction between age/sex class and FA on active period was identified, with flanged males (FM) having a longer active period than adolescents at low FA (*b* ± s.e = -95.90 ± 31.52, CI = -191.77 - -0.03, p = 0.050). A significant interaction between age/sex class and groundwater level on active period was identified. Active period of FM decreases as groundwater level increases (*b* ± s.e = 205.56 ± 44.06, CI = 71.53 – 339.60, p < 0.001). FM have a longer active period than SAF and adolescents when groundwater level is low (FM-adolescent: *b* ± s.e = -163.64 ± 48.95, CI = -312.52 - -14.76, p = 0.020; FM-SAF: *b* ± s.e = 107.74 ± 32.39, CI = 9.21 – 206.27, p = 0.021). Adolescents have a longer active period when groundwater level is high (*b* ± s.e = 95.10 ± 29.92, CI = 4.09 – 186.11, p = 0.033; Fig 5, see Appendix III Table 2 for all significant post-hoc comparisons).

Table 2. Summary of the best supported model for length of orang-utan active period. The variance (s.d.) attributed to the nested random term 'Orang-utan ID' is 504.5 (22.46). Comparisons of the top candidate models can be seen in Appendix III Table 1.

	estimate	std. error	CI	z value	p-value
(Intercept)	585.40	33.56	519.62 – 651.17	17.44	<0.001
Age/Sex Class					
Adolescent	0	0	-	-	-
FM	80.67	44.12	-5.79 – 167.14	1.83	0.067
SAF	9.27	35.58	-60.46 – 79.01	0.26	0.794
UFM	87.79	67.17	-43.87 – 219.45	1.31	0.191
Fire Time					
Post	0	0	-	-	-
Pre	10.27	13.84	-16.85 – 37.39	0.74	0.458
Food Availability	5.48	3.32	-1.04 – 11.99	1.65	0.099
Water Level	-0.10	0.92	-1.91 – 1.71	-0.11	0.914

Age/Sex Class : Fire Time interaction					
Adolescent : Post	0	0	-	-	-
FM : Pre	-21.58	18.70	-58.23 – 15.06	-1.15	0.248
SAF : Pre	32.20	15.78	1.27 – 63.14	2.04	**0.041**
UFM : Pre	-8.45	32.67	-72.49 – 55.58	-0.26	0.796
Age/Sex Class : Food Availability interaction					
Adolescent : Food Availability	0	0	-	-	-
FM : Food Availability	-11.01	4.15	-19.15 – -2.86	-2.65	**0.008**
SAF : Food Availability	-5.62	3.57	-12.62 – 1.38	-1.58	0.115
UFM : Food Availability	-12.25	7.74	-27.43 – 2.92	-1.58	0.114
Age/Sex Class : Water Level interaction					
Adolescent : Water Level	0	0	-	-	-
FM : Water Level	-1.97	0.56	-3.06 – -0.89	-3.55	**<0.001**
SAF : Water Level	-0.83	0.48	-1.77 – 0.12	-1.72	0.085
UFM : Water Level	-0.85	0.78	-2.39 – 0.68	-1.09	0.277
Food Availability : Water Level interaction	0.06	0.08	-0.10 – 0.22	0.73	0.467

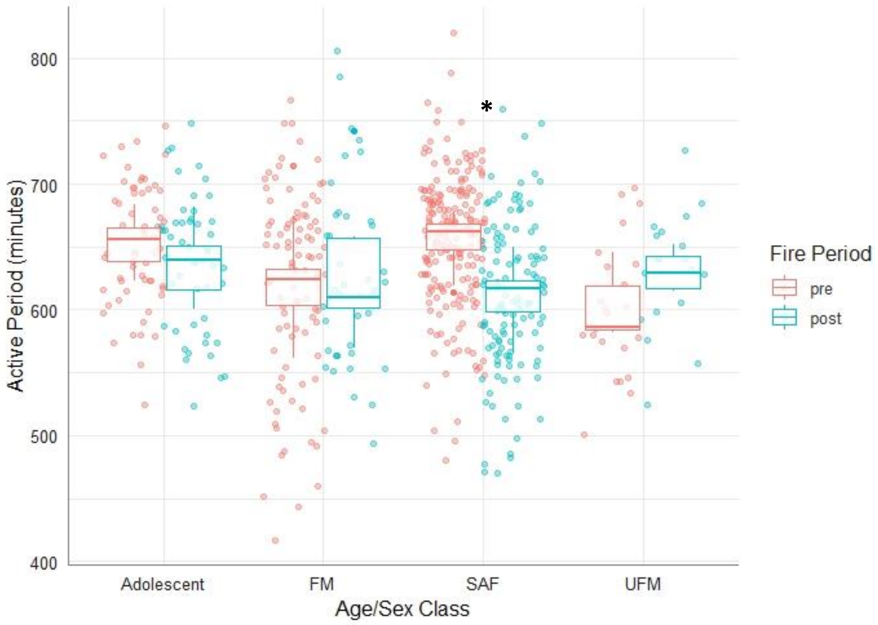


Figure 4. The active period length of each age/sex class split by fire period based on model predictions. Boxplots show the mean active period with hinges of the box representing the 25% and 75% quartiles, and whiskers showing 95% confidence intervals. Points show raw data from each orang-utan follow.

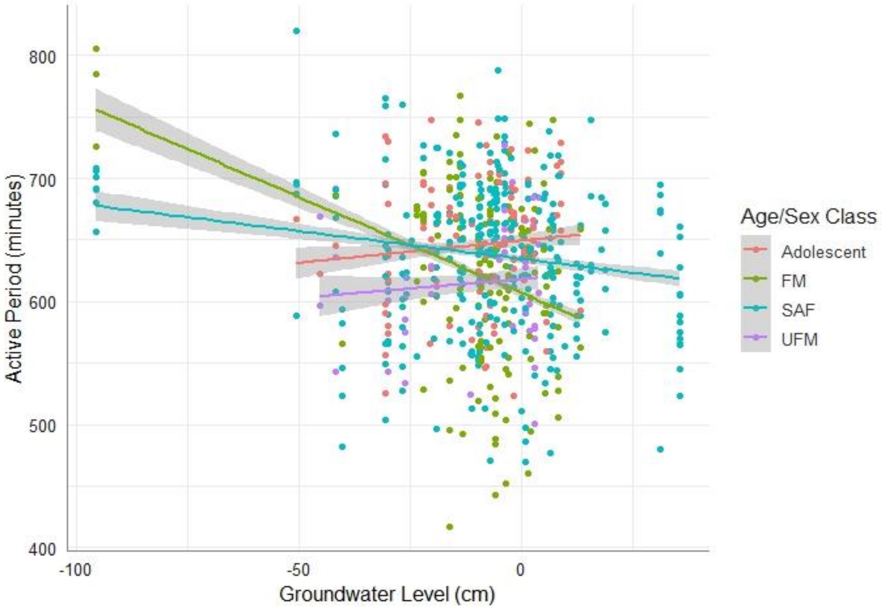


Figure 5. The active period length of each age/sex class across monthly groundwater levels, based on model predictions. Points show raw data from each orang-utan follow. Model predications are represented by linear regression lines with 95% confidence intervals shown.

2.4.2. Activity Budgets

Overall, orang-utans spent most of their active period feeding (mean ± SE = 420 ± 2.9 minutes, corresponding to 66.2 ± 0.4% of the total activity the active period), followed by resting (mean ± SE = 121 ± 2.3 minutes, 19.0 ± 0.4%), travelling (mean ± SE = 65 ± 1.2 minutes, 10.1 ± 0.2%) and other activities (mean ± SE = 30 ± 1.1 minutes, 4.8 ± 0.2%). Time spent on each activity pre- and post-fire can be seen in Table 3.

Table 3. Mean time ± SD spent on each activity pre-fire and post-fire. Time is in minutes and the values in brackets are the mean percentage ± SD of an orang-utan's active period spent doing that activity.

	Pre-fire	**Post-fire**
Feeding	421 ± 87 (665.0 ± 12.1%)	418 ± 72 (68.0 ± 10.3%)
Resting	130 ± 68 (20.1 ± 10.4%)	107 ± 52 (17.3 ± 8.4%)
Travelling	67 ± 35 (10.3 ± 5.1%)	61 ± 30 (9.8 ± 4.5%)
Other	30 ± 30 (4.6 ± 4.5%)	31 ± 29 (5.0 ± 4.7%)

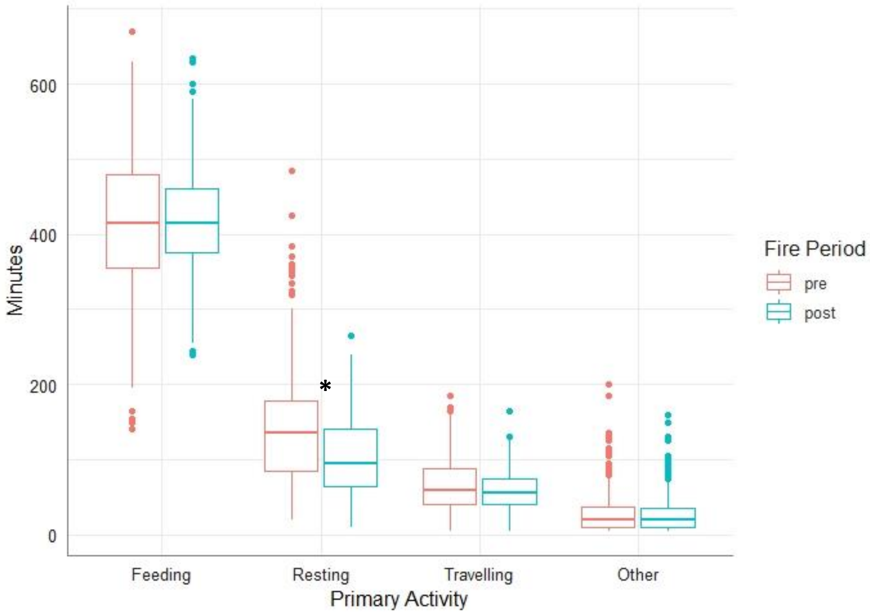


Figure 6. Time spent on each primary activity in the pre-2015 and post-2015 fire period. * indicates significant difference. The fire period explains 4.1% of the variance in resting time due to fixed effects.

Feeding data was normally distributed so a model with a gaussian family was fitted. Inclusion the fixed terms: age/sex class, FA, and groundwater level, with interaction between age/sex and groundwater level, and orang-utan ID as a random term produced the best fitting model (Table 4 for summary of best supported model; see Appendix III Table 4 for a comparison of the models in the top model set). Feeding time decreased as FA increased, however this was a weak relationship and explained just 1.1% of the variance due to fixed effects (*b* ± se = -2.67 ± 1.36, CI = -5.33 – -0.01, p = 0.049). Feeding time decreased as groundwater level increased, for FM and SAF only (FM: *b* ± se = 320.68 ± 55.53, CI = 151.90 – 489.46, p < 0.001; SAF: *b* ± se = 115.94 ± 21.98, CI = 49.13 – 182.77, p < 0.001; Fig 7a).

Table 4. Summary of the best supported model for time spent feeding during an orang-utan's active period. The variance (s.d.) attributed to the nested random term 'Orang-utan ID' is 1051 (32.42). Comparisons of the top candidate models can be seen in Appendix III Table 4.

	estimate	std. error	CI	z value	p-value
(Intercept)	434.13	18.72	397.45 – 470.81	23.20	<0.001
Age/Sex Class					
Adolescent	0	0	-	**-**	**-**
FM	-22.14	19.13	-59.64 – 15.35	-1.16	0.247
SAF	-20.19	12.12	-43.96 – 3.57	-1.67	0.096
UFM	28.79	25.47	-21.14 – 78.71	1.13	0.258
Food Availability	-2.67	1.36	-5.33 – -0.01	-1.97	**0.049**
Water Level	0.01	0.57	-1.10 – 1.11	0.01	0.993
Age/Sex Class : Water Level interaction					
Adolescent : Water Level	0.00	0.00	-	**-**	**-**
FM : Water Level	-2.45	0.71	-3.84 – -1.06	-3.46	**0.001**
SAF : Water Level	-0.89	0.59	-2.05 – 0.27	-1.50	0.133
UFM : Water Level	1.20	0.99	-0.75 –3.14	1.20	0.229

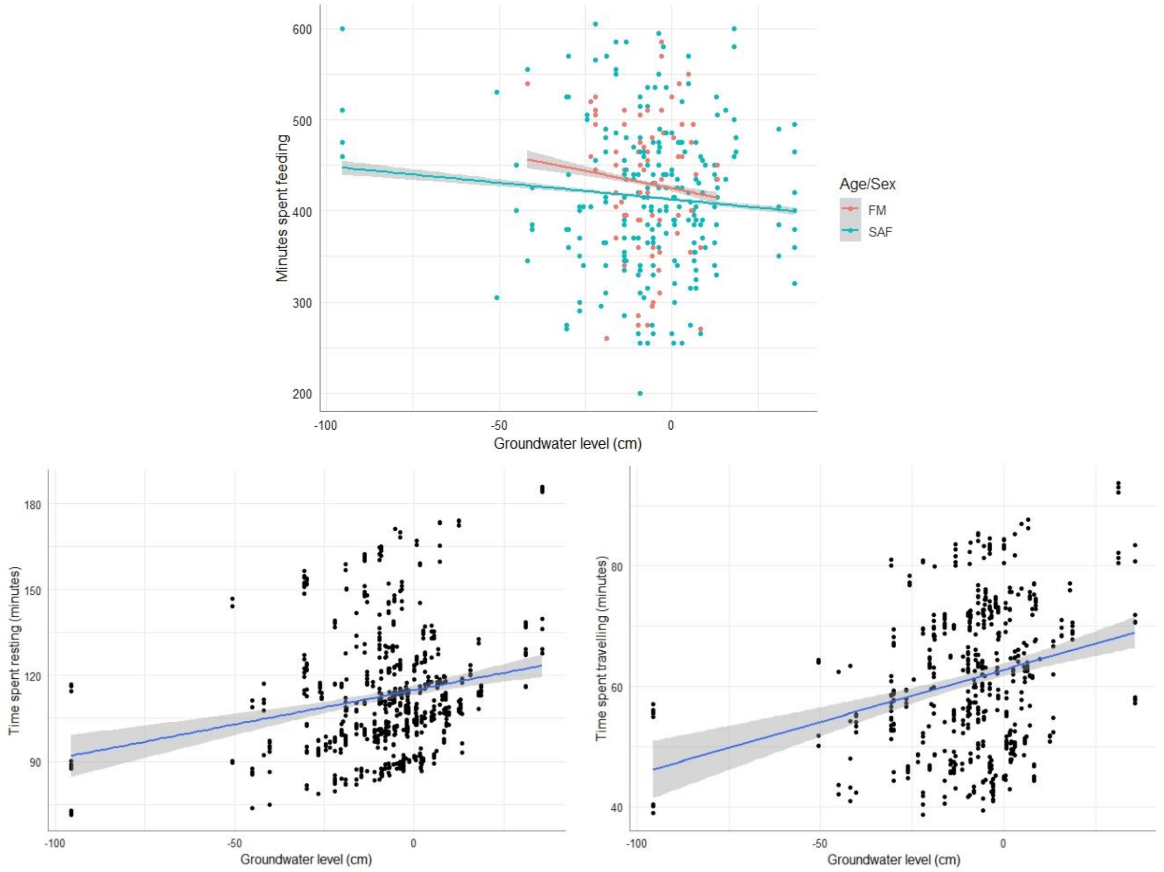


Figure 7. The effect of groundwater level on the time spent; **a.)** feeding; **b.)** resting; **c.)** travelling. Data have been back-transformed from model predictions for **b.)** and **c.)**, for which data were square-root transformed to fit assumptions of normality. Linear regression lines shown with 95% confidence

Resting data were non-normally distributed so was square-root transformed. The orang-utan Gracia was removed from analysis after Cook's distance revealed she had high leverage over the data. A generalised linear mixed model with gaussian error distribution which contained the fixed terms: fire time and groundwater level, and orang-utan ID as a random term, produced the best fitting model (Table 5 for summary of best supported model; see Appendix III Table 5 for a comparison of the models in the top model set). Orang-utans spent more time resting up to nine months post-fire (X^2_{19} = 52.388, p < 0.001; Fig 8b; see Appendix III Table 3 for pairwise comparisons between months). Over the entire four-year post-fire period, orang-utans spent less time resting compared to the pre-fire period (*b* ± se = -1.24 ± 0.22, CI = -1.68 - -0.80, p < 0.001; Fig 6 & 8a). Resting also increased as groundwater level increased, but this explained just 1.3% of the variance due to fixed effects (*b* ± se = 0.02 ± 0.01, CI = 0.01 – 0.03, p < 0.001; Fig 7b).

Table 5. Summary of the best supported model for time spent resting during an orang-utan's active period. The variance (s.d.) attributed to the nested random term 'Orang-utan ID' is 1.084 (1.041). Comparisons of the top candidate models can be seen in Appendix III Table 5.

	estimate	**std. error**	**CI**	**z value**	**p-value**
(Intercept)	4.95	0.273	4.42 – 5.49	18.15	<0.001
Fire Time					
pre	0	0	-	-	-
post	-1.24	0.225	-1.68 – -0.80	-5.53	**<0.001**
Water Level	0.02	0.005	0.01 – 0.03	3.67	**<0.001**

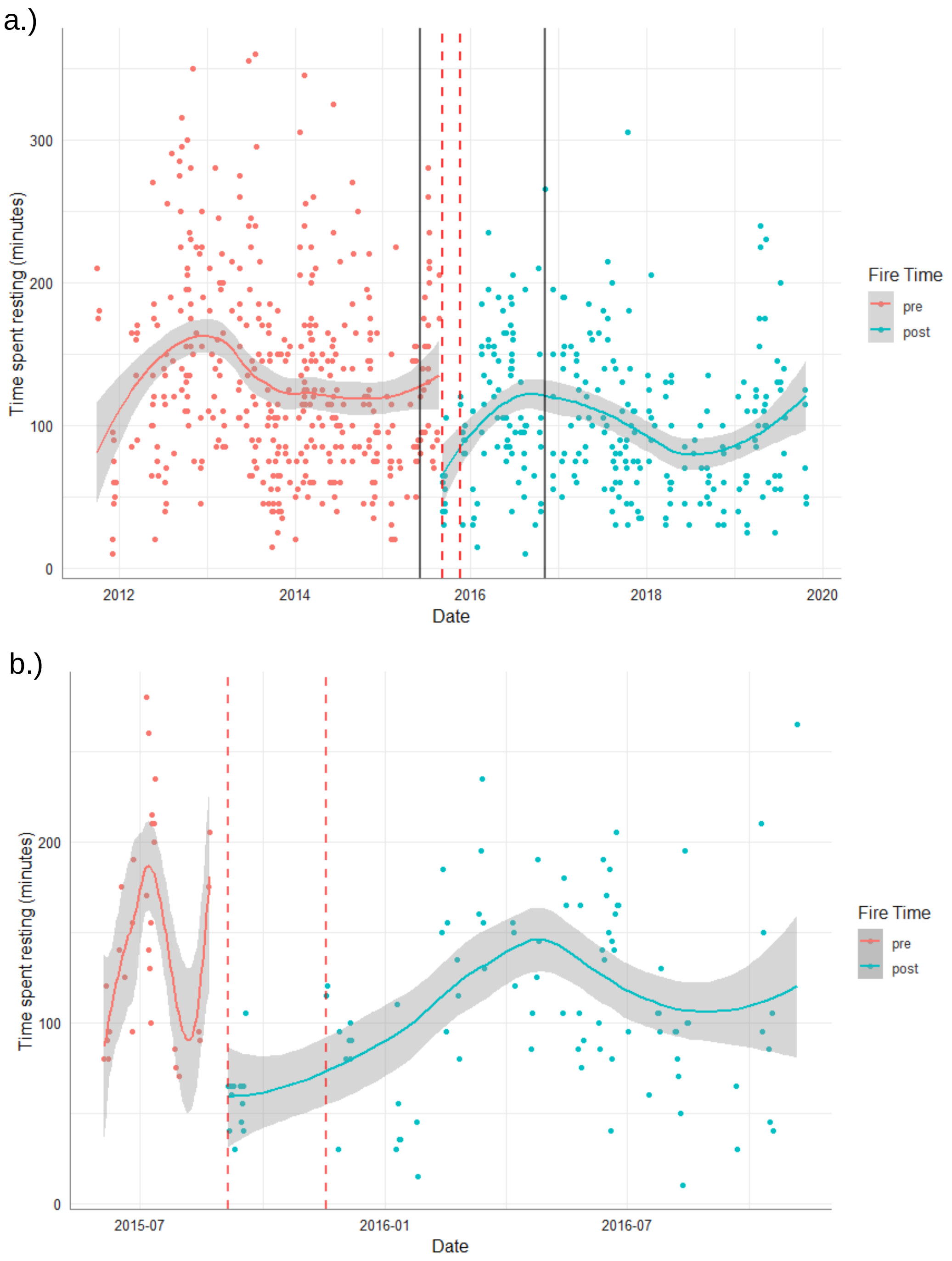


Figure 8. a.) The number of minutes orang-utans spent resting per follow from October 2011 to November 2019, with 'loess' regression lines and 95% confidence intervals. Grey solid lines define the region shown at higher resolution in Figure 8b. **b.)** The number of minutes orang-utans spent resting per follow between September 2015 and November 2016 with loess regression line and 95% confidence intervals. Red dotted lines indicate when the fires occurred.

Travelling data was non-normally distributed so was square-root transformed. Orang-utans Gracia and Indy were removed from analysis after Cook's distance revealed they had high leverage over the data. A generalised linear mixed model with gaussian error distribution which contained the fixed terms: age/sex class, fire period, FA, groundwater level, with interactions between age/sex class and fire period, and orang-utan ID as a random term, produced the best fitting model (Table 6 for summary of best supported model; see Appendix III Table 6 for a comparison of the models in the top model set). An increase in groundwater significantly increased time spent travelling (*b* ± se = 0.01 ± 0.005, CI = 0.0043 – 0.0230, p = 0.004; Fig 7c), although only 1.9% of the variation due to fixed effects was explained by water level.

Table 6. Summary of the best supported model for time spent travelling during an orang-utan's active period. The variance (s.d.) attributed to the nested random term 'Orang-utan ID' is 0.242 (0.492). Comparisons of the top candidate models can be seen in Appendix III Table 6.

	estimate	std. error	CI	z value	p-value
(Intercept)	1.29	0.53	0.256 – 2.323	2.445	0.014
Age/Sex Class					
Adolescent	0	0	-	-	-
FM	-0.54	0.54	-1.588 – 0.508	-1.010	0.312
SAF	-0.20	0.42	-1.025 – 0.620	-0.483	0.629
UFM	-1.05	0.66	-2.345 – 0.252	-1.579	0.114
Fire Time					
post	0	0	-	-	-
pre	0.29	0.42	-0.54 – 1.11	0.68	0.497
Food Availability	0.03	0.04	-0.06 – 0.11	0.66	0.508
Water Level	0.01	0.01	0.004 – 0.023	2.85	**0.004**
Age/Sex Class : Fire Time interaction					
Age_SexAdolescent:fire_timepost	0	0	-	-	-
Age_SexFM:fire_timepre	-0.68	0.59	-1.84 – 0.47	-1.16	0.246
Age_SexSAF:fire_timepre	0.26	0.50	-0.71 – 1.23	0.52	0.603
Age_SexUFM:fire_timepre	0.45	0.87	-1.25 – 2.14	0.52	0.604

2.4.3. Physiological Condition

98.7% of the samples analysed for ketones tested negligible, therefore I was unable to analyse these data statistically. For the two samples that were not negligible, one showed large and the other very large levels of ketones. They both came from the sexually active female ‘Indy’, one in the middle or end of dry seasons. The sample showing large levels of ketones also tested positive for nitrites and trace levels of leukocytes, indicating that Indy may have had an infection at this time. The sample showing very large levels of ketones did not show anything else unusual.

For specific gravity (SG) analysis, data were non-normal so were log-transformed. Inclusion of the fixed terms age/sex class and fire time, and the random term orang-utan ID produced the best fitting model (see Appendix III Table 7 for a comparison of the models in the top model set). SG varied significantly across age/sex classes (Fig 9a). FM and unflanged male (UFM) showed significantly higher SG than adolescents and infants (see Appendix III Table 8 for post-hoc pairwise comparisons). 27% of samples from UFM, 13% from SAF, and 24% from FM showed levels of SG above clinical dehydration levels (> 1.040). No samples from adolescents or infant showed levels of clinical dehydration. SG was significantly lower post-2015 fire compared to pre-fire, indicating that orang-utans were overall more hydrated after the fire, however this was a very weak effect explaining just 2% of the variance due to fixed effects (b ± se = 0.0045 ± 0.0021, CI = 0.0003 – 0.0008, p = 0.035; Fig. 9b). Mean SG pre-fire was 1.025, whereas it was 1.017 post-fire.

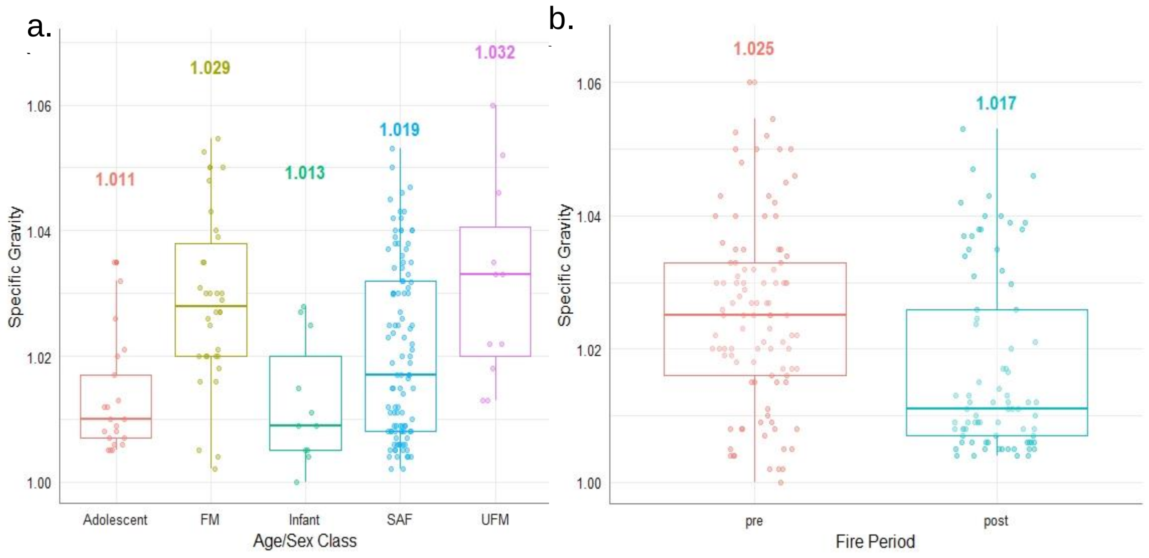


Figure 9. a.) A comparison of SG between age/sex classes. Mean SG for each age/sex class is labelled on the figure. **b.)** A comparison of the SG of urine between pre-fire and post-fire periods. Mean SG for each period is labelled on the figure.

2.5. Discussion

The way in which an animal's activity budget and physiological condition is altered in response to anthropogenic activity is a key question in conservation biology as it can provide an insight into how their fitness may be affected. This study suggests that both orang-utan activity budgets and measures of physiological condition are affected by fire disturbance. Time spent resting significantly increased in the first nine months after the fire event, indicating that orang-utans may have been trying to conserve energy by reducing their activity. In a similar study, Erb *et al.* (2018) showed that orang-utans increased their resting time three months after the 2015 fire period, which also coincided with an increase in urinary ketone levels indicating energy deficit. This study supports and adds to the findings of Erb *et al.* (2018), suggesting that fire causes orang-utans to increase their resting time in the short-term, and up to nine months, after a fire event.

This research builds on previous work by indicating that fire-induced energy conserving strategies may be temporary, as overall, orang-utans decreased their resting time over the full four-year period after the fire event. It is possible orang-utans are able to recover from the fire-induced energy changes and alter their activity budgets according. Some primate behaviour studies suggest that resting behaviour may decrease as animals allocate more time to other activities such as foraging to meet their energy requirements (Strum, 2010; Champion, 2013 unpublished data). However, as I found no effect of fire on feeding time, I cannot be confident in attributing this long-term decrease in resting time to an increase in foraging effort to replace lost energy. Therefore, I suggest examining other measures of foraging behaviour over the long-term, such as changes in diet and calorific intake. Orang-utans may spend more time feeding but ingest poorer quality foods, meaning that they have less time for resting in order to meet energy requirements. A reduction in sexually active female active period was found to be present and increasing throughout the four-year period after the fire event. Primate active period can be influenced by many factors such as social organisation, weather, reproductive status and food availability (FA) (Chivers, 1974, 1980; Lodwick *et al.* 2004). FA has been shown to be an important predictor of orang-utan active period, with active period decreasing as fruit availability decreases (Morrogh-Bernard *et al.* 2009; Vogel *et al.* 2017). Decreasing active period is an energy conserving strategy when energy intake is reduced as orang-utans will spend less time travelling and searching for food when the probability of finding food is low. Furthermore, a potential explanation as to why this was only observed in sexually active females may be that females experience more variable energetic demands through pregnancy and rearing offspring. However, considering evidence of negative energy balance was extremely rare over the entire study period (ketones were found in just 1.3% of samples), reducing active period may not have been an energy conserving strategy in this case. It is possible that orang-utans in the LAHG are able to meet their energy requirements and therefore do not need to continue searching for food and can end their daily activities earlier. This would support the support the finding of a reduction in resting time over the four-year post-fire period.

The minimal presence of ketones in orang-utan urine suggests that LAHG orang-utans were meeting their nutritional requirements. The lack of ketones present in urine samples is unusual compared to previous data from the LAHG. Between 2003 and 2007, ketones were present in 38% of samples and in 36% of the months with data (Harrison *et al.* 2010). The greater presence of ketones in the same population of orang-utans during this period is likely due to ecological stress in the form of illegal logging disturbance. Between 2003 and 2005, large trees were removed for timber and scaffolding, which decreased food availability and resulted in lower orang-utan densities in logged areas and refugee crowding in unlogged areas (Morrogh-Bernard *et al.* 2003; Morrogh-Bernard, 2009; Husson *et al.* 2015). Since then, the orang-utan population has been recovering but has not yet reached carrying capacity (Morrogh-Bernard, unpublished data). Therefore, the habitat quality may be sufficient for orang-utans to meet their energetic requirements, whilst being able to avoid intense competition over areas to establish home ranges and feeding patches. It is important to note that this ketone analysis was semi-quantitative and highly sensitive to reading inaccuracies. Multistix test strips are sensitive to moisture and thus the high humidity of the tropical climate may have impaired any sticks that were not sealed in airtight containers properly. Multistix test strips are also highly dependent on the reader's interpretation, so there is room for human error. Therefore, some samples recorded as negligible may be false negatives. Future research would benefit from investigating changes in other non-invasive, biomarkers of physiological condition. For example, faecal glucocorticoids which can indicate stress (Keay *et al.* 2006; Romano *et al.* 2010), or urinary cytokines and neopterin which signal a pro-inflammatory immune status (van Eeden *et al.* 2001; Behringer *et al.* 2017).

Other ecological factors such as FA and groundwater level also had effects on orang-utan activity budgets. At low FA, flanged males had a longer active period than adolescents. Flanged males usually have the shortest active period of all age/sex classes (Morrogh-Bernard *et al.* 2009), however when FA is low, they may be increasing their active period to increase their foraging effort. This may be essential for meeting energy requirements as flanged males have a much larger body size than other age/sex classes and often travel vast distances in search of receptive females, making their energy expenditure high. I also found a decrease in time spent feeding as FA increased. This was a very weak relationship but is plausible as an increase in FA indicates more higher quality foods in the environment (fruits and flowers), therefore orang-utans may not need to spend so much time eating as they will fulfil their energy requirements sooner compared to when they consume lower quality foods such as bark and leaves (Morrogh-Bernard *et al.* 2009).

The active period of flanged males decreased as groundwater level increased. Flanged males spend much more time travelling on the ground than other age/sex classes as arboreal travel is more energetically expensive due to the large body size and weight of flanged males. This is made more difficult as groundwater increases in the wet season, perhaps forcing flanged males to increase their arboreal travel. If they are expending more energy by travelling arboreally, flanged males may compensate by reducing their active period. Groundwater level also had a significant effect on time spent resting, travelling, and feeding. Resting and travelling behaviour increased, whereas feeding decreased (for flanged males and sexually active females) as groundwater level increased. However, for each behaviour, groundwater level explained < 2.5% of the variance due to fixed effects. It is unlikely groundwater level alone is driving these changes in time allocation. Groundwater level fluctuates seasonally, along with many other peat-swamp variables such as rainfall, food availability, and temperature. It may be that other factors, which correlate with groundwater level but were not included in this study, are more significant drivers of the observed behavioural changes. Future studies should investigate environmental correlates of groundwater level and their effects on orang-utan behaviour.

The specific gravity (SG) of flanged male and unflanged male orang-utan urine was significantly higher than the SG in the urine of sexually active females, adolescents and infants. This indicates that males experience higher levels of dehydration than females and their offspring, this being emphasised by the higher percentage of samples from males showing levels of clinical dehydration (SG > 1.040). Male orang-utans travel much further and have larger range sizes than females (Morrogh-Bernard *et al.* 2009; Singleton and van Shaik, 2002), so may be expending more energy and hence losing more water in the process. Furthermore, flanged males feed less than other age/sex classes so may also have a lower water intake as most of the moisture orang-utans ingest is through consumption of fruit (Morrogh-Bernard *et al.* 2009; Morrogh-Bernard, unpublished data). An overall lower SG of orang-utan urine samples in the post-fire period indicated higher hydration levels after the fire. This result is contrary to my prediction of a higher SG in the post-fire period. As fire period accounted for just 2% of the variance due to fixed effects, it is more plausible that this difference observed is as a result of the variation seen between age/sex class. SG may be lower in the post-fire period as more samples were obtained from sexually active females, adolescents and infants, and less from flanged males and unflanged males in this period. In fact, the percentage of samples obtained from flanged males (which exhibit, on average, higher SG) dropped by 31.5% from the pre to post-fire period. Whereas the percentage of samples from sexually active females increased by 22.9% (Appendix II Table 2; Appendix II Fig. 1). Since adult male orang-utans show significantly higher urinary SG than sexually active females, adolescents and infants, this difference in sample size for each age/sex class is a likely explanation for the lower average SG in the post-fire period.

Overall, evidence suggests that orang-utans employed an energy conserving strategy (in the form of increased resting time) in the initial months after the 2015 forest fire event, and reduced resting time and active period as time after the fire event increased, suggesting a potential ability to recover behaviourally after a fire event. Although a reduction in active period can be interpreted as an energy conserving strategy, in this case it is unlikely due to a lack of evidence of ketosis over the study period. The rare occurrence of ketosis, along with few cases of clinical dehydration, suggest that orang-utans in Sebangau are in good physiological condition. These results suggest that orang-utans display behavioural adaptation to forest fires but have no detectable decline in physiological condition. Future work should focus on investigating other markers of physiological condition such as cortisol, cytokines or neopterin which may better indicate changes in physiological condition. Future work would also benefit from more detailed investigation of the effect of fire on fruiting patterns in areas not directly burnt but affected by smoke and combining this with data on orang-utan diet and feeding behaviour. This would provide a better understanding of any effects of fire on orang-utan nutritional intake and available energy, rather than solely measuring time spent feeding. This study has shown that it is critical to study behavioural and physiological responses to fire over the long-term. Such long-term data can aid in assessing the recovery potential of populations, and when and how to implement conservation action.

Chapter 3: The Impacts of Seasonality and Fire in a Tropical Peat-Swamp Forest on Parasitic Infection in Bornean Orang-utans

3.1. Abstract

Parasitic infection can pose a significant threat to primate populations. Many primates are at risk due to anthropogenic activity such as fire, logging, agriculture, hunting, and the pet trade. It is widely known that anthropogenic activity negatively impacts primates in terms of food availability, density, and ranging, yet the impact of such activities on parasitic infection has scarcely been investigated. Understanding the factors that drive parasitic infection is critical in implementing effective conservation actions and preventing further population declines. The Bornean orang-utan is under severe threat from anthropogenic activity, yet there is very little information on orang-utan-parasite dynamics in the wild. A critical orang-utan habitat, the peat-swamp forest, is rapidly degrading as a result of climate change, extractive processes, and poor fire management. Consequently, peat-swamp forests of Kalimantan experience more severe seasonal variation and fires rage uncontrollably in the dry season each year. I investigated variation in nematode prevalence and intensity between the wet and dry season and before and after a fire event using the Mini-FLOTAC faecal parasite detection technique. Nematode intensity increased after the fire event, and intensity of *Enterobius* spp. was greater in the dry season compared to the wet season. This study was the first to use the Mini-FLOTAC analysis technique in a study on great apes, and it was possible to conduct the entire analysis process in the field. Detection of hookworm sp., *Strongyloides* spp., *Enterobius* spp., *Trichuris* spp. and *Ascaris* sp. are comparable with other orang-utan parasite studies, indicating that the Mini-FLOTAC is a viable and useful tool for investigating wild primate parasites in remote field locations. This study provides an indication that fire and seasonality affect parasitic infection in orang-utans. This area of research would benefit from long-term monitoring to build up a larger dataset over time and across sites in order to anticipate any disease-induced population declines.

3.2. Introduction

Infectious diseases can pose a significant threat to animal fitness, therefore understanding the factors that drive variation in parasitic infection is critical in managing populations of endangered species (Smith *et al.* 2009; Thompson *et al.* 2010). There is a growing understanding that anthropogenic activities are important in affecting parasitic infections (Chapman *et al.* 2005). As human impacts on habitats continue to grow and 61% of non-human primates classed as vulnerable, endangered, or critically endangered (IUCN, 2020), there is an urgency to understand these effects before wild primate populations decline beyond potential recovery. Studying primate parasites in-situ can prove difficult due to invasiveness of techniques and the risk of human to non-human primate disease transmission, yet techniques are being developed to overcome these constraints. Therefore, it is important to monitor populations long-term to track emergence, transmission, and outbreaks of disease. Here I apply a new parasite monitoring procedure, used for the first time in great apes to investigate the impacts of seasonality and a major fire event on gastrointestinal nematode infection in the critically endangered Bornean orang-utan (*Pongo pygmaeus*).

A parasite is an animal or plant which lives in or upon another organism (called its ‘host’) and draws its nutrients directly from it (Bush *et al.* 2001). Parasites can be classified into ectoparasites and endoparasites. Ectoparasites are those which are confined to the exterior of the host’s body, they tend to be arthropods and monogeneans. Endoparasites include those parasites that are confined within the host’s body. They include the more familiar animal parasites such as protozoans, digeneans, cestodes, nematodes, and acanthocephalans. Many bacteria and all viruses are also endoparasitic. The prevalence and intensity of ectoparasites and endoparasites may be influenced most by the environmental conditions during the egg development stage. Many species of both ectoparasites and endoparasites deposit eggs into the environment where they develop into larvae to infect a new host. Conditions such as flooding, drought, humidity and temperature can affect how well eggs develop in the soil or environmental surface and hence influence host infection rates, though the exact directionality of this will depend on the specific life cycle of the parasite. Environments which experience distinct variation in abiotic conditions throughout the year or are subjected to intense anthropogenic disturbance may see differences in parasite prevalence and intensity in hosts over time. For example, in highveld mole-rats (Cryptomys hottentotus pretoriae), seasonality affects the prevalence of ectoparasites and endoparasites differently. Prevalence of an ectoparasitic mite (*Androlaelaps* spp.) was greater in the summer whereas prevalence of an endoparasitic cestode was greater in the winter (*Mathevotaenia* sp.) (Viljoen *et al.* 2011).

It is important to study the drivers of endoparasitic infection in order to understand host population dynamics, behaviour, and the cryptic impacts of anthropogenic disturbance. Seasonality has been the subject of many endoparasite infection studies as factors such as host density, diet, nutritional status, and ranging patterns, as well as environmental temperature, rainfall, and soil conditions vary by throughout the year (Nunn *et al.* 2003; Chapman *et al.* 2005, Altizer *et al.* 2006). Effects of seasonality may vary across different systems. For instance, black and white colobus monkeys (*Colobus guereza*) frequenting wetter areas showed higher levels of gastrointestinal parasitic infection compared to those in drier areas (Chapman *et al.* 2009). Eastern chimpanzees (*Pan troglodyes schweinfurthii)* of the Mahale mountains had a significantly higher prevalence of *Oesophagostomum stephanostomum* in the wet season (Huffman *et al.* 1997). In contrast, other studies have showed higher gastrointestinal parasitic prevalence in Eastern chimpanzees and Western lowland gorillas (*Gorilla gorilla gorilla*) in the dry season (Bakuza and Nkwengulila, 2009; Masi *et al.* 2012). A study on neotropical primates also revealed that gastrointestinal parasitic infection was greater going into the dry season (Martinez-Mota *et al.* 2017). Rainfall and soil state are important seasonal factors affecting the free-living stages of gastrointestinal parasites. Prevalence of *Strongyloides stercoralis* was proposed to be lower in areas with higher rainfall due to water washing away the free-living infective stages in the soil (Khieu *et al.* 2014). A laboratory study showed that the development of *Strongyloides stercoralis* was impaired by submersion of faeces in water (Anamnart *et al.* 2013). In habitats where waterlogging occurs for prolonged periods, such as peat-swamp forests, this may reduce the free-living stages of gastrointestinal parasites. In addition, these environmental factors are known to affect host behaviour which can influence gastrointestinal parasite infection rates. For example, during drier weather, grey-cheeked mangabeys (*Lophocebus albigena*) moved longer distances and used more area which was potentially attributed to faecal avoidance in the environment

(Freeland, 1980). Seasonality is an important influence on environmental conditions and subsequently host behaviour which can affect gastrointestinal parasite infection in variable ways depending on the habitat, host, and parasite species.

The impact of anthropogenic activity on gastrointestinal parasite infection has recently gained more attention. Anthropogenic activity can affect a host's health by reducing resource availability, increasing physiological stress which causes reduced investment in the immune system subsequently increasing infection risk (Gillespie *et al.* 2005; Rode *et al.* 2006). In chronically stressful situations prolonged hypothalamic–pituitary–adrenal axis activity and elevated glucocorticoid concentrations may induce various pathological effects and may eventually affect individual fitness negatively by reducing investment in reproduction and immune function (Romero, 2004; Dhabhar, 2009). Galapagos marine iguanas experienced elevated stress when exposed to low-level anthropogenic disturbance and associated suppression of the immune response (French *et al.* 2010). Anthropogenic activity can also affect host density which, according to epidemiological theory, is a key determinant of the prevalence and richness of gastrointestinal parasites (Anderson and May, 1978; Anderson, 1979; Morand and Poulin, 1998; Poulin, 1998; Packer *et al.* 1999, Nunn *et al.* 2003). Gastrointestinal parasite prevalence and richness in the Tana river red colobus (*Piliocolobus rufomitratus)* and Tana river mangabey (*Cercocebus galeritus*) increased with host density, which was inflated as a result of fragmentation due to logging (Mbora and McPeek, 2009). A higher host density can promote direct transmission of gastrointestinal parasites by increasing host contact rates. It may also lead to more intensive use of the same habitat patches which increases environmental contamination with infective stages from faeces and the likelihood of encountering these infective stages (Anderson and May, 1978; Anderson, 1979; Stoner, 1996; Morand and Poulin, 1998; Poulin, 1998; Packer *et al.* 1999).

Fire, as a form of anthropogenic disturbance, has the potential to elicit the above-mentioned effects, as well as altering the developmental conditions of free-living stages of gastrointestinal parasites. Fire has long been used to control disease outbreaks. For example, controlled burning was used to reduce the free-living stages of gastrointestinal parasites of sheep in Australia (Barger, 1978). Fire has also been used to disrupt the microhabitat of the intermediate host of meningeal brain worm which has devastated populations of deer and elk in South-eastern USA (Weir, 2009). Furthermore, forest damage tends to decrease soil organic carbon content, which is associated with increased infection risk (Buringh, 1984; Khieu *et al.* 2014). Fire can drastically reduce soil carbon content, particularly in habitats such as peat-swamp forests which can burn at and beneath the soil layer due to a high carbon content.

Here, I investigate how seasonality and a major fire event affect gastrointestinal parasite infection in Bornean orang-utans in a peat-swamp forest. Bornean orang-utans are critically endangered as a result of a variety of anthropogenic disturbances. Habitat loss is the orang-utan's major threat, caused by logging, agricultural plantations, infrastructure development, and fire (Ancrenaz *et al.* 2016). Populations are also threatened by hunting and the pet trade (Meijaard *et al.* 2011). Disease may begin to pose a greater threat to wild orang-utans as humans encroach further into their habitat and loss of forest creates additional physiological stress. Very little is known about the gastrointestinal parasites of wild Bornean orang-utans. The studies which have been conducted to date are primarily on Sumatra orang-utans or semi-wild and captive individuals (Rijksen, 1978; Collet *et al.* 1986; Foitova, 2002; Foitova *et al.* 2006; Mul *et al.* 2007; Djojoasmoro and Purnomo, 1998). The consensus drawn from these studies suggest that wild orang-utans have a lower prevalence of gastrointestinal parasites compared to captive individuals, with the most frequently found gastrointestinal parasites being *Strongyloides* spp. and *Balantidium coli.* The disease caused by *Strongyloides* spp. (Strongyloidosis) can be fatal, particularly in young orang-utans, and was the main cause of death during a reintroduction programme in East Kalimantan (Warren, 2001). Other commonly recovered gastrointestinal parasites include the nematodes; hookworm (*Necator americanus/Ancylostoma duodenale*), *Trichuris* spp., *Enterobius* spp., *Ascaris* spp., *Mammomonogamous* spp., and protozoa; *Entamoeba* spp, and *Giardia* spp (Collet *et al.* 1986; Foitová, 2002; Kilbourn *et al.* 2003; Mul *et al.* 2007; Labes *et al.* 2010; Hilser, 2011; Dench *et al.* 2012, unpublished data). This study focusses on gastrointestinal nematodes as these are often the most detrimental to health. Although not always fatal, gastrointestinal nematodes can cause significant problems if an individual's immune system is compromised by stress, suboptimal nutrition, or other illness (Kishimoto *et al.* 2008). Infection with gastrointestinal nematodes has been a significant cause of death in young captive orang-utans, and certain species have been linked with causing pneumonia and peritonitis (Wells *et al.* 1990).

There have been no studies investigating how seasonality and anthropogenic habitat modification influence gastrointestinal nematode infection in orang-utans in a peat-swamp forest. It is important to study peat-swamps as they are a critical habitat for orang-utans. Peat-swamps contain some of the largest remaining populations and highest densities of orang-utans in the world (Johnson *et al.* 2005, Utami-Atmoko *et al.* 2017). Yet, peat-swamps of Borneo are highly disturbed and vulnerable to fire. Logging and agricultural activity drains the naturally high water table causing drying, oxidisation and subsidence of the peat, making it very susceptible to burning in the dry season. Peat can burn for days, months, even years above and below the ground without being detected, so fires spread widely and destroy vast swathes of forest habitat very quickly (Harrison *et al.* 2016). In Kalimantan, only 7.4% of the historical peat-swamp forest area remains (Miettinen *et al.* 2016). Furthermore, given the unique ecological conditions such as high soil pH and seasonal flooding, I cannot assume that the patterns of parasitism seen in other forest types will be present in peat-swamp forests. As the climate warms making seasonal factors more pronounced and anthropogenic habitat modification continues, additional stress may be put on orang-utans, compromising their immunity, and making them more susceptible to gastrointestinal parasitic infection.

Monitoring gastrointestinal parasitic infection in wild populations can be highly challenging. Many studies use methods involving collection and preservation of faecal samples in the field, then exporting samples to a laboratory to be analysed (which may not necessarily be in the country of the field study). This can make regular, long-term monitoring impractical as sample export permits are often difficult and lengthy to obtain, costs can be high and preserving samples require toxic chemicals which can be difficult to dispose of in the field environment. A potential solution may be the Mini-FLOTAC technique (Cringoli *et al.* 2012). The Mini-FLOTAC (combined with use of the Fill-FLOTAC) is a simple, easy-to-use device that is designed for quantitative detection of helminths and protozoa from faeces in limited resource environments (Cringoli *et al.* 2017). The full faecal analysis procedure can be carried out in the field as there is no centrifugation step, only requires a light microscope, and it is not essential to preserve samples. The Mini-FLOTAC is a relatively new technique and so far has been used to investigate gastrointestinal parasites in humans (Barda *et al.* 2013), domestic animals (Cringoli *et al.* 2012; Silva *et al.* 2013), and howler monkeys (*Alouatta pigra*) (Alvarado-Villalobos *et al.* 2017). This is the first time the Mini-FLOTAC technique has been used in a study of great apes. Due to the simplicity and portability of this equipment, more studies of gastrointestinal parasites in wild animal populations could benefit from the utilisation of this equipment. Monitoring gastrointestinal parasitic infection is highly valuable for conservation as it can act as an indicator of ecological stress and the impacts of disturbance (Stuart and Strier, 1995; Cleaveland *et al.* 2002; Chapman *et al.* 2007). Disease is likely to become a greater threat to wild orang-utan populations as anthropogenic habitat modification increases and humans encroach ever further into their habitat. It highly important to understand host-parasite dynamics and monitor disease to anticipate potential population declines of hosts and implement effective control measures to prevent populations falling ever closer to extinction.

Based on the previous research discussed, I generate two hypotheses. Firstly, gastrointestinal nematode infection in orang-utans will be lower in the wet season when the peat-swamp soil is permanently waterlogged, thus creating unfavourable conditions for free-living stages of gastrointestinal nematodes. Secondly, gastrointestinal nematode infection will increase after the fire period due to increased stress compromising the orang-utan immune systems (Erb et al. 2018).

3.3. Methods

3.3.1. Sample Collection and Examination

The study was conducted in the Laboratorium Alam Hutan Gambut (LAHG) research area which lies within the Sebangau forest catchment, Central Kalimantan, Indonesia (2°19'S and 113°54'E). Faecal samples were collected from wild, habituated orang-utans between March and December 2019 on focal individual follows according to Borneo Nature Foundation's (BNF) standard operating procedure (Morrogh-Bernard *et al.* 2002). The study period spanned both the wet and dry season (March-May, December = wet. June–November = dry) and included a major fire event which occurred from August to October. Samples were collected from the same orang-utan on three consecutive days to account for sporadic shedding of eggs by any gastrointestinal nematodes, though this was not always possible (mean ± SE = 1.8 ± 0.2 per individual per follow period; range = 1-4). Samples were usually collected in the morning as orang-utans typically defecate when they wake up. Samples were collected from the ground as quickly as possible to reduce any potential contamination from the environment. Faeces were stored in 50ml vials and taken back to the LAHG research station for examination. GPS point, date, time and orang-utan name, were recorded. Samples were analysed within 12 hours of collection as no fixatives were used to preserve samples and prevent eggs from hatching.

Samples were examined for nematode eggs and larvae using the Mini-FLOTAC technique (Cringoli *et al.* 2017). 2g of faeces was homogenised and then added to 38ml of the flotation solution. Sodium chloride (NaCl) with specific gravity 1.20 was used as a flotation solution as it is non-toxic, making disposal of waste whilst in the field feasible. The faeces were homogenised with the flotation solution and the mixture was pipetted into the reading disk chambers so that each chamber contained 1ml of mixture. After waiting 10 minutes, the top of the reading disk was rotated 90^o to isolate any eggs and larvae which had floated to the surface from faecal debris. The chamber with a smaller area of air bubbles was chosen for examination under a light microscope (Model: GXM180M, Magnification range: x40, x100, x400, x1000). Chambers were scanned systematically, eggs and larvae were identified to the most specific level possible based on morphology, size, shape, and colour. The number of eggs and larvae of each nematode were counted.

3.3.2. Assessment of Gastrointestinal Parasite Community

Gastrointestinal nematode infection was described in terms of prevalence and intensity with respect to the individual orang-utan. Prevalence represents the number of hosts infected with one or more of a particular nematode species/taxonomic group. Intensity is measured as the number of eggs of a particular nematode species/taxonomic group per gram of faeces from an infected host. Intensity does not take into account uninfected hosts (Bush *et al.* 1997).

As samples were taken consecutively (up to four days in a row) to account for any sporadic release of eggs, the maximum egg count and any positive prevalence for that orang-utan's follow period was used for each nematode taxon recovered. A follow period was defined as days spent following a particular orang-utan without changing focal. Prevalence was recorded as binary data for each nematode (1 = present, 0 = absent). Intensity (i.e. the number of eggs g^{-1} for each parasite) was obtained by multiplying the raw egg count by the dilution factor divided by the volume. In this study, 2g faeces was combined with 38ml of flotation solution (dilution factor = 20) and the number of eggs were counted in one 1ml chamber (volume = $1cm^3$), therefore raw egg count was multiplied by 20/1 = 20.

Data were analysed in R version 3.6.3 (R Core Team, 2020). Fisher's exact tests were conducted to determine if seasonality and a fire event impacted gastrointestinal nematode prevalence in orang-utans. Fisher's exact test was required due to the small sample size and lack of variability within groups in the dataset. Data were tested for differences between the wet and dry season, pre-fire and post-fire period, and between parasite taxa. As there was only one sample in the 'wet season post-fire' group, this datapoint was removed as it had potential to skew the data due to it being a small sample size. Zero-inflated negative binomial models were conducted using the *glmmTMB* package (Brooks *et al.* 2017) to determine the factors influencing parasitic intensity. As parasitic intensity data contained an excess of zeros, a zero-inflated model allowed analysis of the data in a way which accounted for a zero egg count because the orang-utan was not infected, as well as the zeros due to the nematode not being present in the environment in which the orang-utan inhabited. Fixed terms included season, fire period and nematode and orang-utan ID was fitted as a random term to account for repeated measures. To determine which model derived from the global model received the most support, the *dredge* function in the package *MuMIn* (Barton, 2019) was used to rank models by AICc after application of the nesting rule (Richards *et al.* 2011; Harrison *et al.* 2018). Model fit was assessed using standard residual plots and Cook's distance to identify particularly influential datapoints. QQ plot residuals did not show significant deviation from the expected distribution (K-S test p = 0.60; Dispersion test p = 0.72; Outlier test p = 0.72). Model outputs were obtained using *tab_model* from *sjPlot (*Ludecke, 2020) of the best supported model and are reported as the incident rate ratio (IRR), standard error (se) and p-value.

3.4. Results

A total of 77 samples were obtained from 14 individual orang-utans. From each follow period for each individual orang-utan, the highest egg counts and a positive prevalence per nematode taxa was taken to form the unrepeated sample for said orang-utan's follow period. Table 7 shows the distribution of raw samples, unrepeated samples and number of individuals across the seasons and fire periods.

Table 7. The number of faecal samples analysed for gastrointestinal nematodes over the entire study period. Raw no. of samples is the total number of samples analysed under the microscope. Unrepeated no. of samples is the number of samples analysed statistically, once a positive prevalence or maximum number of eggs per gram were taken from an orang-utan's follow period. No. of individuals is the number of individual orang-utans from which samples were obtained.

	Raw no. of samples	Unrepeated no. of samples	No. of individuals
Wet season	29	12	8
Dry season	48	22	12
Pre-fire	52	22	12
Post-fire	25	12	9

A total of 5 nematode taxonomic groups were recovered: hookworm sp. (*Ancylostoma duodenale/Necator americanus*), *Strongyloides* spp., *Enterobius* spp., *Trichuris* spp. and *Ascaris* sp. Data on *Ascaris* sp. were not analysed due to low confidence in the accuracy of identification.

3.4.1. Nematode Prevalence

Nematode prevalence varied greatly according to taxonomic group (Fisher's Exact Test, $p < 0.001$, see Appendix IV Table 1 for post-hoc pairwise p-values). Overall, hookworm sp. was the most prevalent, found in 100% of individuals. *Strongyloides* sp. was found in 86%, *Enterobius* spp. in 29% and *Trichuris* spp. in 14% of individuals (Fig. 10).

There was no significant effect of season on nematode prevalence. Hookworm sp. was found in all samples, regardless of season and fire period. *Strongyloides* spp. was found in 75% individuals in the dry season compared to 100% of individuals in the wet season($p = 0.253$). *Enterobius* spp. was found in 33% of individuals in the dry season and 0% in the wet season ($p = 0.117$). *Trichuris* spp. was found in 17% of individuals in the dry season and 0% in the wet season ($p = 0.495$). See Table 8 and Fig. 11 for a summary of the data.

There was no significant effect of fire period on nematode prevalence. *Strongyloides* spp. was found in 83% of individuals in the pre-fire period and 56% of individuals in the post-fire period ($p = 0.331$). *Enterobius* spp. was found in 25% of individuals in the pre-fire period and 33% in the post-fire period ($p = 0.397$). *Trichuris* spp. was found in 22% of individuals in the pre-fire period and 8% in the post-fire period ($p = 0.553$). See Table 8 and Fig. 11 for a summary of the data.

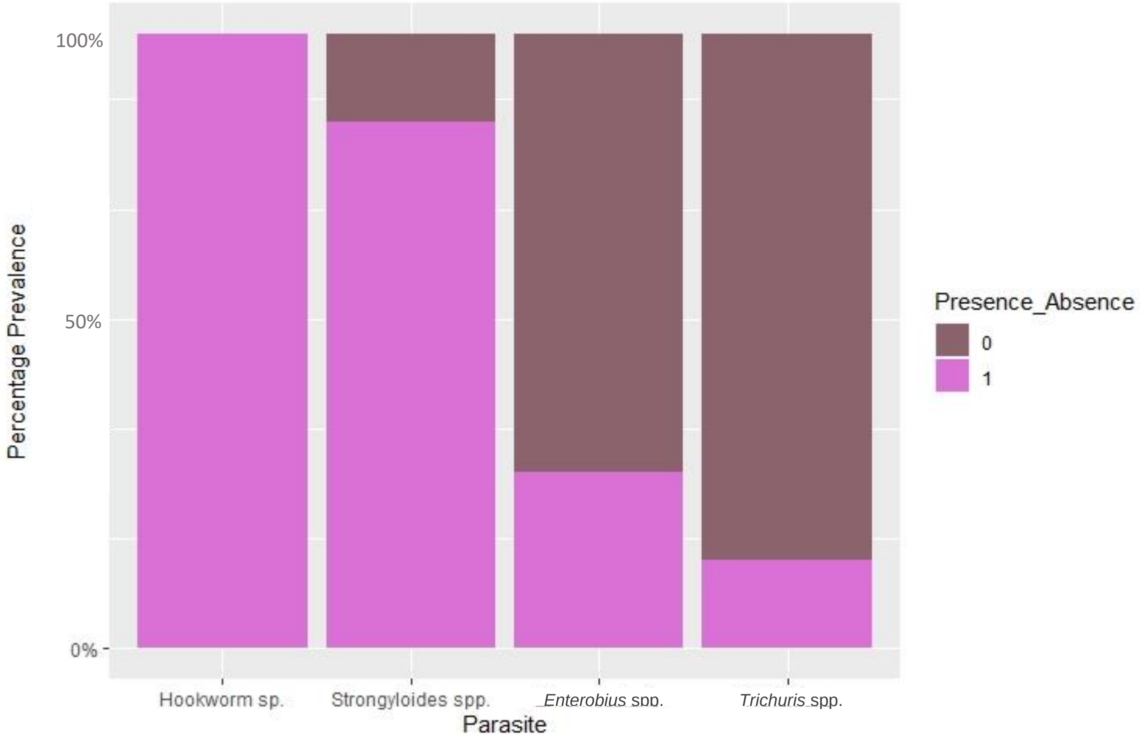


Figure. 10. Percentage prevalence of four nematode taxa with individual orang-utan as the sampling unit. ‘1’ indicates presence of the nematode in the orang-utan, ‘0’ indicates absence. A nematode was said to be present if it was found in at least one sample from that orang-utan.

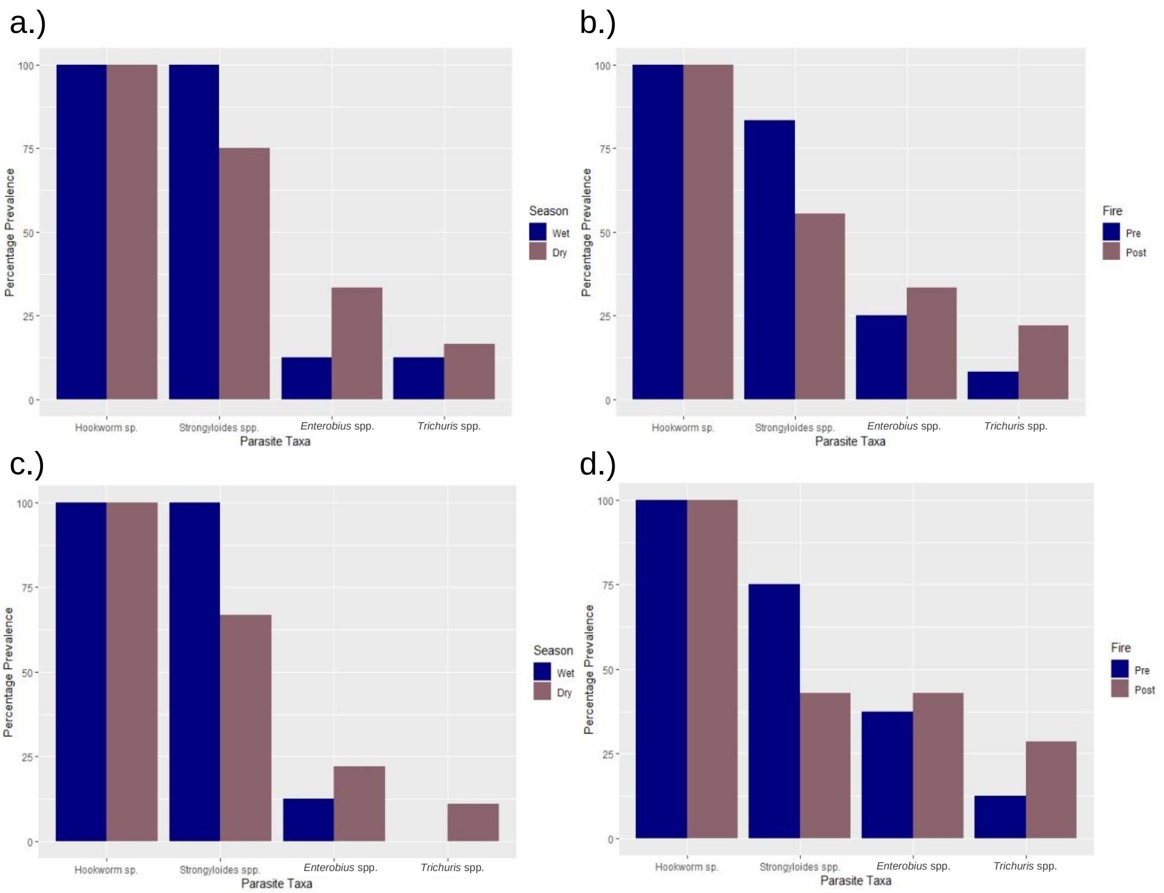


Fig. 11. Percentage prevalence of four nematode taxa with individual orang-utan as the sampling unit. a.) Wet vs dry season. b.) Pre-fire vs post-fire periods. c.) Wet vs dry season pre-fire data only. d.) Pre-fire vs post-fire dry season data only.

Table 8. Percentage prevalence of, and number of individual orang-utans positive for, each nematode taxa in the wet season, dry season, pre-fire period, post-fire period, and overall.

	Hookworm sp.		***Strongyloides* spp.**		***Enterobius* spp.**		***Trichuris* spp.**		**Total no. of individuals**
	%	No. of individuals	%	No. of individuals	%	No. of individuals	%	No. of individuals	
Wet season	100	14	100	8	0	0	0	0	8
Dry season	100	14	75	9	33.3	4	16.7	2	12
Pre fire	100	14	83.3	10	25	3	8.3	1	12
Post fire	100	14	55.6	5	44.4	4	22.2	2	9
TOTAL	100	14	85.7	12	28.6	4	14.3	2	14

3.4.2. Parasitic Intensity

The model with all fixed effects and an interaction between nematode and season received the greatest support (see Appendix IV Table 2 for a comparison of the models in the top model set). Intensity of hookworm sp. was significantly greater than *Strongyloides* spp., *Trichuris* spp., and *Enterobius* spp. (Hookworm sp. – *Strongyloides* spp.: Incident rate ratio (IRR) ± se = 4.60 ± 0.80, $p < 0.001$; Hookworm sp. – *Trichuris* spp.: IRR ± se = 6.95 ± 2.74, $p < 0.001$; Hookworm sp. - *Enterobius* spp.: IRR ± se = 10.29 ± 4.05, $p < 0.001$). Mean intensity of hookworm sp. was 390 eggs per gram (eggs g^{-1}), *Strongyloides* spp. was 102 eggs g^{-1}, *Enterobius* spp. was 125 eggs g^{-1}, and *Trichuris* spp. was 120 eggs g^{-1} (Fig. 12).

There was a significantly greater intensity of *Enterobius* spp. in the dry season compared to the wet season (IRR = 9.59 ± 6.76, $p = 0.002$). However, only one sample tested positive for *Enterobius* spp. in the wet season, therefore I cannot be fully confident in the robustness of this result. No significant differences in intensity of the other taxa between the seasons were found (Fig. 13a).

A significantly greater nematode intensity was found post-fire compared to pre-fire (IRR = 0.64 ± 0.20, $p = 0.027$). Mean intensity pre-fire was 214 eggs g^{-1} whereas mean intensity post-fire was 292 eggs g^{-1}. Mean intensity was consistently higher in the post-fire period for all nematode taxa (Fig. 13b).

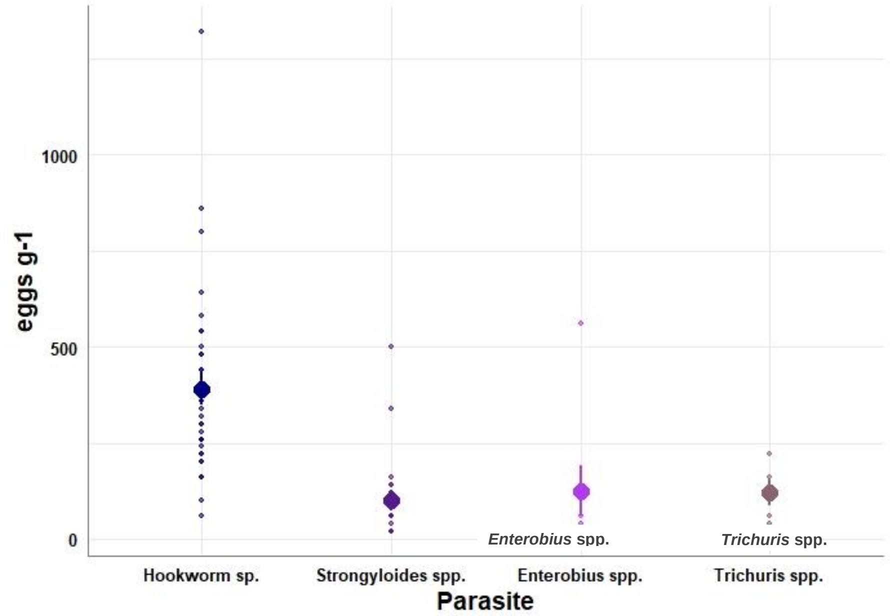
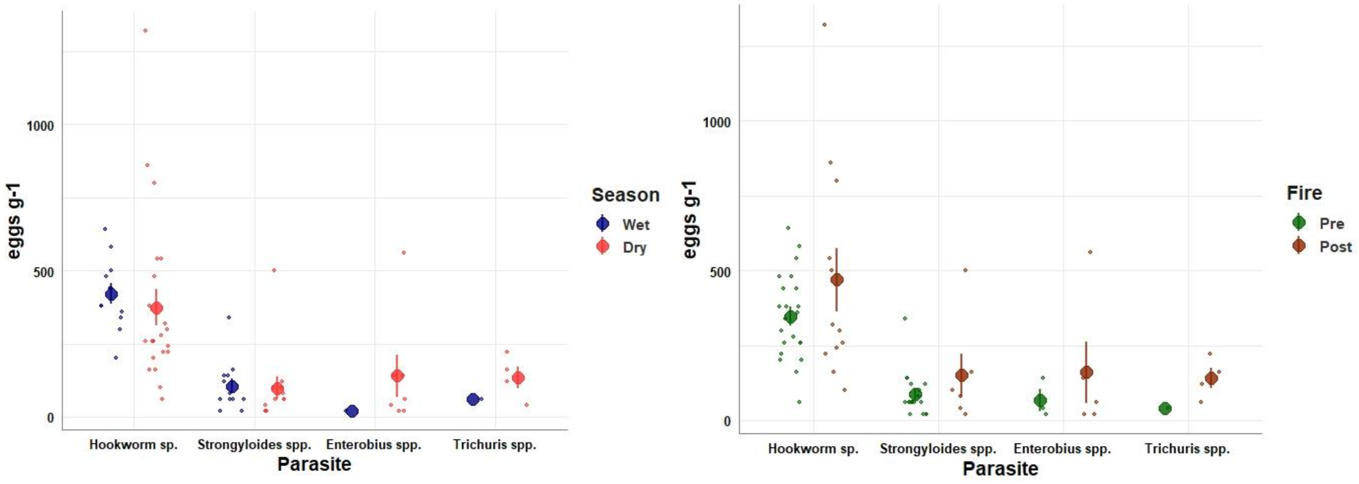


Fig 12. Nematode intensity measured in eggs g^{-1} for each taxa. Small points are raw data from a follow period of an individual orang-utan. Mean and standard error for each nematode are shown as the large point and vertical lines.


a.)

b.)

Fig 13. Nematode intensity measured in eggs g^{-1} for each taxa. a.) Wet vs dry season. b.) Pre-fire vs post-fire periods. Small points are raw data from a follow period of an individual orang-utan. Mean and standard error for each nematode are shown as the large point and vertical lines.

3.5. Discussion

This study elucidates to the possibility that seasonality and fire may influence gastrointestinal parasite intensity in orang-utans, however, I cannot be fully confident in the significance of these results due to the small sample size, particularly the small number of samples in the wet season and post-fire period.

The intensity of *Enterobius* spp. was greater in the dry season compared to the wet season, however only one sample tested positive for *Enterobius* spp. in the wet season, therefore further study with a larger dataset would be required to have confidence in this result. If this effect does indeed hold true, the greater intensity in the dry season may be due to the lifecycle of *Enterobius* spp. Infection by *Enterobius* spp. can occur via self-inoculation (transferring eggs from anus to mouth by scratching), or through exposure to eggs in the environment (soil/leaves contaminated with faeces). During the dry season, less frequent rainfall may allow the infective stages of *Enterobius* spp. to persist longer in the environment as rainfall does not wash them away from leaves or anal surfaces (Khieu *et al.* 2014). Another factor contributing to the lack of confidence in this result is that *Enterobius* spp. eggs are not best detected from faeces. They are primarily found in the perianal skin area and are better diagnosed from a perianal swab. Taking a swab sample would not be possible in a study on wild orang-utans, however since I did detect *Enterobius* spp. eggs in multiple samples across the study, I can be confident in *Enterobius* spp. infection occurring, just not in the patterns of intensity across seasons. Infection with *Enterobius* spp. (Enterobiasis) has been known to cause perianal pruritus, teeth grinding, enuresis, insomnia, anorexia, irritability, and abdominal pain in humans, but can often be asymptomatic (Cook, 1994). Enterobiasis is not often fatal, but orang-utans will likely experience similar symptoms to humans, and severe cases may impact upon their activity patterns, ability to forage and ingest food, compromising their physiological condition.

Nematode intensity was significantly greater in the post-fire period compared to pre-fire period, however the sample size of the post-fire period was very small due to there being only two months in which it was safe to collect data post-fire so I cannot have full confidence in the significance of this effect. It is plausible that that fire as a form of anthropogenic activity may be increasing orang-utans' susceptibility to gastrointestinal parasitic infection. Orang-utans may be more susceptible to infection post-fire due to the toxic smoke affecting their body condition. Erb *et al.* (2018) observed a negative energy balance in the post-smoke period which was more likely attributed to increased energy allocation to immune response or stress hormone production. The indication of a greater nematode intensity in the post-fire period from this study would support the idea put forth by Erb *et al.* (2018) that orang-utans are experiencing a greater allostatic load, rather than experiencing a negative energy balance due to reduced calorific intake, post-fire. Smoke from fires may increase allostatic load by other means also, such a respiratory illness and stress hormone production (Cheyne, 2008; Harvey, 2015). It would be beneficial to investigate other measures of health in wild, fire-affected orang-utans such as cytokines, cortisol and neopterin to identify if orang-utans are more physiologically stressed (van Eeeden *et al.* 2001). This would aid in fully understanding the effects of fire on orang-utan health.

Hookworm sp. having the highest prevalence and intensity of all the nematode taxa found is not likely to be of major detriment to Sebangau orang-utans and is unlikely to impact upon survival and reproduction. Only in cases of very high burden and when an animal's resistance is already lowered can hookworm sp. cause anaemia and death (Cousins, 1972). Although I found a high prevalence of hookworm sp. among individuals, the number of eggs per gram is in the range of a very light infection in humans (1-999 eggs^{-1}; Loukas *et al.* 2006). *Strongyloides* spp. are recognised as the leading cause of parasite-related mortality in juvenile orang-utans, but rarely result in clinical symptoms in adults or sub-adults as their immune system has developed which limits disease severity (AZA Ape Taxon Advisory Group, 2017; Nunn *et al*. 2003). In the one juvenile orang-utan sampled in this study (total of five faecal samples), just one potential *Strongyloides* spp. egg was identified (equivalent to 20 eggs^{-1}). Increasing sampling of wild juvenile orang-utans could be of benefit to assess if *Strongyloides* spp. poses any real risk to wild orang-utan populations as the majority of studies which show *Strongyloides* spp. as a high risk are conducted on grouped-housed, captive orang-utans. Both *Trichuris* spp. and *Enterobius* spp. rarely result in fatalities and were found at very low levels in this study.

There was no significant effect of seasonality or fire on nematode prevalence, however trends in the data were identified. Prevalence of *Strongyloides* spp. seemed to be greater in the wet season, and prevalence of *Enterobius* spp. and *Trichuris* spp. seemed to be greater in the dry season. The sample size of this study was fairly small, therefore this research would benefit from more long-term investigation to increase the sample size and make any effects detectable and results more robust.

These findings show that the Mini-FLOTAC is a promising technique for investigating gastrointestinal parasites in orang-utans. This is the first time the Mini-FLOTAC technique has been used to assess the gastrointestinal parasites of a great ape. The technique was successful in detecting nematodes known to infect orang-utans from previous studies at Sebangau (Hilser, 2011; Dench *et al.* 2012, unpublished data). Here, nematode were detected at relatively high prevalence compared to published ranges. In wild Bornean orang-utans, prevalence of hookworm sp. usually lies within the range of 56-84%, *Strongyloides* spp.: 19-96%, *Enterobius* spp.*:* 2.6-25%, and *Trichuris* spp.*:* 6-14% (Kuze *et al.* 2010; Labes *et al.* 2010; Hilser, 2011; Dench *et al.* 2012, unpublished data). This study detected two of these nematode at a prevalence exceeding the published range (Hookworm sp.: 100%, *Enterobius* spp. 29%). *Strongyloides* spp. and *Trichuris* spp. was found at the higher end of the published ranges (86% and 14% respectively). This suggests that the Mini-FLOTAC is a viable technique for detecting gastrointestinal nematodes in a great ape species and may in fact be more sensitive than other detection techniques such as direct smear, flotation and sedimentation (Labes *et al.* 2010; Hilser, 2011; Dench *et al.* 2012, unpublished data). It is also apparent that the Mini-FLOTAC is a highly useful technique to allow all parasitological analysis to be conduct at the field site, without the need for sample exports and expensive equipment such as centrifuges. This approach is likely to be valuable for future studies of wild primate health and there are plans to use this study to initiate a long-term monitoring project of primate health at BNF's Sebangau research site.

This study was the first to assess the impact of a fire period on gastrointestinal parasitic infection in orang-utans. It would be highly beneficial to continue to monitor this orang-utan population over a long period and in response to other fire events to see if similar trends occur. It is hoped that other field sites can make use of this analysis protocol and compare results with the present study. For example, a major concern of orang-utan parasitological research is the transmission of parasites from reintroduced to wild individuals. Reintroduced individuals often have a greater and more diverse parasite community and thus pose a risk of introducing novel disease wild individuals (Russon, 2009b; Schaumburg *et al.* 2012). Reintroduction sites are often extremely remote and basic, therefore this protocol could be very useful in rapidly and cheaply assessing differences in parasites of wild and reintroduced orang-utans to protect the health of populations.

Peat-swamp forests are becoming increasingly disturbed and fires are becoming ever more frequent and severe. Many sites experience shorter periods waterlogging and are increasingly parched in the dry season, making seasonal effects more pronounced. This study suggests that seasonality affects parasitic intensity of *Enterobius* spp. in orang-utans. Previous studies have investigated the effects of fire on orang-utan movement, distribution, and diet, however, have never considered how fire may affect parasitic infection. These findings suggest that parasitic intensity increases after a fire event, providing evidence towards another mechanism by which fire may negatively impact orang-utan fitness. Although the full consequences of this are unknown, chronic exposure to fires may result in long-term health problems, increased mortality rates and/or decreased birth rates, subsequently contributing to population decline.

Chapter 4 – General Discussion and Recommendations

4.1. General Discussion

Anthropogenic land use change is rapidly increasing the susceptibility of peat-swamp forests to fire, with burnings seen annually in countries such as Indonesia which contains some of the most extensive peat deposits in the world (Herawati and

Santoso, 2011; Warren *et al.* 2017). Not only does the burning of peat-swamps have severe impacts on human health and the global climate, but it has the potential to decimate wildlife populations in a short space of time. Yet, the way in which fire affects animals, in terms of their individual fitness, ability to survive and reproduce is poorly studied. Fire is now considered the greatest threat to the Bornean orang-utan as some of the last remaining strongholds inhabit peat-swamp forests (Johnson *et al.* 2005; Utami-Atmoko *et al.* 2017). The Bornean orang-utan is facing rapid population decline and is currently classified as critically endangered due to anthropogenic activities such as logging, agriculture and hunting (Ancrenaz *et al.* 2016). Therefore, it is critical to understand the mechanisms by which fire is affecting orang-utans in order to effectively conserve remaining populations and peat-swamp forests. This thesis investigated the impact of fire, and other ecological variables, on changes in the behaviour and health of Bornean orang-utans in a tropical peat-swamp. I found that orang-utans increased their resting time in the short-term, up to nine months after a fire event, but decreased resting time and active period over the long-term, four years following a fire event. Results indicate towards a greater gastrointestinal parasite intensity after a fire event, and both activity budgets were affected by seasonal variables such as groundwater level and food availability.

Changes in behaviour and physiology of an animal can indicate fitness consequences and function as an early warning system of ensuing population-level impacts, particularly for species with slow life-histories such as the orang-utan (Galdikas and Wood, 1990). The fact that orang-utans increased their resting time after the fire, but only for up to nine months, suggests that orang-utans are able to adapt to the changes fire creates fairly well and this response can be interpreted as an energy conserving strategy. This finding supports the work of Erb *et al.* (2018) who reported an increase in resting time as an energy conserving strategy at the Tuanan orang-utan research station. Erb *et al.* (2018) described this as an energy conserving strategy due to the greater of ketones, a product of fat catabolism indicating a negative energy balance, in urine samples after the fire event. I did not find any notable presence of ketones indicating that orang-utans in the LAHG are not energetically stressed. Therefore, the energy conserving strategy of increasing resting time may result from other physiological impacts of fire such as smoke inhalation weakening the respiratory system, or it may in fact be an effective way of preventing ketosis. More detailed investigation of diet and calorific intake may assist in understanding if these behavioural changes are related to energy intake or increased energy expenditure on other physiological processes.

As climate change and anthropogenic habitat disturbance progress, the frequency of fire in tropical peat-swamps will continue to increase to reliably annual occurrences. This will be problematic for orang-utans if they must exhibit energy conserving strategies for approximately nine-months after a fire as this would become their almost constant state. Continually increasing resting time to conserve energy post-fire may result in less time allocated to foraging; reducing energy intake, or travelling; reducing chances of social encounters for mating. It may also be important to consider at which life history stage an orang-utan is at when it experiences this alteration in activity budget. For example, if a female with dependent offspring rests more, this may impact the offspring's opportunities for interaction with conspecifics, locomotory development, and learning of what to eat and how to process food. There is even evidence for physical activity being important for cognitive function (van Praag, 2009). This may be particularly important for young orang-utans when the brain is developing most rapidly. Less exercise (i.e. increased resting), can result in poorer learning abilities and therefore could impair the ability of young orang-utans to effectively acquire the skills they need to survive. Even though the increase in resting occurred only over nine months in this study, this may still have an effect on the learning ability of young orang-utans if the fire occurs in a critical period of their development.

The indication of a greater gastrointestinal parasite intensity after a fire event may be due to a higher allostatic load which could create additional physiological stress, increase energy expenditure, and reduce overall fitness. This is a novel study investigating how parasitic infection is affected by fire in orang-utans, therefore further research and larger sample sizes are required to elucidate why this is occurring. A plausible explanation is that host body condition is reduced as a result of the disturbance to habitat caused by fire, hence leaving orang-utans more susceptible to infection. Anthropogenic disturbance has been found to induce physiological stress in many species (e.g. French *et al.* 2010; Jaimez *et al.* 2011), and a poorer body condition has been shown to leave hosts more susceptible to parasitic infection in many taxonomic groups including insects, fish, amphibians, rodents, and with some indication in primates (Beldomenico and Begon, 2010; Eley *et al.* 1989). However, the rare occurrence of ketones over the study period indicates that LAHG orang-utans do not have poor body conditions (at least in terms of energy balances), suggesting there may be additional factors influencing parasitic infection in this orang-utan population. Fire-induced changes in external factors such as rainfall and groundwater level which affect the free-living stages of gastrointestinal parasites may also influence nematode intensity in orang-utans (Khieu *et al.* 2014). However, this study cannot conclusively support this as the sample size was too small. Under the increasingly pronounced effects of climate change, environmental conditions in Bornean forests are likely to become more variable, with an overall increase in rainfall predicted and fires becoming more frequent and severe (Herawati and Santoso, 2011; Sa'adi *et al.* 2020). Although there is no research on the parasitic community in the peat-swamp substrate, one may speculate that peat-swamp parasites are specialised to the annual flooding cycles and acidic conditions. Therefore, changes in rainfall patterns and forest disturbance are likely to affect the life cycles, prevalence, and intensity of peat-swamp parasites and hence influence orang-utan infection rates. If indeed the pattern of greater parasitic intensity after fire events is robust, orang-utan populations may be negatively affected. Death rates may increase due to greater physiological stress, and birth rates may decrease due to lower reproductive investment, resulting in delayed population declines.

As peat-swamp forests show annual patterns of flooding and dry seasons, hydration level can be an important marker of physiological condition. The ability to balance water under difficult environmental conditions such as high temperatures and drought can have consequences on body condition (du Plessis *et al.* 2012). I found that orang-utans had higher hydration levels after a fire event. Since conditions must be very dry in order for the peat-swamp forest to burn, there would be less water in the environment for orang-utans to drink preceding a fire event. Immediately after a fire event, water is likely to be abundant as only the onset of the wet season could extinguish out a fire. Therefore, the hydration levels observed could be related to the environmental conditions that cause a fire to start and end. However, this study investigated hydration over a long-term period, six years pre-fire and four years post-fire. This is too long-term to observe the effects of environmental conditions immediately preceding and following a fire event. Another plausible explanation for this finding is the difference in hydration levels between age/sex classes and an unbalanced age/sex class sample size between the fire periods. Interestingly, male orang-utans were on average less hydrated than females and their offspring. This is likely due to the variable activity patterns between age/sex classes. Males often prioritise mating opportunities over foraging hence travel more to find receptive females, whereas females prioritise foraging and have other demands such as raising offspring. Therefore, I suspect that males lose more water than females. This would benefit from further investigation on age/sex differences in food intake and activity budgets (Morrogh-Bernard *et al.* 2009). Since there were far less samples from male orang-utans in the post-fire period and more from sexually active female orang-utans, this may be the reason for the observed higher hydration levels. This finding would benefit from investigation of hydration levels over a more short-term period and with a more balanced sample from each age/sex class to help elucidate if there is any real difference in hydration levels before and after fires.

I also showed that seasonal variables (food availability and groundwater level) affect orang-utan behaviour and health, and hence are important to account for in studies of effects of anthropogenic change. Climate change and changes in land use such as the creation of logging or oil palm concessions can affect these seasonal variables. It is important to consider the effects of fire disturbance in tandem with the changes to habitat caused by climate change and other anthropogenic disturbance as they are not mutually exclusive. For example, logging activity in the Sebangau forest is what caused the increase in susceptibility of the area to fire as it drained the peatlands (Morrogh-Bernard, 2009). Furthermore, the more intense El Niño Southern Oscillation events and increasing temperatures seen with climate change is what is making fires more severe and frequent (Spessa *et al.* 2015). There is great trepidation about recent approval for the move of Indonesia’s capital city to Kalimantan. Despite promises from the government that no protected forest will be damaged in the process, modification of more land into an urban environment and creating homes for approximately 1.5 million people is expected to have serious negative impacts on some of the last remaining forested areas containing orang-utans (Lyons, 2019). Inevitably, there will be some people making a living by logging, creating plantations, and mining which damage natural forests and increase fire risk.

Therefore, understanding the full effects of fire on wildlife inhabiting peat-swamps will require acknowledgement of other anthropogenic activities and climatic conditions, with their effects on seasonal variables and fire-inducing mechanisms. This appreciation will be critical in preventing fires in peat-swamps to protect the wildlife in this unique habitat.

To conclude, this study shows that fire affects the behaviour and health of Bornean orang-utans over both short-term and long-term periods, but it is unclear to what extent orang-utans suffer physiologically and what a greater gastrointestinal parasite intensity will mean in the long-term. Hence, future studies would benefit from using other markers of physiological condition such as cortisol, cytokines and neopterin to find out if orang-utans show higher stress levels or an increased immune response after a fire period. Investigating more detailed aspects of feeding behaviour such as diet and calorific intake in relation to activity patterns may aid in assessing orang-utan energy balance. As a part of this study, I have set up a fully in-field parasite monitoring protocol which facilitates long-term monitoring of gastrointestinal parasites in wild primates, and can be applied to other parasitological studies of mammals that do not have access to an equipped laboratory. As fires in tropical peat-swamps continue to increase in frequency and severity, adding to the continual loss of habitat caused by logging and plantations, it is essential to continue monitoring wild individuals for changes in behaviour and health, but also critical to conduct population-level assessments to identify any subsequent declines. This is not only important for the Bornean orang-utan, but for other species that inhabit fire-vulnerable habitats. Such information is vital in designing effective conservation strategies to aid with restoration of peat-swamp forests after fires and supporting legislation for the protection of peat-swamps and the wildlife that inhabit them.

4.2. Recommendations for Future Research

Examining long-term changes in orang-utan diet and calorific intake in response to fire

I found that orang-utans were exhibiting energy conserving strategies after the fire event but found no evidence of nutritional stress. My measure of foraging effort was the time spent feeding, which is not necessarily the most informative measure of feeding behaviour or energy intake. Orang-utans can spend more time feeding but ingest food items with lower nutritional value, so in fact may be in a poorer nutritional condition than an orang-utan that spends less time feeding but ingests higher quality food items. Examining other measures of feeding behaviour such as dietary composition and calorific intake should help to show if orang-utans are exhibiting energy conserving strategies in response to nutritional stress. This could be achieved by analysing changes in the proportion of each food class consumed (fruit, flowers, leaves, bark, insects) over time before and after a fire event. It will also be important to consider this alongside changes in the availability of food classes as a result of fire by continuing long-term phenology surveys at the site.

Using alternative biomarkers as measures of physiological condition

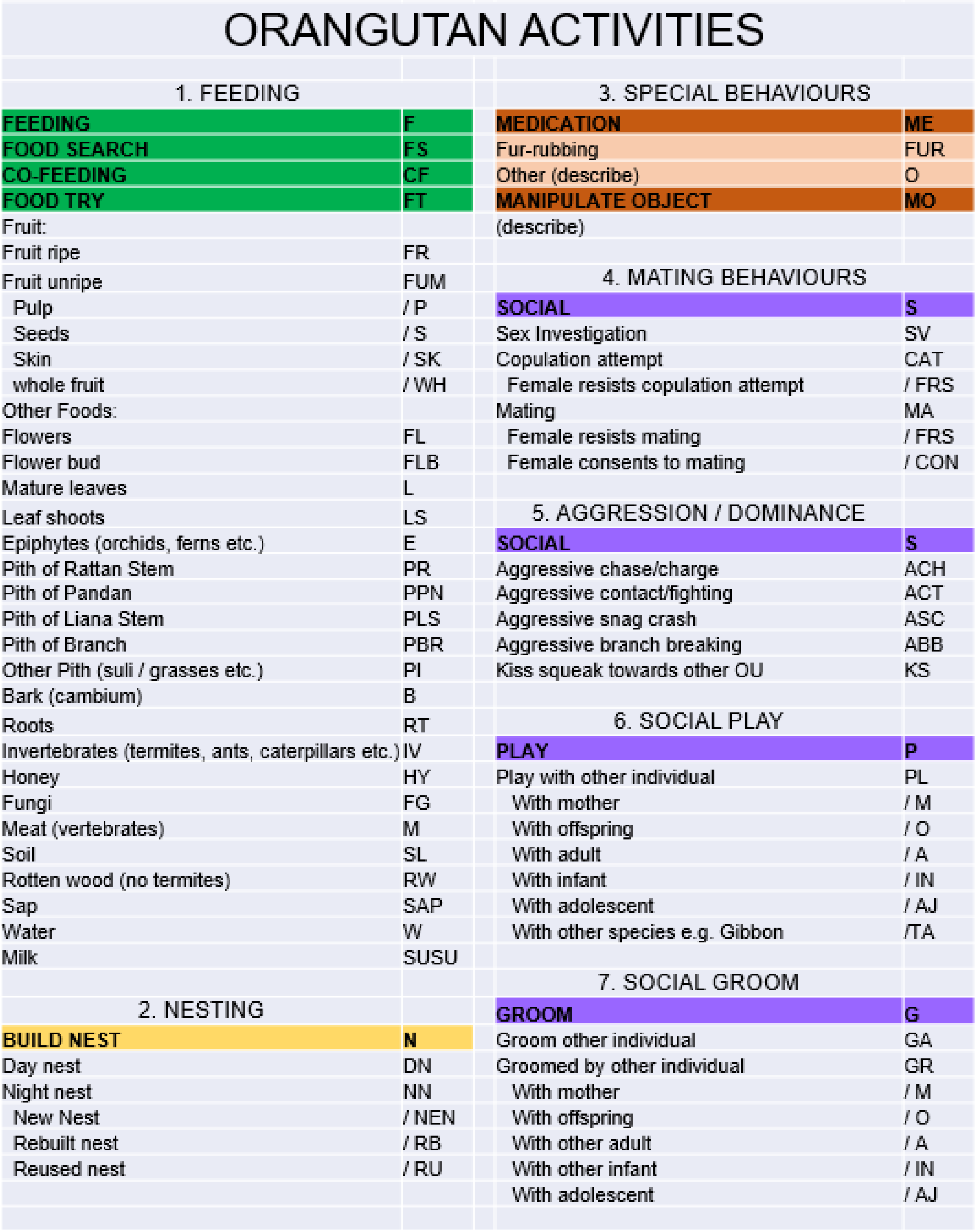
I used ketones as a measure of physiological condition. Nearly all samples tested negligible for ketones, indicating that orang-utans are not experiencing a negative energy balance. However, ketone measurements can be subject to inaccuracies from reading error and humidity damage to the multistix test strips. In addition, I recommend studying the effects of fire on cortisol levels to indicate stress (Jaimez *et al.* 2011), and cytokines and neopterin to indicate an elevated immune response. Increases in cytokines and neopterin have been reported after smoke inhalation and respiratory infection (van Eeden *et al.* 2001; Behringer *et al.* 2017). Therefore, these would act as a good indicator of physiological stress related to the smoke produced from forest fires, rather than just energy balance. Measures of cortisol, cytokines and neopterin can all be obtained from urine or faecal samples, therefore can be obtained non-invasively from wild individuals relatively easily.

Long-term monitoring of parasitic infection in wild primate populations

This study established a protocol for the analysis of faecal samples for gastrointestinal parasites entirely at a field research camp, without the need for expensive equipment or sample export/import permits. This work would benefit from a longer fieldwork period to obtain a greater sample size which would provide more robustness to trends indicated towards in this study. This protocol will help to facilitate the establishment of long-term gastrointestinal parasite monitoring projects to investigate issues such as the impacts of anthropogenic land use change on gastrointestinal parasite infection and transmission of gastrointestinal parasites from reintroduced to wild individuals at release sites.

Appendix I

Appendix I Table 1. Behavioural ethogram. Full list of all possible behaviours recorded on an orang-utan follow. Primary activities in bold and coloured cells, secondary behaviours below primary.



ORANGUTAN ACTIVITIES			
1. FEEDING		3. SPECIAL BEHAVIOURS	
FEEDING	**F**	**MEDICATION**	**ME**
FOOD SEARCH	**FS**	Fur-rubbing	FUR
CO-FEEDING	**CF**	Other (describe)	O
FOOD TRY	**FT**	**MANIPULATE OBJECT**	**MO**
Fruit:		(describe)	
Fruit ripe	FR		
Fruit unripe	FUM	4. MATING BEHAVIOURS	
Pulp	/ P	**SOCIAL**	**S**
Seeds	/ S	Sex Investigation	SV
Skin	/ SK	Copulation attempt	CAT
whole fruit	/ WH	Female resists copulation attempt	/ FRS
Other Foods:		Mating	MA
Flowers	FL	Female resists mating	/ FRS
Flower bud	FLB	Female consents to mating	/ CON
Mature leaves	L		
Leaf shoots	LS	5. AGGRESSION / DOMINANCE	
Epiphytes (orchids, ferns etc.)	E	**SOCIAL**	**S**
Pith of Rattan Stem	PR	Aggressive chase/charge	ACH
Pith of Pandan	PPN	Aggressive contact/fighting	ACT
Pith of Liana Stem	PLS	Aggressive snag crash	ASC
Pith of Branch	PBR	Aggressive branch breaking	ABB
Other Pith (suli / grasses etc.)	PI	Kiss squeak towards other OU	KS
Bark (cambium)	B		
Roots	RT	6. SOCIAL PLAY	
Invertebrates (termites, ants, caterpillars etc.)	IV	**PLAY**	**P**
Honey	HY	Play with other individual	PL
Fungi	FG	With mother	/ M
Meat (vertebrates)	M	With offspring	/ O
Soil	SL	With adult	/ A
Rotten wood (no termites)	RW	With infant	/ IN
Sap	SAP	With adolescent	/ AJ
Water	W	With other species e.g. Gibbon	/TA
Milk	SUSU		
		7. SOCIAL GROOM	
2. NESTING		**GROOM**	**G**
BUILD NEST	**N**	Groom other individual	GA
Day nest	DN	Groomed by other individual	GR
Night nest	NN	With mother	/ M
New Nest	/ NEN	With offspring	/ O
Rebuilt nest	/ RB	With other adult	/ A
Reused nest	/ RU	With other infant	/ IN
		With adolescent	/ AJ

8. OTHER SOCIAL

SOCIAL	**S**
Touch / non-aggressive contact e.g. hug	TC

9. AGGRESSION TOWARDS ANOTHER ANIMAL

AGGRESSION TOWARDS OTHER ANIMAL	**ATA**
Kiss squeak towards other animal	KS
Threatening other animal, e.g. charge, snagcrash, shaking branches etc.	TH

10. INDEPENDENT PLAY

PLAY	**P**
Independent play, e.g. swinging, twirling	IPS
Independent play with object	IPO

11. TRAVEL

TRAVELLING	**T**
Tree sway	TT
Clambering	CLA
Climbing / Descending	CLI
Brachiating	BR
Quadrupedal Walking	QW
Bipedal Walking	BI

12. AGGRESSION TOWRDS OBSERVER / PERSON

AGGRESSION TOWARDS OBSERVER	**ATO**
AGGRESSION TOWARDS OTHER PERSON	**AOP**
Kiss squeak towards observer or other person	KS
Threatening researcher or other person, e.g. charge, snagcrash, shaking branches etc.	TH
Unknown	**U**
In nest	/N
Lost	**L**
Other (describe)	**O**

13. VOCALISATION

VOCALISATION	**V**
Kiss Squeak	KS
Kiss Squeak + Grunt	KS/ GRNT
Kiss Squeak + Grumph	KS/ GRPH
Chomp	CH
Grumph	GRPH
Gork	GORK
Grumble	GRBL
Long call	LC
Lork	LK
Soft hoot / whimper	HW
Cry	CY

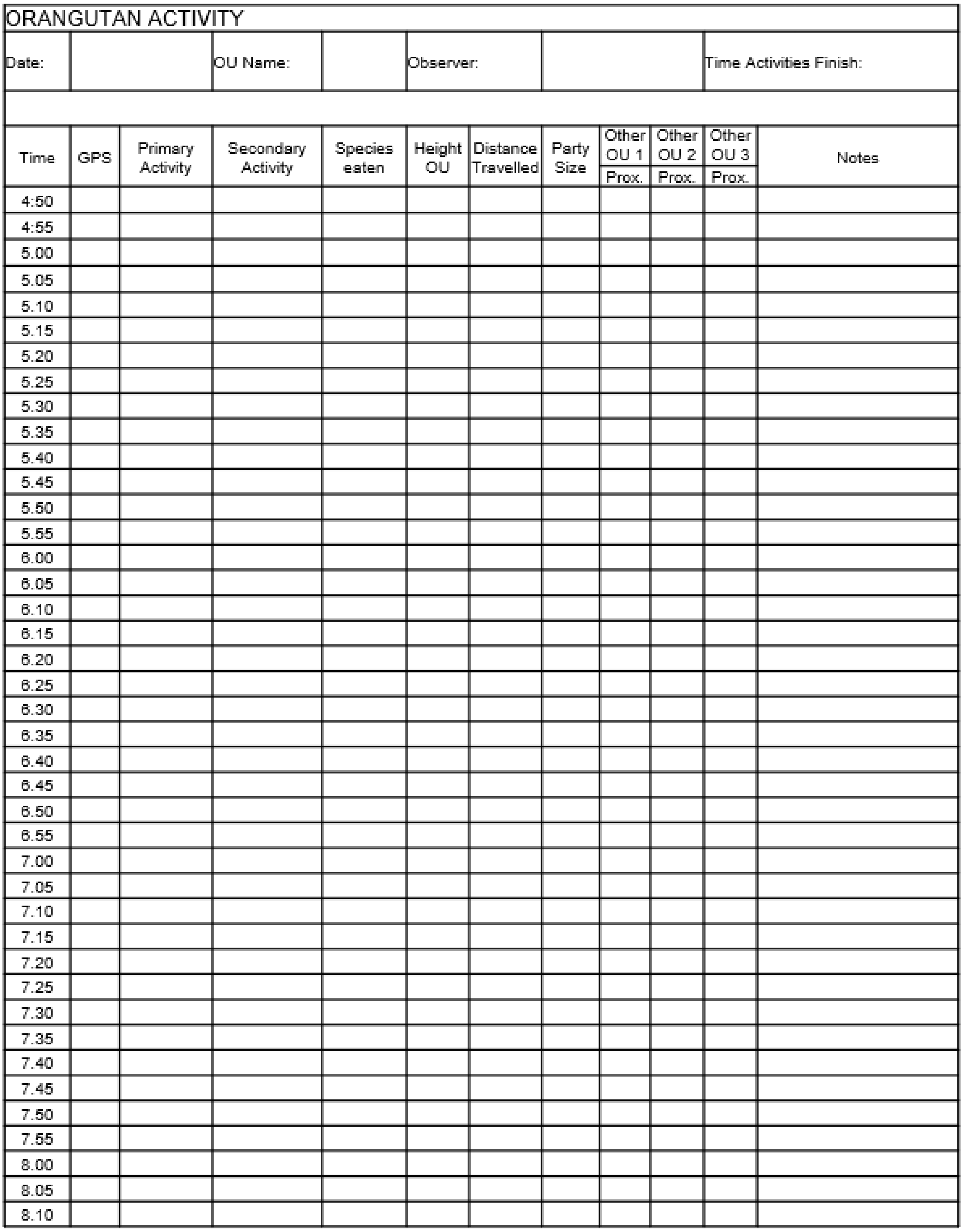
14. OTHER

DEFECATE / URINATE	**DU**
GROOM	**G**
Self-groom	SG

15. RESTING

RESTING	**R**
Sitting	SI
Standing	ST
Lying Down	LD
Hanging	HA
Quadrupedal	Q
Clinging ventrally	CLV
Clinging dorsally	CLD
Unknown	U
Tree / branch	/ TR
Liana	/ LI
Ground	/ G
Nest / sarang	/ N
On mother (infant)	/ M
Other (specify)	/ O

Appendix I Table 2. Example of a behavioural data collection sheet.



ORANGUTAN ACTIVITY											
Date:			OU Name:		Observer:					Time Activities Finish:	
Time	GPS	Primary Activity	Secondary Activity	Species eaten	Height OU	Distance Travelled	Party Size	Other OU 1	Other OU 2	Other OU 3	Notes
								Prox.	Prox.	Prox.	
4:50											
4:55											
5.00											
5.05											
5.10											
5.15											
5.20											
5.25											
5.30											
5.35											
5.40											
5.45											
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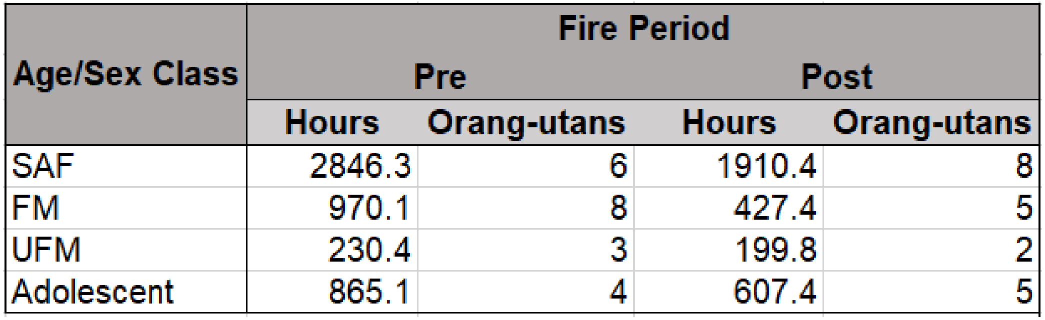
7.35											
7.40											
7.45											
7.50											
7.55											
8.00											
8.05											
8.10											

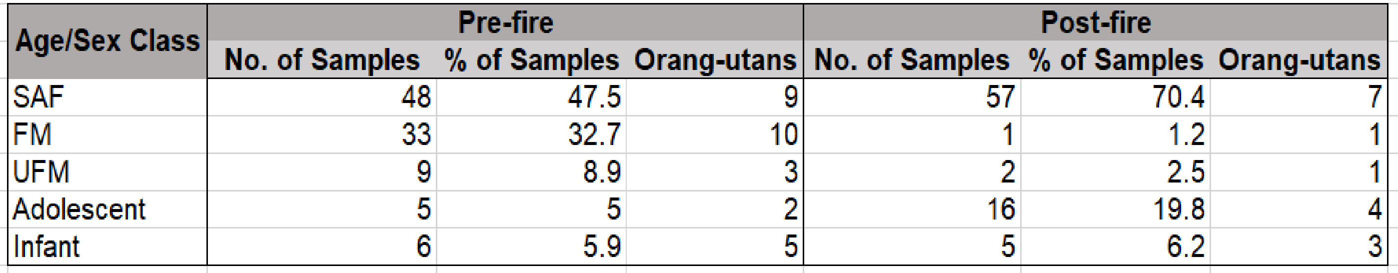
Appendix II

Appendix II Table 1. The total number of follow hours and sample size of orang-utans for each age/sex class in the pre-fire and post-fire periods.

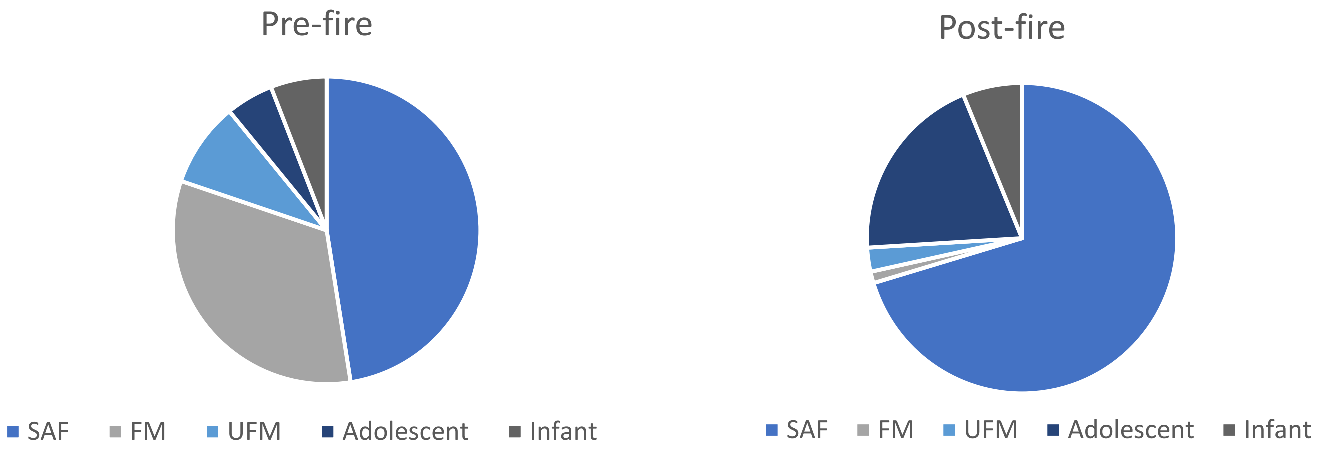


Age/Sex Class	Fire Period			
	Pre		Post	
	Hours	Orang-utans	Hours	Orang-utans
SAF	2846.3	6	1910.4	8
FM	970.1	8	427.4	5
UFM	230.4	3	199.8	2
Adolescent	865.1	4	607.4	5

Appendix II Table 2. The total number of urine samples, percentage of samples, and number of orang-utans of each age/sex class in the pre-fire and post-fire periods for specific gravity analysis.



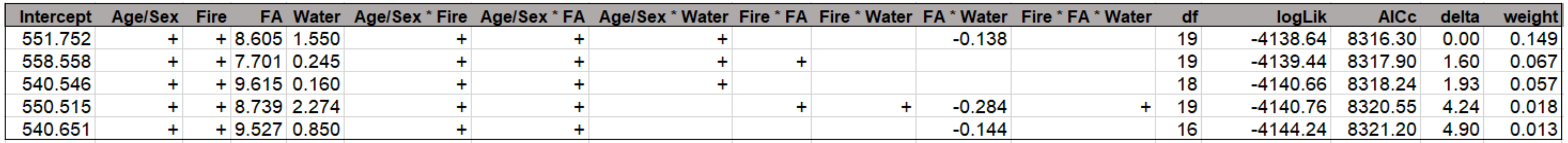
Age/Sex Class	Pre-fire			Post-fire		
	No. of Samples	% of Samples	Orang-utans	No. of Samples	% of Samples	Orang-utans
SAF	48	47.5	9	57	70.4	7
FM	33	32.7	10	1	1.2	1
UFM	9	8.9	3	2	2.5	1
Adolescent	5	5	2	16	19.8	4
Infant	6	5.9	5	5	6.2	3



Appendix II Figure 1. A comparison of the proportion of samples from each age/sex class in the pre-fire and post-fire periods.

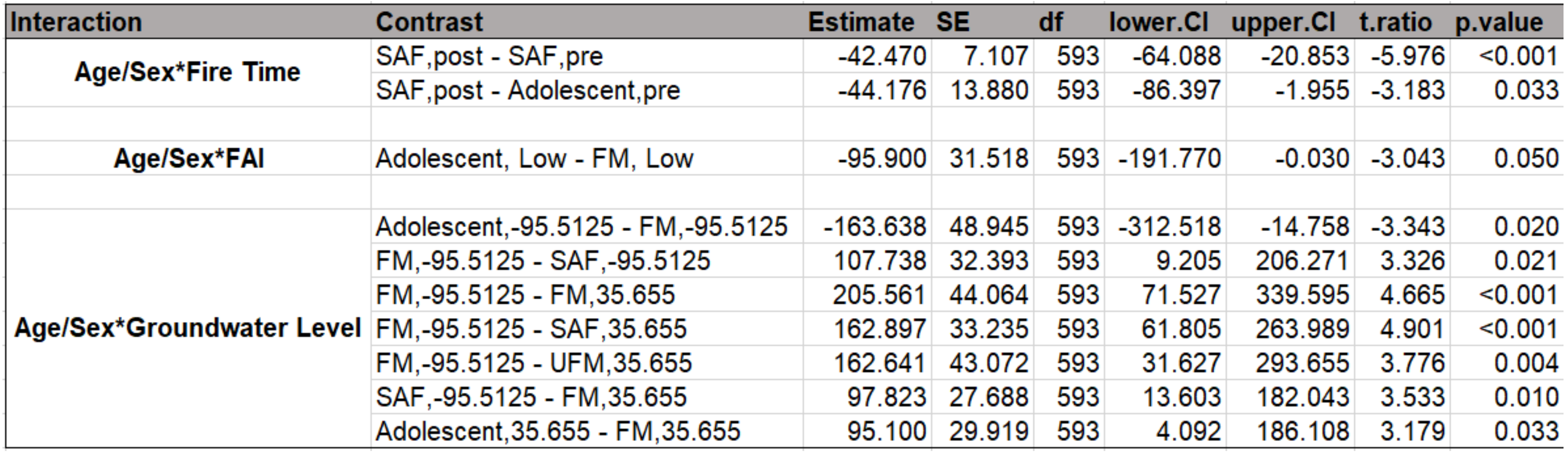
Appendix III

Appendix III Table 1. Model selection summary for the analysis identifying the predictors of orang-utan active period length. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



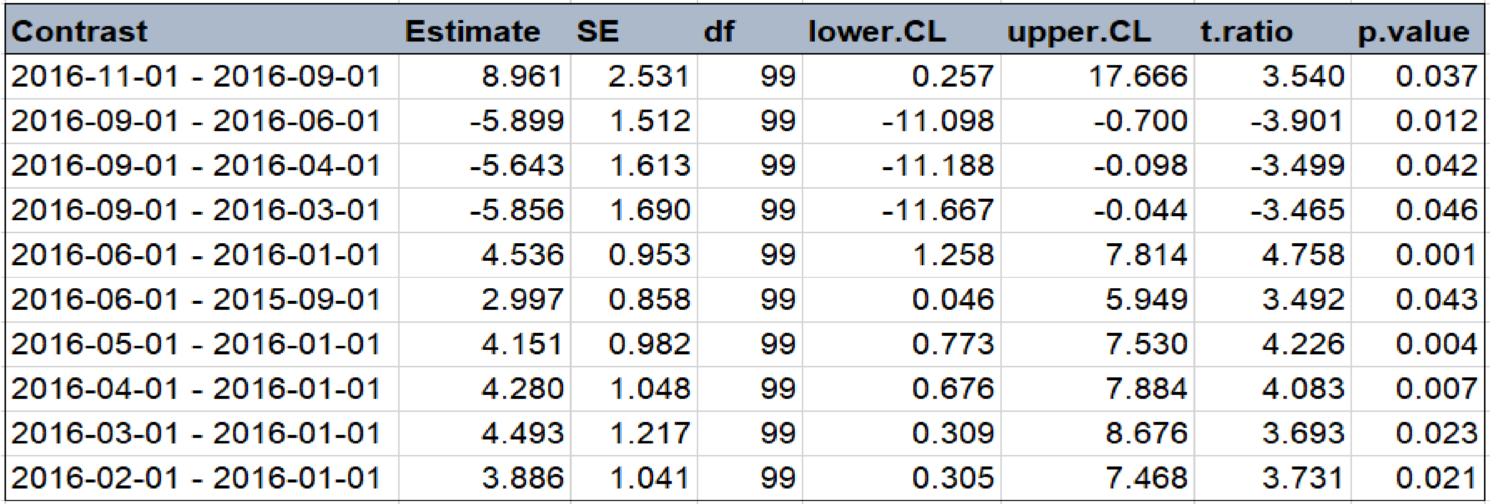
Intercept	Age/Sex	Fire	FA	Water	Age/Sex * Fire	Age/Sex * FA	Age/Sex * Water	Fire * FA	Fire * Water	FA * Water	Fire * FA * Water	df	logLik	AICc	delta	weight
551.752	+	+	8.605	1.550	+	+	+			-0.138		19	-4138.64	8316.30	0.00	0.149
558.558	+	+	7.701	0.245	+	+	+	+				19	-4139.44	8317.90	1.60	0.067
540.546	+	+	9.615	0.160	+	+	+					18	-4140.66	8318.24	1.93	0.057
550.515	+	+	8.739	2.274	+	+		+	+	-0.284	+	19	-4140.76	8320.55	4.24	0.018
540.651	+	+	9.527	0.850	+	+				-0.144		16	-4144.24	8321.20	4.90	0.013

Appendix III Table 2. Post-hoc pairwise comparisons of length of active period across levels of fire period, age/sex categories, food availability and groundwater level. Significant interactions shown only.



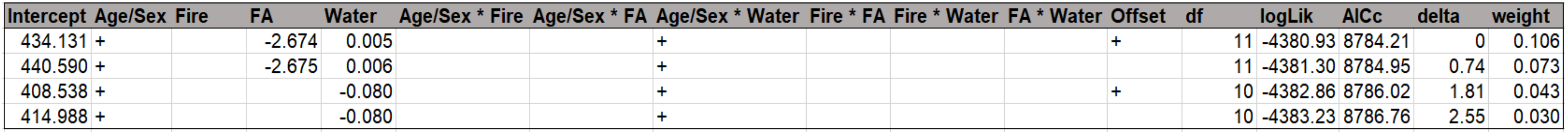
Interaction	Contrast	Estimate	SE	df	lower.CI	upper.CI	t.ratio	p.value
Age/Sex*Fire Time	SAF,post - SAF,pre	-42.470	7.107	593	-64.088	-20.853	-5.976	<0.001
	SAF,post - Adolescent,pre	-44.176	13.880	593	-86.397	-1.955	-3.183	0.033
Age/Sex*FAI	Adolescent, Low - FM, Low	-95.900	31.518	593	-191.770	-0.030	-3.043	0.050
Age/Sex*Groundwater Level	Adolescent,-95.5125 - FM,-95.5125	-163.638	48.945	593	-312.518	-14.758	-3.343	0.020
	FM,-95.5125 - SAF,-95.5125	107.738	32.393	593	9.205	206.271	3.326	0.021
	FM,-95.5125 - FM,35.655	205.561	44.064	593	71.527	339.595	4.665	<0.001
	FM,-95.5125 - SAF,35.655	162.897	33.235	593	61.805	263.989	4.901	<0.001
	FM,-95.5125 - UFM,35.655	162.641	43.072	593	31.627	293.655	3.776	0.004
	SAF,-95.5125 - FM,35.655	97.823	27.688	593	13.603	182.043	3.533	0.010
	Adolescent,35.655 - FM,35.655	95.100	29.919	593	4.092	186.108	3.179	0.033

Appendix III Table 3. Post-hoc pairwise comparisons of time spent resting over a short-term period after the 2015 fire event. Months encompass the range September 2015 – November 2016. Significant comparisons shown only.



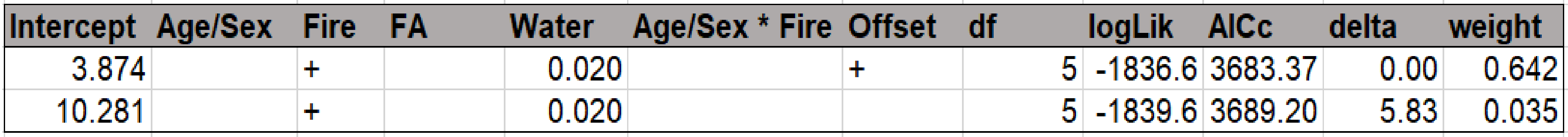
Contrast	Estimate	SE	df	lower.CL	upper.CL	t.ratio	p.value
2016-11-01 - 2016-09-01	8.961	2.531	99	0.257	17.666	3.540	0.037
2016-09-01 - 2016-06-01	-5.899	1.512	99	-11.098	-0.700	-3.901	0.012
2016-09-01 - 2016-04-01	-5.643	1.613	99	-11.188	-0.098	-3.499	0.042
2016-09-01 - 2016-03-01	-5.856	1.690	99	-11.667	-0.044	-3.465	0.046
2016-06-01 - 2016-01-01	4.536	0.953	99	1.258	7.814	4.758	0.001
2016-06-01 - 2015-09-01	2.997	0.858	99	0.046	5.949	3.492	0.043
2016-05-01 - 2016-01-01	4.151	0.982	99	0.773	7.530	4.226	0.004
2016-04-01 - 2016-01-01	4.280	1.048	99	0.676	7.884	4.083	0.007
2016-03-01 - 2016-01-01	4.493	1.217	99	0.309	8.676	3.693	0.023
2016-02-01 - 2016-01-01	3.886	1.041	99	0.305	7.468	3.731	0.021

Appendix III Table 4. Model selection summary for the analysis identifying the predictors of the time orang-utans spend feeding. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



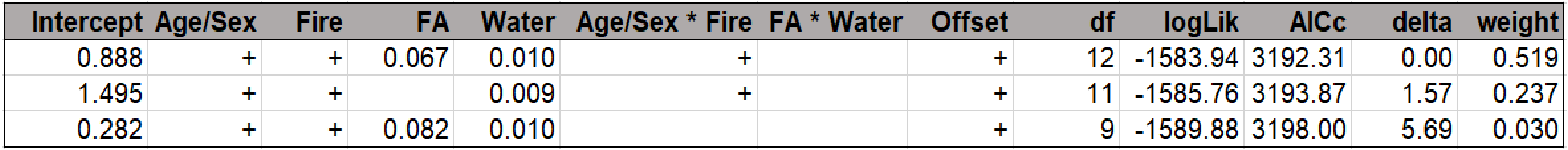
Intercept	Age/Sex	Fire	FA	Water	Age/Sex * Fire	Age/Sex * FA	Age/Sex * Water	Fire * FA	Fire * Water	FA * Water	Offset	df	logLik	AICc	delta	weight
434.131	+		-2.674	0.005			+				+	11	-4380.93	8784.21	0	0.106
440.590	+		-2.675	0.006			+					11	-4381.30	8784.95	0.74	0.073
408.538	+			-0.080			+				+	10	-4382.86	8786.02	1.81	0.043
414.988	+			-0.080			+					10	-4383.23	8786.76	2.55	0.030

Appendix III Table 5. Model selection summary for the analysis identifying the predictors of the time orang-utans spend resting. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



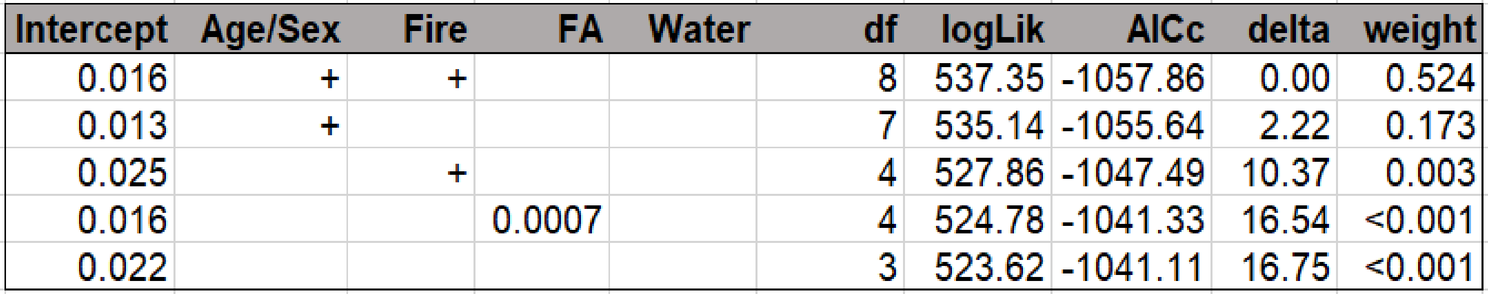
Intercept	Age/Sex	Fire	FA	Water	Age/Sex * Fire	Offset	df	logLik	AICc	delta	weight
3.874		+		0.020		+	5	-1836.6	3683.37	0.00	0.642
10.281		+		0.020			5	-1839.6	3689.20	5.83	0.035

Appendix III Table 6. Model selection summary for the analysis identifying the predictors of the time orang-utans spend travelling. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



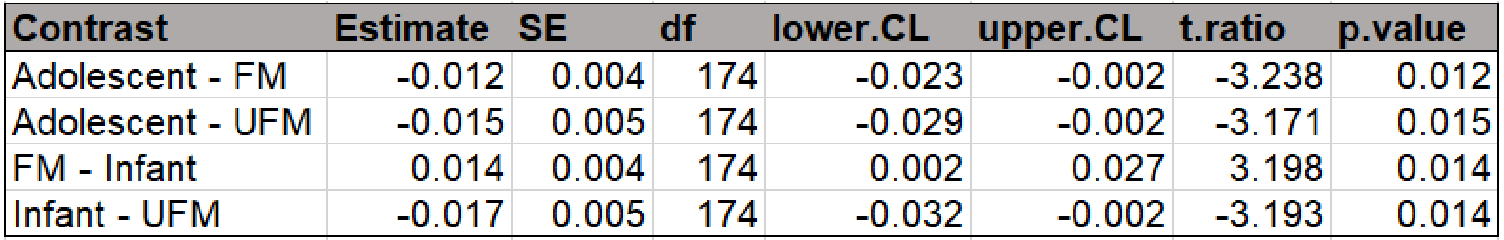
Intercept	Age/Sex	Fire	FA	Water	Age/Sex * Fire	FA * Water	Offset	df	logLik	AICc	delta	weight
0.888	+	+	0.067	0.010	+		+	12	-1583.94	3192.31	0.00	0.519
1.495	+	+		0.009	+		+	11	-1585.76	3193.87	1.57	0.237
0.282	+	+	0.082	0.010			+	9	-1589.88	3198.00	5.69	0.030

Appendix III Table 7. Model selection summary for the analysis identifying the predictors of urine specific gravity. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



Intercept	Age/Sex	Fire	FA	Water	df	logLik	AICc	delta	weight
0.016	+	+			8	537.35	-1057.86	0.00	0.524
0.013	+				7	535.14	-1055.64	2.22	0.173
0.025		+			4	527.86	-1047.49	10.37	0.003
0.016			0.0007		4	524.78	-1041.33	16.54	<0.001
0.022					3	523.62	-1041.11	16.75	<0.001

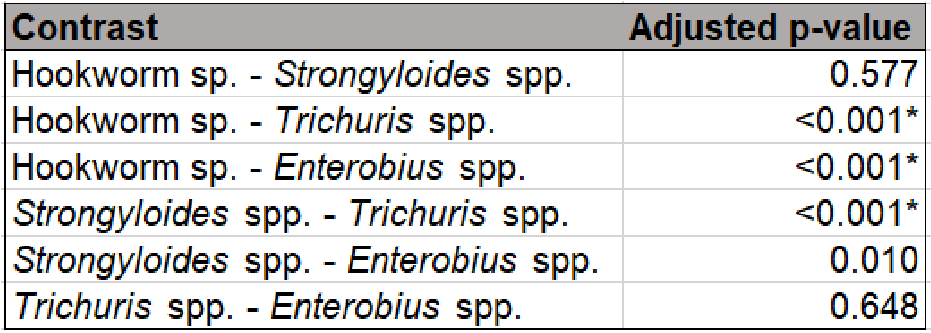
Appendix III Table 8. Post-hoc pairwise comparisons of specific gravity across levels of fire period, age/sex categories, and groundwater level. Significant comparisons shown only.



Contrast	Estimate	SE	df	lower.CL	upper.CL	t.ratio	p.value
Adolescent - FM	-0.012	0.004	174	-0.023	-0.002	-3.238	0.012
Adolescent - UFM	-0.015	0.005	174	-0.029	-0.002	-3.171	0.015
FM - Infant	0.014	0.004	174	0.002	0.027	3.198	0.014
Infant - UFM	-0.017	0.005	174	-0.032	-0.002	-3.193	0.014

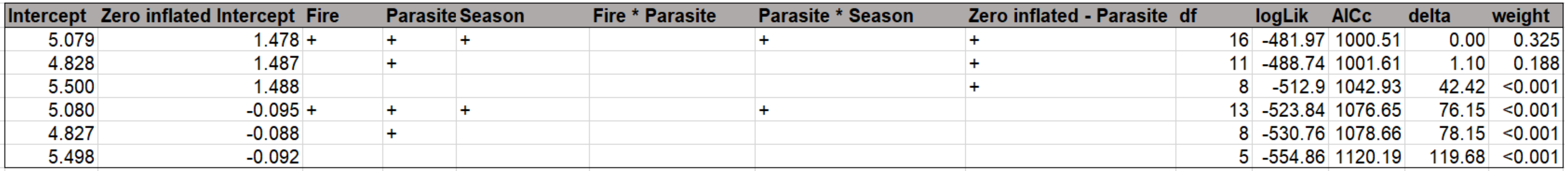
Appendix IV

Appendix IV Table 1. Post-hoc pairwise comparisons of the prevalence of each nematode taxa. * = significance at the adjusted p-value.



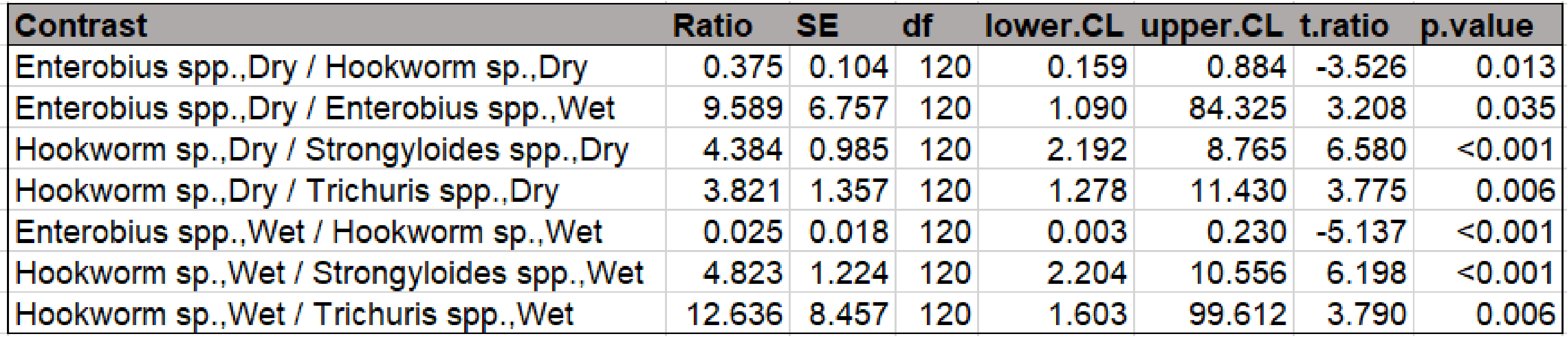
Contrast	Adjusted p-value
Hookworm sp. - *Strongyloides* spp.	0.577
Hookworm sp. - *Trichuris* spp.	<0.001*
Hookworm sp. - *Enterobius* spp.	<0.001*
Strongyloides spp. - *Trichuris* spp.	<0.001*
Strongyloides spp. - *Enterobius* spp.	0.010
Trichuris spp. - *Enterobius* spp.	0.648

Appendix IV Table 2. Model selection summary for the analysis identifying the predictors of nematode intensity in eggs g^{-1}. The models presented are those retained after application of the nesting rule (Richards *et al.* 2011) and selection for models with delta <6 (Harrison *et al.* 2018).



Intercept	Zero inflated Intercept	Fire	Parasite	Season	Fire * Parasite	Parasite * Season	Zero inflated - Parasite	df	logLik	AICc	delta	weight
5.079	1.478	+	+	+		+	+	16	-481.97	1000.51	0.00	0.325
4.828	1.487		+				+	11	-488.74	1001.61	1.10	0.188
5.500	1.488						+	8	-512.9	1042.93	42.42	<0.001
5.080	-0.095	+	+	+		+		13	-523.84	1076.65	76.15	<0.001
4.827	-0.088		+					8	-530.76	1078.66	78.15	<0.001
5.498	-0.092							5	-554.86	1120.19	119.68	<0.001

Appendix IV Table 3. Significant post-hoc pairwise comparisons of nematode intensity with the nematode*season interaction.



Contrast	Ratio	SE	df	lower.CL	upper.CL	t.ratio	p.value
Enterobius spp.,Dry / Hookworm sp.,Dry	0.375	0.104	120	0.159	0.884	-3.526	0.013
Enterobius spp.,Dry / Enterobius spp.,Wet	9.589	6.757	120	1.090	84.325	3.208	0.035
Hookworm sp.,Dry / Strongyloides spp.,Dry	4.384	0.985	120	2.192	8.765	6.580	<0.001
Hookworm sp.,Dry / Trichuris spp.,Dry	3.821	1.357	120	1.278	11.430	3.775	0.006
Enterobius spp.,Wet / Hookworm sp.,Wet	0.025	0.018	120	0.003	0.230	-5.137	<0.001
Hookworm sp.,Wet / Strongyloides spp.,Wet	4.823	1.224	120	2.204	10.556	6.198	<0.001
Hookworm sp.,Wet / Trichuris spp.,Wet	12.636	8.457	120	1.603	99.612	3.790	0.006

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