

The Gunung Palung Orangutan Project: Twenty-five years at the intersection of research and conservation in a critical landscape in Indonesia

Cheryl D. Knott^{a,b,c,d,e,*}, Erin E. Kane^{a,c,d}, Mariamah Achmad^c, Elizabeth J. Barrow^{c,d}, Meredith L. Bastian^{a,d,f}, Josephine Beck^{c,d}, Andrea Blackburn^{a,d}, Terri L. Breeden^c, Nancy Lou Conklin Brittain^g, Jennifer J. Brousseau^{c,d,h}, Ella R. Brown^{c,d,o}, Michelle Brown^{d,i}, Laura A. Brubaker-Wittman^{a,d}, Gail A. Campbell-Smith^{c,d,j}, Andrew de Sousa^c, Andrea L. DiGiorgio^{a,d,k}, Cathryn A. Freund^{c,l}, Victoria I. Gehrke^c, Aly Granados^{c,d,m}, John Harting^{c,d,aa}, Faye S. Harwell^{a,d}, Andrea Johnson^{c,d}, Petrus Kanisius^c, James R. Kemsey^c, Sulidra Frederik Kurniawan^c, Desi Kurniawati^c, Timothy G. Laman^{c,d,n}, Andrew J. Marshall^{o,x,y,z}, Ranti Naruri^c, Caitlin A. O'Connell^{a,d,p}, Brodie J. Philp^{c,d}, Edi Rahman^c, Riyandi^q, Natalie J. Robinson^{a,c,d}, Amy M. Scott^{a,d}, Katherine S. Scott^{c,d,r}, Tatang Mitra Setia^s, Wuryantari Setiadi^t, Endro Setiawan^{u,w}, Ibrahim Sumardi^u, Robert Rodriguez Suro^{a,c,d}, Frederik Wendi Tamariska^c, Melissa Emery Thompson^v, Betsy Yaap^{c,d}, Tri Wahyu Susanto^{c,d,s}

^a Department of Anthropology, Boston University, MA, USA

^b Department of Biology, Boston University, MA, USA

^c Gunung Palung Orangutan Conservation Program, MA, USA/Yayasan Palung, Ketapang, West Kalimantan, Indonesia

^d Gunung Palung Orangutan Project, Cabang Panti Research Station, West Kalimantan, Indonesia

^e Women's, Gender and Sexuality Program, Boston University, MA, USA

^f Smithsonian's National Zoo and Conservation Biology Institute, Washington DC, USA

^g Department of Human Evolutionary Biology, Harvard University, MA, USA

^h Department of Forest Resources and Environmental Conservation, Virginia Polytechnic Institute and State University, VA, USA

ⁱ Department of Anthropology, University of California Santa Barbara, CA, USA

^j International Animal Rescue, Ketapang, West Kalimantan, Indonesia

^k Princeton University, NJ, USA

^l Department of Biology, Wake Forest University, NC, USA

^m Department of Forest Resources Management, University of British Columbia, Canada

ⁿ Museum of Comparative Zoology, Harvard University, MA, USA

^o Department of Anthropology, University of Michigan, MI, USA

^p Department of Biological Sciences, Human and Evolutionary Biology, University of Southern California, CA, USA

^q Faculty of Mathematics and Science, Tanjungpura University, Pontianak, West Kalimantan, Indonesia

^r Department of Social Sciences, Oxford Brookes University, United Kingdom

^s Biology Faculty, Universitas Nasional, Jakarta, Indonesia

^t Eijkman Institute for Molecular Biology, Jakarta, Indonesia

^u Gunung Palung National Park Office, Ketapang, West Kalimantan, Indonesia

^v Department of Anthropology, University of New Mexico, NM, USA

^w Biology Study Program, Graduate School, Universitas Nasional, Jakarta, Indonesia

^x Department of Ecology and Evolutionary Biology, University of Michigan, MI, USA

^y Program in the Environment, University of Michigan, MI, USA

^z School for Environment and Sustainability, University of Michigan, MI, USA

^{aa} Pacific Biosciences, Menlo Park, CA, USA

* Corresponding author at: Department of Anthropology, Boston University, 232 Bay State Road, Boston, MA 02215, USA.

E-mail address: knott@bu.edu (C.D. Knott).

ARTICLE INFO

Keywords:
Orangutan
Rainforest
Long-term research
Critically endangered
Non-invasive
Conservation

ABSTRACT

The Gunung Palung Orangutan Project has conducted research on critically endangered wild Bornean orangutans (*Pongo pygmaeus wurmbii*) since 1994 in Gunung Palung National Park, West Kalimantan, Indonesia. A major goal of our broad-ranging research on orangutan behavior and ecology is to understand how the unique rainforest environment of Southeast Asia, characterized by dramatic changes in fruit productivity due to unpredictable mast fruiting, impacts orangutan behavior, physiology, and health. Much of our research has been devoted to the development of non-invasive techniques and an integrated biology approach – using hormonal assays, fecal processing, nutritional analysis, genetics, and behavioral ecology – and has led to an increased understanding of the ecological and evolutionary pressures shaping orangutan adaptations. Our results show that the extended life history and very slow reproductive rate of orangutans are adaptations to their environment. Orangutans in the Gunung Palung landscape, as elsewhere across Borneo and Sumatra, also face a series of conservation challenges, including extensive habitat loss and the illegal pet trade. We highlight how our investigations of orangutan health status, ecosystem requirements, and the assessment of orangutan density using ground and drone nest surveys have been applied to conservation efforts. We describe our project's direct conservation interventions of public education and awareness campaigns, sustainable livelihood development, establishment of village-run customary forests, investigation of the illegal pet trade, and active engagement with Indonesian government organizations. These efforts, in concert with the development of local scientific and conservation capacity, provide a strong foundation for further conservation as orangutans face a challenging future.

1. Introduction

Primates are important to biodiversity conservation, are flagship species for protected areas, and contribute to ecosystem function (Supriatna and Ario, 2015). Long-term field research is critical to protect endangered species, and some of the longest running projects have been on wild primates (Wrangham and Ross, 2008). Such projects provide data illuminating physiological and ecological processes impacting wildlife, data which can and should enable impactful conservation action. Integrating research and conservation is paramount for orangutans given their extended life histories. With a lifespan of 50 years or more, first birth in females at age 15, slow growth, and the longest inter-birth interval of any mammal (Galdikas and Wood, 1990; Knott and Harwell, in press; van Noordwijk et al., 2018), orangutans are particularly vulnerable to extinction (Marshall et al., 2009). Here, we highlight how the Gunung Palung Orangutan Project (GPOP) has intertwined research and conservation to help safeguard a critically important population of Bornean orangutans.

The very name orangutan, translating to “person of the forest” in Indonesian and Malay, underscores that the fate of this great ape rests on protection of their rainforest habitat. During the Pleistocene, orangutans were distributed across Asia, but are now restricted to the islands of Borneo and Sumatra in Indonesia and Malaysia (Knott and Kahlenberg, 2011). In 2016, the Bornean orangutan (*Pongo pygmaeus*) was classified as Critically Endangered on the IUCN Red List and listed on Appendix I of CITES (Ancenaz et al., 2016), joining the already critically endangered Sumatran orangutan (*Pongo abelii*). In 2017, an isolated population of Sumatran orangutans was defined as a genetically distinct species, the Tapanuli orangutan (*Pongo tapanuliensis*), instantly becoming the most endangered ape (Nater et al., 2017; Wich et al., 2019). Bornean orangutan populations, specifically, decreased over 60% from 1950 to 2010 with an additional 22% decline projected to occur between 2010 and 2025 (Ancenaz et al., 2016).

Seven main threats drive orangutan population decline: human population pressure, logging-related forest loss, forest conversion for agriculture, forest fires, hunting, the illegal pet trade, and weak law enforcement (Ancenaz et al., 2016; Freund et al., 2016; Marshall et al., 2006; Meijaard et al., 2011a; Nelleman et al., 2007; Norconk et al., 2020; Rijksen and Meijaard, 1999; Wich et al., 2008). Over the past 50 years, timber extraction and rainforest conversion to monoculture plantations contributed to the destruction of at least 80% of Bornean and Sumatran rainforests (Ancenaz et al., 2016; Curran et al., 2004; Gaveau et al., 2014; Wich et al., 2012). Of remaining wild orangutan populations, 75% are outside of protected areas (Meijaard et al., 2012) in forests being rapidly logged and converted for agriculture (Ancenaz et al., 2016).

1.1. Gunung Palung National Park (GPNP)

In 1937, 30,000 ha of land surrounding Mt. Palung (Gunung Palung in Indonesian) were designated a Natural Reserve Area, becoming officially demarcated in 1978. By 1981, the area was renamed a Wildlife Reserve, and expanded to 90,000 ha. In 1990, the Wildlife Reserve was declared a National Park, and in 2014 expanded to 108,044 ha. GPNP was initially contained entirely within the Ketapang Regency, but in 2007, 81% of the Park shifted to the newly created Kayong Utara Regency (Fig. 1).

GPNP and the surrounding landscape is a United Nations Great Ape Survival Project conservation priority area, representing one of the world's most important blocks of orangutan habitat and one of the only remaining tracts of intact lowland Dipterocarp rainforest in Borneo. It contains one of the last viable orangutan populations and safeguards other endangered species including gibbons, sun bears, proboscis monkeys, pangolins, and tarsiers (Blundell, 1996). It serves as a water catchment, providing clean water to surrounding regions, and is a regional buffer against climate change, with deep peat forests acting as carbon sinks and mitigating flooding and damage to coastal farmlands from tidal salinity. Despite its conservation designation, illegal logging, hunting, and encroaching oil palm plantations threaten GPNP's biodiversity.

The Gunung Palung Orangutan Project (GPOP) was established in 1994 by Cheryl Knott, after an initial pilot study in 1992. The research project is based at the Cabang Panti Research Station (1°13'S, 110°7'E, elevation 0–1116 m) in west-central GPNP. In 1984, Mark Leighton founded the station in collaboration with the Indonesian Institute of Sciences, with permission and cooperation from the Ministry of Forestry (Leighton and Darnaedi, 1996). Leighton's research at Cabang Panti continued until 1996. A second long-term study, the One Forest Project, was established here by Andrew Marshall in 2000. Our primary rainforest site sits on the upper branches of the Air Putih River, at the western base of the valley between Mt. Palung (1116 m) and Mt. Panti (1050 m). Cabang Panti was initially reached only by canoe, but is now also accessible by a 12.4 km trail from Tanjung Gunung, a Buginese village on the edge of the Park (Fig. 1). The research area encompasses 3400 ha, with 96.7 km of trails (Fig. 2). Additional research is also conducted in a 1100 ha area of secondary and degraded forest with a history of illegal logging along the Rangkong River between Tanjung Gunung and Cabang Panti. The Park's proximity to the Java Sea and its relatively small, isolated mountain range, results in elevational compression of plant communities and distinct ecological zones (Grubb, 1977; Marshall, 2009).

This site was chosen for its habitat diversity, distinguished by geology, soil type, drainage, elevation, plant species, forest structure, and

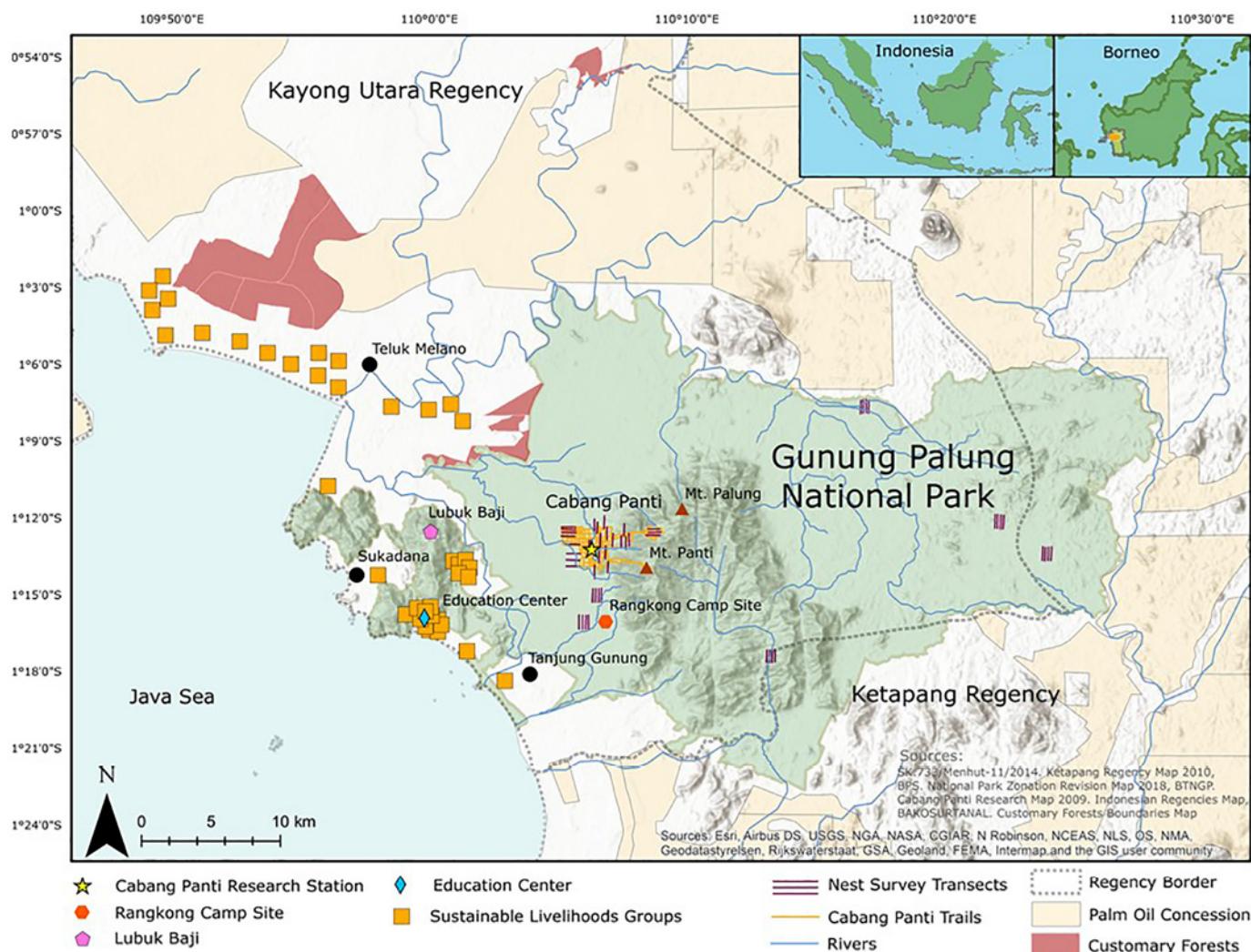


Fig. 1. Map of the Gunung Palung conservation landscape, showing the location of the research area within the National Park, research area trail system, nest survey transects, the access trail to the station from the village of Tanjung Gunung, and our secondary research area along the Rangkong River. The conservation landscape depicted includes surrounding oil palm concessions, the location of our customary forests, Lubuk Baji camp, our Environmental Education Center, and our sustainable livelihoods groups.

phenology (Fig. 2). Forest types include 1) *peat swamp*: nutrient-poor, bleached white soils, overlain by variable amounts of organic matter (5–10 m asl), 2) *freshwater swamp*: nutrient-rich, seasonally flooded, poorly drained, gleyic soils (5–10 m asl), 3) a small amount of *heath forest*: nutrient-poor, sandstone on mossy soil (0–50 m asl, with some higher elevation patches), 4) *alluvial bench*: nutrient-rich, sandstone and granite-derived soil within the floodplain of the *Air Putih*, with a high clay content on sparse patches of shale (0–50 m asl), 5) *lowland sandstone*: well-drained sandstone-derived soils with a high clay content and occasional patches of shale (20–200 m asl), 6) *lowland granite*: well-drained, granite-derived soils (200–400 m asl), 7) *upland granite*: well-drained, granite-derived soils (350–800 m asl), and 8) *montane*: largely granite-derived soils (750–1116 m asl) (Cannon and Leighton, 2004; Marshall et al., 2014). The Park also includes brackish water swamp forest and mangrove habitat outside of the research area (Leighton and Darnaedi, 1996).

Indonesia experienced catastrophic deforestation over the last century, losing an average of 1.52 million ha of forest annually (Sumargo et al., 2011). Kalimantan (Indonesian Borneo) has one of the highest deforestation rates, losing 30.7% of intact forest from 1973 to 2010 (Gaveau et al., 2014). Dipterocarp trees, which grow up to 70 m and constitute over 85% of timber exports from Indonesia, are targeted for

logging (Curran et al., 1999). Typically, small teams hand-log these trees, drag them through the forest, and transport them via rivers (Hiller et al., 2004).

GPNP lost nearly 11% of its area to agriculture and durian plantations by 1989 (Fawzi et al., 2018) and 1–2.4% of the Park and buffer zone were lost annually between 1988 and 2002 (Curran et al., 2004). El Niño-related drought in 1997 led to forest fires, exacerbating forest loss and destroying 30% of the old-growth forest in GPNP, with an additional 1.1% lost to fires in 2015 (Fawzi et al., 2019). The fall of President Suharto in 1998, precipitated by the Asian economic crisis of 1997, compromised government management of protected areas throughout Kalimantan (Nellemann et al., 2007). Illegal logging and mining increased with political turmoil, and from 2000 to 2004 GPNP experienced substantial illegal logging (Nellemann et al., 2007). Most logging occurred in the Park's northern and western regions, but logging on the *Air Putih* River also increased in the 2000s, and by 2003 selective hand-logging reached Cabang Panti's trail system. Because this posed an immediate threat to researcher and staff safety, we were forced to shut down until the national government became involved and logging subsided (Nellemann et al., 2007). The station was rebuilt in 2007, spearheaded by Andrew Marshall, and both long-term projects resumed research.

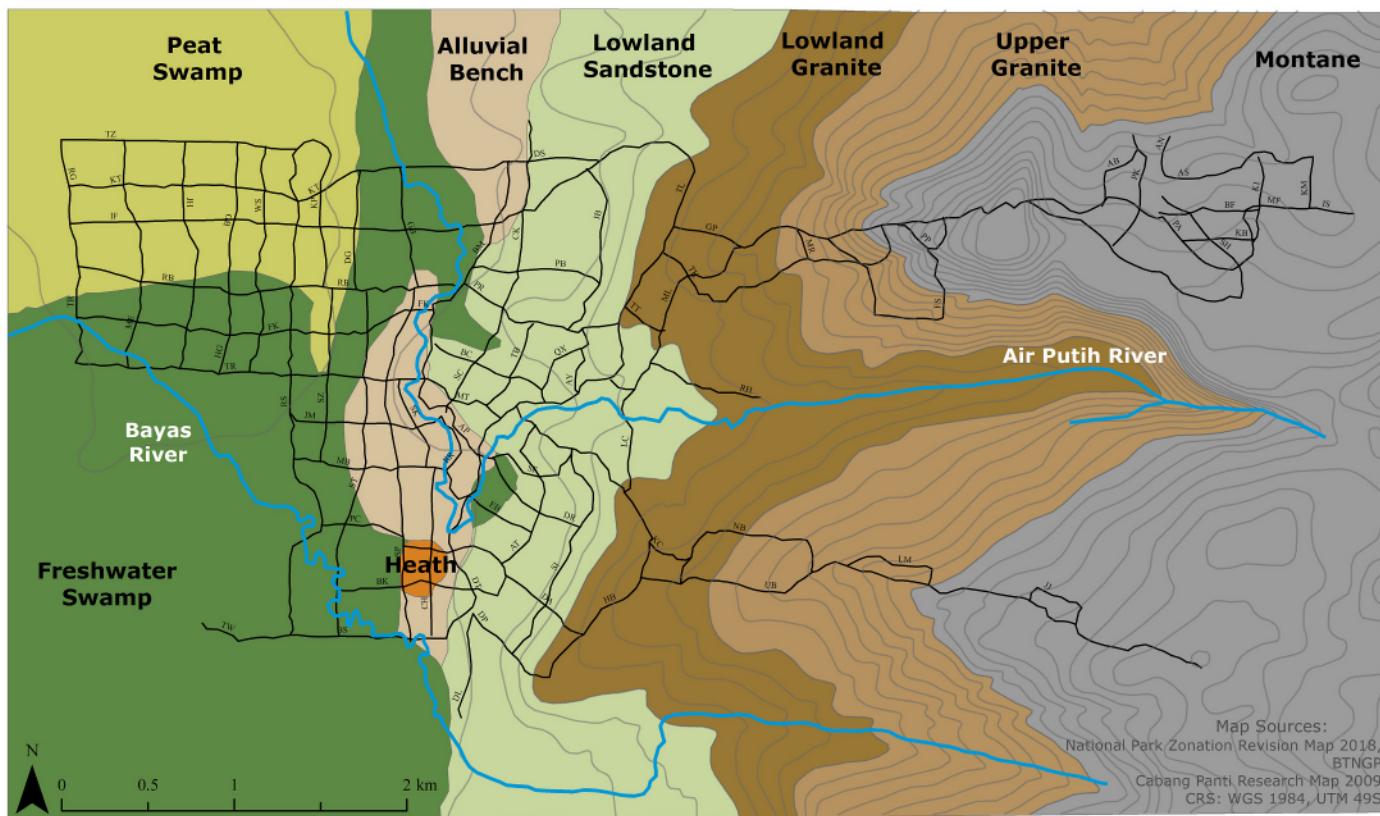


Fig. 2. Map of research area showing trail network around the Cabang Panti Research Station, with habitats and elevation delineated.

Despite this history of logging in the National Park, our research area has remained largely intact, although Bornean ironwood trees (*Eusideroxylon zwageri*) were selectively hand-logged before 1980. Conditions throughout GPNP have significantly improved: between 2011 and 2017 annual forest loss decreased to 0.12 - 0.21% (Fawzi et al., 2018). Formerly-logged areas in GPNP have regenerated, and by 2018 secondary forest composed 26% of the Park's area (Fawzi et al., 2019). Logging along the western border, where our conservation activities are concentrated (Yoshikura et al., 2016), has largely been eliminated and remote sensing detected no deforestation in GPNP from 2015 to 2018 (Fawzi et al., 2019). GPNP is an integral component of the largest network of protected lowland rainforest in Indonesian Borneo (Curran et al., 2004).

2. Orangutan habitat and nutritional requirements

The overarching goal of GPOP is to understand how orangutan biology is influenced by the rainforest habitat they occupy and to apply this knowledge to further their conservation. We explore the relationship between environment and orangutan behavior, energetics, and physiological processes, including growth and reproduction (Figs. 3 and 4). One of the benefits of a long-term field project is the ability to develop novel, complex, and difficult to implement methods that may require long timeframes for pilot testing, methodological adjustment, and collection of adequate sample sizes. Thus, we also detail here, as one of the main outcomes of the project, some of the methodological advances that we have helped pioneer (Knott et al., in press).

Orangutans are followed using all-day focal observations, from night-nest to night-nest. Bout lengths and 5-min point samples are collected on primary and secondary activities, positional behavior, substrate, height, vocalizations, and social interactions, with *ad libitum* comments recorded on rare or unusual behaviors. Food samples, urine, and feces are collected and analyzed for physiological and chemical properties (Knott et al., in press). In August 2016, iPads replaced paper

data sheets (Scott et al., 2016). More than 8250 focal follows have been conducted, with 83,759 h of observation on over 200 wild orangutans (DiGiorgio, 2019; Knott, 1998; Knott et al., 2008; Knott et al., 2010; Knott et al., 2019; O'Connell, 2018; Scott et al., 2019).

2.1. Phenological monitoring of food availability and ranging behavior

Orangutans live in forests characterized by dramatic changes in food availability, a consequence of 'mast fruiting' events which occur irregularly and unpredictably, on average every 3.7 years at GPNP (Curran and Leighton, 2000). During these events, triggered by the El Niño-Southern Oscillation weather phenomenon, up to 88% of large trees (especially in the dominant canopy family *Dipterocarpaceae*) fruit synchronously (Ashton et al., 1988; Curran et al., 1999). We measure fruiting and flowering patterns by collecting phenological data on two large samples of trees, figs, and lianas. The first is site-wide phenological monitoring established in 1985 by Leighton (Cannon and Leighton, 2004) and reassessed and expanded in 2000 by Marshall et al. (2014), encompassing 70 randomly placed plots, with five 20 m × 50 m and five 100 m × 20 m in each of the main habitat types. We characterize phenology using the 25 genera orangutans most frequently consume to avoid inflating food availability with rarely or never eaten genera. The second phenological dataset is focused on 1083 stems in which orangutans have been directly observed to feed, distributed over 17 transects across 6 habitats, established by Knott (1998) and updated by DiGiorgio and Knott (2019). This ecological context is critical for understanding orangutan biology and ranging patterns.

The large home ranges and semi-solitary nature of orangutans make research and conservation challenging. With heterogeneous habitats and high temporal and spatial variability in fruiting, orangutans travel widely, taking advantage of local fruiting peaks (Leighton and Leighton, 1983; Singleton et al., 2009). Because orangutans regularly move outside the study site, and between habitats (Marshall et al., 2014),

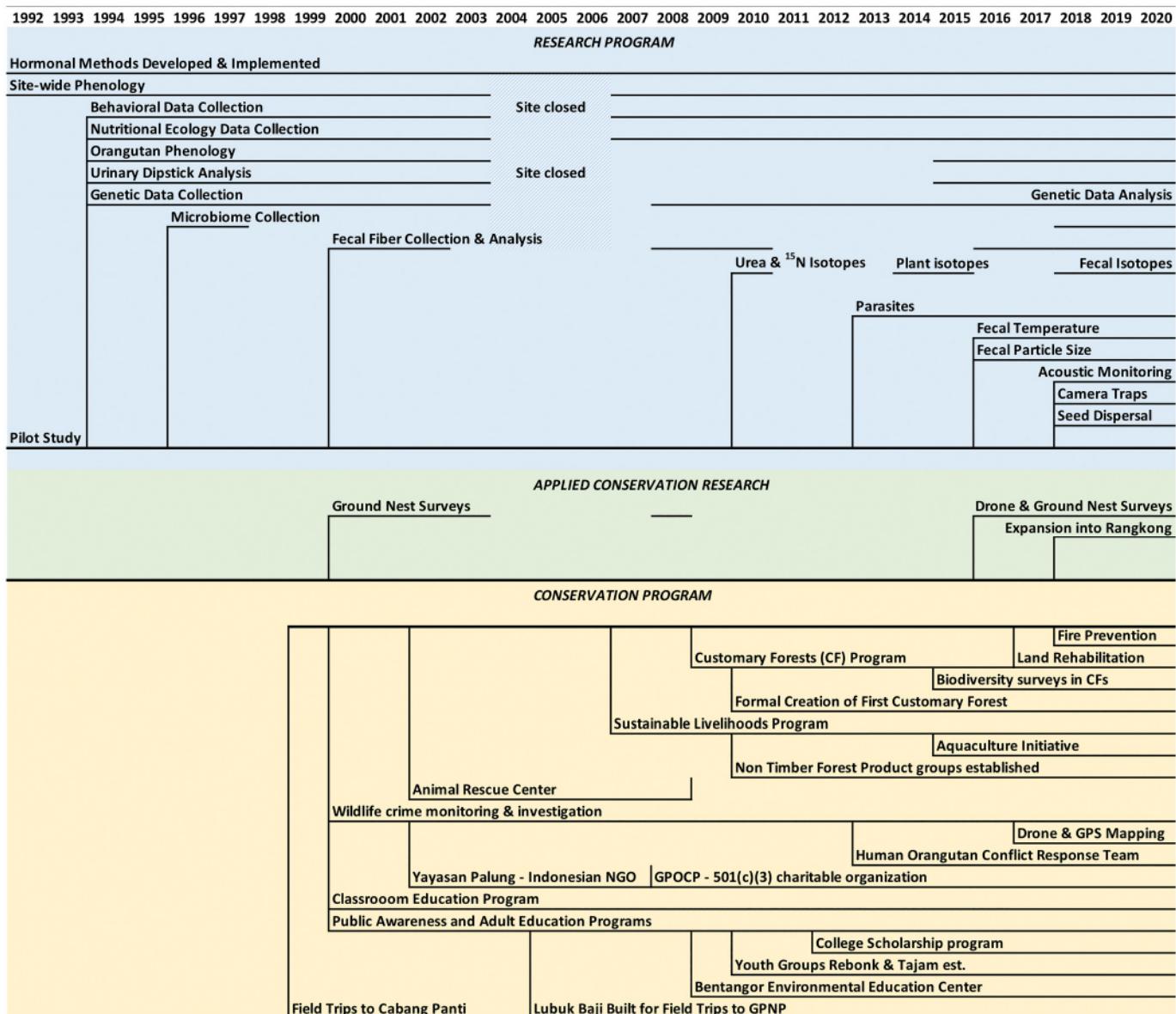


Fig. 3. Timeline of research and conservation activities as part of the Gunung Palung Orangutan Project.

continual population monitoring, considering density, is essential for long-term research. Individuals forage and find mates across expansive home ranges. In GPNP, adults encounter another orangutan on just 25% of focal follows. Female orangutan home ranges at GPNP overlap by 68% on average, but individuals use the same 200 m × 200 m area on just 2.4% of days, reflecting scramble competition for resources and active avoidance (Knott et al., 2008). Female home ranges are at least 600 ha, likely an underestimate because individuals routinely leave the study area (Knott et al., 2008). Males may maintain habitat fidelity for several years; however typical home range sizes are unknown, as they exceed the sizes of orangutan study sites, but are likely 2500–4000 ha (Singleton and van Schaik, 2001). Increased understanding of orangutan ranging behavior in relation to spatiotemporal food distribution is essential to decide when an area is 'big enough' for conservation.

Our ongoing examination of orangutan movement patterns, diet, and seeds in feces is revealing how orangutans provide ecosystem services via seed dispersal (Blackburn et al., 2020). As large-bodied frugivores, orangutans have important ecological roles, as both seed dispersers and seed predators, however there are many research gaps in our understanding of these mutualisms and antagonisms (McConkey, 2018). Research has remained undeveloped with regards to spatial and

temporal patterns of orangutan fruit selection in relation to seed dispersal and seed shadows. Orangutans engage in at least two forms of seed dispersal: seed spitting and seed swallowing, however we know little about the orangutan's seed disperser effectiveness in either of these modes and secondary dispersal processes are unknown. Current research efforts are beginning to develop our understanding of these processes.

2.2. Determination of nutritional requirements

As orangutan habitat rapidly decreases, some habitats must be prioritized for conservation protection (Duffy et al., 2007). Measures of diet and energy intake, expenditure, and balance, are fundamental for understanding individual and population viability (Knott, 2005a). However, characterizing orangutan diets is challenging because they eat over 1600 different types of plants and show substantial inter-site dietary variability (Russell et al., 2009), with over 300 species and 151 genera eaten at Gunung Palung. During behavioral follows, we mark each new feeding tree or liana with an aluminum tag and record the GPS location. Although we have tagged over 50,000 trees and lianas in our study area, each month the majority of trees in which orangutans feed have never been previously tagged. Specifically, looking at the 17

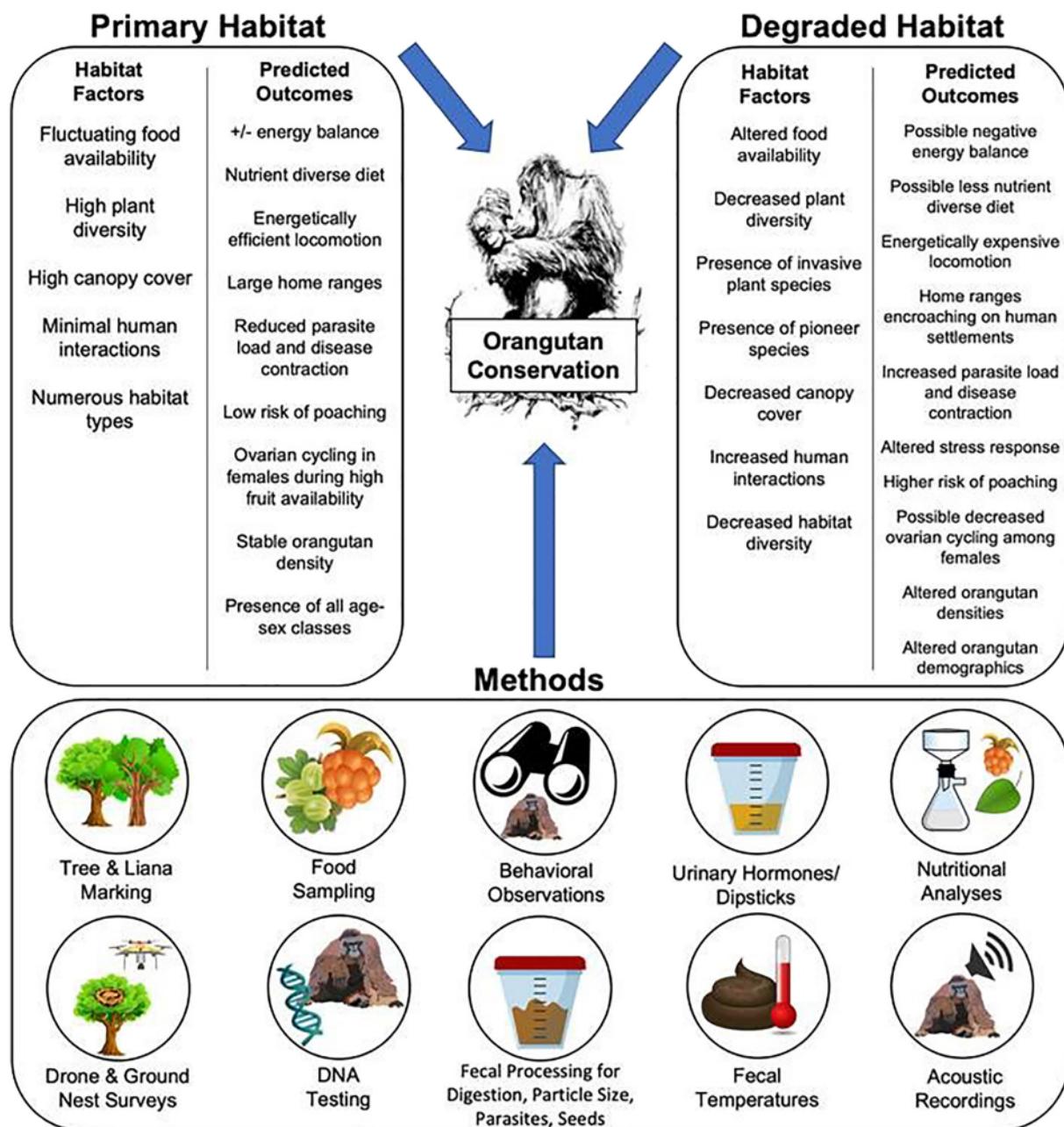


Fig. 4. Methods used to obtain measures of orangutan habitat, physiology, and behavior, with predicted outcomes in primary and degraded habitats.

individual orangutans with the most independent feeding observations (500–7000) showed that even after 24 months of observations or more, approximately 75% of trees in which individual orangutans fed had never been tagged before. This finding supports the interpretation that orangutans' semi-solitary social structure is related to their dietary focus on the small, widely dispersed trees found in their habitat.

Collection of detailed data on caloric and nutrient intake is critical to understanding orangutan nutritional requirements and how they are met in specific habitats and areas with varying levels of anthropogenic disturbance. Thus, during focal follows we collect data from each feeding bout on the height and diameter at breast height of the tree or liana, food type, genus, species, part, percentage eaten, feeding rates, and bout length (DiGiorgio et al., 2020; Knott, 1998). We collect, photograph, and measure plant samples to catalog species characteristics, and collect samples which are separated, weighed by component parts, and dried to determine wet and dry weight. We conduct food

chemistry analyses, which we use to determine kilocalories eaten per feeding bout and total daily nutrient and caloric intake (Conklin-Brittain et al., 2006; Knott, 1998). Daily values range between 1793 and 8422 kcal during periods of low and high food availability, respectively (Knott, 1998). We have collected data on over 70,000 orangutan feeding bouts, weighed and measured 2102 food samples, and analyzed the nutrient content of 218 plant foods.

We have demonstrated that, at GPNP, orangutans' energy intake fluctuates dramatically, and that nutrient and caloric availability influence their ranging behavior (Knott, 1998). Orangutans maximize calorie intake during periods of high fruit availability while maintaining an overall 10.1:1 ratio of non-protein energy (NPE) to protein energy (PE) (DiGiorgio, 2019). Only a small number of orangutan foods actually have this ratio of NPE:PE. Thus, not only are foods that approximate this ratio important, but it is essential that orangutans have access to complementary foods and foods with varying nutrient proportions to

balance their diet. This information can be used for habitat prioritization, identifying appropriate rehabilitant release sites, and determining the species composition for reforestation and corridors (DiGiorgio and Knott, 2019).

3. Health monitoring

Measuring physiological and disease status can demonstrate how anthropogenic processes impact the health and long-term viability of endangered populations. Because ethics preclude capturing great apes for evaluation, non-invasive methods for physiological assessment are critical to conservation management. Developing and refining non-invasive measures to assess health, physiology, and reproductive function has been a hallmark of our project since its inception (Emery Thompson and Knott, 2008; Knott, 1996; Knott, 1997; Knott, 1998), and our methods are now used at other orangutan sites (Harrison et al., 2010; Vogel et al., 2016) and with other primate taxa (Emery Thompson et al., this issue; Higham, 2016).

Because orangutans are largely solitary, they minimize energetic resources allocated to immune system maintenance. For example, orangutans maintain much lower white blood cell counts than African apes (Nunn et al., 2000). This may result in a diminished immune response, leaving them vulnerable during unnaturally high levels of contact with conspecifics or humans. In anthropogenic landscapes, orangutans travel more on the ground (Ancrenaz et al., 2014; Loken et al., 2013) potentially increasing contact with disease vectors from humans, orangutans, and other wildlife. As orangutans are forced into more fragmented habitats, measuring their physiological and disease status gives us critical insight into how habitat loss and human-orangutan interactions affect population health and long-term viability.

3.1. Non-invasive urinary and fecal measures

With increasing concern about exposure to zoonanthroponotic and zoonotic disease vectors, developing quick, inexpensive, non-invasive ways to assess health, even in unhabituated orangutans, is important. Non-invasive urine and feces collection are foundational to our monitoring of orangutan physiology and health. We use urinary dipstick analysis, developed for human clinical settings, to measure disease parameters in orangutans (Harrison et al., 2010; Kaur and Huffman, 2004; Knott, 1998; Krief et al., 2005; Leendertz et al., 2010). These measures provide rapid indicators of health and nutrient depletion (Knott, 1996; Naumenko et al., 2019). We also monitor fecal temperature as a proxy for internal body temperature (Harwell et al., 2019).

Ketones, produced by fat breakdown during weight loss, are detected in the urine of wild orangutans in GPNP during periods of low caloric intake (Knott, 1998), demonstrating that individuals respond to energetic stress by catabolizing their fat stores. Periods of low food intake may also lead to protein deficits, which we demonstrated by measuring the ratio of urea to creatinine in urine and urinary stable nitrogen ¹⁵N isotope values (Vogel et al., 2012a). Orangutans at GPNP recycle nitrogen during periods of low food availability and individuals may experience tissue wasting, using body nitrogen stores for energy (Vogel et al., 2012a; Vogel et al., 2012b). Prolonged tissue wastage can lead to death, highlighting the risks of degraded or marginal habitats. To further illuminate orangutans' physiological response to fluctuating fruit availability, we are assessing digestive efficiency by measuring the proportion of dietary fiber to fiber excreted in feces and quantifying fecal particle size (Weary et al., 2017).

3.2. Endocrine markers of reproductive health

Orangutans give birth approximately once every eight years (van Noordwijk et al., 2018), an extremely slow reproductive rate, leaving them particularly vulnerable to extinction. At our project's outset, human reproductive ecologists had demonstrated a close relationship

between female energetic status and ovarian function (Ellison, 1990) that had not yet been directly investigated in wild non-human primates. Inter-birth intervals were considered relatively fixed, and primarily controlled by photo-period, though data from captive orangutans showed faster reproduction in energetically-rich environments (Anderson et al., 2008; Knott, 2001). Thus, we hypothesized that fluctuations in fruit productivity and long periods of low food availability explained orangutans' long inter-birth intervals.

We developed methods to collect urine and dry it on filter paper for later laboratory analysis, and to extract ovarian hormone metabolites to characterize female reproductive state (Knott, 2005b). Once electricity became available at the site, we added frozen sample preservation. We conducted one of the first studies of ovarian function in wild primates, developing now-widespread techniques (Emery Thompson, 2013; Higham, 2016). This study revealed close correspondence between female ovarian function, energy intake, and expenditure (Knott, 1999; Knott et al., 2009), driven by physiological and behavioral responses to changes in fruit availability (Knott, 1998) and confirming that orangutan reproduction is strongly tied to environmental variability. Orangutans at GPNP only conceive when fruit is abundant and they have relatively high reproductive hormone levels (Knott et al., 2009). During fruit-poor periods, hormone levels are likely sufficiently suppressed to prevent conception and ovarian cycling. Furthermore, reproductive rates, and by extension population persistence and species survival, are constrained by females' ability to obtain sufficient resources to sustain reproductive costs. If environmental degradation leads to lower energy intake, this would impact ovarian function and could further extend orangutan inter-birth intervals, increasing their extinction risk.

3.3. Energetic and stress hormones

Identifying sources and impacts of environmental stress is essential to monitoring animal health. The stress response is a protective, adaptive response to external or internal stressors that is not in itself a sign of illness, but repeated activation can have negative fitness consequences under some conditions, such as in highly degraded habitats (Beehner and Bergman, 2017). Thus, investigating whether there are differences in glucocorticoid levels in orangutans living in primary versus degraded habitats, and whether there are any associated health or fitness outcomes should be an important goal of conservation scientists (Beehner and Bergman, 2017). Cortisol and other glucocorticoids are metabolic hormones that are regularly used to assess stress in wild animals non-invasively using urine and feces. But, glucocorticoids are produced in response to multiple stressors, including social and nutritional stress, so attributing elevations in glucocorticoids to a specific cause can be problematic (Dantzer et al., 2016). This is more straightforward in orangutans, because they are semi-solitary and it is easier to isolate occasions of potential social stress (O'Connell and Knott, 2017).

To assess, interpret, and contextualize stress and glucocorticoid responses, we helped pioneer a new technique to measure C-peptide. Excreted and measured in urine, C-peptide is produced in direct proportion to insulin (Melani et al., 1970). Research on orangutans at GPNP provided the first thorough validation of urinary C-peptide as a measure of energy balance in wild primates, demonstrating that orangutans' monthly C-peptide averages correlate positively with fruit availability and estimated caloric intake (Emery Thompson and Knott, 2008). We can now connect habitat-wide measures of food availability with individuals' physiological state while considering other influences, including energy spent on ranging or immune function.

Measuring urinary cortisol, C-peptide, and other hormonal, behavioral, and ecological variables, reveals how seasonal fruit shortages and caloric constraints impact the pace of reproduction. It also facilitates identification of the sources and consequences of the stress response. For example, we estimate daily energy expenditure based on time spent in different activities and body positions (Knott, 1999). Because logged forests have more and larger canopy gaps, orangutans may need to

descend to the ground to travel between food trees and spend more time climbing (Ancrenaz et al., 2014). Orangutans, especially females, use more energetically expensive locomotor behavior in logged forests (Rao and van Schaik, 1997). Thus, navigating degraded forests may increase orangutans' energy expenditure in forests that potentially provide less food, increasing metabolic stress. Understanding how orangutan foraging and ranging interact with energetic stress and health also enables cross-population and cross-species comparison to determine how stress varies with ecology, behavior, and life history.

3.4. Parasites

Parasite infection reflects habitat disturbance in many primate taxa (Gillespie et al., 2005; Labes et al., 2009; Nunn and Altizer, 2006). Evidence is accruing that intestinal parasites have adverse effects on wild primate fitness, including increased glucocorticoids (Friant et al., 2016; Müller-Klein et al., 2019) and reduced fertility (Akinyi et al., 2019). As habitats shrink and primates become increasingly threatened, non-invasive monitoring of fecal samples for intestinal parasites can provide a useful proxy for population health (Howells et al., 2010). Although chronic parasite infection may be the norm in many species, establishing baseline levels, including inter-individual variation, enables tracking deviation from this norm (Gillespie, 2006).

We began analyzing fecal samples for parasites in GPNP in 2013, establishing patterns of parasite prevalence and species richness during a period of fruit abundance (O'Connell, 2018). While all samples contained intestinal parasites, orangutans showed no outward signs of ill health. We have continued parasite monitoring, comparing periods of high and low fruit abundance to assess how changing ecology and energetic status influence parasite infection. Some parasite taxa may increase during low fruit compared to high fruit periods (*Enterobius* sp.), while others increase in certain age-sex classes (*Trichuris* sp.). Evaluating parasite dynamics over time, in conjunction with other health measures, documents how changing environmental conditions and anthropogenic factors impact orangutan health.

4. Applied conservation research

4.1. Ground and drone nest surveys for monitoring of population density

Accurately estimating orangutan densities and population size is essential to assess their conservation status. However, direct counting methods are not feasible as orangutans are cryptic, occur at low densities, and cannot be captured, marked, and released ethically. Because they build nightly sleeping nests, orangutan population size can be assessed through transect-based nest counts (van Schaik et al., 1995). Extrapolation to population estimates relies on accurate estimates of parameters including nests built per day, nest decay time, and proportion of nest builders in the population. Between 1997 and 2002, we collected data from GPNP to establish these parameters for Bornean orangutans and in 2001, conducted the first Park-wide assessment of orangutan density, surveying 14 sites across different habitat types and levels of disturbance. We introduced the current method in which trained observers walk transects in both directions, minimizing chances of missing nests. We estimated that approximately 2500 orangutans live in GPNP, and an additional 2500 orangutans live in forests outside the Park (Johnson et al., 2005). Orangutan density was estimated at 3.0 individuals/km², with densities ranging from 2.4 ind/km² in montane forest to 4.1 ind/km² in primary peat swamp. We conducted ground nest censuses, considering additional variables, in 2002, 2003 (Felton et al., 2003), 2010, and 2016.

Nest counts are time-consuming (Meijaard et al., 2011b), costly, require trail cutting for transects, and are restricted by accessibility. Drone survey methods developed in Sumatra mitigate these challenges (Koh and Wich, 2012). We pilot-tested drone-based nest surveys in GPNP in 2016 and 2017, comparing ground and aerial surveys across

four sites in different habitats. After demonstrating the feasibility of drone surveys of orangutan nests, we surveyed eight habitats with matched ground and drone nest transects in 2019, and are generating habitat specific conversion factors to estimate orangutan populations. Drones also facilitate monitoring of forest degradation, illegal activity inside the Park, and forest fires, thus characterizing orangutan distribution and forest status to better target conservation efforts.

4.2. Orangutan use of degraded habitats

Orangutans respond flexibly to anthropogenic habitat destruction by utilizing degraded forests, though they require intact forests nearby. Although most orangutan populations occur outside protected areas (Meijaard et al., 2012), our understanding of orangutan ecology in disturbed habitats is poor (Meijaard et al., 2010; Spehar et al., 2018). Orangutans use logged forests to varying degrees, depending on logging duration and timing (Husson et al., 2009). Logging alters forest structure by removing large fruit-producing trees and changing plant community composition (Felton et al., 2003). Figs (*Ficus* spp.) are the most commonly eaten fruit by orangutans in GPNP; their asynchronous fruiting pattern makes them an important resource, especially when other fruits are unavailable. The 56 species of *Ficus* in GPNP are mostly hemiepiphytes growing on large host trees (Laman and Weible, 1998). When large trees are logged, so are their strangler figs, removing a key orangutan food source. Our study of matched logged and unlogged forests showed logged forests lost both timber trees and orangutan feeding trees, resulting in lower food availability and 21% lower orangutan nest density (Felton et al., 2003).

To expand our understanding of orangutans in degraded habitats, we are establishing a second research area in selectively logged forests between the village of Tanjung Gunung and the Cabang Panti Research Station, along the Rangkong River (Fig. 1). Orangutans are often found here, even when scarce in the primary forest, corroborating previous research demonstrating orangutan population resilience in lightly logged areas (Ancrenaz et al., 2010). We will examine how and why orangutans utilize these degraded areas. Although these landscapes may have lower biodiversity, they have high potential conservation value for orangutans and other species (Meijaard et al., 2010). We hypothesize use is driven by increased food availability from pioneer and invasive species like *Bellucia pentamera*, which thrives in canopy gaps caused by hand-logging (Dillis et al., 2017) and produces large crops of sugar-rich fruits at considerably higher frequencies than any native plant taxon (Dillis et al., 2018). When orangutans leave protected forest to forage in human-disturbed habitat, they risk human-orangutan conflict, including poaching, which has been shown to have a major negative impact on orangutan populations (Marshall et al., 2006). While habitat loss may push orangutans into anthropogenic landscapes, they may also be pulled in by temporary increases in food availability caused by human actions.

Although orangutans are studied at sites with a range of habitat disturbance profiles, it is rare to be able to study the same sub-population across a gradient of habitat disturbance. Gunung Palung National Park has both relatively pristine core areas and anthropogenically disturbed peripheral areas, and orangutans make regular use of both. We have established comparable transects in pristine and degraded areas to measure human disturbance, food species diversity, and phenology. We are initiating more expansive and detailed study of orangutans in these disturbed areas, complementing our long-term study of orangutans in primary forest. We will assess genetics to determine whether orangutans from the primary forest use this degraded habitat, and examine population relatedness. Bio-acoustic monitoring is being used to identify orangutan male presence by recording long calls, and can measure differences in human noise and animal biodiversity between disturbed and undisturbed forest (Gómez et al., 2018; Spillmann et al., 2017). Similarly, camera traps can help assess terrestrial travel and monitor human use, both are expected to occur more often in degraded or disturbed habitat (Loken et al., 2013). Research is ongoing,

but we anticipate physiological health measures in the degraded area compared to baseline measures from the main study area will be particularly revealing about the costs of habitat degradation and provide valuable insight into ecological impacts of human disturbance around protected areas like GPNP. Because our conservation efforts often involve working with landowners at the National Park boundaries, expanding our research in this area will enable us to implement new strategies to reduce human-orangutan conflict and to provide education about the conservation value of forest regrowth (Ancrenaz et al., 2010).

5. Conservation interventions

Throughout West Kalimantan, short-term economic interests incentivize unsustainable exploitation of natural resources, export timber, oil palm, and minerals at alarming rates, debilitate the ecosystem, and destroy biodiversity, leaving local people without long-term economic options. Communities are forced to encroach on GPNP and clear forest for subsistence. Because Indonesian law forbids private ownership of forest and does not recognize customary land ownership, community land is consistently threatened with conversion to timber concessions or oil palm plantations. Although deforestation has slowed from its peak a decade ago, poaching and habitat loss still threaten orangutans in and around GPNP. Much of the Park's buffer zone has been converted to oil palm plantations, or has been designated for future conversion (Fig. 1), despite the presence of orangutans and ongoing use by local communities for traditionally harvested forest products.

To address these threats, in 1999 we established the Gunung Palung Orangutan Conservation Program (GPOCP), known locally as *Yayasan Palung* (Palung Foundation). Our main office is in the town of Ketapang, with a satellite office in Pampang Harapan, a village in the Kayong Utara regency approximately 30 min by motorbike from the village closest to the research station. We conduct scientific, data-driven interventions (Fig. 5) based on the Orangutan Indonesia Conservation Strategies and Action Plan 2007–2017 (Indonesian Ministry of Forestry, 2009) and IUCN Best Practice Guidelines for the Prevention and Mitigation of Conflict between Humans and Great Apes (Hockings and Humle, 2009). We follow the Open Standards for the Practice of Conservation framework (Conservation Measures Partnership, 2013) to identify interventions to combat threats, taking a landscape level approach to conservation. Our staff of over 35 are almost entirely Indonesians from the local community, with many working for GPOCP for over 10 years, allowing implementation of conservation solutions tailored to the local context.

5.1. Environmental education

Our conservation program began in 1999 when we brought groups of high school students and teachers to the research station for environmental education. This expanded into school visits in Ketapang and the GPNP buffer zone, and we developed a well-tested repertoire of activities exposing students to the extraordinary local flora and fauna. In-school programming includes classroom activities and field trips for elementary, junior and senior high school students, and themed puppet shows for kindergarten and early-elementary students.

We also bring environmental education into the formal education system, inspiring environmental stewardship in the next generation. On average, we annually reach over 5000 children through over 100 classroom visits. We also hold teacher workshops to develop local capacity for conservation education. Because habitat destruction around GPNP often occurs in hard-to-access and sparsely populated areas, since 2015 we have conducted multi-day expeditions to take our conservation message to remote locations. We sometimes partner with the medical clinic *Alam Sehat Lestari* (ASRI, or Health in Harmony) for health screenings during these visits. In 2015 alone, these expeditions reached 1519 students across 24 schools, with significant knowledge gains about orangutans and substantial shifts towards more positive attitudes

towards conservation (Freund et al., 2019).

In 2005, we built a more accessible destination within GPNP, the Lubuk Baji camp (Fig. 1), to satisfy increased demand for field trips. Students climb past multiple waterfalls to a "tree house" complete with tree trunk staircases and railings made from gnarled branches. Groups spend several nights here, learning to identify plants and animals, testing water quality, and conducting environmental observations. Many participating students are from communities where local forests have been cut down, or significantly degraded, and people are increasingly disconnected from the forest ecosystems providing them with clean water, food, medicines, and household products. Our field trips educate future environmental stewards on the role healthy forests play in their lives. The facility is also a destination for local and international eco-tourism and is now run by the National Park. After the establishment of the Kayong Utara Regency in 2007, we purchased land for the Bentangor Environmental Education Center in the village of Pampang Harapan, near the Park (Fig. 1). School groups come here for field trips and it is also a center for adult education, meetings, and workshops and our sustainable livelihood activities, including organic gardening plots and our seedling nursery. In 2019 alone, we hosted 26 field trips here, serving 866 students and 21 adults.

Since 2012, we have provided undergraduate scholarships to deserving, under-privileged youth in our region to attend Tanjungpura University in Pontianak, the provincial capital, through the West Bornean Orangutan Caring Scholarship (WBOCS) program. So far, we have awarded 43 scholarships, with 7 graduates. WBOCS is developing a generation of university-trained young adults with a commitment to and concern for orangutans and their habitat. Students intern at our office, research station, or with conservation partners for one month annually and write senior theses related to orangutans or habitat protection. Because students are drawn from diverse majors, including law, forestry, education, international relations, sociology, geography, biology, and computer software, these scholarships foster multidisciplinary local support for conservation. Some graduates are now valued members of our permanent staff.

5.2. Conservation awareness

Early in our project we began conservation programming for adults to reach decision-makers and local leaders and develop environmentally conscious behavior in communities around GPNP. GPOCP hosts weekly radio shows engaging citizens on local conservation issues (e.g. forest fires, oil palm development, flooding related to deforestation) through talk shows and guest presentations. These reach approximately 400,000 listeners each month across the GPNP landscape. We also produce an Indonesian language printed newsletter, *MiAS*, focusing on conservation issues, and publish articles weekly in Indonesian print and online media. Awareness campaigns include billboards about conservation issues, posters and calendars, and a comic book about the illegal pet trade. Our social media posts in Indonesian and English reach wide Indonesian and international audiences.

To spur long-term change, we run targeted events in local communities in remote areas adjacent to the Park. These events include school programs for students and village discussions about forests, climate change, the National Park, non-timber forest products, and issues of conservation and sustainability. During our 'road shows,' we project environmental films and discuss conservation issues with the community during and after the film. These are major events for small villages and draw large crowds, sometimes up to 1000 people.

We also run conservation youth volunteer groups in Ketapang and Kayong Utara. These groups were established in 2010 to reach and educate youth beyond the formal education system. Youth receive training in organizational skills, ecotourism, and media, and help implement our public outreach events. For example, during Orangutan Caring Week in 2019, our volunteers, WBOCS students, and staff held a week-long event with traditional dance, music, talk shows, quiz nights,



Fig. 5. Threats to orangutans and their habitat in Gunung Palung National Park and strategies used to mitigate them by the Gunung Palung Orangutan Conservation Program.

book and movie discussions, and a mobile library, all with rainforest and orangutan conservation themes. For International Orangutan Day, volunteer groups developed an interactive theater performance about orangutan conservation held on the beach on the Park's western edge. Our volunteers' creative delivery of conservation content spreads our message across age and ethnic groups.

5.3. Customary forests

Many villages around GPNP, and elsewhere in Indonesia, border forest where communities traditionally obtain forest products. However, because Indonesian law neither allows private ownership of forests nor recognizes traditional land ownership, forests continually risk conversion to oil palm plantations or timber concessions. Since 2007, GPOCP has helped communities gain legal title to use forest lands through the Customary Forest (*Hutan Desa*) Initiative. Forests surrounding national parks are protected from conversion into oil palm by legally leasing management rights to communities. Designating and developing local conservation areas reduces Park encroachment and mitigates threats from human population pressure, land-use changes, and deforestation. Our staff train communities in forest management and regulations, and provide technical and legal assistance for proposals and meetings with local governments.

Through this process we facilitated the first Customary Forest decree in West Kalimantan in 2010. Seven customary forests are now certified, protecting 7962 ha of land. Although this bureaucratic process can be arduous and lengthy, it is one of our most impactful conservation tools. The program empowers local communities to protect and sustainably use forest resources, incentivizes sustainable resource management, and develops conservation awareness. It creates a strategic network of protected forests surrounding GPNP and strengthens Park protection. Landscape-level conservation is enhanced by establishing routes between GPNP and outlying areas, building connectivity between

customary forests, reforesting areas heavily impacted by wild fires, and establishing wildlife corridors.

5.4. Sustainable livelihoods

Communities around GPNP lack economic alternatives to logging and palm oil production, driving deforestation. Additionally, most villages are located on unproductive former rainforest. Because repeated planting of crops leaches soil nutrients, villages clear and burn more forest for agriculture. Since preventing extractive activities in GPNP and other forests can lead to livelihood loss for communities relying on forest products, we promote alternative income-generating activities and sustainable agriculture. This mitigates the threat of changing land-use and lessens the need for illegal poaching and trafficking.

In 2011–2012, GPOCP started developing Non-Timber Forest Product (NTFP) Artisan Groups. Households produce traditional handicrafts made out of *pandanus* and *nipah* palm plants and coconut shells. We have also created NTFP groups in the customary forests, producing organic food products like coconut oil, coffee, cassava chips, and honey. We provide training in design, quality control, business management, and community organizing, help groups attend regional marketing events, and develop agreements with local cooperatives for marketing and capital provision. Products are sold regionally, nationally, and internationally. Some of our lead artisans can sustain their families entirely through sales and by training other artisans. Our artisans have become community leaders in high demand, with national and international recognition.

Our Environmental Education Center is the nexus for this programming, providing training in organic farming and other techniques for sustainable, environmentally-friendly livelihoods. Our organic farming plot demonstrates production of higher crop yields on existing lands, techniques that have been adopted by 15% of our initial target community. We also display a biogas system, fuel-efficient stove, and low-

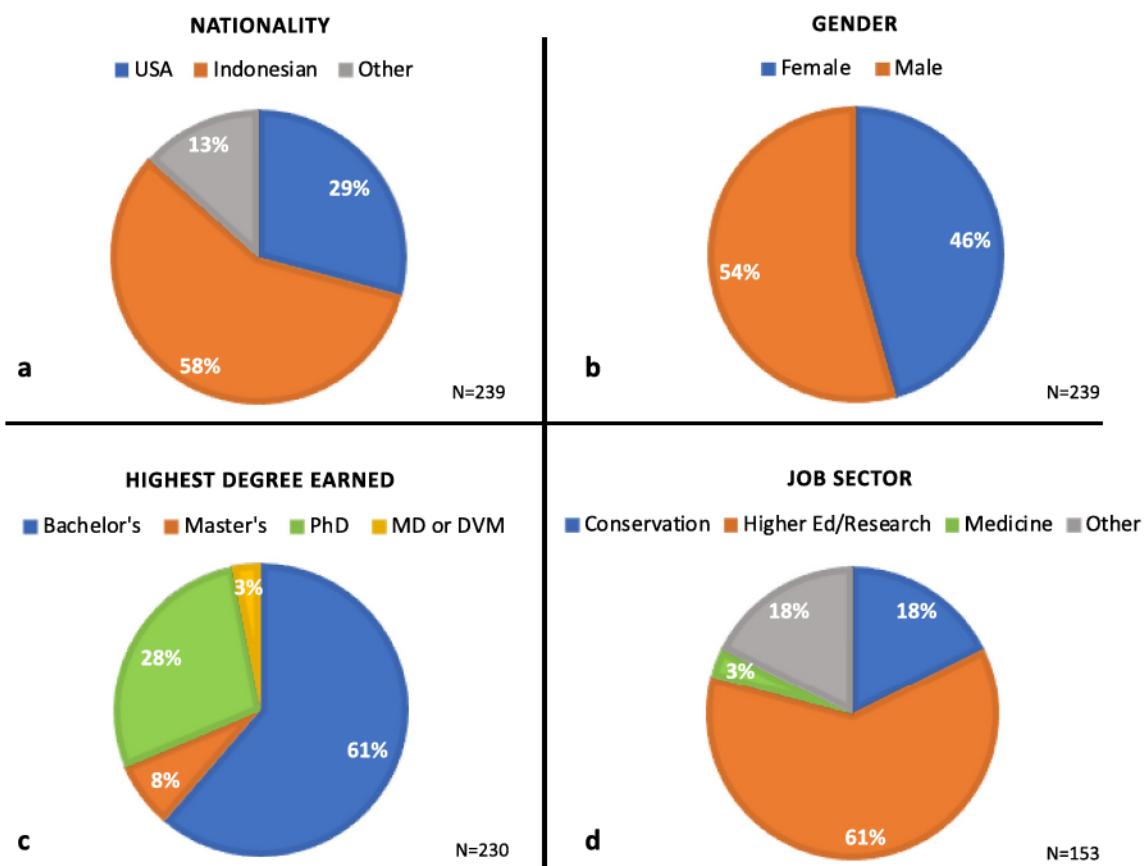


Fig. 6. Breakdown of a) nationality b) gender c) highest degree earned (or in progress) and d) eventual job sector of researchers across all projects at Cabang Panti Research Station from 1986 to 2020. Data used for 'a' and 'b' provided by the Gunung Palung National Park Bureau. Data for 'c' and 'd' are shown for individuals whose status could be determined.

impact fish farming system. As of 2019, 22 households had participated in a fish farming cooperative, with over 10,000 fish bred across 47 ponds in three main villages. With ingenuity and market independence, communities create income-generating activities using local technologies with little start-up cost and develop local markets for their products.

5.5. Wildlife crime investigations

Deforestation degrades and fragments forest, displacing orangutans into forest-agricultural borders. This can lead to negative human-orangutan interactions including crop-raiding and poaching (Campbell-Smith et al., 2011; Campbell-Smith et al., 2012; Norconk et al., 2020; Wich et al., 2008). Recent surveys in villages abutting the Park revealed that 16% of participants had seen orangutans within 500 m of their gardens; 81% of this subgroup reported that orangutans had eaten or damaged their crops. This fosters negative attitudes about orangutans (Campbell-Smith et al., 2010) and can lead to orangutan injury and killing, despite wildlife protection laws. With orangutans' extremely long inter-birth interval, reproduction occurs too slowly to recover from a loss of more than 1% of the population annually (Marshall et al., 2009). An estimated 750–3500 orangutans are killed in Kalimantan each year (Meijaard et al., 2011a), almost certainly exceeding births, and threatening species survival (Meijaard et al., 2012).

In 2001, we started a wildlife investigation program to combat orangutan killings, including the killing of females to capture and sell infants for the illegal pet trade (Freund et al., 2016). Through field investigations and an extensive network, GPOCP gathers information and evidence about the endangered wildlife and orangutan trade, and assists local authorities confiscating animals and prosecuting offenders. When we began identifying illegally-held orangutans, authorities could not

confiscate them because they lacked animal holding facilities. In 2002, we built an animal transit center for this purpose and between 2008 and 2014 we helped confiscate 133 illegally-held orangutans (Freund et al., 2016), and dozens of gibbons, monkeys, birds, and other wildlife. Because poorly enforced wildlife protection laws weaken incentives to abide by them (Meijaard et al., 2012), with partners in West Kalimantan we have trained and urged local and national governments to fully enforce orangutan protections. In June 2010, we contributed to the successful prosecution of a wild orangutan trader sentenced to one year in prison and a \$100 fine. This was the first time full charges were brought against an orangutan trader in West Kalimantan and set a precedent across Indonesia: the threat of jail and fines could deter poorly paid workers from participating in the wildlife trade. In 2009, we transferred transit center management to International Animal Rescue (IAR), whose veterinary staff focus on the welfare of rescued orangutans while we focus on investigations and uncovering illegal trade routes.

6. Impacts of research on long-term conservation

6.1. Research presence/illegal logging deterrent

The presence of a research station increases protection of surrounding habitat (Wrangham and Ross, 2008) and the conservation of GPNP has benefited from long-term research by our project and other researchers including Mark Leighton, Lisa Curran, David Peart, Andrew Marshall, Daniel Gavin, and the students and assistants they have trained and supported (Fig. 6). Researchers bring government attention and protection to the station, and the presence of foreign researchers studying local wildlife contributes to local pride and investment in parks. Research stations also depend on local communities, and

economies benefit from researchers' purchase of goods and services (Kasenene and Ross, 2008). Many men living in villages around GPNP have engaged in illegal logging (Hiller et al., 2004), but now some of these men, trained and employed by GPOP, are champions for conservation in their communities.

6.2. Multi-stakeholder coordination and involvement

Our long-term presence and demonstrated commitment to the region has forged close ties with local agencies and communities. Research is approved by the Indonesian Ministry of Research and Technology and foreign researchers register with local police and government agencies. Our research is supported by sponsors and counterparts in academic and scientific institutions including Universitas Tanjungpura in Pontianak, West Kalimantan, and the Eijkman Institute for Molecular Biology and Universitas Nasional in Jakarta. We work closely with the GPNP Bureau (BTNGP), and the research station is jointly managed by Yayasan Palung and BTNGP. We support National Park rangers stationed in GPNP and provide training in research methods, particularly during nest and drone survey collaborations, where they are project coordinators and team members. Many collaborations and workshops build capacity for effective Park management, including orangutan survey techniques, wildlife documentation, GIS analysis, and plant identification. We also benefit from BTNGP employees' expertise. Researchers regularly meet with National Park authorities to discuss threats to the Park and strategies to combat them. BTNGP also partners on many of our community projects. Additionally, we provide Park officials with data, photographs, and video for government meetings on biodiversity, and facilitate participation at international orangutan and biodiversity conferences. We share research findings, conservation solutions, and expertise in person, fostering trust and building relationships.

At the regional level, the Natural Resources Conservation Department (BKSDA) is our long-time strategic partner in wildlife crime investigation. They have legal authority to rescue and confiscate orangutans and other endangered animals, so we report case findings to them and coordinate with IAR. Our conservation staff also work with ASRI on conservation education, sharing materials and knowledge about orangutans and partnering on some regional expeditions. Fauna and Flora International – Indonesia is a GPOCP program partner and we collaborate to develop customary forests in different regions. Artisan activities are implemented in close coordination with government and industry entities that invest in groups and extend their market access. Perhaps our most important partners are our community members. Communities are both project partners and stakeholders for the Customary Forest Initiative and NTFP Artisan Groups. All projects are designed with community input, and most activities are community-driven with GPOCP providing training, facilitation, and guidance.

6.3. Student training and personnel capacity building

Our research station and conservation project provide scientific training for Indonesian and foreign students (Fig. 6). The orangutan research project has trained 59 undergraduates, 32 post-graduates, 10 master's students, 16 PhD students, and 4 post-docs, both Indonesian and foreign. Of all 239 individuals, both foreign and Indonesian, who have conducted research at the Cabang Panti Research Station, 79% have gone on to do additional work in conservation or research. In addition, GPOP has taught specialized skills to 41 Indonesian field and laboratory assistants. Many of the field staff have an elementary level education, but are now experts at orangutan observation, plant species identification, and the use of scientific tools. Our research and conservation programs employ more than 35 Indonesian staff, further building local knowledge and support for orangutan conservation in the region. Many members of our team have gone on to important positions at partner organizations, been elected to local political offices, and built conservation careers across Indonesia and internationally. The research

station provides an entrée for young people into conservation and wildlife ecology with far-reaching implications, and has been a magnet for several generations of conservation scientists over the past 40 years.

6.4. Challenges and long-term prospects for orangutan conservation

Running a long-term field research and conservation program is not without its challenges. Relationships depend on both the field and social skills of whomever is on the ground at any particular moment. Indonesian government officials change frequently; relationships and trust must be rebuilt with every management change. Securing funding to provide for long-term project support is an additional challenge. We primarily rely on grants that must be re-applied for every 1–2 years, and lack the financial support of a large institution. We are grateful to our steady funders who recognize the value of long-term research and provide us with consistent funding to make a significant impact on wild orangutan research and conservation. Everywhere conservation action is needed there is a complex list of problems that can only be addressed through long-term investment, sincerity, and commitment.

Threats to orangutan populations linger on the horizon. Climate change poses a challenge for orangutans across much of their range. Because it includes higher elevation forests, GPNP will remain a refuge for wild orangutans, even under the most dire climate change scenarios (Santika et al., 2017). The capital of Indonesia is slated to move to East Kalimantan, also on Borneo, which will likely increase pressure on forests for agricultural expansion. However, it may also bring increased ecotourism and attention to the plight of Indonesia's most iconic species, increasing the will to conserve these unique animals. Orangutan conservation helps protect the habitats they occupy, thus safeguarding biodiversity and conserving ecosystems. Although the chances of wild orangutans' survival may seem slim, we remain hopeful that the tide is turning. Fortunately, we can do more than just hope: we can continue to build our vision 'to create a human community that is aware and motivated to conserve orangutans, their habitat, and biodiversity.'

Role of funding source

Our research and conservation work was supported by grants from the Adventure Travel Conservation Fund; American Society of Primatologists; Ape Alliance and Great Ape Film Initiative; Arcus Foundation (G-PGM-1911-3073, G-PGM-1708-2235, G-PGM-1506-1327, G-PGM-1104-36, 1104-36/PID-01853, 0902-30); Association of Zoos and Aquariums Conservation Endowment Fund (13-1159, 11-1063) and Conservation Grants Fund (15-1296); Awely Foundation; Balikpapan Orangutan Society-Canada; Balikpapan Orangutan Society-USA; Bay and Paul Foundations; Cheyenne Mountain Zoo; Cleveland Metroparks Zoo; Columbus Zoo and Aquarium; Conservation, Food and Health Foundation; Conservation International; Disney Conservation Fund; Explorers Club; Feyerabend Foundation; Focused on Nature; GLOBIO - Focus Foundation; GRASP Ian Redmond Conservation Award; Hollomon Price Foundation; Houston Zoo; IDEA WILD; Indonesia Climate Change Trust Fund; International Primatological Society Southwick Grant and Jacobsen Award; International Union for the Conservation of Nature; Jean-Marc Vichard Conservation and Development Award; Keidanren Nature Conservation Fund; LSB Leakey Foundation; Mary Erskine Grant; Margot Marsh Biodiversity Fund; Andrew W Mellon Foundation; Mohamed bin Zayed Species Conservation Fund; Nacey Maggioncalda Foundation; National Geographic Society (EC-53921R-18, ECO690-14, GEFNE68-13, 8564-08, C113-07, C49-04, 7054-01, C2-01, Chairman's Award, 6058-97, 6029-97, 5746-96, 5321-94); National Science Foundation (BCS 1638823, 1540360, BCS-0936199, 643122, 9414388); Ocean Park Conservation Fund; Orangutan Conservancy; Orangutan Foundation International; Orangutan Odysseys; Orangutan Outreach; Orang Utan Republik Foundation; Oregon Zoo; Papoose Foundation; Phoenix Zoo; Primate Conservation International; Prince Bernhard Nature Fund; Remembering Wildlife; Riverbanks Zoo and Gardens; Sea

World Busch Gardens Conservation Fund; Seneca Park Zoo; Sigma Xi; Tides Foundation; USAID - IFACS; US Fish and Wildlife Service (F19AP00798, F18AP00898, F15AP00812, F13AP00920, F12AP00369, 96200-0-G249, 96200-9-G110, 98210-8-G661, 98210-7-G185, 98210-4-G960, 98210-4-G745, 98210-1-G976, 98210-1-G051); Wenner-Gren Foundation; Whitley Fund for Nature; Wildlife Conservation Network; Woodland Park Zoo Partners for Wildlife; Zoo Atlanta; Zoo New England, internal grants from Boston University and Harvard University as well as through private donations. Study sponsors had no role or influence in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the paper for publication.

Policy and ethics

This research was approved by the Standing Committee on the Use of Animals in Research and Teaching at Harvard University, Protocol No. 95-04 and by Boston University's Institutional Animal Care and Use Committee (IACUC), Protocol numbers 11-045 and 14-043.

CRediT authorship contribution statement

Cheryl D Knott: Writing - original draft, Writing - review & editing, Visualization, Supervision, Software, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis, Data Curation, Conceptualization; **Erin E Kane:** Writing - review & editing, Supervision, Software, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis, Data Curation; **Maria-mah Achmad:** Supervision, Project Administration, Methodology, Investigation; **Elizabeth J Barrow:** Writing - review & editing, Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis, Data Curation; **Meredith L Bastian:** Supervision, Project Administration, Methodology, Investigation; **Josephine Beck:** Supervision, Project Administration, Methodology, Investigation; **Andrea Blackburn:** Writing - review & editing, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Terri L Breedon:** Writing - review & editing, Supervision, Project Administration, Methodology, Investigation, Funding Acquisition; **Nancy Lou Conklin Brittain:** Supervision, Methodology, Investigation; **Jennifer J Brousseau:** Supervision, Project Administration, Methodology, Investigation; **Ella R Brown:** Supervision, Project Administration, Methodology, Investigation, Data Curation; **Michelle Brown:** Supervision, Project Administration, Methodology, Investigation, Data Curation; **Laura A Brubaker-Wittman:** Writing - review & editing, Investigation; **Gail A Campbell-Smith:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition; **Andrew de Sousa:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition; **Andrea L DiGiorgio:** Writing - review & editing, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Cathryn A Freund:** Writing - review & editing, Visualization, Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Victoria Gehrke:** Writing - review & editing, Supervision, Project Administration, Methodology, Investigation, Funding Acquisition; **Alys Granados:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **John Harting:** Supervision, Project Administration, Methodology, Investigation; **Faye S Harwell:** Writing - review & editing, Visualization, Investigation, Formal Analysis; **Andrea Johnson:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Petrus Kanisius:** Writing - review & editing, Investigation; **James R Kemsey:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Funding Acquisition; **Sulidra Frederik Kurniawan:** Visualization, Investigation; **Desi Kurniawati:** Investigation; **Timothy G Laman:** Writing - review & editing, Visualization, Methodology; **Andrew J Marshall:** Writing - review & editing, Supervision,

Project Administration, Methodology, Investigation, Formal Analysis; **Ranti Naruri:** Supervision, Project Administration, Methodology, Investigation; **Caitlin A O'Connell:** Writing - review & editing, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Brodie J Philip:** Supervision, Project Administration, Methodology, Investigation; **Edi Rahman:** Supervision, Project Administration, Methodology, Investigation; **Riyandi:** Project Administration, Investigation; **Natalie J Robinson:** Writing - review & editing, Visualization, Investigation, Data Curation; **Amy M Scott:** Writing - review & editing, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Katherine S Scott:** Supervision, Project Administration, Methodology, Investigation; **Tatang Mitra Setia:** Project Administration; **Wuryantari Setiadi:** Project Administration; **Endro Setiawan:** Project Administration, Investigation; **Ibrahim Sumardi:** Project Administration; **Robert Rodriguez Suro:** Visualization, Methodology, Investigation, Funding Acquisition; **Frederik Wendi Tamariska:** Supervision, Project Administration, Methodology, Investigation; **Melissa Emery Thompson:** Writing - review & editing, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Betsy Yaap:** Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis; **Tri Wahyu Susanto:** Visualization, Supervision, Project Administration, Methodology, Investigation, Funding Acquisition, Formal Analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Universitas Tanjungpura (UNTAN), the Eijkman Institute for Molecular Biology, the Universitas Nasional, Indonesia (UNAS), the Directorate of Natural Resource Conservation and Ecosystems (KSDAE) – Ministry of Environment and Forestry, the Gunung Palung National Park office (BTNGP), M. Ari Wibawanto, Dadang Wardhana, Setiohindrianto Prabani, Franky Acil Zamzani, Wawan Setiawan, Rizki Wahyudi, the Natural Resource Conservation Office, West Kalimanatan office (BKSDA), the Indonesian Institute of Sciences (LIPI), the Center for Research and Development in Biology (PPPB), and the Ministry of Research and Technology/(National Research and Innovation Agency (RISTEK/BRIN)) for their sponsorship and support and for granting permission to conduct research in Gunung Palung National Park. Thank you to our collaborating organizations International Animal Rescue (IAR)/YIARI, Clinic ASRI/Health in Harmony, and Fauna and Flora International (FFI). We thank all the dedicated Research Managers: Mary Ford, Christine Perez, Sera Blair, Helga Peters, Hayley Hendrickson, Rebecca Walder, Page Van Meter, Sholly Gunter, Sunny Sanderson; Research Assistants: Chloe Tuck, Margaret Gavin, Rebecca Ingram, Rebecca Curtis, Tori Bakley, Dania Abizaid; Field Assistants: Rhanda, Surdarwin, Karya, Asfandi, Rudi, Morni, Uthay, Sumen, Raden Jono, Ismono, Tady, Hermanto, Asraff, Endit, Dagul, Ipin, Sa, Sidi, Albani, Sarifindi, Muhammad Harissan, Hardianto, Supianto, Surya, Suharto, Mariyadi, Alex, Akauliang, Andi Abdul Sabta Pelari, Supianto (Dang), Yogi Saputra, Sahril Ramadani; Field Laboratory Assistants: Marsandi, Miran Campbell-Smith, Muhammad Rusda Yakin, Agus Trianto, Muhammad Syainullah, Rinta Islami, Sumihadi; Data Managers and Assistants: Jennifer Burnaford, Lydia Beaudrot, Elizabeth Johnson, Rachel Bennett, Victoria Zdanowicz. We thank GPOCP/YP Directors: James McCaul, Jason Morris, Tito Purwanto Indrawan, Samuel Hamy, Victoria Dauncy, Sofyan Embik; Managers: Asep Mulyadi, Hartanti, Hudi Danu Wuryanto, Monalisa Pasaribu; Staff: Ade Akhmad Ilyasak, Ade Yuliani, Agus Lujito, Andre Ronaldo, Asbandi, Asman, Bambang, Edward Tang, Giovanni Fiocco, Hajeral, Haning Pertiwi, Hendri Gunawan, Heri Handoko, Idris, Jainuddin, Jhon Lay Hery, Kristanto,

Kurniawan Tanjung, Mahendra, Muhammad Rizal Alqadrie, Mulyono Yusuf, Musanif Effendi, Nani Wujianti, Nano Sudarno, Nur Asni, Ridwan, Risya Rejita, Rudi Hartono, Rusita, Salmah Sos, Samri Bin Djema, Selvia Arisanti, Simon Tampubolon, Sri Wahyuni, Sutina Melly Shen, Suyandi, Sy. Abdul Samad, Syahik Nurbani, Tori'in, Tri Nugroho, Wawan Angriyandi, Widra Yolanda, Yunita Kusuma Dewi, Yupita; Students and Collaborators: Erin Vogel, Brooke Crowley, Roberto Delgado, Wartika Rosa Farida, Annika Felton, Linda Engström, Adriano Lameira, Kim Nouwen, Taufiq Purna Nugraha, Karmele Llano Sanchez, Herawati Sudoyo, Eva Topelberg, Serge Wich; Board Members: Yan Sukanda, Yudo Sudarto, H. Bachtiar, Barita Oloan Manulang, S. Suci Utami Atmoko, Darmawan Liswanto, Sugardjito, Dedy Darnaedi, Adi Mulya, Dadan Kusnandar, Yudo Sudarto, Yohanes Terang, Diah Permatas, Sonya Kahlenberg, Noemi Rosa, Rebecca Martin. Finally, C Knott thanks Richard Wrangham, Peter Ellison, Carel van Schaik, and Mark Leighton for their early support of the project.

References

Akinyi, M.Y., Jansen, D., Habig, B., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Costs and drivers of helminth parasite infection in wild female baboons. *J. Anim. Ecol.* 88, 1029–1043.

Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., Lackman, I., 2010. Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *Plos ONE* 5 <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0011510>.

Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A.J., Ross, J., Samejima, H., Loken, B., Cheyne, S.M., Stark, D.J., Gardner, P.C., Goossens, B., Mohamed, A., Bohm, T., Matsuda, I., Nakabayasi, M., Lee, S.K., Bernard, H., Brodie, J., Wich, S., Fredriksson, G.M., Hanya, G., Harrison, M.E., Kanamori, T., Kretschmar, P., Macdonald, D.W., Riger, P., Spehar, S., Ambu, L.N., Wilting, A., 2014. Coming down from the trees: is terrestrial activity in Bornean orangutans natural or disturbance driven? *Sci. Rep.* 4, 4024.

Ancrenaz, M., Gumal, M., Marshall, A.J., Meijaard, E., Wich, S.A., Husson, S., 2016. *Pongo pygmaeus*. Bornean Orangutan. The IUCN Red List of Threatened Species 2016, e.T17975A123809220.

Anderson, H.B., Emery Thompson, M., Knott, C.D., Perkins, L., 2008. Fertility and mortality patterns of captive Bornean and Sumatran orangutans: is there a species difference in life history? *J. Hum. Evol.* 54, 34–42.

Ashton, P.S., Givnish, T.J., Appanah, S., 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting. *Am. Nat.* 132, 44–66.

Beehner, J.C., Bergman, T.J., 2017. The next step for stress research in primates: to identify relationships between glucocorticoid secretion and fitness. *Horm. Behav.* 91, 68–83.

Blackburn, A., Susanto, T.W., Knott, C.D., 2020. Orangutan seed dispersal in Gunung Palung National Park, Borneo, Indonesia: Dispersal quantity, germination rates, gut transit times, and dispersal distance. In: Frugivores and Seed Dispersal Symposium, p. 26. Uttarakhand, India.

Blundell, A., 1996. A preliminary checklist of mammals at Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan. *Trop. Biodivers.* 3, 251–260.

Campbell-Smith, G., Simanjorang, H.V.P., Leader-Williams, N., Linke, M., 2010. Local attitudes and perceptions toward crop-raiding by orangutans (*Pongo abelii*) and other nonhuman primates in Northern Sumatra, Indonesia. *Am. J. Primatol.* 72, 866–876.

Campbell-Smith, G., Campbell-Smith, M., Singleton, I., Linkie, M., 2011. Apes in space: Saving an imperilled orangutan population in Sumatra. *PLoS ONE* 6.

Campbell-Smith, G., Sembiring, R., Linkie, M., 2012. Evaluating the effectiveness of human-orangutan conflict mitigation strategies in Sumatra. *J. Appl. Ecol.* 49, 367–375.

Cannon, C.H., Leighton, M., 2004. Tree species distributions across five habitats in a Bornean rain forest. *J. Veg. Sci.* 15, 257–266.

Conklin-Brittain, N.L., Knott, C.D., Wrangham, R.W., 2006. Energy intake by wild chimpanzees and orangutans: Methodological considerations and a preliminary comparison. In: Höhmann, G., Robbins, M., Boesch, C. (Eds.), *Feeding Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge, pp. 445–471.

Curran, L.M., Leighton, M., 2000. Vertebrate responses to spatio-temporal variation in seed production by mast-fruiting Bornean Dipterocarpaceae. *Ecol. Monogr.* 70, 101–128.

Conservation Measures Partnership, 2013. Open Standards for the Practice of Conservation. Conservation Measures Partnership.

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

Curran, L., Trigg, S., McDonald, A., Astiani, D., Hardiono, Y., Siregar, P., Caniago, I., Kasischke, E., 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303, 1000–1003.

Dantzer, B., Westrick, S.E., Kesteren, F.v., 2016. Relationships between endocrine traits and life histories in wild animals: insights, problems, and potential pitfalls. *Integr. Comp. Biol.* 56, 185–197.

DiGiorgio, A.L., 2019. Nutrient Goals of Wild Bornean Orangutans at Gunung Palung National Park: A Case for Nutrient Balancing. Boston University, Cleveland, OH.

DiGiorgio, A., Knott, C.D., 2019. Nutrient goals of wild Bornean orangutans at Gunung Palung National Park: a case for nutrient balancing. *Am. J. Phys. Anthropol.* 168, 59.

DiGiorgio, A., Upton, E.M., Suanto, T.W., Knott, C.D., 2020. Wild Bornean orangutan (*Pongo pygmaeus wurmbii*) feeding rates and the marginal value theorem. *Am. J. Primatol.* e23183.

Dillis, C., Marshall, A.J., Rejmánek, M., 2017. Change in disturbance regime facilitates invasion by *Bellucia pentamera* Naudin (Melastomataceae) at Gunung Palung National Park, Indonesia. *Biol. Invasions* 19, 1329–1337.

Dillis, C., Marshall, A.J., Webb, C.O., Grote, M.N., 2018. Prolific fruit output by the invasive tree *Bellucia pentamera* Naudin (Melastomataceae) is enhanced by selective logging disturbance. *Biotropica* 50, 598–605.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébaud, E., Loreau, M., 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol. Lett.* 10, 522–538.

Ellison, P.T., 1990. Human ovarian function and reproductive ecology: new hypotheses. *Am. Anthropol.* 92, 952–993.

Emery Thompson, M., 2013. Comparative reproductive energetics of human and nonhuman primates. *Annu. Rev. Anthropol.* 42, 287–304.

Emery Thompson, M., Knott, C., 2008. Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. *Horm. Behav.* 53, 526–535.

Emery Thompson, M., Müller, M.N., Machanda, Z.P., Otali, E., Wrangham, R.W., 2020. The Kibale chimpanzee project, Uganda: over thirty years of research, conservation, and change. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2020.108857> (this issue).

Fawzi, N.I., Husna, V.N., Helms, J.A., 2018. Measuring deforestation using remote sensing and its implication for conservation in Gunung Palung National Park, West Kalimantan, Indonesia. *EES* 149, 012038.

Fawzi, N.I., Indrayani, A.M., DeKay, K., 2019. Forest change monitoring and environmental impact in Gunung Palung National Park, West Kalimantan, Indonesia. *Jurnal Ilmu Lingkungan* 17, 197–204.

Felton, A.M., Engstrom, L.M., Felton, A., Knott, C.D., 2003. Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol. Conserv.* 114, 91–101.

Freund, C., Rahman, E., Knott, C., 2016. Ten years of orangutan-related wildlife crime investigation in West Kalimantan, Indonesia. *Am. J. Primatol.* 79, 26620.

Freund, C., Achmad, M., Kanisius, P., Naruri, R., Tang, E., Knott, C., 2019. Conserving orangutans one classroom at a time: evaluating the effectiveness of a wildlife education program for school-aged children in Indonesia. *Anim. Conserv.* 23, 18–27.

Friant, S., Ziegler, T.E., Goldberg, T.L., 2016. Changes in physiological stress and behaviour in semi-free-ranging red-capped mangabeys (*Cercopithecus torquatus*) following antiparasitic treatment. *P Roy Soc B* 283, 20161201.

Galdikas, B.M.F., Wood, J.W., 1990. Birth spacing patterns in humans and apes. *Am. J. Phys. Anthropol.* 83, 185–191.

Gaveau, D.L.A., Sloan, S., Moliedena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M.N.W., Meijaard, E., 2014. Four decades of forest persistence, clearance and logging on Borneo. *PLoS One* 9, e101654.

Gillespie, T.R., 2006. Non-invasive assessment of gastro-intestinal parasite infections in free ranging primates. *Int. J. Primatol.* 27, 1129–1143.

Gillespie, T.R., Chapman, C.A., Greiner, E.C., 2005. Effects of logging on gastrointestinal parasite infections and infection risk in African primates. *J. Appl. Ecol.* 42, 699–707.

Gómez, W.E., Isaza, C.V., Daza, J.M., 2018. Identifying disturbed habitats: a new method from acoustic indices. *Ecological Informatics* 45.

Grubb, P.T., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8, 83–107.

Harrison, M.E., Morrogh-Bernard, H.C., Chivers, D.J., 2010. Orangutan energetics and the influence of fruit availability in the nonnesting peat-swamp forest of Sabangau, Indonesian Borneo. *Int. J. Primatol.* 31, 585–608.

Harwell, F.S., Gotama, R., Scott, K.S., Philp, B., Knott, C.D., 2019. Body temperature estimates for Bornean orangutans (*Pongo pygmaeus wurmbii*) from internal fecal temperature measurements. *Am. J. Phys. Anthropol.* 168, 99.

Higham, J., 2016. Field endocrinology of nonhuman primates: past, present, and future. *Horm. Behav.* 84, 145–155.

Hiller, M.A., Jarvis, B.C., Lisa, H., Paulson, L.J., Pollard, E.H.B., Stanley, S., 2004. Recent trends in illegal logging and a brief discussion of their causes. *J. Sustain. For.* 19, 181–212.

Hockings, K., Humle, T., 2009. Best Practice Guidelines for the Prevention and Mitigation of Conflict Between Humans and Great Apes. IUCN SSC Primate Specialist Group. Gland, Switzerland.

Howells, M., Pruetz, J., Gillespie, T., 2010. Patterns of gastro-intestinal parasites and commensals as an index of population and ecosystem health: the case of sympatric western chimpanzees (*Pan troglodytes verus*) and guinea baboons (*Papio hamadryas papio*) at Fongoli, Senegal. *Am. J. Primatol.* 73, 173–179.

Husson, S.J., Wich, S.A., Marshall, A.J., Dennis, R.D., Ancrenaz, M., Brassey, R., Gumal, M., Hearn, A.J., Meijaard, E., Simorangkir, T., Singleton, I., 2009. Orangutan distribution, density, abundance and impacts of disturbance. In: Wich, S.A., Utami, S.S., Setia, T.M., van Schaik, C.P. (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 77–96.

Indonesian Ministry of Forestry, 2009. Orangutan Indonesia: Conservation Strategies and Action Plan, 2007–2017. Ministry of Forestry, Jakarta, Indonesia.

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

Kasenene, J., Ross, E.A., 2008. Community benefits from long-term research programs: a case study from Kibale National Park, Uganda. In: Wrangham, R.W., Ross, E.A. (Eds.), *Science and Conservation in African Forests: the Benefits of Longterm Research*. Cambridge University Press, Cambridge, pp. 99–114.

Kaur, T., Huffman, M., 2004. Descriptive urological record of chimpanzees (*Pan troglodytes*) in the wild and limitations associated with using multi-reagent dipstick test strips. *J. Med. Primatol.* 33, 187–196.

Knott, C., 1996. Monitoring health status of wild orangutans through field analysis of urine. *Am J Phys Anthropol* Supplement 22, 139–140.

Knott, C.D., 1997. Field collection and preservation of urine in orangutans and chimpanzees. *Trop Biodivers* 3, 95–102.

Knott, C.D., 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *Int. J. Primatol.* 19, 1061–1079.

Knott, C.D., 1999. *Reproductive, Physiological and Behavioral Responses of Orangutans in Borneo to Fluctuations in Food Availability*. Harvard University, Cambridge, MA.

Knott, C.D., 2001. Female reproductive ecology of the apes: implications for human evolution. In: Ellison, P.T. (Ed.), *Reproductive Ecology and Human Evolution*. Aldine de Gruyter, New York, pp. 429–463.

Knott, C.D., 2005a. Energetic responses to food availability in the great apes: implications for hominid evolution. In: Brockman, D.K., van Schaik, C.P. (Eds.), *Primate Seasonality: Implications for Human Evolution*. Cambridge University Press, Cambridge, pp. 351–378.

Knott, C.D., 2005b. Radioimmunoassay of estrone conjugates from urine dried on filter paper. *Am. J. Primatol.* 67, 121–135.

Knott, C.D., Harwell, F.S., 2020. Ecological risk aversion and the evolution of great ape life histories. In: Hopper, L., Ross, S. (Eds.), *Chimpanzees in Context*. University of Chicago Press, Chicago (in press).

Knott, C.D., Beaudrot, L., Snaith, T., White, S., Tschauner, H., Planansky, G., 2008. Female-female competition in Bornean orangutans. *Int. J. Primatol.* 29, 975–997.

Knott, C.D., Emery-Thompson, M., Wich, S.A., 2009. The ecology of reproduction in wild orangutans. In: Wich, S.A., Utami, S.S., Setia, T., Mitra, van Schaik, C. (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 171–188.

Knott, C.D., Emery Thompson, M.E., Stumpf, R., McIntyre, M.H., 2010. Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *P Roy Soc B* 277, 105–113.

Knott, C.D., Kahlenberg, S.M., 2011. Orangutans: understanding forced copulations. In: Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S., Stumpf, R. (Eds.), *Primates in Perspective*. Oxford University Press, New York, pp. 290–305.

Knott, C.D., Scott, A.M., O'Connell, C.A., Scott, K.S., Laman, T.G., Riyandi, Susanto, T. W., 2019. Possible male infanticide in wild orangutans and a re-evaluation of infanticide risk. *Sci. Rep.* 9, 7806.

Knott, C.D., Scott, A.M., O'Connell, C., Susanto, T.W., Kane, E.E., in press. Field laboratories for non-invasive wildlife and habitat health assessment and conservation. In: Wich, S.A., Piel, A.K. (Eds.), *Conservation Technology*. Oxford University Press, Oxford.

Koh, L.P., Wich, S.A., 2012. Dawn of drone ecology: low-cost autonomous aerial vehicles for conservation. *Trop Conserv Sci* 5, 121–132.

Krief, S., Huffman, M.A., Sevenet, T., Guillot, J., Bories, C., Hladik, C.M., Wrangham, R. W., 2005. Noninvasive monitoring of the health of *Pan troglodytes schweinfurthii* in the Kibale National Park, Uganda. *Int. J. Primatol.* 26, 467–490.

Labes, E., Hegglin, D., Grimm, F., Nurcahyo, W., Harrison, M., Bastian, M., Deplazes, P., 2009. Intestinal parasites of endangered orangutans (*Pongo pygmaeus*) in Central and East Kalimantan, Borneo, Indonesia. *Paristol* 137, 123–135.

Laman, T., Weiblen, G.D., 1998. Figs of Gunung Palung National Park (West Kalimantan, Indonesia). *Trop Biodivers* 5, 247–299.

Leendertz, S.A.J., Metzger, S., Skjerve, E., Deschner, T., Boesch, C., Riedel, J., 2010. A longitudinal study of urinary dipstick parameters in wild chimpanzees (*Pan troglodytes verus*) in Côte d'Ivoire. *Am. J. Primatol.* 72, 689–698.

Leighton, M., Darnaedi, D., 1996. Gunung Palung National Park, West Kalimantan, Indonesia, Special Issue. *Trop Biodivers* 3, 141–143.

Leighton, M., Leighton, D., 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific Publications, Boston, pp. 181–196.

Loken, B., Spehar, S., Rayadin, Y., 2013. Terrestriality in the Bornean orangutan (*Pongo pygmaeus morio*) and implications for their ecology and conservation. *Am. J. Primatol.* 75, 1129–1138.

Marshall, A.J., 2009. Are montane forests demographic sinks for Bornean white-bearded gibbons *Hylobates albiventer*? *Biotropica* 41, 257–267.

Marshall, A.J., Nardiyono, Engstrom, L.M., Pamungkas, B., Palapa, J., Meijaard, E., Stanley, S.A., 2006. The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biol. Conserv.* 129, 566–578.

Marshall, A.J., Lacy, R., Ancrenaz, M., Byers, O., Husson, S.J., Leighton, M., Meijaard, E., Rosen, N., Singleton, I., Stephens, S., Taylor-Holzer, K., Utami Atmoko, S.S., van Schaik, C.P., Wich, S.A., 2009. Orangutan population biology, life history, and conservation. In: Wich, S.A., Utami, S.S., Setia, T., Mitra, van Schaik, C. (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 311–326.

Marshall, A.J., Beaudrot, L., Wittmer, H.U., 2014. Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. *Int. J. Primatol.* 35, 1178–1201.

McConkey, K.R., 2018. Seed dispersal by primates in Asian habitats: from species, to communities, to conservation. *Int. J. Primatol.* 1–27 <https://link.springer.com/article/10.1007/s10764-017-0013-7>.

Meijaard, E., Albar, G., Nardiyono, Rayadin, Y., Ancrenaz, M., Spehar, S., 2010. Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLOS ONE* 5.

Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S.S., Nurcahyo, A., Tjiu, A., Prasetyo, D., Nardiyono, Christie, L., Ancrenaz, M., Abadi, F., Antoni, I.N.G., Armayadi, D., Dinato, A., Ella, Gumelar, P., Indrawan, T.P., Kussaritano, Munajat, C., Priyono, C.W.P., Purwanto, Y., Puspitasari, D., Putra, M.S.W., Rahmat, A., Ramadani, H., Sammy, J., Siswanto, D., Syamsuri, M., Andayan, N., Wu, H., Wells, J.A., Mengersen, K., 2011a. Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLOS ONE* 6.

Meijaard, E., Mengersen, K., Buchori, D., Nurcahyo, A., Ancrenaz, M., Wich, S., Atmoko, S.S.U., Tjiu, A., Prasetyo, D., Nardiyono, Hadiprakarsa, Y., Christie, L., Wells, J., Albar, G., Marshall, A.J., 2011b. Why don't we ask? A complementary method for assessing the status of great apes. *PLOS ONE* 6.

Meijaard, E., Wich, S., Ancrenaz, M., Marshall, A.J., 2012. Not by science alone: why orangutan conservationists must think outside the box. *Ann. N. Y. Acad. Sci.* 1249, 29–44.

Melani, F., Rubenstein, A., Oyer, P.E., Steiner, D.F., 1970. Identification of proinsulin and C-peptide in human serum by a specific immunoassay. *Proceedings of the National Academy of Sciences USA* 67, 148–155.

Müller-Klein, N., Heistermann, M., Strube, C., Morbach, Z.M., Lilie, N., Franz, M., Ostner, J., 2019. Physiological and social consequences of gastrointestinal nematode infection in a nonhuman primate. *Behav. Ecol.* 30, 322–335.

Nater, A., Mattle-Greminger, M.P., Nurcahyo, A., Nowak, M.G., de Manuel, M., Desai, T., Groves, C., Pybus, M., Sonay, T.B., Roos, C., Lameira, A.R., Wich, S.A., Askew, J., Davila-Ross, M., Fredriksson, G., de Valles, G.d., Casals, F., Prado-Martinez, J., Goossens, B., Verschoor, E.J., Warren, K., S., Singleton, I., Marques, D.A., Pamungkas, J., Perwitasari-Farajallah, D., Rianti, P., Tuuga, A., Gut, I.G., Gut, M., Orozco-terWengel, P., van Schaik, C.P., Bertranpetti, J., Anisimova, M., Scally, A., Marques-Bonet, T., Meijaard, E., Krutzen, M., 2017. Morphometric, behavioral, and genomic evidence for a new orangutan species. *Curr. Biol.* 27, 3487–3498.

Naumenko, D., Watford, M., Atmoko, S., Erb, W., Vogel, E., 2019. Evaluating ketosis in primate field studies: validation of urine test strips in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). *Folia Primatol.* 91, 159–168.

Nelleman, C., Miles, L., Kaltenborn, B.P., Virtue, M., Ahlenius, H. (Eds.), 2007. *The Last Stand of the Orang-utan - State of Emergency: Illegal Logging, Fire and Palm Oil in Indonesia's National Parks*. UN Environment Programme.

van Noordwijk, M.A., Utami Atmoko, S.S., Knott, C.D., Kuze, N., Morrogh-Bernard, H.C., Oram, F., Schuppli, C., van Schaik, C.P., Willems, E.P., 2018. The slow ape: high infant survival and long inter-birth intervals in orangutans. *J. Hum. Evol.* 125, 38–49.

Norconk, M.A., Atsalis, S., Tully, G., Santillán-Doherty, A., Waters, S., Knott, C.D., Ross, S.R., Shabee, S., Stiles, D., 2020. Reducing the live primate trade: actions for primatologists. *Am. J. Primatol.* 82 (1), e23079.

Nunn, C., Altizer, S.M., 2006. *Diversity and Characteristics of Primate Parasites, in Infectious Diseases in Primates: Behavior, Ecology and Evolution*. Oxford University Press, Oxford.

Nunn, C.L., Gittleman, J.L., Antonovics, J., 2000. Promiscuity and the primate immune system. *Science* 290, 1168–1170.

O'Connell, C.A., 2018. *The Costs and Benefits of Sociality Explored in Wild Bornean Orangutans (*Pongo pygmaeus wurmbii*)*. Boston University, Boston.

O'Connell, C.A., Knott, C.D., 2017. Examining social stress through self-directed behavior in wild orangutans. *Am. J. Phys. Anthropol.* 162, 302–303.

Rao, M., van Schaik, C.P., 1997. The behavioral ecology of sumatran orangutans in logged and unlogged forest. *Trop Biodivers* 4, 173–185.

Rijksen, H.D., Meijaard, E., 1999. *Our Vanishing Relative: The Status of Wild Orangutans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Boston.

Russon, A.E., Wich, S.A., Ancrenaz, M., Kanamori, T., Knott, C.D., Kuze, N., Morrogh-Bernard, H.C., Pratje, P., Ramlee, H., Rodman, P., Sawang, A., Sidiyasa, K., Singleton, I., van Schaik, C.P., 2009. Geographic variation in orangutan diets. In: Wich, S.A., Utami, S.S., Setia, T., Mitra, van Schaik, C. (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 135–156.

Santika, T., Meijaard, E., Budiharta, S., Law, E.A., Kusworo, A., Hutabarat, J.A., Indrawan, T.P., Struebig, M., Raharjo, S., Huda, I., Sulhani, Ekaputri, Trison, A.D., Stigner, S.M., Wilson, K.A., 2017. Community forest management in Indonesia: avoided deforestation in the context of anthropogenic and climate complexities. *Glob Environ Change* 46, 60–71.

van Schaik, C.P., Priatna, A., Priatna, D., 1995. Population estimates and habitat preferences of orangutans based on line transects of nests. In: Nadler, R.D., Galikas, B.F.M., Sheeran, L.K., Rosen, N. (Eds.), *The Neglected Ape*. Plenum Press, New York and London, pp. 129–147.

Scott, K.S., DiGiorgio, A., Knott, C.D., 2016. Can technology help us understand the orangutan? Using iPads for data collection in Gunung Palung National Park, West Kalimantan. In: Joint Meeting of the 26th Congress of the International Primatological Society and the 39th Annual Meeting of the American Society of Primatologists. Chicago, IL.

Scott, A.M., Susanto, T.W., Knott, C.D., 2019. Are male orangutans a threat to infants? Mother-offspring interactions with males in wild *Pongo pygmaeus wurmbii*. *Int. J. Primatol.* 40, 435–455.

Singleton, I., van Schaik, C., 2001. Orangutan home range size and its determinants in a Sumatran swamp forest. *Int. J. Primatol.* 22, 877–911.

Singleton, I., Knott, C.D., Morrogh-Bernard, H.C., Wich, S.A., van Schaik, C.P., 2009. Ranging behavior of orangutan females and social organization. In: Wich, S.A., Utami, S.S., Setia, T., Mitra, van Schaik, C. (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford University Press, Oxford, pp. 205–214.

Spehar, S.N., Sheil, D., Harrison, T., Louys, J., Ancrenaz, M., Marshall, A.J., Meijaard, E., 2018. Orangutans venture out of the rainforest and into the Anthropocene. *Sci. Adv.* 46, e1701422.

Spillmann, B., van Schaik, C.P., Setia, T.M., Sadjadi, S.O., 2017. Who shall I say is calling? Validation of a caller recognition procedure in Bornean flanged male orangutan (*Pongo pygmaeus wurmbii*) long calls. *Bioacoustics* 26, 109–120.

Sumargo, W., Nanggara, S.G., Nainggolan, F.A., Apriani, I., 2011. Indonesian Forest Portrait: 2000–2009. Forest Watch, Indonesia.

Supriatna, J., Ario, A., 2015. Primates as flagships for conserving biodiversity and parks in Indonesia: lessons learned from West Java and North Sumatra. *Primate Conservation* 29, 123–131.

Vogel, E.R., Crowley, B.E., Knott, C.D., Blakely, M.D., Larsen, M.D., Dominy, N.J., 2012a. A noninvasive method for estimating nitrogen balance in free-ranging primates. *Int. J. Primatol.* 33, 567–587.

Vogel, E.R., Knott, C.D., Crowley, B.E., Blakely, M.D., Larsen, M.D., Dominy, N.J., 2012b. Bornean orangutans at the brink of protein bankruptcy. *Biol. Lett.* 8.

Vogel, E.R., Alavi, S.E., Utami-Atmoko, S.S., van Noordwijk, M.A., Bransford, T.D., Erb, W.M., Zulfa, A., Sulistyo, F., Farids, W.R., Rothman, J.M., 2016. Nutritional ecology of wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peat swamp habitat: effects of age, sex, and season. *Am. J. Primatol.* 1–20.

Weary, T.E., Wrangham, W.R., Clauss, M., 2017. Applying sieving fecal particle size measurement to frugivores: a case study of the eastern chimpanzee (*Pan troglodytes schweinfurthii*). *Am. J. Phys. Anthropol.* 163, 510–518.

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

Wich, S., Gaveau, D., Abram, N., Ancrenaz, M., Baccini, A., 2012. Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean orang-utan? *PLoS ONE* 7.

Wich, S.A., Fredriksson, G., Nowak, M.G., 2019. The Tapanuli orangutan: status, threats, and steps for improved conservation. *Conservation Science and Practice* 1, e33.

Wrangham, R.W., Ross, E.A. (Eds.), 2008. *Science and Conservation in African Forests: The Benefits of Longterm Research*. Cambridge University Press, Cambridge.

Yoshikura, T., Amano, M., Chiikaraishi, H., Supriyanto, B., Wardhana, D., 2016. Evaluation of appropriate identification of deforestation agents and drivers for designin REDD+ readiness activities through an examination of the area around Gunung Palung National Park, Indonesia. *Open J For* 6, 106–122.