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LETTER FROM THE EDITOR

On behalf of the editorial board and our faculty liaison, Professor Jill Shapiro, I am excited to present this fourth volume of *Sapient*, the Undergraduate Journal of Biological Anthropology. This journal was established to allow students in all academic fields to submit original articles related to human variation and genetics, evolutionary theory and history, and primate behavior and ecology, and paleoarchaeology and orphology.

This year, we have worked towards several goals. First, we have continued to expand the *Sapient* community by encouraging students from campuses around the world to submit to our journal. Second, we have expanded our online and social media presence. Finally, we have tried to incorporate more primary research articles into our journal and to expand the topics of our secondary research articles. We look forward to continuing to provide undergraduate students the opportunity to read and write sophisticated research articles in the field we love.

— Sarah Ricklan

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~~Ten~~ Eleven Years of *Homo floresiensis*

Laura Hunter, Columbia University

"In a hole in the ground there lived a Hobbit. Not a nasty, dirty, wet hole, filled with the ends of worms and an oozy smell, nor yet a dry, bare, sandy hole with nothing in it to sit down on or to eat: It was a Hobbit-hole."

– J.R.R. Tolkien, The Hobbit, or, There and Back Again

Introduction

In a field as reliant upon chance and infrequent finds as paleoanthropology, every new discovery is inexorably followed by an academic clambering to come to the best possible understanding of the data. Even a single tooth or fragment of bone can be the impetus of a lively, and sometimes heated, debate. However, ever so often, there is a discovery that calls into question our core assumptions and forces us to either find a way to reconcile this new find with our previous ideas or to shape a new foundational understanding. It was in the wake of one of these discoveries that the field of evolutionary biology took root – in 1859 when Darwin's publication of *On the Origin of Species* shattered the contemporary view that all species on earth sprouted fully formed from God's head. Over a century later, there still remain swathes of people clinging to this worldview that Darwin tore asunder. In the wake of that knowledge, it does not seem unreasonable – in fact, it seems very human – for a group of paleoanthropologists to argue contentiously following the eleven year-old discovery of a specimen that seems to be too young and too small and too far from the cradle of civilization.

This paper will outline the discovery, announcement, and subsequent intellectual debate about the group of specimens widely designated under the species name *Homo floresiensis.* It will outline the original find and publication in 2004, the subsequent find less than a year later, the theories posed by the discoverers, and the alternate interpretations proposed by their contenders. This includes the theories that the type specimen is a microcephalic, a cretin, a case of Laron's syndrome, or – as most recently speculated – an individual with Down's syndrome. Finally, I will express my own stance with regard to the Hobbit from Flores.

A Curious Find

On the island of Flores in Indonesia, there is a limestone cave 30m wide, 25m long, and 40m deep, nestled at the base of a hill on the southern edge of the Wae River Valley (Brown *et al.*, 2004; Morwood *et al.*, 2005; Aiello, 2010). This cave – called Liang Bua or "Cold Cave" – was formed approximately 600ka and exposed by action of the Wae Racang River approximately 190ka (Aiello, 2010). It is in Liang Bua on September 2, 2003, when a local worker toiling under the supervision of Wahyu Saptomo, digging 5.9m deep in Sector VII of their cave site, stuck his trowel in the dirt and hit bone. Careful excavation following the initial strike of the trowel revealed the skull of an individual who looked very human but appeared very small (Brown *et al.*, 2004; Callaway, 2014).

The skull uncovered – given the designation LB1 – sustained some damage from the trowel strike, which removed part of the superior vault and the frontonasal region, extending down to the alveoli of the maxillary incisors, which were never recovered (Brown *et al.*, 2004; Brown, 2012). Additionally, there is clear post-mortem damage to the right side of the cranial vault and the right posteriolateral margin of the foramen magnum, and the mandible sustained some distortion (Falk *et al.*, 2009; Kaifu *et al.*, 2011; Brown, 2012). In spite of all this damage, however, Brown *et al.* (2004) determined that the skull belongs to an adult, based on full fusion of the sphenooccipital synchondrosis, adult dentition, and complete epiphyseal fusion.

The damage was not extensive enough to prevent Brown *et al.* (2004) from thoroughly examining and describing the skull in detail. LB1 has a face that belonged to the genus *Homo* – with reduced prognathism relative to *Australopithecus* – but its cranial capacity of 380 to 417cm3 is shockingly low, about the average weight of an adult chimpanzee's (Brown *et al.*, 2004; Falk *et al.*, 2005; Morwood and Jungers, 2009; Callaway, 2014; fig. 1). A closer analysis reveals what Brown *et al.* (2004, pp. 1055) famously hailed as a "unique combination of primitive and derived features." The cranial vault is long and low, with the maximum breadth located at the supramastoid region, the bone of the calvarium thick posteriorly. A deep fissure separates the mastoid process from the petrous crest of the tympanic bone, and a recess bilaterally separates the tympanic plate and entoglenoid pyramid. Perhaps most contentious of all, the mandible clearly lacks a mental protuberance (chin), the presence of which largely considers an autapomorphy of the species *Homo sapiens* (Brown *et al.*, 2004; Morwood *et al.*, 2005; Morwood and Jungers, 2009; fig. 1). All of these features resemble those of *H. erectus* (sensu lato), but coincide with traits that seem further derived, reminiscent of *H. sapiens*, including the breadth and depth of the glenoid fossa and the lack of a straight-bar supraorbital torus (Brown *et al.*, 2004, fig. 1). The teeth are even stranger, with bifurcated mandibular P3s resembling those of Indonesian *H. erectus* and Dmanisi coupled with a rotated maxillary P4, unique to this individual (Brown *et al.*, 2004; Morwood *et al.*, 2005, fig, 1).

To confound things further, the team at the Liang Bua dig site did not just find the skull, but also discovered a femur, tibia, fibula, patella, a partial pelvis, incomplete hands and feet, vertebrae and rib fragments, and a clavicle (Brown *et al.*, 2004, fig. 2). While the team had high hopes that these post-cranial specimens would provide clarity regarding the taxonomic status of the LB1 skull, they seem only to daze and confuse. The pelvis is short and broad with a marked lateral flare, described as most resembling the ancient *Australopithecus afarensis*, which lived in Africa a million years before *H. erectus* (Brown *et al.*, 2004). The femora appear to be too short to match the other skeletal remains it accompanied, especially compared to the length of the foot, which is strikingly long and lacks the longitudinal arch present in *H. erectus* and possibly even in *Au. afarensis* (Brown *et al.*, 2004; Morwood and Jungers, 2009, fig. 2). A cross section of the tibia reveals a distinctly oval shape, and all long bones appear to be "robust," or mediolaterally thick (Brown *et al.*, 2004; Morwood *et al.*, 2005, fig. 2). Perhaps most interestingly, the thoracic cage is bell-shaped – compared to the barrel shape seen in *H. sapiens* – and the clavicle is short and double curved, a formation that most resembles those of extant non-human apes (Brown *et al.*, 2004, fig. 2).

In light of such unique anatomy, the primary discoverer Peter Brown decided to give it the species name *Sundanthropus floresianus*. However, upon some deliberation, it was determined that the specimen should be placed in the genus *Homo* and that the word *floresianus* was inappropriate given its translation to "flowery anus" (Callaway 2014). The resident archaeologist Mike Morwood expressed some desire to name the new species *Homo hobbitus* as a nod to the tiny men in the J.R.R. Tolkien books, of which the last movie had recently debuted in theaters after eight years of filming (Aiello, 2010). Ultimately, the species name published in their unveiling paper on October 28, 2004 was *Homo floresiensis*, although the media did have a field day referring to the new find as "the Hobbit from Flores."

The announcement of the discovery of *Homo floresiensis* renewed public fascination with human evolution, with headlines like "The Little People of Flores" and "*Homo tomthumbus*" presented in newspapers alongside the usual political updates and inflation figures. In the paleoanthropological community, the news was somewhat less well-received, with many sure that it was a hoax and others suggesting that the LB1 skull was not representative of the population that inhabited that area just 50ka (Henneberg and Thorne, 2004; Jacob *et al.*, 2006; Callaway, 2014; Sutikna *et al.*, 2016).

However, on October 2, 2005 – just under a year after the publication of the initial paper – Morwood *et al.* (2005) announced the discovery of further remains from Liang Bua, consisting of a new mandible (LB6/1), a radius, a tibia (LB8), a handful of carpals, a few isolated teeth, and the right humerus, right ulna, and left fibula of the holotype specimen LB1 (Morwood *et al.*, 2005). The earliest of these remains dates to 95-74ka, expanding the range of time *H. floresiensis* inhabited the area significantly (Morwood *et al.*, 2005). The latest of the remains were discovered below the Holocene sequence, beneath tuffaceous silt deposits at the 12ka mark. These silts correspond to a volcanic eruption that drove the pygmy elephants (Stegadon) of Flores – and perhaps *H. floresiensis* as well – to extinction (Morwood *et al.*, 2004; Morwood *et al.*, 2005). Much like the discovery of the post-cranial bones during the original find, these new skeletal elements – consisting of nine to fourteen individuals (Morwood *et al.*, 2005; Morwood and Jungers, 2009; Baab and McNulty, 2009) – serve only to further confound the paleoanthropological community.

The LB6/1 mandible sustained some post-mortem damage to the left coronoid process and condyle and the left central incisor was lost prior to discovery, but it is clear that upon death, this individual had all of their adult teeth (Morwood *et al.*, 2005). The tooth row is more V-shaped than that of the LB1 mandible, and on the whole it is somewhat smaller, but otherwise, their similarities are significant. Both specimens appear to be megadont for mandibles of their size, both lack a mental protuberance, and both have bifurcated, mesiodistally elongated P3s (Brown *et al.*, 2004; Morwood *et al.*, 2005; Morwood and Jungers, 2009). Notably, Morwood *et al.* (2005) identified multiple mental foramina on the LB6/1 mandible – a trait commonly seen in *H. erectus* (sensu stricto) – but the morphology of the premolars resembles that of *Australopithecus* and *H. habilis*, further exemplifying Brown *et al.*'s (2004, pp. 1055) "unique combination of primitive and derived features."

The postcranials in this new find sing the same unique tune. The carpals appear to most resemble those of *Australopithecus* and *H. habilis*, lacking the derived "boot-shaped" trapezoid commonly seen in *H. sapiens* – although the absence of *H. erectus* carpals in the fossil record leaves their own anatomy a mystery (Morwood *et al.*, 2005; Tocheri *et al.*, 2007; Morwood and Jungers, 2009; Orr *et al.*, 2012, fig. 2). The LB8 tibia – though damaged at the medial condyle and medial malleolus – is estimated to be about 216mm and determined to belong to an individual who stood at about 109cm, a height very close to that of LB1, who measures to 106cm based on femur length. Additionally, the LB8 tibia resembles LB1 in its oval cross section and mediola-teral thickness (Morwood *et al.*, 2005, fig. 2).

This mediolateral thickness is additionally found in the humerus, ulna, and fibula attribut-ed to the holotype specimen LB1 (Morwood *et al.*, 2005, fig. 2). The humerus and ulna had been noted but not fully excavated by the release of Brown *et al.*'s paper a year prior, and the newly discovered fibula matches the first in length almost exactly (Brown *et al.*, 2004; Morwood *et al.*, 2005, fig. 2). While the unearthing of the fibula and ulna were welcomed gladly, it is the humerus that offers the most compelling new information concerning the anatomy of LB1. It sustained some post-mortem damage to the anterior head, tubercle, and the midshaft, but is ultimately free of distortion, allowing for an accurate measurement of humerofemoral index – a comparative measurement of the length of the upper and lower limbs (Morwood *et al.*, 2005, fig. 2). This reveals an index of 85.4, stunningly high for such a late-living hominin and equal to that of A.L. 288-I (*Australopithecus afarensis*) (Morwood *et al.*, 2005; Argue *et al.*, 2006; Morwood and Jungers, 2009). Equally bizarre is the degree of humeral torsion, which, at 110 degrees, is significantly less than modern humans (141-1780) but within range for the brachiator *Hylobates* and the quadruped *Macaca* (Morwood *et al.*, 2005, fig. 2).

Of all these traits oddly primitive features of the collection of specimens under the species name *Homo floresiensis*, however, the most contentious remains the cranial capacity of 380-417cm3 (Brown *et al.*, 2004; Falk *et al.*, 2005; Morwood and Jungers, 2009; Callaway, 2014), particularly in light of the archaeological evidence found alongside the bones. Small faunal re-mains – including those of fish, frogs, snakes, tortoises, rodents, and bats – were found, some of their bones charred, indicating the possible presence of fire or even cooking in Liang Bua con-temporaneous with *H. floresiensis*. Additionally, the skeletal remains of 17 juvenile Stegadon with cut marks evident on the bones indicate that the inhabitants of Liang Bua hunted big game (Morwood *et al.*, 2004; Morwood *et al.*, 2005).

This hunting was likely accomplished by the stone tools recovered in a massive density of 5,500 artifacts per m^3 from the same layer of sediment as *H. floresiensis*, including simple flakes, points, perforators, blades, microblades that were perhaps hafted as barbs, and struck bifaces from small radial cores. These tools are continuous from 95-74ka to 12ka and their disappearance corresponds with those of *H. floresiensis* and Stegadon (Morwood *et al.*, 2004; Morwood *et al.*, 2005, fig. 3). Older, heavier percussion tools – including a massive chopper – were discovered in deposits that predate *H. floresiensis*, dated to 102.4 ± 0.6k. There were no hominin remains found with these tools, and therefore there is no way to determine who exactly left them behind (Morwood *et al.*, 2004). In fact, many argue that there are no hominin remains that can explain the presence of the stone tools found in conjunction with *H. floresiensis*, as a hominin with as small a cranial capacity as LB1 would not be capable of making them (Martin *et al.*, 2006a). Henneberg and Thorne (2004) argued that the tools must belong to *H. sapiens* – whose skeletal remains are found on the island of Flores in the early Holocene – but there are no pigments or adornments characteristic of *H. sapiens* found in conjunction with the tools (Morwood *et al.*, 2004; Morwood *et al.*, 2005).

Some argue that the stone tools found in Liang Bua are continuous with those discovered at Mata Menge, an archaeological site just 50km away (Brumm *et al.*, 2006). The tools of this site are dated to 840-700ka and are made up of 487 artifacts (Brown *et al.*, 2004; Brumm *et al.*, 2006). There are five core types, described as similar to the Oldowan tools of East Africa and made using a cobble or old core as a hammer-stone, striking flakes across core faces by direct free-hand percussion (Brumm *et al.*, 2006). Their similarity to the tools discovered in Liang Bua lies in their emphasis on freehand reductions of cores both bifacially and radially, as well as in the maximum dimension of the flake scars (Brumm *et al.*, 2006; Morwood and Jungers, 2009). Both sites make use of volcanic/metavolcanic fluvial cobbles as their primary raw material, although that may be because they occupy the same island and therefore have access to the same resources (Brumm *et al.*, 2006).

Though establishing continuity over a span of about 840-700ka is impressive, both sites are located on the island of Flores, which does not aid in any insight onto how exactly the mak-ers of the tools got there in the first place. How exactly did the Hobbit from Flores wander so far from the cradle of civilization?

An Unexpected Journey

The island of Flores is at least 19km from the other islands of the Sunda Shelf, even with the sea levels 100-125m lower than they are today (Baab and McNulty, 2009; Morwood and Jungers, 2009). Therefore, the only way that *H. floresiensis*' predecessor could have happened upon Flores was by sea. While it has been demonstrated that it is possible to build a raft capable of traveling 1000km using only the lithics associated with *H. erectus*, it was modern *H. sapiens* that achieved this, and there is no clear evidence that it was within the motivation or cognitive power of *H. erectus* to do so (Dennell *et al.*, 2014). Another theory – which does not depend on raft-building capabilities – is that the ancestor of *H. floresiensis* could have accidentally gotten swept up in a tsunami or cyclone and rode a natural raft of vegetation to the shores of Flores. There is a host of anecdotal evidence indicating this is a very real possibility, including the case of a pregnant woman found clinging to a floating sago tree, five days after the 2004 tsunami in Japan (Morwood, 2009; Dennell *et al.*, 2014).

According to this theory, the most likely route for the *H. floresiensis* ancestor to take is from Vietnam/Cambodia to the tectonically active island of Sulawesi to Flores (Dennell *et al.*, 2014; fig. 4). This is further supported by the fact that the prevailing ocean currents in the Sunda Shelf run from north to south, and Sulawesi lies just north of Flores (Dennell *et al.*, 2014, fig. 4). Because there are *H. erectus* skeletal remains on the island of Java, it is tempting to believe that the ancestor of *H. floresiensis* hopped islands in the Sunda Shelf from Java to Lombok to Sumbawa to Flores (Morwood *et al.*, 2004, fig. 4), but the nature of the ocean currents moving from north to south makes west to east travel less likely, supporting the notion that *H. floresiensis* came to the island of Flores from Vietnam/Cambodia, rather than from Java to Lombok to Sumbawa. The nail in the coffin of the Java island-hopping proposal lies in the evidence of a volcanic eruption in the Sunda Shelf 900ka, corresponding to the arrival of Stegadon florensis and the Mata Menge toolmakers on Flores (Aiello, 2010). However, there is no evidence of hominins on Sulawesi prior to *H. sapiens* 30ka – perhaps this island is the next place to look in pursuit of shedding light on the mystery of *H. floresiensis* (Morwood and Jungers, 2009; Aiello, 2010; Jungers, 2013;

Dennell *et al.*, 2014).

Insular Dwarfism

Given the location of the find and the erectine features of the skeletal remains, Brown *et al.* (2004) concluded that *H. floresiensis* was a group of *H. erectus* that stumbled upon the island of Flores and underwent insular dwarfism – the observation that small-bodied species tend to become giant and large-bodied species tend to become small on islands (Bromham and Cardillo, 2007).

To many, this hypothesis is well supported by the nature of how *H. floresiensis* likely arrived on the island. Insular dwarfism is often predicated by a founder population reaching an island and becoming reproductively isolated from the original population (Argue *et al.*, 2006), which was likely the situation for *H. floresiensis* if it truly did get swept across the Sunda Shelf on the wave of a tsunami. Moreover, there were a wealth of insular dwarf and giant species that lived with *H. floresiensis* on Flores, including dwarf Stegadon, a species of giant rats, and a species of giant storks (Van Heteren, 2013), all of which indicate that insular dwarfism was a common occurrence on the island.

Though some (Jacob *et al.*, 2006) have argued that the island is too small to sustain a pop-ulation that long-lasting, 19 stable hunter-gatherer populations with more than one individual per km^2 have been documented (Van Heteren, 2008). Additional concerns that Flores is not isolated enough or that the population on Flores did not have enough time to evolve into an insular dwarf population (Jacob *et al.*, 2006) have been met handily. The Stegadon of Flores migrated to the island only once over the duration of *H. floresiensis*' presence on the island, proving that the level of isolation is high, and logistically, a single colonization of Flores by hominins is just as likely as multiple (Van Heteren, 2008; Baab and McNulty, 2009). Eighty thousand years has been shown to be enough time to develop a unique morphology (Bromham and Cardillo, 2007), so the possi-ble 840ka that *H. floresiensis* may have remained on the island of Flores appears to be more than enough time to do so (Aiello, 2010).

Brown *et al.*'s (2004) argument at the time of publication, however, relied largely on examination of the morphology of *H. floresiensis*, with an emphasis on the features it shared with *H. erectus*. Among the cranial traits, this includes the long, low cranial vault with thickness that may have result in a sagittal keel, the deep fissure separating the mastoid process from the pe-trous crest, and the recess bilaterally separating the tympanic plate and entoglenoid pyramid (Brown *et al.*, 2004). The subsequent discovery of the LB6/1 mandible the following year would reveal the presence of multiple mental foramina, as commonly seen in *H. erectus* (sensu stricto) (Morwood *et al.*, 2005). A recent paper (Kaifu *et al.*, 2015) published less than a month prior to the submission of this paper revealed that the teeth of *H. floresiensis* bear a striking resemblance to those of Java *H. erectus*. The features of the dentition that seem to exemplify this particularly appear to be the more circular P4 crown, the P4 transverse crest, equal-sized M1s and M2s, and the moderately wide alveolar arcade (Kaifu *et al.*, 2015).

For the proponents of the insular dwarfism hypothesis, the puzzling aspects of *H. floresiensis*' anatomy can be justified by the four characters of all insular animals: size change relative to ancestor, heterochronic features, low gear locomotion, and reversals to ancestral state (Van Heteren, 2013). *H. floresiensis* is certainly smaller than the proposed ancestor *H. erectus*, and based on body mass estimations, an omnivore like *H. floresiensis* on an island the size of Flores would have a body mass between that of an insular dwarfed carnivore (4.5kg) and an insular dwarfed herbivore (67.7kg) (Van Heteren, 2008). This estimated body mass falls close to the value of 36kg that Brown *et al.* (2004) had previously proposed for LB1, lending traction to this theory. Furthermore, *H. floresiensis* conforms to the body size expected for a dwarfed *H. erectus*, based on a study of insular dwarf primates. In this study, the three largest primates reduced to 52%, 61%, and 80% of their original size when dwarfed on an island – *H. floresiensis* is notably 52% of the size of Indonesian *H. erectus*, matching the size reduction of the largest primate perfectly (Bromham and Cardillo, 2007).

Further skeletal oddities can be explained by heterochrony, which is signaled by features displaying differences from adults (Van Heteren, 2008). Van Heteren (2008) reasons that heterochrony in *H. floresiensis* may be responsible for its low humeral torsion, as an early halt in bone development may not provide ample opportunity for the muscles of the limbs to shape the bone. Low gear locomotion over uneven terrain may have resulted in mediolaterally thick long bones and a broad pelvis (Van Heteren, 2013).

The strongest morphological argument against the insular dwarfism hypothesis is that reversals to ancestral state cannot account for all of the pre-erectus features present in the skeleton of *H. floresiensis*, including the limb proportions, megodontia, and foot and shoulder morphology (Aiello, 2010; Jungers, 2013). Nevertheless, it has been shown that *Homo* limb proportions overlap with non-human primate limb proportions at small sizes, perhaps explaining the *Australopithecus*-like proportions of *H. floresiensis* without an ancestral or pathological explanation (Holliday and Franciscus, 2009). Additionally, dental evidence indicates that dwarfs are typically megadont relative to their non-dwarf counterparts.

Perhaps unshockingly, the most contentious of the pre-erectus features present in *H. floresiensis* is the endocranial capacity. According to most island models, the estimated brain size of LB1 is too small for its body size (Martin *et al.*, 2006b; Montgomery, 2013). Arguments that the brain may have necessitated shrinking because it is so energetically expensive (Bromham and Cardillo, 2007; Van Heteren, 2013) have been met with skepticism, as the primate brain is associated with higher innovative thought, a cognitive advantage that may outweigh its energetic cost, especially on an island inhabited by predators like the Komodo dragon (Argue *et al.*, 2006; Montgomery, 2013).

Bromham and Cardillo (2007) and Weston and Lister (2009) have shown that the endocranial capacity of the extinct dwarf hippos on Madagascar are up to 30% smaller than their mainland counterparts when scaled to equivalent body mass.

They applied this situation to a *H. erectus* with a body mass of 60kg and an endocranial capacity of 991cm3. When reduced 62% to a body size of 23kg, the resulting brain size was 704cm3, which, when reduced 30%, was con-verted to 493cm3 (Bromham and Cardillo, 2007; Weston and Lister, 2009). However, comparisons between hominins and non-primate species are not necessarily straight forward, as they as-sume a perhaps erroneous conservation of genetic, behavioral, developmental, and physiological constraints acting on brain sizes (Montgomery, 2013). In light of this knowledge, scaling based on data from seven mainland/island pairs of primates revealed that a *H. erectus* with LB1's endocranial capacity would be about 12.7kg, significantly smaller than the 36kg body mass estimate (Brown *et al.*, 2004; Montgomery, 2013).

Controversy Emerges

Without a reasonable evolutionary justification for such a small endocranial capacity, the paleoanthropological community turned to pathological explanations. Not long after the publication of *H. floresiensis*' debut paper, Henneberg and Thorne (2004) suggested that the brain of LB1 resembled that of a microcephalic Minion from Crete and that many of the cranial traits – including vault thickness, mandibles lacking mental protruberances, and supraorbital torus – are present in modern Australo-melanesians. This served as the first publication questioning the conclusions of Brown *et al.* (2004), but perhaps the best-known paper to do so was published in 2006 by Jacob *et al.*

This 2006 paper by Jacob *et al.* challenged Brown *et al.*'s (2004, pp. 1055) "unique combination of primitive and derived features," and suggested that perhaps they were "a combination of characters that are not primitive but instead regional, not unique but instead found in modern human populations… and not derived but strikingly disordered developmentally" (Jacob *et al.*, 2006, pp. 13426). Jacob *et al.*'s (2006) usurpation of Brown *et al.*'s (2004) data was two-pronged: a) establish that *H. floresiensis* could simply be a regional *H. sapiens* and b) demon-strate that *H. floresiensis*' unique characteristics are the result of a developmental disorder.

Jacob *et al.* (2006) revealed that the deep fissure separating the mastoid process from the petrous crest of the tympanic bone – a feature that Brown *et al.* (2004) noted as distinctly *H. erectus* – is commonly observed in Australians and Tasmanians, as well as the recess between the tympanic plate and entoglenoid pyramid. The absence of a true chin is seen in a striking 93.4% of the Rampasasa population, and dental anomalies – including spaces between the teeth and hy-pocone reduction of the maxillary molars – are common among the pygmies of the area. Further-more, enlarged and block-like P3 teeth are common worldwide in *H. sapiens* and bifurcated pre-molars are frequent enough in modern day to be part of the standard Arizona State University dental recording system – seen in up to 37% of the population in some regions (Jacob *et al.*, 2006).

In pursuit of proving developmental disorder, Jacob *et al.* (2006) identified a short list of features in LB1 that could be the result of weak muscle attachments. This list included LB1's low degree of humeral torsion, lack of well-defined femoral gluteal lines, and the oval cross-sections and mediolateral thickness of the long bones – which were identified as the result of a compromise between weak muscle development and a need for support. This suite of features is accompanied by advanced suture closure, dental rotation commonly seen in *H. sapiens* with developmental abnormality, and cranial asymmetry that exceeds clinical norms, particularly at the frontal, nasal, occipital, and parietals (Jacob *et al.*, 2006).

Though Jacob *et al.*'s 2006 paper is short and relatively simple, it has proved seminal, en-couraging many to determine exactly which pathology could explain LB1's host of bizarre features.

Microcephaly

As the endocranial capacity of LB1 is only 380 to 417cm3 (Brown *et al.*, 2004; Falk *et al.*, 2005; Morwood and Jungers, 2009; Callaway, 2014), it seems reasonable to posit that microcephaly may be the cause of LB1's unique traits.

Microcephaly is a disorder of multiple etiologies, producing short individuals with normal sized faces and small braincases (Henneberg and Thorne, 2004). There are over 400 associated genetic syndromes, typically with an autosomal recessive inheritance that causes it to occur more frequently in small, inbred populations (Argue *et al.*, 2006; Martin *et al.*, 2006a; Martin *et al.*, 2006b). Microcephaly is typically divided into primary (or high functioning) microcephaly and secondary (or low functioning) microcephaly (Argue *et al.*, 2006; Martin *et al.*, 2006a). Primary microcephaly is typically present at birth and identified by a narrow, sloping forehead and point-ed vertex. The extent of mental deficiencies in these individuals varies, and they typically have a normal lifespan (Argue *et al.*, 2006). By contrast, secondary microcephaly develops post-natally and is characterized by reduced number and shallow appearance of gyri and small frontal lobes. These individuals typically suffer from profound mental deficiencies and die at an early age (Argue *et al.*, 2006).

In the case of LB1 – an individual of short stature – it may be wise to put a focus on the microcephalic syndromes that involve some sort of dwarfism. The two most well-studied are Seckel Syndrome and Majeskwi's microcephalic osteodysplastic primordial dwarfism type II (MOPD II) (Argue *et al.*, 2006; Martin *et al.*, 2006b). Seckel Syndrome is a rare autosomal reces-sive disorder characterized by a short but proportionate stature, a small jaw, a beak-like nose, ab-normally large eyes, absence of some teeth, and clubbed feet (Argue *et al.*, 2006). By comparison, MOPD II is characterized by a height of 100-110cm, a small jaw with poor chin development, missing teeth, thin bones, a small femoral head and short femoral neck, and a high and narrow pelvis with small iliac wings (Argue *et al.*, 2006; Martin *et al.*, 2006b).

It is clear upon reading this list of diagnostic skeletal characteristics that LB1 does not meet all requirements. LB1 does not have the proportionate stature nor clubbed feet of Seckel Syndrome, and although the nasal bone is damaged, there is no reason to assume that it is beak-like in shape (Argue *et al.*, 2006). Where the forearms of an MOPD II microcephalic are disproportionately short, those of LB1 are disproportionately long. Additionally, the MOPD II high and narrow pelvis with small iliac wings is in direct contrast with the short and broad pelvis of LB1, complete with a lateral flare of the iliac wings (Argue *et al.*, 2006).

The skeletal elements of *H. floresiensis* do not seem to coincide well with any known form of dwarfing microcephaly, but it is in the examination of LB1's brain that the debate becomes truly interesting. Falk *et al.* (2005) performed an analysis of a virtual endocast of the cranium, comparing it to those of great apes, *H. erectus*, *H. sapiens*, *Au. africanus*, *Au. aethiopicus*, a pygmy, and a microcephalic. They adjusted the sizes of all virtual endocasts so that they matched their 417cm3 measurement of LB1's cranial capacity and began comparison. Ultimately, they determined that the endocast most resembled *H. erectus* – wider caudally than rostrally, wider ventrally than dorsally, long and low, but lacking the derived occipital expansion of *H. erectus* – and found that it least resembled their microcephalic, which had a pointed frontal lobe, a compressed occipital lobe, and a flattened posterior end. Notably, they found that LB1 had an enlarged Broddman's Area 10, which is associated with higher cognition processes (Falk *et al.*, 2005).

Falk *et al.* (2005)'s paper was followed by two major criticisms. First, the brachycephaly they described in LB1 was found variably in microcephalics and that Broddman's Area 10 was enlarged in seven out of nineteen microcephalics studied in a subsequent paper (Weber *et al.*, 2005). Second, the microcephalic that Falk *et al.* (2005) chose for their study was not representa-tive of primary microcephaly, as they had claimed (Martin *et al.*, 2006a). The European microcephalic obtained from AMNH was a plaster cast rather than the real skull, and the calotte of the cast appeared to be paler than the cranial base and had cranial sutures that did not line up properly. Inductively coupled mass spectrometry (ICP-MS) revealed that the calotte and the cranial base of the plaster cast were from different batches of plaster (Martin *et al.*, 2006a; Martin *et al.*, 2006b; Holloway, pers. comm.; fig. 5).

In addition to a poor choice in materials, the cranium belonged to Jakob Moegele from the village Plattenhardt, who died at the young age of ten (Martin *et al.*, 2006b; Holloway, pers. comm.). This early death – especially compared to LB1's estimated age of 30 – indicates that Jakob likely had secondary microcephaly, rather than primary microcephaly (Martin *et al.*, 2006a). Furthermore, Jakob's endocast exhibits unusual features that are not commonly seen on microcephalics, including few gyral indentations, a pointed frontal pole, a cerebellum hanging low and at a sharp angle, and an enlarged foramen magnum – indicative of cerebellar malformation (Martin *et al.*, 2006b). Jakob's endocranial capacity was only 260cm3 (Martin *et al.*, 2006b; Holloway, pers. comm.). When prompted as to why Falk *et al.* (2005) opted not to use a half endocast of 400cm3, taken from a real skull rather than a plaster cast, they responded that they were unable to determine the location of the midline (Holloway, pers. comm.).

About five years following, Vannucci *et al.* (2011) published a paper after careful examination of LB1 compared to a host of microcephalics. According to their study, LB1 has cerebel-lar protrusion and frontal breadths within microcephalic range and clearly pathological features – including prominent gyri recti of the frontal lobes, asymmetry of the temporals, and a keel-like dorsal expansion on the brain stem that is unique to this specimen (Vannucci *et al.*, 2011; Holloway, pers. comm.). Ultimately, it was determined that LB1 appears to be small like *Australopithecus* but organized like *H. sapiens* (Vannucci *et al.*, 2011), indicating that LB1 must be a microcephalic of some form, as convergent evolution as extensive as the organization of *H. sapiens*' brain seems untenable.

Cretinism

While microcephaly is certainly the most well-known pathology possibly afflicting LB1, it is not the only one in the running. In 2008, Obendorf *et al.* suggested that myxoedematrous endemic (ME) cretinism may be the cause of LB1's unique anatomy. Cretins are born without a functioning thyroid due to iodine deficiency during neo-natal development (Obendorf *et al.*, 2008; Aiello, 2010; Brown, 2012). These individuals typically have short and broad hands and feet, delayed epiphyseal fusion, a hypoplastic ilium, and a dwarfed stature (~82-161cm) due to extreme growth retardation (Brown, 2012). Cretinism is particularly common in Indonesia due to an iodine deficiency serious enough that iodized salt was introduced into select areas in 1927 and has been mandated by law since 1994 (Obendorf *et al.*, 2008).

Among the features identified in both LB1 and cretins are a depressed nasal bridge, open anterior fontanelles, a thick cranial vault, skull asymmetry, the absence of frontal sinuses, under-developed chin, and increased thickness in long bones (as seen in experimental thyroidextomy) (Obendorf *et al.*, 2008). The humerofemoral index of cretins is 78, not a far cry from LB1's 87, and although cretin feet are described as absolutely small, relative to the femur they are large, resulting in a foot-to-femur length of 76-84%, compared to LB1's 78% and the 53% found in healthy *H. sapiens* (Obendorf *et al.*, 2008). Obendorf *et al.* (2008) additionally determined that 5% of ME cretins in a Negrito pygmy population would have a cranial capacity below 500cm3, based on the idea the cretinism reduces the brain size by 50% and assuming 5% of the population have a cranial capacity at 1000cm3 or lower. Contributions to the list of cretin features identified in LB1 were made by Oxnard *et al.* in 2010. They noted that the clavicle is short in relation to width with a longitudinal twist and that the femoral head and neck were more medially inclined than those of a healthy *H. sapiens* (Oxnard *et al.*, 2010).

Following these publications, Peter Brown himself addressed the question of cretinism in LB1, pointing out that a fair number of features that were recognized as diagnostic of cretinism are simply the result of post-mortem damage to the skeleton. He made it clear that the medial end of the clavicle is partly crushed, resulting in the appearance of a lack of epiphyseal fusion where there truly is one. Furthermore, the open anterior fontanelle, depressed nasal bridge, and absent frontal sinus are all simply the consequences of damage to the cranium sustained during excava-tion (Brown, 2012).

Tackling the features typically associated with cretinism, Brown (2012) asserted that the delayed epiphyseal fusion and hypoplastic ilia of cretins were simply not present in LB1, whose acetabulum, iliac crest, and ischial ramus are all fused fully where a cretin of 30 years would not have full fusion. Features never used as a diagnostic of cretinism were cranial thickness and significantly reduced brain size, and while the math behind the notion that 5% of cretins could have a cranial capacity of 500cm3 was sound, there have been no documented cases of a cretin having such a small cranial capacity and therefore no evidence that such a small brain size is even viable (Brown, 2012). Lastly, the feet of LB1 are not only large relative to the femur, but large abso-lutely, where cretin feet are not, and the underdeveloped chin of a cretin is not homologous to the complete absence of a mental protuberance in LB1.

While it was admirable and clever to look into an illness that affects the modern people indigenous to the same area as LB1, it is also worth noting that the iodine deficiencies in Indonesia are associated with agricultural populations consuming cassava, which contain cyanogenic glucocides and are associated with a higher incidence of hypothyroidism (Brown, 2012). Not only is there no evidence that *H. floresiensis* participated in agriculture, but there is also no way that cassava could be eaten in Flores thousands of years ago, as the food was introduced to Asia in the 17th century (Brown, 2012).

Laron's Syndrome

Much like Cretinism, Laron's syndrome is a condition resulting from a hormone imbalance (Hershkovitz *et al.*, 2007), but where Cretinism's is associated with a non-functioning thyroid, Laron's syndrome is a situation in which the body has normal to high levels of human growth hormone but no receptors for it in the liver, leading to a deficiency of insulin-like growth factor (IGF-I) (Hershkovitz *et al.*, 2007; Falk *et al.*, 2009). As with microcephaly, Laron's syn-drome is most prevalent in areas with a high level of inbreeding – as may be expected of a founder population on a small island. However, Laron's syndrome is not associated with any mental deficiencies and is characterized by small head and stature, osteoporosis, muscle underdevelopment, thin bones, and a protruding forehead (Falk *et al.*, 2009).

Based on Laron's Syndrome patients followed over a span of 45 years, Hershkovitz *et al.* (2007) created a list of 34 features diagnostic to Laron's syndrome and found that *H. floresiensis* meets 33 of them, including reduced prognathism, rounded supraorbital rims, pronounced supra-orbital torus, small teeth, a marked lateral flare of the ilium, thick long bones with weak muscle attachment, and underdeveloped mandible. An Israeli cohort of female Laron's syndrome pa-tients exhibit heights ranging from 95cm to 136cm, encompassing the estimated heights of LB1 (106cm) and LB8 (109cm) (Morwood *et al.*, 2005; Hershkovitz *et al.*, 2007). The teeth of Laron's Syndrome patients notably have both unique features of the premolars – bifurcated P3s and rotated P4s – and their crania exhibit the unique fissure separating the mastoid process from the petrous crest of the tympanic plate as well as the presence of a recess between the tympanic plate and entoglenoid pyramid (Hershkovitz *et al.*, 2007).

While the evidence of Laron's syndrome in Hershkovitz *et al.* (2007) appears quite convincing, scathing criticism followed. Falk *et al.* (2009) noted that Herskovitz *et al.*'s (2007) assessment did not include six of the ten traditional diagnostic criteria for Laron's syndrome – a protruding forehead, a saddle nose, small hands and feet, broke/disordered deciduous teeth, irregular growth and crowding of permanent teeth, delicate long bones, and decreased bicondylar-biparietal ratio. The protruding forehead diagnostic of Laron's syndrome stands in direct contrast with the sloping forehead present on LB1, prompting speculation over whether Hershkovitz *et al.* (2007) conflated a pronounced supraorbital torus with a pronounced forehead (Falk *et al.*, 2009; Van Heteren, 2013). In fact, a not insignificant number of Laron's syndrome traits that Hershkotivz *et al.* (2007) claim are present in LB1 seem to be the result of misinterpretation. As stated by Brown (2012), it is not possible to determine the exact shape of LB1's nasal bones due to dam-age sustained in its excavation, and therefore there is no clear indication whether LB1's nose was saddle-shaped or not. The facial height and prognathism of LB1 are reduced relative *Australopithecus*, not reduced compared to *H. sapiens*, as is the case for Laron's syndrome patients, and the small mandible and retrognathic chin of Laron's syndrome patients are in contrast to the proportional mandible but absent chin of LB1. Furthermore, the marked lateral flare of LB1 is fun-damentally different in shape than that of Laron's syndrome patients (Falk *et al.*, 2009, fig. 6). Curiously, the limb proportions of Laron's syndrome patients are determined by sitting height divided by stature, characterized by a high degree of variability and therefore a wholly unreliable metric to compare with the humerofemoral index of LB1 (Falk *et al.*, 2009; Van Heteren, 2013).

The bicondylar-biparietal ratio of is not directly addressed in Hershkovitz *et al.* (2007), but it is worth noting that this is reduced to 59.7 (females) and 63.8 (males) in Laron's syndrome patients because the maximum cranial breadth is located dorsally on the parietal bones. However, the maximum breadth of LB1 is located at the supramastoid region, resulting in a bicondylar-biparietal of 88.7, higher than the corresponding values for healthy *H. sapiens* (females: 75.4 and males: 73.7) (Falk *et al.*, 2009; Van Heteren, 2013). Certainly this is not a case of reduced bicon-dylar-biparietal ratio. Additional features that are diametrically opposed in Laron's syndrome patients and LB1 are the small hands and feet characteristic of Laron's syndrome compared to LB1's absolutely large feet, the short first metatarsal of Laron's syndrome compared to LB1's short fourth metatarsal, the thin bones of Laron's syndrome compared to LB1's mediolaterally thick long bones and cranial vault, and the delayed suture closure of microcephalic Laron's syn-drome patients compared to the full – if not advanced – suture closure in LB1 (Brown *et al.*, 2004; Jacob *et al.*, 2006; Falk *et al.*, 2009; Van Heteren 2013).

Down's Syndrome

Just last year, Eckhardt *et al.* (2014) and Henneberg *et al.* (2014) published two companion papers, the first asserting that LB1 is clearly a developmental singularity, and the second claiming that LB1 had Down's syndrome, based on the degree of facial asymmetry, disproportionately short femora, small endocranial capacity, lack of longitudinal arches, and brachycephaly as a result of developmental compromise (Henneberg *et al.*, 2014). While these papers do not seem to be receiving much academic attention and dispute, other than a brief paper asserting that the mandibular morphology is not consistent with that of a *H. sapiens* with Down's syndrome (Westaway *et al.*, 2015), they are worth mentioning to exemplify the fact that proposed pathologies to explain LB1 are still emerging.

Author's Stance

The truth of the matter is that the list of possible pathologies that could be affecting LB1 are endless, and continued pursuit of discovering the illness that best fits the unique features exhibited in LB1 may in fact be hindering the investigation of other aspects of this find, including a closer analysis of the associated artifacts. There is a distinct possibility that *H. floresiensis* is not a small *H. erectus* or a pathological *H. sapiens* but a species in its own right, evolved in the Late Pliocene or Early Pleistocene and descended from *H. habilis* or *Australopithecus*, as concluded by many researchers (Argue *et al.*, 2006; Baab and McNulty, 2009; Martinez and Hamsici, 2008; Argue *et al.*, 2009; Morwood and Jungers, 2009; Jungers, 2013; Westaway *et al.*, 2015).

Many cladistic and statistical analyses of *H. floresiensis* propose that it is an early member of the genus *Homo*, evolving either after *H. rudolfensis* but before *H. habilis* or alternatively after *H. habilis* (Martinez and Hamsici, 2008; Argue *et al.*, 2009). The many ancestral features of *H. floresiensis*, particularly the morphology of the axial skeleton and the limb proportions, seem to indicate that its ancestor preceded African *H. erectus* skeleton KNM-WT 15000, and the skeletal remains discovered in Dmanisi, Georgia suggest that a more ancestral hominin population may have dispersed out of Africa (Baab and McNulty, 2009; Morwood *et al.*, 2009). The Dmanisi specimens – while not nearly as diminutive as *H. floresiensis* – stand at a meager 145-166cm compared to *H. erectus*' 185cm, and their endocranial capacities (612-775cm3) are below the *H. erectus* average (1100cm3). Additionally, specimens from the Sangriran and Bapang For-mations of Java, Indonesia share dental characteristics with Dmanisi that appear to be less derived than seen in East Turkana *H. erectus* (Baab and McNulty, 2009).

With the possible presence of pre-erectus *Homo* in Asia, the very notion of which calls in to question our understanding of hominin migration across history, *H. erectus* is no longer the only candidate for founding population on the island of Flores approximately 900ka (Dennell *et al.*, 2014). The stone tools of Mata Menge and Liang Bua, which are described as resembling the Oldowan tools of Eastern Africa (attributed to both *H. erectus* and *H. habilis*), have another potenetial maker (Brumm *et al.*, 2006).

Conclusion

In 1856, just a meager three years prior to the publication of Darwin's *On the Origin of Species*, an ancient skeleton was discovered in the Neander Valley in Germany. With the notion of human evolution absent from the public consciousness, the prevailing theory was that this was a Cossack horseman with a bad case of rickets that bowed his bones, the pain causing him to fur-row his brows so frequently that the bone over his eyes became hyper-developed.

Thirty years later, the discovery of fossils on the island of Java in Indonesia sparked a wealth of controversy, some claiming that this was the missing link between man and ape, others claiming it belonged to a primitive branch unrelated to humans, and still others claiming that it was a giant gibbon.

These are just two examples of the hurried controversy that arises each time we discover a specimen that does not align with the prevailing understanding of human evolution. In the wake of eleven years of heated debate, the question remains: Is *H. floresiensis* a unique species, an insular dwarf of *H. erectus*, a microcephalic dwarf, or perhaps even something else? No matter the end result, debate will continue, as it always does.

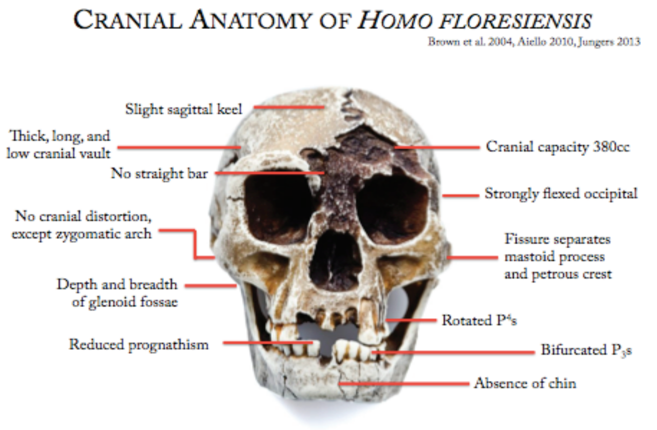

Fig. 1. Cranial anatomy of *Homo floresiensis* based off descriptions from Brown *et al.* (2004), Aiello (2010), and Jungers (2013). Photo courtesy W.L. Jungers.

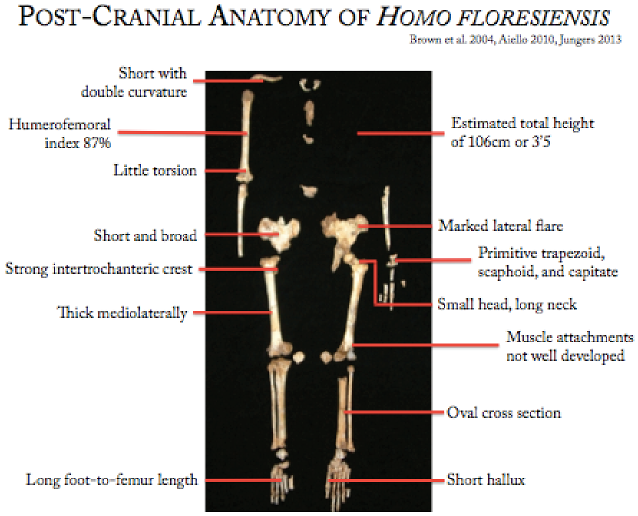

Fig. 2. Post-cranial anatomy of *Homo floresiensis* based off descriptions from Brown *et al.* (2004), Aiello (2010), and Jungers (2013). Photo courtesy W.L. Jungers.

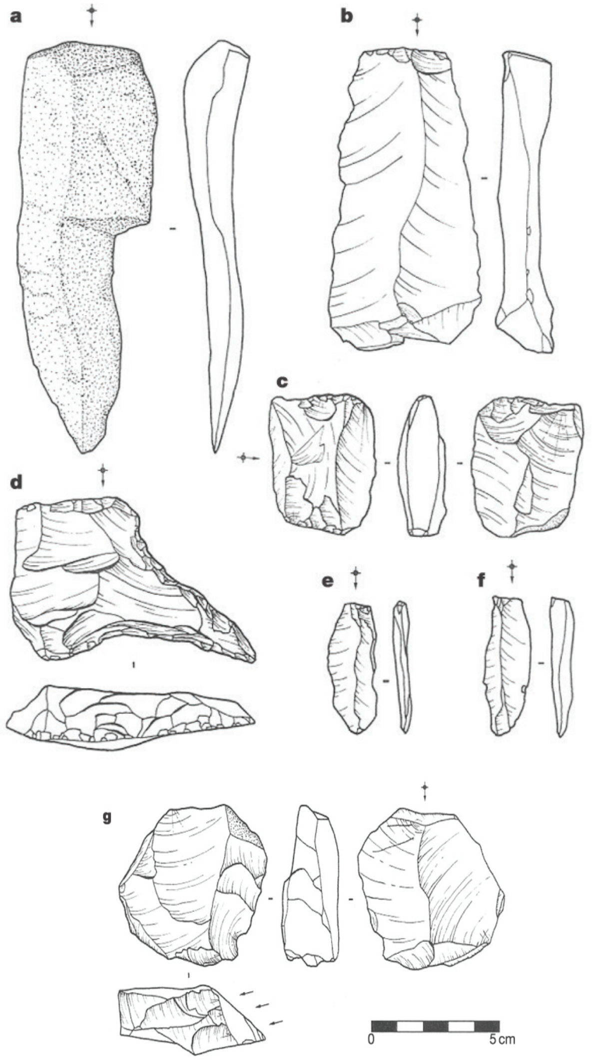

Fig. 3. Tools associated with *H. floresiensis*. a, b, Macroblades. c, Bipolar core. d, Perforator. e, f, Microblades. g, Burin core for producing microblades. Arrows indicate position of striking platforms, where knappers detached the flakes from cores by direct percussion using hammerstones. Modified from Morwood *et al*., 2004.

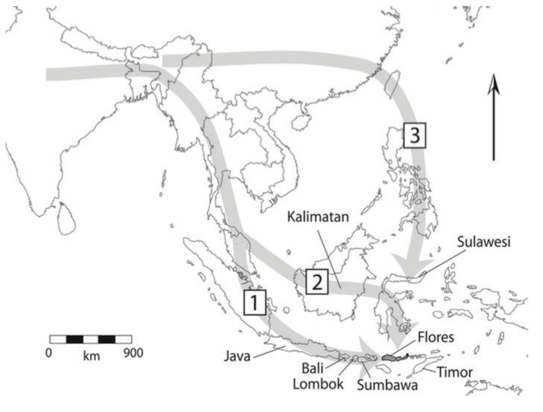

Fig. 4. Map of Southeast Asia showing the location of islands discussed in the text, and the three proposed routes of dispersal for taxa arriving on Flores: 1) eastward from Java, 2) from Kalimantan via Sulawesi and 3) from China via the Philippines and Sulawesi. Taken from Dennell *et al*., 2014.

Fig. 5. Comparison of the original microcephalic skull in Stuttgart (left; Staatliches Museum für Naturkunde, 5297/25523) with the cast held in the collections of the American Museum of Natural History, New York (right; AMNH No. 2792a). Note the clear difference in coloration of the calotte compared to the rest of the skull in the AMNH cast. Taken from Martin *et al*., 2006b.

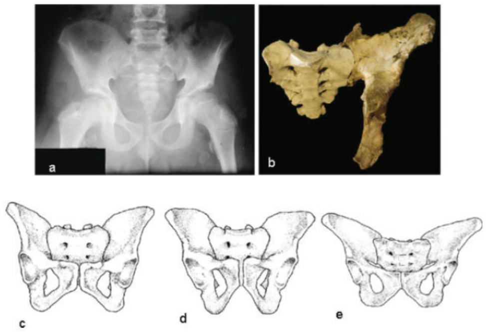

Fig. 6. (a) Radiograph of a 22-year-old man with Laron Syndrome (modified from Kornreich et al., 2008); (b) left ox coxae of LB1 articulated with a cast of the sacrum of AL 288-1 (Australopithecus afarensis); (c) female pelvis; (d) male pelvis; (e) australopithecine pelvis (c-e adapted from Lovejoy, 2005). The similarity between b and e is noteworthy. Modified from Falk et al., 2009.

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Explaining the Sex Differential in Mental Health Diagnosis Among Military Personnel: An Evolutionary Framework

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Background

Over the last decade and a half of the US's involvement in overseas military engagements, the American public has once again turned its attention to the experience of US military personnel both at home and abroad. Furthermore, as a result of the lowest mortality rates in the history of warfare, that focus has increasingly shifted to the far less visible scars of war (Gawande, 2004). Discussions of mental health have seen a resurgence in popularity as the medical community learns more about the causes and effects of conditions such as post-traumatic stress disorder and depression, particularly as they affect military personnel. With that focus comes the realization that people of certain demographics are at a much higher risk for receiving such mental health diagnoses. In particular, female military personnel exhibit much higher rates of depression and anxiety disorders than their male counterparts (Otto, O'Donnell, Ford, and Ritschard, 2010). This paper investigates possible explanations for this sex differential using an evolutionary framework for human behavior.

This research is relevant because of the annually increasing rates of women serving in war zones around the world. As a result of these greater numbers and the recent decision to remove all gender restrictions to combat service, women's health is receiving greater attention within the military healthcare system than ever before (Committee on Health Care for Underserved Women, 2012). Furthermore, effective and scientifically sound approaches to women's healthcare are essential to maintaining a healthy and high-performing military population.

In this paper I will investigate the relationship between women's stress responses in a military environment and the resulting mental health issues. The very nature of the military career field entails an increased exposure to stressors that simply do not exist in most civilian settings. It is therefore reasonable to suspect that sex difference in stress response may be a determinant of mental health variance that is not seen to the same extent in the general population. Since many sex differences have their roots in biology, examining stress response through an evolutionary lens offers an important glimpse into how once-favorable stress responses can produce harmful results in a modern war environment.

PTSD and Psychological Trauma in Female Veterans

As females enter the military in increasing numbers, they bring unique healthcare needs with them. As more attention is being directed towards questions of women's health at war, their mental health is being carefully analyzed to detect trends in pre-deployment, during deployment, and post-deployment levels of stress, depression, anxiety, and trauma (Ritchie and Naclerio, 2015). The November 2010 Medical Surveillance Monthly Report (MSMR) provides an analysis of mental health conditions in the US military from 2000-2009. It found that the rates of mental health diagnoses for maladjustment, anxiety, depressive, and personality disorders were twice as high among women relative to their male counterparts (Armed Forces Health Surveillance Branch, 2010). Figure 1 of the Armed Forces Health Surveillance Branch (2010) Report shows the breakdown by category and gender in rates of mental health diagnoses per 100,000 person-years from 2000-2009. In all but one category (alcohol/substance abuse), female military personnel exhibit higher rates of mental health diagnoses than their male counterparts.

It is possible that these differences in mental health diagnoses may persist within the population at large, suggesting potentially non-military sources. Yet the research suggests that the deployment experience itself is the disproportionately harmful factor for returning female veterans. The October 2009 MSMR presented a cohort study in which the rates of illnesses and injuries among women in the two years following their return from deployments to Iraq and Afghanistan were compared to their "expected rates" based on their pre-deployment health condition (controlling for the higher rates of female mental health diagnosis in the broader population). The study found that women returning from deployments experienced higher rates of anxiety, depression, and episodic mood disorders than expected based on their pre-deployment condition, indicating the likelihood of causative factors present within the deployment environment (Armed Forces Health Surveillance Branch, 2009). These higher rates for women hold true when compared with their male counterparts returning from deployment, strongly indicating a sex-based difference (Armed Forces Health Surveillance Branch, 2009). Figure 2 of the Armed Forces

Health Surveillance Branch (2009) Report shows the mental health diagnosis rate difference per 1000 person-years of the post-deployment women relative to the other two cohorts of pre-deployment women and post-deployment men. The data indicates that women returning from deployment had the highest rates of mental health diagnoses in each category. This further supports the claim that the sex differential is the result of more than just pre-existing sex differences within the population at large. Rather, it is the result of a deployment environment uniquely damaging to women's mental health.

The damaging nature of the deployment environment on women's mental health seems to persist even after controlling for factors such as combat exposure. A study by Vogt *et al.* (2011) specifically measured the differing rates of mental health diagnosis between men and women as a factor of combat exposure. This study of 2,000 US service members recently returned from tours in Afghanistan found that there was no significant relationship between combat-related stressors (such as firing a weapon, being fired on, witnessing injury or death, etc.) and sex in the prediction of post-traumatic stress symptoms, mental health functioning, or depression (Vogt *et al.*, 2011). This study suggests that female service members are no more likely to experience negative mental health effects from combat than are their male counterparts, thereby necessitating an alternate explanation for the sex differential in the rates of diagnosis.

Tend and Befriend Stress Response Model

While "fight or flight" is the most commonly known behavioral model for stress response, substantial evidence suggests that an additional pathway may signal relationship "gaps" in which positive social bonds are weak or inaccessible and prompts affiliation to reduce one's stress response (Taylor, 2006). Called "tend and befriend," this biobehavioral model entails humans (and especially women) responding to stress by tending to offspring and affiliating with conspecifics to strengthen social bonds (Taylor, 2006). This model treats affiliative behavior as the product of a biological signaling system tasked with maintaining positive relationships. According to this model, oxytocin acts as an affiliative hormone (promoting pro-social behavior) that reacts to the presence of social distress by encourage social contact as a coping mechanism, thereby reducing the negative effects of that stress response (Taylor, 2006). Figure 3 from Taylor's (2006) study describes the mechanistic pathway of the biobehavioral model, particularly emphasizing oxytocin's feedback loop to promote affiliation in response to gaps in positive social relationships. Notably, when those affiliative efforts of promoting social contact are unsuccessful or met with hostility, this exacerbates the problem and heightens the stress response.

From an evolutionary perspective, the "tend and befriend" stress response would likely increase reproductive fitness, as tending to one's offspring increases the probability of that offspring's survival (Taylor, 2006). In fact, oxytocin, the hormone at the center of the attachment-caregiving system, has been clearly shown to enhance this maternal behavior (Taylor *et al.*, 2000). The evolutionary advantage to "befriending" lies in the significant physical and mental health benefits associated with the formation of strong social bonds in times of stress (Taylor, 2006). These benefits include lower risk of mortality than those in social isolation (Taylor, 2007) and greater health benefits overall (Cohen & Wills, 1985).

Thesis

A different perspective on the negative experiences of female service members during and post-deployment is needed to better understand their higher rates of mental health diagnoses relative to their male counterparts. In the present study, an evolutionary medicine framework is used to better understand how certain evolved characteristics of female stress response may exacerbate war-zone trauma and further limit the coping processes available to female service members.

The primary methodology of this study will be to critically examine relevant literature to test the hypothesis that the increased rates of mental health diagnoses experienced by female military personnel can be attributed in part to the tendency for women to favor the "tend and befriend" stress response strategy in a deployment-zone environment that doesn't provide the needed social support to make that strategy effective.

My hypothesis will be supported if the literature meets three requirements. (1) The available research must demonstrate that the "tend and befriend" stress response is a strong explanatory model for women. (2) Since the "tend and befriend" biobehavioral model requires high levels of social support to reduce the stress response, it must be shown that female military personnel experience a lack of social support during and/or post-deployment. (3) The literature must show that the lack of social support and the resulting heightened stress response can result in the higher rates of mental health diagnosis in female military personnel.

Review of the Literature

The "Tend and Befriend" Stress Response in Women

As stated in the introduction, the "tend and befriend" biobehavioral model is particularly appealing from an evolutionary framework because the natural results of tending to one's offspring and strengthening social bonds would seem to have direct benefits to one's reproductive fitness. Recent research suggests that women may be significantly more likely to utilize the "tend and befriend" stress response compared to men (Morrison, 2009; Smeets *et al.* 2009). In a study comparing how stress coping varies between genders, Tamres, Janicki, and Helgeson (2002) conducted a meta-analysis of 50 studies of sex differences in coping mechanisms published between the years 1990 and 2000. Table 1 shows the categories of coping mechanisms that the study included and the statistical significance of the sex difference. Women were more likely to cope with stress by seeking emotional support and verbally reaching out to others compared with men, who tended to withdraw when under stress (Tamres, Janicki, and Helgeson, 2002). This conclusion is noteworthy because it demonstrates the relatively higher importance of emotional support for women coping with stress. These emotional support-seeking stress coping mechanisms are behaviors predicted using the "tend and befriend" biobehavioral model, further supporting the model's favorability.

In seeking to understand the evolutionary relevance of the "tend and befriend" biobehavioral model, we must examine both the proximate and ultimate explanations of the behavior. On the level of proximate explanations, women would be expected to rely more strongly on oxytocin-mediated stress responses than men (Taylor, 2006). Estrogen strongly enhances the effects of oxytocin within the endocrine system and as discussed before, oxytocin plays an important role in the affiliative behavior inherent to maternal care (Taylor, 2006). As an ultimate explanation, it makes sense that females would rely on the "tend and befriend" stress response because evolutionarily, the large sexual division of labor in which women were primarily responsible for childcare would have promoted behaviors that directly resulted in higher offspring survival rates. Therefore, behaviors such as "tend and befriend" that favored infant survivorship would likely have been selected for in women.

Social Support for Female Military Personnel

The "tend and befriend" stress response mechanism relies on the formation of social bonds in response to a stressor and minimizes the negative effects of the body's natural stress reaction. Lacking social support can heighten stress response (Taylor, 2006). Social ostracism is a highly detrimental social reality for many women while deployed (Ritchie and Neclerio 2015). Women working in predominantly male career fields often encounter a substantial amount of either outright hostility or passive lack of engagement from their male colleagues (Ritchie and Neclerio 2015). This is likely even more true when breaking into combat positions previously held only by men. Cognitive psychologists have studied the negative effects of ostracism in great detail. Recent evidence links the experience of ostracism and the body's experience of physical pain to a central pain mechanism that can be visible via MRI (Eisenberger and Lieberman, 2004; Wesselmann *et al.*, 2003). Both experiencing ostracism and observing it in others has been found to activate the dorsal anterior cingulate cortex as well as the anterior insula, the same areas of the brain that show evidence when someone experiences physical pain (Eisenberger and Lieberman, 2004; Wesselmann *et al.*, 2003). The severing of the social support networks that humans rely on is therefore a painful and psychologically harmful experience.

Additionally, social support may be severed in the post-deployment period as well. Research by Cotton, Skinner, and Sullivan (2000) looked to female veterans within the Veterans Affairs (VA) healthcare system to understand the determinants of the social support level these women felt in their post-military life. The researchers found that certain factors associated with leaving the military (such as chronic familial strains, economic difficulties with housing and paying bills, unemployment, etc.) greatly contributed to these women's lack of social support (Cotton, Skinner, and Sullivan, 2000). Social support can also be affected by the era in which the women served. Table 2 shows the breakdown in variables the study used to measure social support in female veterans from across military eras. One interesting result was that those veterans from the Vietnam era reported far lower levels of social support than those who served during the Persian Gulf (Cotton, Skinner, and Sullivan, 2000). Numerous factors may be at play here, including the public perception of the war (broad societal support for the war in Vietnam being lower overall and therefore affecting the social report soldiers received from friends and family) as well as the perceived acceptability of their occupation as a result of changing gender norms (it being more socially acceptable for women to serve in the military during the Persian Gulf compared to Vietnam) (Cotton, Skinner, and Sullivan, 2000). Nevertheless, these data lend credence to the idea that female military personnel, both former and present, are disproportionately affected by a lack of social support in their lives.

Social Support and Mental Health Diagnosis

The final claim I will analyze is whether the lack of social support that leads to a heightened stress response could substantially contribute to the higher rate of mental health diagnoses in female military personnel. A review by Cohen and Wills (1985) found that there is indeed a positive association between social support and well-being. Furthermore, social support is critical for a positive recovery from posttraumatic stress symptoms. Studies of chimpanzees undergoing stress tests have found that the presence of a friendly conspecific in the same room during the stressful stimuli greatly decreases the observed stress response (Sapolsky, 2004). An additional study by Brewin, Andrews, and Valentine (2000) found that in humans, a lack of social support was twice as likely to predict the later development of long-term traumatic symptoms as the severity of the trauma itself. This points to the relevance of social support in promoting an easier recovery from trauma.

Implications for Further Research and Policy Reform

Summary of Research

Relevant findings in this area (and as described in an earlier section) suggest that there is a strong evolutionary incentive for women to utilize the "tend and befriend" behavioral response to stress (Morrison, 2009; Smeets *et al.* 2009; Tamres, Janicki, and Helgeson, 2002; Taylor, 2006). The natural result of this tendency is that women likely rely more than would otherwise be expected on social bonds to cope with stress. The social isolation and lack of support experienced by women during and post-deployment described earlier combined with women's reliance on the "tend and befriend" stress response model likely exacerbates the pre-existing social isolation often experienced by veterans upon their return to civilian life. Finally, since female military personnel continue to exhibit long-term traumatic symptoms at an ever-increasing rate, it's logical to conclude that these increasing rates are likely linked to the lack of social support experienced by female military personnel during and post-deployment.

When seeking explanation for behaviors through an evolutionary framework, the major limitation is that such explanations are not easily proven empirically and sufficiently causative. Furthermore, the demonstration of one biobehavioral model (in this case the "tend and befriend" stress response) does not preclude the existence of other factors that may influence the observed data. Some possible factors include perceived violation of culturally mandated gender norms and trauma resulting from the high prevalence of sexual assault within the armed forces (Kimerling *et al.*, 2007). In fact, these contributing factors can be responsible for further eroding the social support for women returning from deployment and exacerbating the effects of the psychological trauma initially experienced.

Significance for Military Policy

The results of this study indicate that there is significant room for improvement within the military as well as in the broader culture in providing greater social support for female military personnel. As a vital component of the modern-day

US military, female service members deserve a health care system that recognizes their unique mental health needs. Healthcare providers should receive more information about the uniquely elevated importance of social bonds for women serving in the stressful deployment and post-deployment environment. Questions as to the strength of these bonds should be incorporated into the primary health care surveys used by physicians working with female military personnel and regarded as a critical treatment assessment tool when working with service members suffering from post-traumatic stress symptoms.

Another area of improvement lies in the dedicated efforts of the armed forces to expand its ranks of female service members. This would likely result in stronger social bonds with coworkers overall as more women would be able to form healthy same-sex social bonds that are often more easily attained and preserved. Critical mass theory often touts the figure of 30% as being the target percentage of women within governments and industry needed to make a real difference on policy and culture more broadly (Dahlerup 2006). Recent Department of Defense data (from 2011) calculate the percentage of women serving on active duty across branches as 14.5% (Ritchie & Naclerio 2015). Though more research needs to be done on the military context to have an accurate idea of the necessary critical mass, 30% is a good goal with which to start. Attempting to reach this target percentage of women within the military could minimize the effects of the male-dominated environment by promoting a culture of female empowerment and reducing women's feelings of social isolation and ostracism within the military ranks.

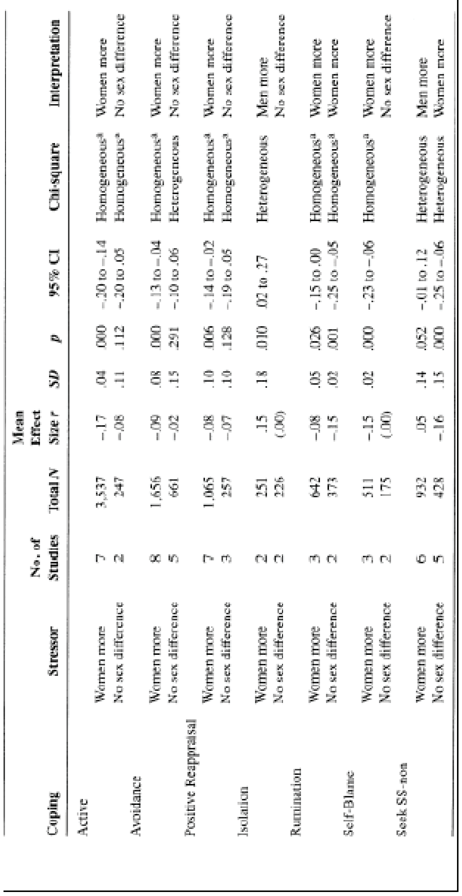
The difficulty lies in attracting more women to the military. How does one approach changing cultural perceptions of acceptable careers for women? I would argue that the answer could be found in a number of fields. Incorporating more women into recruitment advertisements and hiring more female recruiters are both excellent strategies to encourage more women to view the military as a potential career path. Another area of focus is in the retention of the female military personnel serving currently. Recognizing this as a priority, both the Navy and Marine Corps have tripled paid maternity leave to 18 weeks and the Air Force has recently implemented a new policy guaranteeing that women won't have to deploy for at least a year following the birth of a new child ("Carter Announces 12 Weeks Paid Maternity Leave," 2016). More policy reforms are needed that focus on women's uniquely difficult experience balancing home and work within military life in order to further improve female retention rates. Yet perhaps one of the best strategies is for the military to better advertise the advantages it already offers to career-minded women. One of the major advantages for women pursuing a career in the military is the complete absence of a wage gap. This is due to the fact that pay is public knowledge and raises are non-negotiable (an area in which women tend to lag behind their male colleagues within the civilian sector) due to the pre-determined and strict rubrics for pay based on rank and number of years' experience for all military personnel. By implementing more policies focused on the recruitment and retention of the many women who would excel in a military career, the military will be equipped to promote a culture of inclusion for women that supports them in times of physical and emotional stress, improving health outcomes overall.

Nevertheless, critical mass theory fails to recognize the role that a small number of high-profile individuals can play. Called "token women," these leaders are able to garner broad-based support on promoting women's interests within institutions and leading to broad-based cultural change (Bratton 2005). This is particularly relevant to a military setting in which women are less likely than men to reach high level promotions. Research by Hosek (2001) indicates that about 45% of white male officers become majors in their careers, while only about 31% of white women do. While lower female retention rates overall likely affect this, it is clearly more difficult for women to reach higher levels of leadership within the military. Part of this is due to the important role that combat experience plays in service members' evaluations for and against promotion, with combat exposure being a virtual prerequisite for most high-ranking positions. It is partially because of this that the recent decision to open all combat positions to women may be of immeasurable importance in creating a pro-woman military culture. As more women enter combat they become eligible for high-level positions that will enable them to have a real voice in enacting the military policy change necessary to create the strong social support critical for female service members' success.

This is just the beginning of a rich line of further inquiry. As we seek to understand more about the mental health of service members from all demographics, potential institutional reforms will present themselves as positive moves in the direction of both diversifying the US military and improving the health and well-being of service members overall.

Tables and Figures

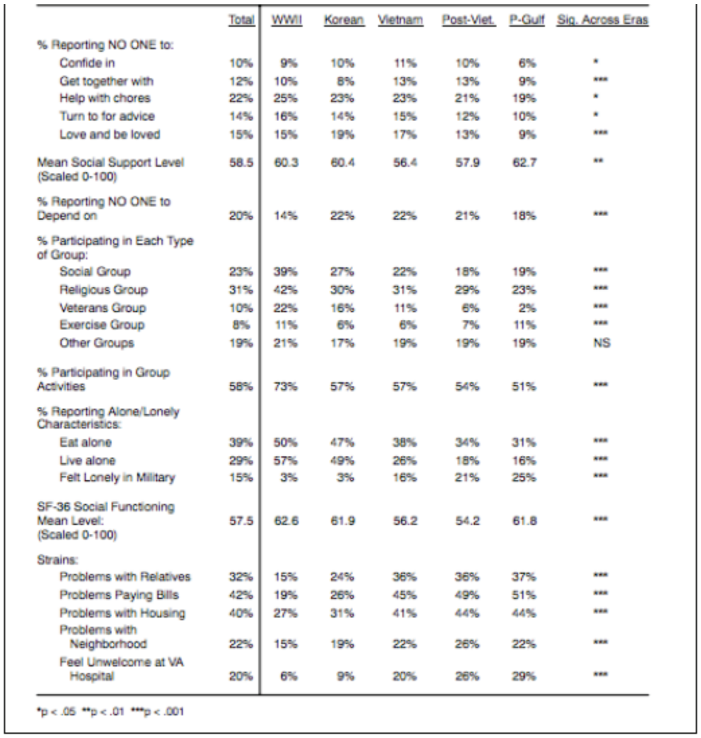
TABLE 1. Meta-analysis of sex differences in coping behaviors by stressor appraisal[1]



Coping	Stressor	No. of Studies	Total N	Mean Effect Size r	SD	p	95% CI	Chi-square	Interpretation
Active	Women more	7	3,537	−.17	.04	.000	−.20 to −.14	Homogeneous[a]	Women more
	No sex difference	2	247	−.08	.11	.112	−.20 to .05	Homogeneous[a]	No sex difference
Avoidance	Women more	8	1,656	−.09	.08	.000	−.13 to −.04	Homogeneous[a]	Women more
	No sex difference	5	661	−.02	.15	.291	−.10 to .06	Heterogeneous	No sex difference
Positive Reappraisal	Women more	7	1,065	−.08	.10	.006	−.14 to −.02	Homogeneous[a]	Women more
	No sex difference	3	257	−.07	.10	.128	−.19 to .05	Homogeneous[a]	No sex difference
Isolation	Women more	2	251	.15	.18	.010	.02 to .27	Heterogeneous	Men more
	No sex difference	2	226	(.00)					No sex difference
Rumination	Women more	3	642	−.08	.05	.026	−.15 to .00	Homogeneous[a]	Women more
	No sex difference	2	373	−.15	.02	.001	−.25 to −.05	Homogeneous[a]	Women more
Self-Blame	Women more	3	511	−.15	.02	.000	−.23 to −.06	Homogeneous[a]	Women more
	No sex difference	2	175	(.00)					No sex difference
Seek SS-non	Women more	6	932	.05	.14	.052	−.01 to .12	Heterogeneous	Men more
	No sex difference	5	428	−.16	.15	.000	−.25 to −.06	Heterogeneous	Women more

[1] Modified from Tamres *et al.*, 2002.

TABLE 2. Distribution of select study variables across military eras[2]



	Total	WWII	Korean	Vietnam	Post-Viet.	P-Gulf	Sig. Across Eras
% Reporting NO ONE to:							
Confide in	10%	9%	10%	11%	10%	6%	*
Get together with	12%	10%	8%	13%	13%	9%	***
Help with chores	22%	25%	23%	23%	21%	19%	*
Turn to for advice	14%	16%	14%	15%	12%	10%	*
Love and be loved	15%	15%	19%	17%	13%	9%	***
Mean Social Support Level (Scaled 0-100)	58.5	60.3	60.4	56.4	57.9	62.7	**
% Reporting NO ONE to Depend on	20%	14%	22%	22%	21%	18%	***
% Participating in Each Type of Group:							
Social Group	23%	39%	27%	22%	18%	19%	***
Religious Group	31%	42%	30%	31%	29%	23%	***
Veterans Group	10%	22%	16%	11%	6%	2%	***
Exercise Group	8%	11%	6%	6%	7%	11%	***
Other Groups	19%	21%	17%	19%	19%	19%	NS
% Participating in Group Activities	58%	73%	57%	57%	54%	51%	***
% Reporting Alone/Lonely Characteristics:							
Eat alone	39%	50%	47%	38%	34%	31%	***
Live alone	29%	57%	49%	26%	18%	16%	***
Felt Lonely in Military	15%	3%	3%	16%	21%	25%	***
SF-36 Social Functioning Mean Level: (Scaled 0-100)	57.5	62.6	61.9	56.2	54.2	61.8	***
Strains:							
Problems with Relatives	32%	15%	24%	36%	36%	37%	***
Problems Paying Bills	42%	19%	26%	45%	49%	51%	***
Problems with Housing	40%	27%	31%	41%	44%	44%	***
Problems with Neighborhood	22%	15%	19%	22%	26%	22%	***
Feel Unwelcome at VA Hospital	20%	6%	9%	20%	26%	29%	***

*p < .05 **p < .01 ***p < .001

[2] Modified from Cotton *et al*., 2000.

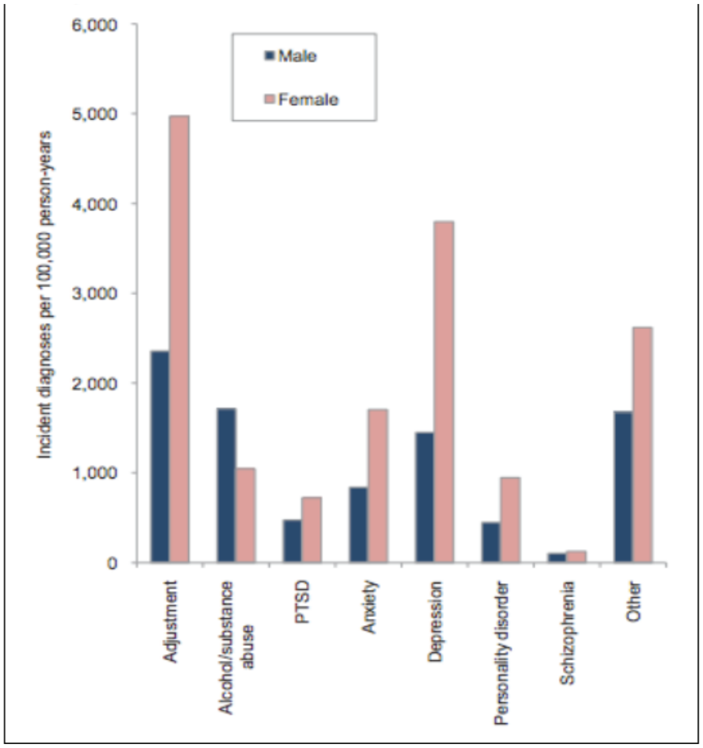


Fig. 1. Incidence rates of mental disorder diagnoses per 100,000 person-years, by category and gender, active component, U.S. Armed Forces, 2000-2009. Taken from Otto, O'Donnell, Ford, and Ritschard, 2010.

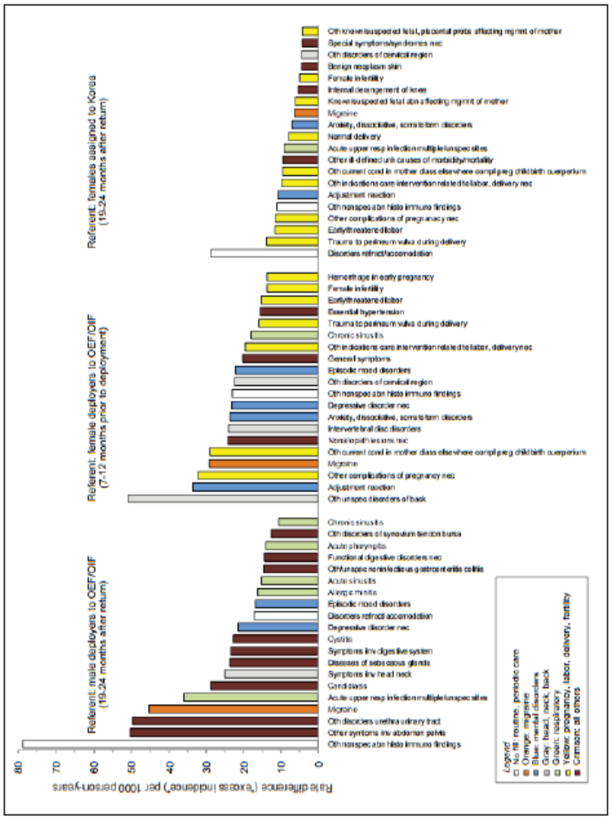


Fig. 2. Conditions with largest rate differences ("excess incidence"), among female OEF/OIF deployers, 19-24 months after returning from OEF/OIF, in comparison to adjusted referent rates. Taken from Armed Forces Health Surveillance Branch, 2009.

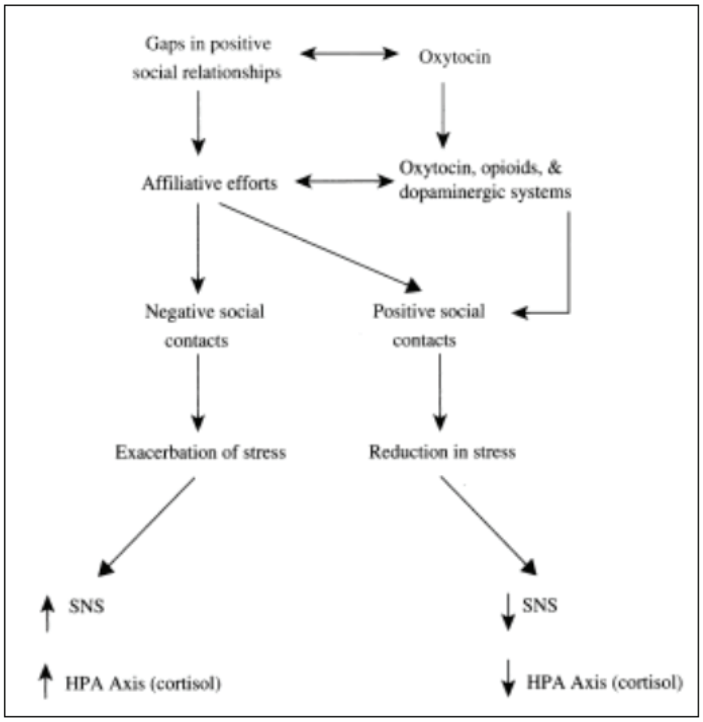


Fig. 3. Model of affiliative response to stress. Taken from Taylor, 2006.

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Time Heals All Wounds: Age-Related Changes in Health Outcomes for Wild Chimpanzees

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Introduction

Throughout life, individuals of any species must devote energy to various biological tasks that are crucial to their own survival, and, more importantly, to the survival of their genes. For primates in particular, these include growth, maintenance, reproduction, physical activity, and storage for later use. As individuals age, the priority of each task changes, and energetic trade-offs must be made to accommodate finite energy acquisition. For example, growth is the top priority very early in life, especially for primates who have large, expensive brains (Weisbecker and Goswami, 2010), while reproduction does not matter very much yet. In contrast, mature individuals mostly expend energy on maintenance of their already-grown bodies (which includes basal metabolic rate, immune function, muscle growth, etc.) and reproduction (Hawkes, 2003). Older individuals' maintenance costs increase as their bodies begin to deteriorate (Emery Thompson, *et al.*, 2007). In this paper, I will explore the relationship between aging and maintenance costs, or, more specifically, the energetic costs of adverse health events such as enduring illness and wounds, in a wild population of Eastern chimpanzees (*Pan troglodytes schweinfurthii*). This has important implications both for understanding our own similarities and differences with our closest cousins, and for conservation efforts on their behalf.

Predictions

I hypothesize that there are age-related changes in the likelihood of acquiring a viral respiratory infection for wild chimpanzees, such that young and old individuals are more susceptible. Infants would have a higher likelihood because their adaptive immunity is not yet fully functional (Djuardi, *et al.*, 2010), and past-prime adults would be susceptible because their energetic cost of bodily maintenance is much higher than younger individuals (Emery Thompson, *et al.*, 2007). Life history theory would predict this U-shaped relationship due to the changing allocation of energy to bodily maintenance over an individual's life. I predict that the probability of being observed with a respiratory infection would be highest for infants and past-prime individuals.

The severity of those respiratory infections should also change with age. Again, the youngest and oldest individuals should have the highest probability of being observed with a severe respiratory infection over the course of the study period for the same reasons mentioned above.

I hypothesize that there are also age-related changes in the likelihood of sustaining an open wound. Adults, especially males, would sustain the most wounds because of frequent intragroup and intergroup fighting (Wrangham and Peterson, 1996). Juveniles would have the next highest number of wounds due to reckless play behavior that would lead to more frequent snare wounds (Muller, 2000). I predict that the probability of being observed with an open wound would be highest for prime adults and juveniles.

The probability of having a severe wound should also be highest for these groups, given that wounds from fighting and snares are largely the most debilitating types of wounds recorded during this study period (Muller, 2000).

Lastly, I hypothesize that there should be age-related effects on the healing time for wounds. The amount of time it takes for an open wound to heal should increase linearly with age as overall bodily maintenance costs increase and finite energetic resources necessary for repair are spread thin. To test this hypothesis, I created the "healing index" measure, which is the number of days per year an individual is seen with a new wound over the number of total days they were seen with a wound that year. Smaller fractions are an easily calculable proxy for slower healing times, because each new wound is present for a higher number of days. This measure was verified by counting healing time in days by hand for each of five individuals who sustained multiple wounds during a 15-month period of the study. Higher average numbers of days needed for a wound to heal did indeed correspond with smaller healing indices. Thus, I predict that healing index should decrease as age increases. All of these hypotheses are tested against the null hypothesis that there is no relationship between aging and health outcomes, but rather that there are other physiological or behavioral factors at play.

Methods

The Kanyawara community of wild chimpanzees has been studied continuously by the Kibale Chimpanzee Project (KCP) since 1987. Their home range consists of about 37.8 km2 of forest (Wilson, Hauser, and Wrangham, 2001) in Kibale National Park (0°34' N, 30°21'E) near the base of the Ruwenzori Mountains in western Uganda. The site mainly includes moist deciduous forest, interspersed with secondary forest, grassland, and swamp, at an average elevation of 1,500 meters above sea level (Chapman and Wrangham, 1993).

In this paper, I include KCP health data from January 1995 to December 2007. During this period, individuals were well-habituated and individual identification was reliable (Chapman and Wrangham, 1993). For each day of observation, trained field assistants assigned each individual a health score: one (healthy), two (cough or sneeze), three (diarrhea), four (wound), or five (other) on daily behavior sheets. 71 individuals, ranging in age from <one year to 64 years old, who had any adverse health condition over the course of the study period were included in the analysis. 29 of these individuals were male and 42 were female.

For my data extraction, I used the field assistants' comments on the KCP behavior sheets to assign a severity code to each sick day. Notes for coughing bouts consisting of phrases such as "coughing very much," "terrible cough," or "productive cough" were coded as severe, whereas "coughed once" or "dry cough" were not, creating a binary distinction for severity. Any indication that a wound was particularly debilitating (i.e., a snare wound, or a wound sustained from a fight that left the individual "badly off") was coded as severe, and the rest were not. In addition, as of April 2015 a new health code scale was introduced, which I retroactively applied to this 1995-2007 dataset: one through four remained the same, while five (swelling or boil), six (limp), and zero (other) were added. This made the health coding used in this analysis, especially that for wounds, more specific and accurate. Also, when reviewing the comments on the behavior sheets, I added sick day entries that had been missing beforehand, making this the most complete health dataset for the Kanyawara community to date.

Some entries were removed because they were deemed irrelevant to this study or incorrect. For example, any health score two's that were noted because an individual screamed so loudly they coughed, or coughed while eating food, were removed because the cause of the coughing bout was likely not a viral respiratory infection, but rather some other throat irritation. Four's with no explanatory comment were removed because they could not be analyzed, and any entry with an indication that the entry was a mistake (i.e., appeared to be the estrus, rather than health, score marked in the wrong location or if it was meant to be another individual) was removed as well. When calculations factored in days observed for each individual, such as the healing index, all individuals who were seen fewer than 40 days that year were removed so that random outliers would not skew the data. This benchmark was deemed appropriate because the majority of individuals were observed for more than 40 days each year during the study period.

In general, the age categories used in this study are those considered standard in the field (Goodall, 1986). Age categories were delineated as zero to <five years (infant), five to <10 years (juvenile), 10 to <15 years (adolescent), and 15 and above (adult). However, while Goodall (1986) suggests that 33 years should be used as the cutoff for past-prime adults based on her work with the chimpanzee community at Gombe National Park, Tanzania, there is evidence that shall be discussed in detail below that indicates that an older cutoff might be more appropriate here considering Kanyawara's particular demographic trends (Muller and Wrangham, 2014). Because of this, analyses were performed using both the Gombe cutoff of 33 years and a new Kanyawara cutoff of 45 years for comparison.

In determining the effects of age on health outcomes, I controlled for sex in all analyses and included fruiting season as well for respiratory infections in a re-analysis of the data. Other factors, such as rank and gregariousness, were not controlled for at this time. All analyses, which included generalized linear models and generalized linear mixed models, were performed using SPSS (version 22), and those for respiratory infections and their severity were re-analyzed using R (version 3.2.0).

Results

Respiratory infections

There was a linear relationship between age category and the probability of an individual showing signs of a respiratory infection during an observation day when controlling for sex. Age category and the interaction between sex and age category were both highly significant ($p<0.001$), with 35- to 45-year-old females having the highest probability of having a respiratory infection (Fig. 1). The pairwise differences among all age categories were significant.

With the Gombe past-prime adult cutoff of 33 years, the same linear trend appeared (Fig. 2). Age category was still significant ($p=0.004$), while sex was not.

There was a linear relationship between age category and the likelihood of having a severe respiratory infection when controlling for sex. Age category was significant ($p=0.001$), while sex was not (Fig. 3). However, when dividing the adult age groups into 10-year units, as done above, the results showed the same trend but were no longer significant.

When using the Gombe cutoff, the positive linear trend disappears, and instead it appears that the probability of having a severe respiratory infection decreases in the oldest individuals, but with lots of individual variation (Fig. 4). Neither age category nor sex was significant.

Wounds

Adolescents (individuals aged 10 to <15 years) had the highest probability of being observed with a wound, when controlling for sex, and individuals under age 15 were all more likely to have a wound than older individuals (Fig. 5). Age category and the interaction between sex and age category were both highly significant (both $p<0.001$). Juvenile and adolescent males by far had the highest probability of sustaining a wound.

With the Gombe age cutoff for past-prime individuals, the same trends are observed. Again, age category and the interaction between sex and age category are both highly significant (both $p<0.001$), with juvenile and adolescent males having the highest probability of sustaining a wound (Fig. 6).

For wound severity, there was no significant difference between any age categories or between the sexes, as each had a relatively equal probability of sustaining a severe wound. This applied when using both the Kanyawara and Gombe age categories.

Juveniles had the lowest healing index, while all other age categories were relatively the same when controlling for sex (Fig. 7). However, for this measure, age category only approached significance ($p=0.053$), while sex was significant ($p=0.006$). Males had a lower mean healing index than females (0.547 vs. 0.738, respectively).

When using the Gombe age cutoff, juveniles still had the lowest healing index of all age categories (Fig. 8). However, age category was more significant than sex ($p=0.035$ vs. $p=0.046$, respectively).

Discussion

In the Kanyawara community, age did affect the likelihood of contracting a respiratory infection, with individuals becoming more susceptible, especially to severe infections, as they got older. This is supported by life history theory, because of the fact that the immune system is extremely expensive (Muhlenbein & Watts, 2010). When general maintenance costs rise as the body becomes more decrepit, an individual can become more immunocompromised. While it is expected that the youngest individuals should be immunocompromised as well due to their underdeveloped adaptive immunity, there might be other factors protecting infants from acquiring infections, such as only socializing with their mothers and thus reducing risk of transmission. It is interesting that 35- to 45-year-old females would have the highest probability of having a respiratory infection of any age-sex category given that they are not the oldest individuals, but perhaps this is the tipping point when their energetic costs of reproduction start to compete with the rising cost of maintaining their bodies, thus leaving less energy available for immune responses. Also, it should be noted that the sample size of individuals above the age of 45 in this study was very small (n=7).

Though the energetic trade-offs of life history theory account for the trends for respiratory infections, wounds seemed to have a different influence. For both the probability of sustaining a wound and for the amount of time it took for a wound to heal, age category mattered, but there was no continuous trend over the course of an individual's life. Instead, behaviors characteristic of certain life stages increased risk. Individuals who were old enough to be independent from their mothers but still too young to refrain from reckless play behavior (i.e., juveniles and adolescents) (Bloomsmith, *et al.*, 1994) were most likely to get wounded, and the largest culprit was accidentally stumbling across a snare in the forest (Muller, 2000). Males, whose play behavior is often more active (Bloomsmith, *et al.*, 1994), were particularly susceptible. While probability of a severe wound did not seem to change across age categories, the fact that juveniles, especially males, took longer to heal indicates that the wounds they sustain were indeed more serious.

The statistical analyses performed in this study were not sufficient to determine whether Goodall's (1986) past-prime adult cutoff of 33 years or a Kanyawara-tailored cutoff of 45 years would be more appropriate for this community, but the only difference in the trend of the results when both categorizations were applied was in respiratory infection severity. Thus, future investigation of what is proper for a past-prime age cutoff for wild chimpanzees is necessary. While there is presently little information on the subject, the existing evidence shows that the Kanyawara chimpanzees tend to live much longer than their counterparts at Gombe (Muller and Wrangham, 2014). Unlike the Gombe population, this community is free from SIV and has not suffered the damaging effects of human intrusion as much as at other field sites. Because of this, the Kanyawara dataset includes individuals who are much older than at other sites, potentially showing trends that do not exist elsewhere.

When looking at the effects of age on health outcomes, I controlled for sex because it has been shown that the presence of body size dimorphism in primates correlates with dietary niche differentiation regarding fauna consumption (Kamilar and Pokempner, 2008). Given that adult chimpanzees exhibit a body size dimorphism of about 1.25 (Pusey, *et al.*, 2005) and that 80% of meat, a preferred food, is indeed consumed by adult and adolescent male chimpanzees (Teleki, 1973), a difference in energy intake between the sexes would be expected. This would therefore influence the amount of energy available for fighting off infections and healing wounds. In a re-analysis of the data, I also controlled for fruit season because it has been shown to affect infectious disease rates at Gombe (Lonsdorf, *et al.*, 2011).

It would have been beyond the scope of this study to include all factors that might influence respiratory infections and wound healing time, but here I offer suggestions for further research directions. First of all, there is evidence that male rank is associated with parasite richness, which is an indicator of more general immune function (Muhlenbein and Watts, 2010). As more energy is diverted towards high levels of testosterone in order to increase or maintain dominance, and thus to increase reproductive success, energy must be taken away from bodily maintenance (Wingfield, *et al.*, 1990). I predict that higher-ranking male individuals in this community would have more respiratory infections, especially severe ones. They are probably involved in more fights in order to maintain rank, but since snare wounds seemed to be the most common type of injury in the Kanyawara community, I would predict to see a longer healing time for snare wounds in high-ranking individuals.

In addition, individual gregariousness might have an effect on the likelihood of acquiring a respiratory infection, as it has been shown that core-ranging individuals in larger party sizes tend to be most susceptible when there are outbreaks (Rushmore, *et al.*, 2013). If controlling for gregariousness, I predict that adult females, who generally stay in small party sizes with only their young (Furuichi, 2009), would be less likely to acquire a respiratory infection than males.

It has been argued that human interaction increases the likelihood of chimpanzees acquiring infectious diseases, and as such, data taken by human observers are affected by the observers themselves (Goldberg, *et al.*, 2007). However, Lonsdorf, *et al.* (2011) showed that human contact had no effect on health outcomes at Gombe, so it was not included as a variable here. The Kanyawara community has also never been provisioned (R. Wrangham, pers. comm.).

There were limitations to the dataset that could have affected the results shown here that should be addressed in future studies. Ideally, we would have observation data for every individual on every day throughout the study period to confirm all of the instances of respiratory infections and wounds, but that would be impossible given the nature of studying wild populations. However, as the saying goes, the absence of evidence is not necessarily evidence of absence. Also, the comments on the behavior sheets were not always detailed enough to provide unequivocal information for this study. In order to code for severity, I had to assume that every time an entry included certain vocabulary it was severe, and entries that did not include these phrases were not. This might explain the lack of trend for wound severity and the relatively large standard errors for both respiratory infection and wound severity.

Confirmations of a healed wound on a certain day were also few and far between, so I often had to assume that once an individual started receiving a health score of one, they had healed. Nevertheless, sometimes an individual was not observed for a long time after sustaining a wound, or there would be conflicting scores on different observers' behavior sheets. The healing index is useful because it bypasses the challenge of determining an official day of completed healing, but it is limited because it does not account for the cases in which an individual is no longer observed regularly, or if they have new and old wounds at the same time. In the future, my hope is that this study spotlights the kind of information that is useful to record on the behavior sheets out in the field, and that the healing index is modified in order to account for its current shortcomings.

Chimpanzees are the closest extant relatives of the human species and as such, we share a number of traits with them, including many almost identical aspects of our immune systems (Puente, *et al.*, 2005). However, humans possess a number of unique characteristics, including an extended lifespan well beyond reproductive age (Finch, 2010), and we do not yet know how our energy allocation is affected accordingly. Human senescence is remarkable, and as of yet, we know very little about its evolutionary underpinnings (Emery Thompson, *et al.*, 2007). By studying age-related changes in health outcomes for chimpanzees, we can better understand those minute but potentially significant differences between human and chimpanzee immune systems and other health-related mechanisms.

Moreover, studying chimpanzee health for its own sake is crucial for conservation. Eastern chimpanzees are currently classified as endangered on the IUCN Red List of Threatened Species (Wilson, *et al.*, 2014), and are not only important for learning about ourselves, but for maintaining the health of the ecosystems they inhabit. By understanding which individuals are more susceptible to infectious diseases or who struggle more to heal after being wounded, we will be increasingly equipped to protect chimpanzees with targeted conservation efforts, better education for local human community members and ecotourists, and more proper care when these animals are in captivity.

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Tables and Figures

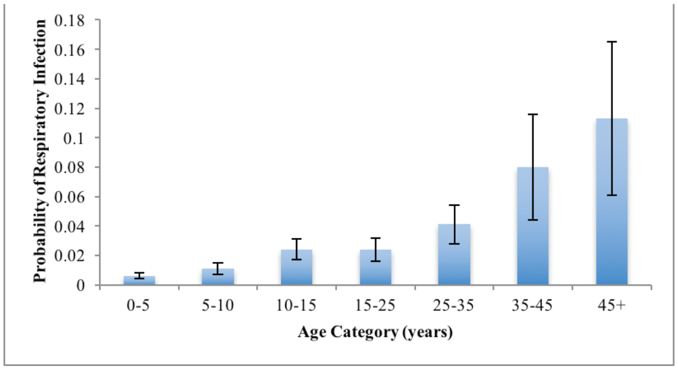

Fig. 1. Probability of sustaining a respiratory infection by age categories using the Kanyawara cutoff for old age.

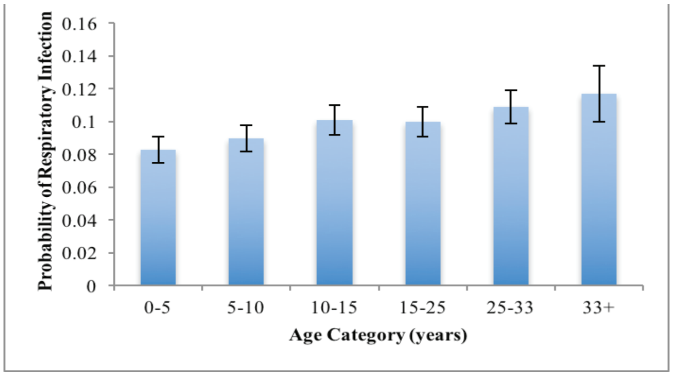

Fig. 2. Probability of sustaining a respiratory infection by age categories using the Gombe cutoff for old age.

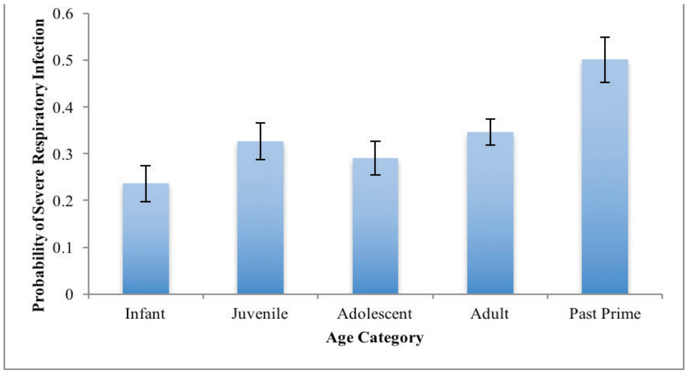

Fig. 3. Probability of sustaining a severe respiratory infection by age categories using the Kanyawara cutoff for old age.

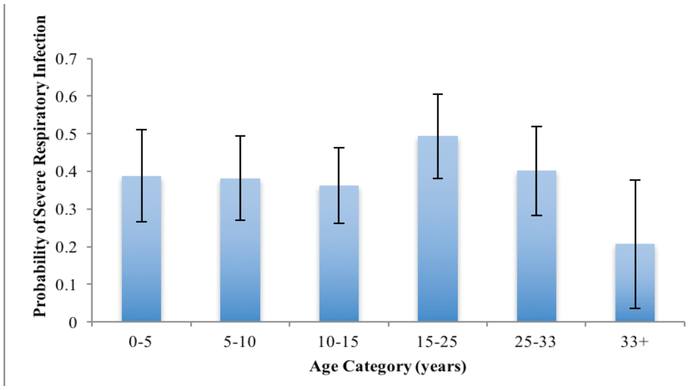

Fig. 4. Probability of sustaining a severe respiratory infection by age categories using the Gombe cutoff for old age.

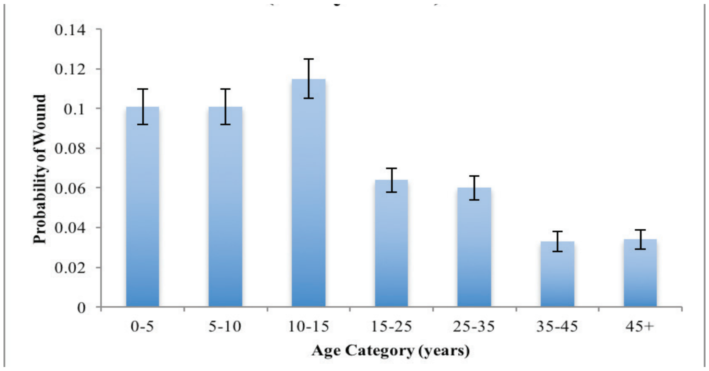

Fig. 5. Probability of sustaining a wound by age categories using the Kanyawara cutoff for old age.

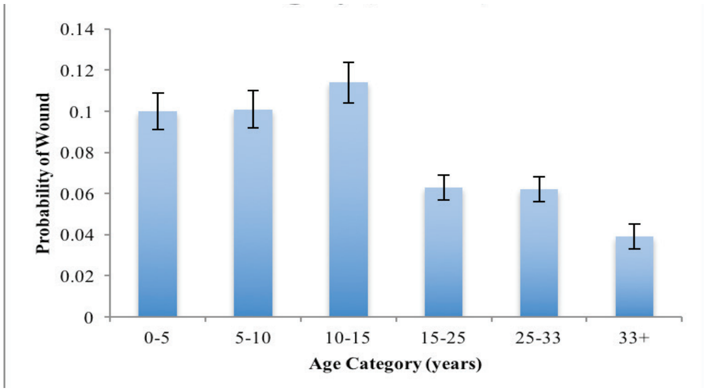

Fig. 6. Probability of sustaining a wound by age categories using the Gombe cutoff for old age.

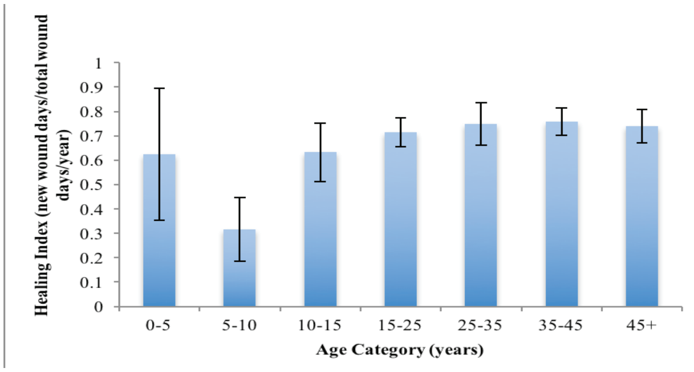

Fig. 7. Healing index score by age categories using the Kanyawara cutoff for old age. Lower healing indices indicate a longer time was necessary for a wound to heal.

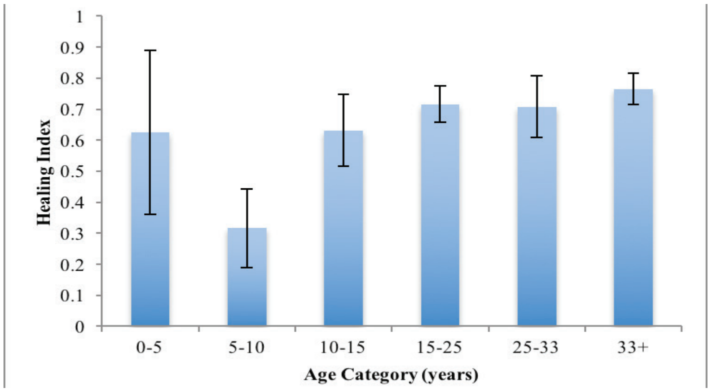

Fig. 8. Healing index score by age categories using the Gombe cutoff for old age.

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The Effects of Kin Selection on Primate Social Behavior: Theory, Method, and Future Discussions

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Introduction

Darwin, known for his indefatigable capacity to defend, with force and grace, his theory of natural selection against all manner of criticism, recognized "one special difficulty" (Darwin, 1859, p. 236): that of the sterile worker caste of eusocial insects. These taxa, in which a vast majority of individuals devote themselves entirely to the reproductive output of the queen (Wilson 1975), represent par excellence an apparent difficulty for Darwinian natural selection—how do traits that do not principally benefit and that sometimes even harm the individuals possessing them evolve? This question is germane to the study of a wide variety of taxa in which cooperative and altruistic behaviors are observed. Primates, a highly social order of mammal, are perhaps second only to the eusocial insects in terms of research effort devoted to solving this apparent paradox. In this review, I will attempt to address the efficacy of one body of theory, which may provide a partial solution to this paradox, in its application to the study of primate social behavior—namely, kin selection theory.

The central tenet of kin selection theory is that selective forces operate as if to maximize 'inclusive fitness:' the sum of 'direct' fitness benefits to individuals and the 'indirect' fitness benefits that they receive via their genetic kin (Hamilton 1964; Maynard Smith 1964). 'Indirect' fitness benefits are proportional to actual genetic relatedness, meaning that closely related kin will have a greater impact on inclusive fitness than more distantly related kin. The implication for cooperative and altruistic behaviors is that they should be directed primarily (in the case of mutualistic cooperation) or solely (for true altruism) towards related individuals. Despite some strident criticism on the theoretical front (e.g. Wilson & Wilson 2007; Nowak *et al.* 2010), there is a near consensus among evolutionary biologists that kin selection theory, in its general form, is both useful and entirely amenable to Darwin's theory of natural selection (e.g. Abbot *et al.* 2011; Gardner *et al.* 2011). I will not, therefore, treat the fundamental principles of kin selection theory as controversial. The question at hand, rather, is whether or not the theory is an appropriate and testable framework from which to approach the study of cooperative and altruistic behavior in primates. I will argue that, indeed, it is, but that kin selection—as evolutionary force and as theory —is, respectively, constrained and limited in many ways. Consequently, a number of criteria must be met to provide strong positive evidence that kin selection is the best explanation for the evolution of a cooperative behavior. I will conclude by suggesting some ways that the study of kin selection in primates might be expanded and improved upon, so as to better elucidate the extent of its action.

The Theoretical Value of Kin Selection Theory in Primatology

Primates, in that they are highly social animals that display various types of cooperative and altruistic behavior, are, at the very least, suitable subjects in the search for kin selection forces at play. I here follow Langergraber's (2012) use of 'cooperation' and 'altruism:' 'cooperation' is behavior that increases the lifetime direct fitness of individuals other than the individual performing the behavior regardless of its impact on the actor's own lifetime direct fitness; 'altruism' increases the lifetime direct fitness of recipients while necessarily decreasing the lifetime direct fitness of the actor. Altruism, then, is merely a special case of cooperation. Although not technically necessary, I will at times refer to 'true altruism.' My purpose in doing so is two-fold: to avoid confusion with behaviors that are often described as 'altruistic' since they result in a temporary decrease in direct fitness, but which ultimately result in a lifetime direct fitness benefit (e.g. Trivers' (1971) 'reciprocal altruism'), and because behaviors are often assumed to be altruistic without good reason or evidence.

Potentially kin-selected behaviors that have been studied in primates can be understood as falling on a continuum, with potential proxies of cooperation on one end and behaviors that are ostensibly definitive examples of true altruism on the other. The former category is exemplified by composite sociality indices (CSIs) which attempt to determine the affiliative strength of dyadic relationships by comparing summed rates of interaction (e.g. proximity, contact, grooming) to mean rates across all dyads (Silk *et al.* 2006). These indices may be crude proxies for the cooperative nature of dyadic relationships. Some behaviors, on the other hand, such as interventions in dominance interactions by adult individuals on behalf of juveniles who are unable to reciprocate (e.g. Chapais *et al* 1997, 2001), are more likely to be actually altruistic. As will be discussed, kin selection theory has the potential to explain the preferential distribution of cooperative behaviors—on both ends of this spectrum—towards closely related individuals, and thus the evolution of such behaviors. Studies on truly altruistic behaviors, however, have the greatest potential to test the action of kin selection, as they are much more difficult to explain under alternative theoretical constructs. Other potentially cooperative behaviors that primates exhibit—all of which have been studied in the context of kin selection—include, but are not limited to, grooming, coalition forming, food sharing or tolerated co-feeding, voluntary rank reversals, and dynamics during dispersal or group fission events (e.g. Bélisle 2002; Bélisle & Chapais 2001; Combes & Altmann 2001; Pope 2000; Silk 1982; Silk *et al.* 2013; Widdig *et al.* 2006).

In addition, primates may be particularly adept at kin-recognition, as they are equipped with highly evolved social intelligence and cognition (Byrne 2000). Although not necessary for individuals to act preferentially towards kin, kin-recognition may greatly facilitate their doing so and thereby accelerate the action of kin selection forces (Hamilton, 1964; Waldman 1987). Kin-recognition mechanisms are commonly lumped into the categories of "phenotype matching," in which individuals use a 'kin-template' of some phenotypic cue and check for similarity to this template to assess relatedness (without necessarily having a cognitive concept of relatedness), or "familiarity-based" mechanisms, in which individuals treat others with whom they have been familiarized as related (e.g.

Langergraber 2012). I second Tang-Martinez's (2001) criticism of this scheme, which points out that any mechanism by which identity is discerned will involve familiarization to a phenotypic cue specific to the identity-category in question. The notable difference, then, though perhaps largely semantic, is whether individuals use cues that are specific to the individual identity of others or whether they can recognize cues that are generalizable on the family level (sensu 'kin-templates'). In the former case, individuals are unlikely to recognize as kin others with whom they have not become individually acquainted during the course of development (sensu "familiarity-based mechanisms"). If, however, individuals recognize family-specific cues, then familiarization with particular individuals may not be necessary for recognition of these individuals as kin (Mateo 2002).

Although there is strong evidence that non-human primates recognize familiar individuals as kin, whether they can use family-specific cues to identify related individuals (regardless of individual familiarization with them) is unclear. For example, primates living in female philopatric societies consistently behave preferentially towards maternal kin, with whom they are familiarized via matrilineal social ties, but not towards paternal kin, with whom they are less likely to be acquainted (for review, see Berman 2011 and Langergraber 2012; see Strier 1994 for critique of a cercopithecine bias inherent in such generalizations). This pattern provides indirect but strong evidence that primates do not use family-specific cues in kin-discrimination. One might expect that use of family-specific cues might maximize potential inclusive-fitness benefits, as individuals could cooperate or avoid conflict with related individuals with whom they are not individually acquainted. It is worth noting, however, that the energetic costs of generating and recognizing such cues may be greater than their benefits if individuals are already acquainted with many close relatives who satisfy their needs for cooperative help (Chapais & Bélisle 2004). Whatever the cue used, however, primates are thought to be particularly adept at recognizing the identity of other individuals and the quality of their relationships with these individuals (Byrne 2000). Such abilities might facilitate particularly efficient kin-discrimination, if not recognition of relatedness per se. This makes primates attractive as potential models of kin-selected behavior. Relative to research effort devoted to delimiting the extent of kin-bias and testing kin selection as an ultimate explanation of behavior, however, the literature on proximate mechanisms by which primates discriminate between kin and non-kin is surprisingly meagre, and deserves further study.

Regardless of the of the proximate mechanisms used for kin-discrimination, kin selection theory is the best existing model that provides an adaptive ultimate explanation of behaviors that are truly altruistic in terms of direct lifetime fitness. No good alternative model has been proposed to explain why a behavior would evolve that causes an individual to act to increase the lifetime reproductive success of others while decreasing their own. Although 'group selection' models repeatedly resurface (e.g. Wilson and Wilson 2007)—arguing that individuals might act altruistically if doing so provides a 'group fitness' advantage—closer inspection reveals them to be both theoretically and empirically flawed. If an altruistic trait is by definition a detriment to the lifetime direct fitness of the individual bearing it, its underlying genes will quickly be selected against unless propagated as copies in other 'vehicles' (Dawkins 1982). Kin selection theory specifies that related individuals, proportional to their relatedness coefficients, are reliable such vehicles (Hamilton 1964). On the other hand, as Dawkins (1982) argues, it is not necessarily the case in nature that 'groups' constitute coherent 'vehicles' of replicating genetic material; consequently, it is hard to imagine how individually maladaptive traits and their genetic antecedents could propagate themselves within a group without specifying which individuals in such a group are receiving a fitness advantage from them. If they are propagated via genetically similar individuals within the group, and thus provide an advantage to the group as a whole, then what is actually being described is kin selection, since this genetic similarity is almost certainly the result of relatedness through shared descent (Dawkins 1982; Maynard Smith 1976). Indeed, kin selection theory has been able to describe all putative examples of group selection, but not vice-a-versa (Gardner *et al.* 2011), indicating that group selection models are useless at best, and incoherent at worst. Kin selection models, on the other hand, provide a logically coherent explanation for truly altruistic behavior. If, then, a truly altruistic behavior is reported between non-related individuals in non-human animals, it is likely that the behavior either actually provides some direct fitness benefit to the actor (and is thus not truly altruistic), or it is an instance of maladaptive altruism (Bertram 1982).

Kin selection theory may also explain the preferential distribution of non-altruistic cooperative behavior towards kin, but must compete in this context with alternative theoretical explanations. Clutton-Brock (2009) proposes mutualism, reciprocity (or 'delayed benefits'), and manipulation as the three primary alternatives to kin selection as explanations of cooperative behavior in animal societies. In mutualism, both participants in a cooperative interaction receive immediate benefits that exceed the cost of participation. Brown and Vincent (2008) describe how mutualistic cooperation can evolve if costs and benefits are shared more or less evenly between participants, and the latter outweigh the former. Second, various models proposing reciprocity, or 'delayed benefits,' describe behaviors that are initially costly to one of the participants, who will receive benefits that exceed the initial cost of participation at some later point. These benefits come either from the individuals who benefited from the original cooperative act, as in 'direct reciprocity' (Trivers 1971), or from individuals aware of these original acts and possibly the reputation of the participants as reliable cooperators, as in 'indirect reciprocity' (Nowak & Sigmund 2005). Finally, individuals might cooperate under duress from manipulation or coercion; that is, the costs of cooperating might be less than the costs of punishment for not cooperating (Clutton-Brock & Parker 1995). The common element in all of these ultimate explanations of cooperative behavior is that it is actually to the direct fitness benefit of the actor to cooperate. Hence, they are necessarily unable to explain truly altruistic behavior. They are, however, logical ultimate explanations of non-altruistic cooperative behavior, which can work either in tandem with, or in the absence of, kin selection forces. Their action is well documented in non-human primates (Berman 2010; Chapais & Bélisle 2004; Langergraber 2012).

These alternative explanations also have an advantage over kin selection theory in their capacity to explain cooperative behavior between non-related individuals (Clutton-Brock 2009). As kin selection theory posits that cooperative behavior will be selected for because of its positive impact on the fitness

of related individuals, it is understood that kin selection cannot explain behaviors that are not preferentially directed towards kin. Where cooperative behavior seems to be distributed without regards to relatedness, then, mutualism, reciprocity, and manipulation should be borne in mind as alternative ultimate explanations. Even if a behavior is preferentially distributed towards kin, but commonly occurs between non-kin, it is likely that one of these processes is ultimately responsible, either wholly or in conjunction with kin selection. (Chapais 2001)

The purpose of the preceding section has been two-fold: to describe the suitability of primates as models in studies of potentially kin-selected behavior, and to describe the explanatory potential of kin selection theory concerning different categories of cooperative behavior, all of which occur in non-human primates. In the section that follows, I will attempt to delineate a framework for assessing hypotheses rooted in kin selection theory that is logically consistent with the strengths and limitations I have claimed for it. In the process, I will evaluate some existing studies according to their relative success in meeting a number of criteria included in this framework. It is my hope that in doing so, I will highlight both the merits and weaknesses of existing methodologies commonly used to address the question of kin selection's role in shaping primate social behavior.

Testing Kin Selection Theory in Primates

Any test which purports to provide evidence in support of kin selection as the likely ultimate explanation of a cooperative behavior should ideally demonstrate that (1) said behavior is distributed preferentially towards related individuals, (2) this preferential distribution is not simply an artifact of (i.e. is independent of) other variables such as rank or spatial proximity, and (3) the behavior tends to confer an inclusive fitness advantage on individuals exhibiting it. Inclusive fitness would ideally be measured in terms of the relative lifetime reproductive output or lifespan of individuals plus appropriate fractions of the same such data from their kin. Alternatively, it may be possible to infer the inclusive fitness benefits of a behavior by observing how contextual differences in the cost-to-benefits ratio of a behavior influence the distribution of said behavior in relation to relatedness. In practice, demonstrating each of these components may not be feasible within the scope of a single study. Still, the quantitative demonstration of each component, assuming consistency in the taxa and behaviors studied, would provide the strongest evidence that a cooperative behavior is indeed selected for, at least in part, because of its inclusive fitness benefits. For reasons discussed in the previous section, I will cautiously advance Chapais' (2001) suggestion that truly altruistic interactions have the greatest potential of meeting these requirements. Finally, various constraints on kin-preferential distributions of cooperative behaviors, such as those delineated by Chapais and Bélisle (2004), should be taken into account when interpreting the data. It is my belief that collecting and evaluating data on cooperative behaviors according to this framework provides the best potential for accurate descriptions of kin selection's importance for the evolution of cooperative behaviors in non-human primates relative to other ultimate explanations.

To provide evidence that kin selection is the likely ultimate mechanism underlying a cooperative behavior, it is first necessary to demonstrate that individuals distribute this cooperative behavior preferentially towards related individuals. Many behaviors that meet this requirement have been documented in non-human primates. For example, there is strong evidence that cooperation is distributed according to matrilineal social bonds in female-philopatric cercopithecine monkeys, such as vervets, baboons, and macaques (Berman 2011; Langergraber 2012). Silk (1982), in her classic study of captive female bonnet macaques, found that reciprocal grooming was higher among individuals of similar rank when they were related, and that individuals were more likely to provide support and assume greater risk in aggressive interactions on behalf of related than non-related individuals. Thus, this study meets the first criterion in demonstrating evidence that kin selection can explain reciprocal grooming and coalitionary support.

Silk (1982) rightly observes, however, that kin selection alone is insufficient in explaining the evolution of these behaviors. Females frequently groomed unrelated females of higher rank and would intervene on behalf of unrelated females against females of lower rank. Chapais and Bélisle (2004) argue that these so-called 'conservative coalitions' often form between unrelated females because optimal partners must have attributes that are not necessarily related to kinship (e.g. rank or size). Although Silk originally referred to these behaviors as forms of 'altruism,' her data show that they are actually forms of non-altruistic cooperation: females experienced significantly less harassment from higher-ranking females whom they frequently groomed. In other words, grooming is a form of manipulation. Consequently, ultimate explanations that posit direct lifetime fitness benefits must be considered alongside kin selection, especially since these behaviors are often directed towards non-related individuals. In sum, the demonstration of kin-bias, while necessary to support kin-selection hypotheses, is not sufficient to do so.

Although kin-biases may often characterize the distribution of a cooperative behavior, it is possible that these patterns are actually the artifacts of lurking variables, such as rank or spatial proximity. Accordingly, tests should control for variables that may incidentally bias the distribution of cooperative behaviors towards kin. Chapais (2001) demonstrates why this is fundamental to the study of cooperation between matrilineal kin: maternal kinship often positively correlates with spatial proximity. It may often be the case, then, that individuals engage in cooperative behaviors with kin merely because kin are more readily available than non-kin. Furthermore, if these behaviors are not altruistic, then kin-selection is not necessary as an ultimate explanation. The same logic holds for kin-biases observed in the formation of coalitions, which may arise solely because closely related individuals are similarly ranked and thus mutually benefit from forming conservative coalitions with each other (Chapais 2001; Chapais & Bélisle 2004). The correlation of such variables with kinship is not necessarily evidence that indirect fitness benefits do not play a role in the evolution of a behavior. Yet, if tests are to provide strong positive evidence for the importance of these benefits, they must demonstrate that kinship remains a significant positive determinant of cooperation after controlling for potentially confounding variables.

Many studies have indeed met this criterion. Bernstein *et al.* (1993), for example, found that, though proximity correlated positively with maternal kinship in rhesus macaques, affiliative interactions between kin were higher than predictions based on proximity alone. Similarly, Silk and her colleagues (2006) found that female baboons groom adjacently ranked close kin more frequently than adjacently ranked non-kin. These findings indicate that the behaviors in question may provide indirect fitness benefits to individuals, and may experience stronger positive selection than would be expected if they provided direct benefits alone. It is not always certain, however, whether they actually provide such indirect benefits. That Bernstein and his colleagues found the same positive relationship between kinship and rates of aggressive interaction, independent of proximity, makes this point clear. For obvious reasons, aggression towards kin is unlikely to confer indirect fitness benefits. Again, kin-biased distributions of cooperative behavior, even when independent of potentially confounding variables, constitute necessary but insufficient support of ultimate explanations grounded in kin selection theory.

It is worth considering whether tests of kin selection should also control for the effects of parental care, particularly between mothers and their infants. In a study of captive sooty mangabeys, Ehardt (1988) found that females preferentially groomed and were groomed by kin only before removal of mother-infant interactions from the data analysis. Kin-biased distributions of cooperative behavior that are heavily skewed by maternal care, like those that are merely artifacts of proximity correlates, may be explained without reference to indirect fitness benefits. This contention is in line with theoretical definitions of altruism that exclude parental care (e.g. Bertram 1982; Trivers 1971) on the basis that such care necessarily confers a direct fitness benefit on the parent. Ensuring the survival and welfare of offspring is, after all, a way of ensuring that one's reproductive output is not, as it were, for naught. On the other hand, other definitions of altruism include parental care (e.g. Dawkins, 1979; Maynard Smith 1964; Wilson 1971) on the basis that it incurs a direct fitness cost on the parent, since energy spent on caring for offspring reduces energy available for investment in future reproduction. Even if parental care is not altruistic, however, it likely always confers indirect fitness benefits via increased offspring quality, and is therefore at least cooperative (Chapais 2001). Kin selection, therefore, cannot be ruled out as an explanation of cooperative behaviors which are kin-biased only when mother-infant interactions are included. Nevertheless, it is also not entirely evident that alternative ultimate mechanisms, which only require direct fitness benefits, are not wholly responsible. Strong evidence for kin-selection hypotheses, then, will not depend on mother-infant interactions alone.

Beyond providing evidence for a kin-preferential distribution of cooperative behavior that is independent of confounding variables, it is necessary to demonstrate that the behavior in question confers an inclusive fitness advantage on individuals exhibiting it. Ideally, inclusive fitness effects should be assessed directly using data on lifetime reproductive output or reproductive lifespan, taking into account both direct and indirect effects for all included individuals. One might then relate these data to differences in the way individuals distribute cooperative behavior in relation to kin. In practice, however, such an analysis would require large amounts of precise data on behavior, life history, and relatedness.

Some analyses have approximated this method in making the connection between kin-biased cooperation and inclusive fitness benefits. Pope (2000), for example, using long-term genetic and demographic data on female red howlers, found that females in long-established coalitions had significantly higher reproductive output than females in newly established coalitions. These long-established coalitions were also characterized by a significantly higher average degree of relatedness than new coalitions (mean $r = 0.44$). One can infer, therefore, that membership in these older coalitions, which are maintained through active territory defense and harassment of unrelated intruders, confers substantial inclusive fitness benefits. This study, however, failed to establish a quantitative relationship between reproductive success and specific cooperative behaviors, making it impossible to rule out ecological factors, as Pope concedes. Combes and Altmann (2001), on the other hand, used 25 years of demographic data on savannah baboons to test different hypotheses regarding rank-reversals commonly observed between aging mothers and their mature daughters, which were independent of loss in relative or absolute rank due to changing group dynamics. The rank-reversals were consistently more likely to happen between mothers and adjacently ranked daughters than between adjacently ranked unrelated females ruled out the hypothesis that rank reversals were simply the by-product of physical deterioration. Instead, rank-reversals were well-predicted by models which used Hamilton's rule and residual reproductive values to predict the age at which mothers should 'consensually' reverse ranks with daughters to maximize inclusive reproductive output. Assuming that such rank reversals had no significant impact on the fitness of related individuals beyond mother-daughter dyads, this study provides strong evidence that kin selection is the best ultimate explanation of these rank reversals.

An alternative method to demonstrating the impact of kin-biased cooperation on inclusive fitness is the reverse: demonstrating how differences in the costs-to-benefits ratio of a behavior in different contexts influence the distribution of this behavior in relation to kin. Hamilton's rule predicts that individuals should distribute cooperative behaviors with high direct costs relative to indirect benefits only towards the closest of kin, if at all. On the other hand, individuals might distribute behaviors that are of relatively low direct cost towards more distantly related kin. It is important to recognize, however, that various factors may constrain the distribution of cooperative acts in relation to kin (Chapais & Bélisle 2004), such that it is difficult to predict how such distributions will actually react to changes in costs-to-benefits ratios.

Chapais and Bélisle (2004) review two of their previous experiments (Bélisle & Chapais 2001; Bélisle 2002) on tolerated co-feeding according to the method discussed above. In the first experiment, female Japanese macaques of different rank were given the opportunity to co-feed from a translucent box with holes on opposite sides. Rates of co-feeding were significantly related to degree of kinship, but rates of co-feeding between aunts and nieces ($r = .25$) were similar to those of non-kin. In the second experiment, the same dyads were used but now fed from a box with adjacent holes, supposedly lowering the cost of monopolizing the food source. As expected, rates of co-feeding were significantly lower and restricted to mother-daughter pairs. These data may suggest that the distribution of tolerated co-feeding is sensitive to assessments of inclusive fitness benefits. Although it is an inherently difficult task, differences in costs-to-benefits ratios (at least in the context of Hamilton's rule) would ideally be measured in terms of lifetime direct fitness. Chapais and Bélisle infer that the contextual change between experiments represents a decrease in relative costs because supplants and chases by the subordinate individual were significantly lower in the second experiment. This difference, however, may not translate to an actual difference in terms of lifetime direct fitness. The risks of making such assumptions notwithstanding, this represents a useful experimental approach for assessing the relationship between cooperative behavior and inclusive fitness benefits. Alternatively, it might be possible to use observational data to assess how individuals distribute a cooperative behavior in relation to kin across a variety of contexts that affect the relative costs and benefits of deploying this behavior, though I am not aware of any examples.

As suggested by Chapais (2001), truly altruistic behaviors have the greatest capacity to meet each of the aforementioned requirements, if indeed they are truly altruistic. (Chapais uses the term 'unilateral altruism,' which I shall treat as synonymous with 'true altruism.') In line with his own suggestion, Chapais and his colleagues (1997, 2001) have conducted experiments on a behavior that they argue is truly altruistic—the aggressive intervention of mature female Japanese macaques in dominance interactions between juvenile peers. These studies have shown that this behavior is preferentially distributed towards kin, with rates of intervention declining significantly with degree of relatedness. Assuming that adults incur a direct fitness cost by intervening, which their juvenile relatives cannot eventually compensate, it is likely that adults are ultimately motivated to intervene by indirect fitness benefits. However, lest my third criterion be abandoned, it is still preferable to demonstrate these costs and benefits in terms of lifetime direct fitness, rather than to assume they are present. In addition, to claim that kin selection is the only existing ultimate mechanism producing true altruism is not to claim that all truly altruistic acts can be explained by kin selection. As stated earlier, altruistic acts may be maladaptive—the result of proximate mechanisms such as genetic mutation, developmental processes, or forces in the physical or social environment. Bertram (1982) reminds us that altruistic behaviors that do not confer an inclusive fitness advantage may in fact be maladaptive. It is, for this reason, necessary to quantitatively demonstrate inclusive fitness benefits before accepting that kin selection is the ultimate mechanism producing a cooperative behavior.

Finally, when interpreting the data, it is important to recognize that a number of factors constrain actual distributions of cooperative behavior towards kin, often making optimal distributions unachievable for subjects and unknowable for researchers. Chapais and Bélisle (2004) review a number of these constraints: limited time available for cooperation, the diminishing returns inherent in directing cooperative behavior towards individuals who are not in great need of it, and the unavailability of distantly related kin. These factors may explain why the deployment of cooperative behaviors are so frequently observed to decrease dramatically below r values of 0.5, that of parents and offspring or full-siblings (see Chapais & Bélisle 2004, fig. 16.1). In addition, the distribution of truly altruistic behaviors is likely constrained by the preference of individuals to cooperate in ways that do not incur direct fitness costs. Chapais and Bélisle contend that the design of the aforementioned intervention studies (Chapais *et al.* 1997, 2001) mitigated the effect of each constraint: a wide array of kin categories were available, intervention was not costly in terms of time, individual needs could not be satisfied by closer kin because only a single related individual was available during any experiment, and interventions were truly altruistic. It is possible, however, that while actual constraints were mitigated, perceived constraints were not. For example, mature individuals may have forgone intervention due to lack of familiarization with distantly related kin, rather than an evaluation of relative costs and benefits. In other words, they do not perceive spatially proximate, but distantly related kin as such. Though exceedingly difficult, then, it may be necessary to control for actual and perceived constraints to observe optimally kin-biased distributions of cooperation.

Conclusion and Future Directions

My intentions in the previous sections were firstly to develop a theoretical justification for the use of kin selection theory in the study of primate social behavior, and secondly to provide a framework, logically consistent with this rationale, by which tests of kin selection hypotheses can be evaluated. I have argued that a number of criteria are necessary (but insufficient in isolation from each other) to demonstrate strong positive confirmation of such hypotheses. Namely, it is necessary to demonstrate that a cooperative behavior is directed preferentially towards kin, to carefully control for variables that may incidentally generate this kin-biased distribution, and to demonstrate an inclusive fitness benefit incurred by individuals exhibiting the behavior. Studies that do not meet each criterion may provide partial evidence in support of kin selection hypotheses, and alternative hypotheses should still be considered even when all three are met. Nevertheless, one should be skeptical of strong claims that kin selection is the best ultimate explanation for the evolution of any particular cooperative behavior if these claims are not backed by data that meet any of these criteria. While many studies have indeed demonstrated kin-biased cooperative behaviors (Berman 2010; Langergraber 2012), very few have attempted to directly quantify the impact of these behaviors on inclusive fitness (e.g. Combes & Altmann 2001; Pope 2000). Researchers should devote future effort towards providing this level of analysis where there are sufficient data and where kin-biased cooperation is well documented, such as in female-philopatric cercopithecine monkeys. In addition, better descriptions of the proximate mechanisms used by primates to discriminate amongst their kin are needed, since these mechanisms are the actual substrates which are shaped by—and which constrain the action of—ultimate processes such as kin selection.

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Feeding Party Size, Diet, and Resource Patch Use of Black-Handed Spider Monkeys (*Ateles geoffroyi*) in Costa Rican Lowland Wet Forest

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Introduction

Spider monkeys (*Ateles spp.*) form one of the most widespread genera of neotropical primates, but they are still threatened by habitat destruction, hunting, and low reproductive rates (Collins, n.d.). In fact, 40% of *Ateles* species and subspecies are either endangered or critically endangered compared to 17% of all neotropical primates (Collins, n.d.). Knowing the monkeys' movement patterns, along with their most important food species and information about their fission-fusion social structure is important to determine appropriate methods for their conservation. This is especially important since large frugivorous primates, such as *Ateles*, are highly sensitive to habitat disturbance and fragmentation (Michalski and Peres, 2005).

Spider monkeys are ripe fruit specialists, although they have been known to vary their diet when fruit is scarce (Chapman *et al.*, 1995; Chapman, 1988). Fruit is generally more patchily distributed than lower quality foods such as leaves, so spider monkeys' highly frugivorous diet contributes to their difficulty surviving in small patches (Collins, n.d.). Temporal and spatial variation in food abundance and quality affect spider monkeys' diet, social structure, mating, and life history strategies (Sterling *et al.*, 2013). Specifically, they split into feeding parties based on food availability (Chapman and Lefebvre, 1990). This social system, called fission-fusion, is seen in many Old and New World primates and reduces intragroup competition when large food patches are sparse (Sterling *et al.*, 2013). This is because spider monkeys compete aggressively for access to food trees (Klein and Klein, 1977 as cited in Chapman and Lefebvre, 1990) and agonistic interactions between individuals increase as the number of monkeys in a tree increases (Symington, 1988). Another proposed explanation for their fission-fusion social system is to reduce ranging costs since larger groups must travel farther to find a large enough patch to sustain the entire group (Asenio *et al.*, 2009). Size and composition of spider monkey fission-fusion groups are far more fluid than those of most other non-human primates and are matched only by chimpanzees (Symington, 1988). As such, they have been the subject of many studies focussing on their fission-fusion dynamics and subgroup sizes. Some studies have found a strong positive correlation between spider monkey feeding party size and the diameter at breast height (DBH) of feeding trees (Symington, 1988). Others have found that the relationship is dependent on tree species (Wallace, 2008), and still others have found no relationship at all (Asenio *et al.*, 2009).

While studies have already been conducted on the feeding ecology of spider monkeys elsewhere in the Osa Peninsula (Riba-Hernandez and Stoner, 2005; Weghorst, 2007), little is known about the monkeys around Piro Research Station where they seem to be thriving. The goal of this study is to gain a better understanding of resource use by the black-handed spider monkey as well as their ranging, foraging, and social behaviors by observing them during feeding bouts and mapping their resource distribution. This study will provide preliminary findings pertaining to feeding party size, diet, and ranging behavior of the spider monkeys around Piro Research Station which can be applied to conservation efforts in the Osa Peninsula and elsewhere where spider monkeys are endangered. We tested the hypothesis that patch size influences feeding party size and predicted that larger feeding parties would be found at larger food patches.

Methods

Study Site

This study took place in the Osa Peninsula off of Costa Rica's southern Pacific Coast. The Osa Peninsula covers less than one thousandth of a percent of the total surface area of the Earth, yet is home to 2.5% of the planet's biodiversity (Lanier, 2014). Piro Research Station (08°24.244'N, 83° 20.195'W) is located on the south-western coast of the Osa Peninsula and is surrounded by primary and secondary lowland wet rainforest. As much of the 3.6 km2 surrounding Piro Research Station were covered as possible by using all available hiking trails.

Study Subjects

All data were collected from one community of black-handed spider monkeys living in the vicinity of Piro Research Station. A total of 71 individuals were observed in 33 feeding parties over a period of eight days from June 28 to July 5, 2015. Given the nature of the spider monkeys' fission-fusion social structure, it is more than likely that the same individuals were observed multiple times throughout the study period. We were unable to control for this effect because the monkeys were wild, free-ranging, and not marked or tagged in any way so there was no way of identifying specific individuals. Within a feeding party, individuals were aged by relative body size and sexed by observing the external genitalia with adult females possessing an enlarged white clitoris, and adult male genitalia consisting of a less conspicuous pair of darkly-coloured testicles. Females with infants were considered one individual since infants do not feed from trees like adults do.

Data Collection

Trails were walked between approximately 6:00 am and 6:00 pm each day. The date, time of day, and the part of the tree being eaten (ripe fruit, unripe fruit, new leaves, mature leaves, flowers, and in one case the pith of a young branch) were recorded each time a visible feeding party was encountered. A feeding party was defined as any group of individuals simultaneously feeding in a single patch with a patch defined as a single tree (Symington, 1988). Feeding group composition was recorded taking into account the total number of individuals and the age and sex of each when possible. GPS coordinates of the feeding tree were read using a Garmin GPS 72H handheld GPS. In cases where the feeding tree was inaccessible due to excessive downed woody debris or steep terrain, the GPS coordinates of the point on the trail from which the monkeys were observed was recorded instead. To estimate patch size, DBH of the feeding tree was measured where possible using a DBH tape. DBH has been found to be a reliable estimate of crown volume when determining food availability in a patch (Symington, 1988; Wallace, 2008). Phenological characteristics of the feeding tree were also recorded including the presence or absence of ripe fruit, un-ripe fruit, fruit on the ground, new leaves, mature leaves, and flowers. Photos of each feeding tree were also taken for later identification of genus and/or species.

Data Analysis

A linear regression was performed to determine the amount of variation in feeding party size caused by patch size (DBH). Mean feeding party size (± SD) was calculated for each food type and across food types. To determine whether food type has an effect on feeding party size, a one-way analysis of variance (ANOVA) and Tukey's honest significant difference post-hoc analysis were conducted between all food types observed being consumed more than once during the study (ripe fruit, unripe fruit, flowers, and leaves) with feeding party size as the test variable. Diet composition was determined based on frequency of observed feeding events. All numerical data analyses were performed using Microsoft Excel 365 computer software. The distribution of feeding patches was mapped using Google Earth (7.1.5.1557) computer software.

Results

Feeding Party Size

An average feeding party size of 2.2±1.7 (mean±SD) was found to feed at trees with an average DBH of 41.9±30.9 cm. Almost half of all feeding parties consisted of only one monkey while another quarter were groups of two. One fifth of feeding parties was made up of three or four monkeys, while only one group of five, and one group of nine were observed. A linear regression found no significant relationship between feeding party size and patch size ($y = 0.0118x + 1.6235$, $r = 0.20$, $p = 0.35$) with only 4% of variation in feeding party size being attributable to variation in patch size (Fig. 1). However, while a one-way ANOVA showed that the effect of food type on feeding party size was only approaching significance at the $p<0.05$ level ($F_{3,7} = 2.8476$, $p = 0.0562$), Tukey's HSD post-hoc analysis indicated a significant difference ($p = 0.034$) in mean feeding party size between leaves (1±0) and ripe fruit (3.5±3.0; Table 1). Notably, leaves were only observed being consumed by solitary monkeys.

Diet Composition

Flowers made up one third of the monkeys' diet, the highest proportion of any food type, with leaves, ripe fruit and unripe fruit each making up a significant portion of the remaining two thirds and the pith of young branches accounting for 3% (Fig. 2). All flowers consumed were of the *Symphonia globulifera* species. They ate the ripe fruit of the royal palm (*Attalea butyracea*), guava (*Guajava psidium*), and *Virola kos-chnyi*, and the unripe fruit of the royal palm and *Melastoma* (family Melastomataceae). They also ate the new leaves of the Ficus (family Moraceae). The monkeys also consumed the unripe fruit, new and mature leaves, and pith of several other unidentified tree species.

Resource Distribution and Ranging Behavior

A few patterns emerge upon viewing the daily sight-ings data and map of spider monkey feeding locations (Fig. 3). It was common to see feeding groups of varying sizes on Las Tortugas trail in the early morning (between 6:00 and 6:30 am), and around Piro Research Station around midday (between 12:30 and 2:00 pm). Monkeys were sighted at various times of the day throughout the forest to the north of the road, but were never observed in the area to the west of the road. Five of the 26 observed feeding trees were visited more than once over the course of the study period.

Discussion

Feeding Party Size

Our results do not support the hypothesis that feeding party size is influenced by patch size, but may have been hindered by the short period of data collection and relatively small number of data points. While a positive relationship between patch size and feeding party size has been documented for at least four other primate species (Symington, 1988; Chapman *et al.*, 1995), a study of A. geoffroyi in Costa Rica supported the current study's results finding no relationship between subgroup size and the DBH of feeding trees (Asenio *et al* ., 2009). Wallace (2008) found differences in this relationship among tree species; subgroup size of *Ateles chamek* in Bolivia increased significantly with patch size for only two out of eight studied tree species. Explanations for spider monkeys adjusting their feeding party size according to feeding tree size include the reduction of ranging costs (Asenio *et al.*, 2009; discussed in the "Resource Distribution and Ranging Behaviour" section below), and the reduction of intragroup competition (Symington, 1988). Intragroup competition has long been considered the reason for the existence of fission-fusion sociality in spider monkeys since they must compete for access to food trees (Klein and Klein, 1977 as cited in Chapman and Lefebvre, 1990). Symington (1988) has also shown that agonistic interactions occur almost exclusively in crowded trees. Based on a long-term study of *A. geoffroyi* in Santa Rosa National Park in Costa Rica, Chapman *et al* . (1995) concluded that subgroup size is limited by habitat-wide resource distribution and abundance rather than individual patch size. In this case, larger groups would be found at large patches when the patches are clumped, but not when they are widely dispersed (Chapman *et al* ., 1995).

Overall, the average feeding party size (for all food types) of 2.2±1.7 found in our study is lower than the 3.15 to 7.3 range reported by prior studies of spider monkeys (White 1986; Chapman *et al.*, 1995; Iwanaga and Ferrari, 2001; Weghorst, 2007; Asenio *et al.*, 2009). However, these numbers all take into account subgroups of varying types (feeding, foraging, and resting), while our data represents feeding parties only. The difference may also be due to the current study's short time span. Chapman *et al.* (1995) reported monthly average subgroup sizes of *A. geoffroyi* in Santa Rosa National Park, Costa Rica as low as 2.3 individuals. This is very similar to our study's result and suggests the potential for seasonal differences in subgroup size. This notion is supported by the findings of Asenio *et al.* (2009) which state that subgroups are, on average, larger in the wet season than in the dry season. Since our study took place during the transition from the dry to the wet season and we found that average feeding party size was largest for ripe fruits, it is possible that seasonal fruit availability influenced our results. Given the intensely fruit-dominated diets reported in other studies of spider monkeys (White, 1986; Symington, 1988; Chapman *et al.*, 1995; Link *et al* ., 2012), it is probably more accurate to compare their findings to our study's average feeding party size for ripe fruit only (3.5±3.0) instead of our average feeding party size across all food types.

Diet Composition

The current study found a shockingly low proportion of ripe fruit in the diet of spider monkeys around Piro Research Station (19.7%) compared to most other studies of spider monkeys which report a range of 71.4-92.4% (White, 1986; Symington, 1988; Chapman *et al.*, 1995; Link *et al.*, 2012). However, Chapman *et al.* (1995) reported monthly proportions of fruit in the diet as low as 13.7% which is closer to, and even lower than, the results of our study. One study of *A. geoffroyi* in the Osa Peninsula found that from July to September, the flower nectar of the *S. globulifera* tree accounted for 86-100% of spider monkeys' feeding time (Riba-Hernandez and Stoner, 2005) which is approximately three times the amount reported here, but spans a longer time period.

Conversely, proportions of leaves (24.24%) and flowers (33.33%) in the diet were much higher than previously reported (White, 1986; Chapman *et al* ., 1995; Link *et al.*, 2012), although results varied. Prior studies reported 0.3-14% flowers and 3.1-16.63% leaves in spider monkeys' diets with the highest leaf consumption found in the dry season (White, 1986; Chapman *et al.*, 1995; Link *et al.*, 2012). The major differences in diet composition are likely caused by the short study period combined with the fact that our study was carried out during the transition between the dry and wet seasons. However, it has been noted that spider monkeys exhibit lots of month-to-month variation in diet (Chapman *et al* ., 1995; Chapman, 1988). Spider monkeys prefer ripe fruit, but adjust their diet seasonally to include more leaves in the dry season when fruit is scarce (White, 1986; Chapman, 1988; Symington, 1988). The beginning of the wet season also cor-responds with a major flush of new leaves in lowland tropical wet forests (Boinski and Fowler, 1989) which, combined with fruit scarcity, probably contributed to the high proportion of leaves consumed during our study. The high flower consump-tion can be explained by the fact that *S. globulifera* is one of the most common trees on the Osa Peninsula (Hartsthorn, 1983 as cited in Riba-Hernandez and Stoner, 2005) and flowers mostly from July to September (Riba-Hernandez and Stoner, 2005). The monkeys' dependence on *S. globulifera*, at least during this time of the year, contradicts Chapman's (1988) assertion that spider monkeys tend to rely on species that occur at low densities.

Resource Distribution and Ranging Behavior

While our data was not sufficient to make broad assumptions about the monkeys' ranging behaviour or resource distribution, we were able to detect some patterns in their movement. Seeing groups of spider monkeys consistently in the same location on Las Tortugas trail very early in the morning, soon after the monkeys wake up, may indicate the presence of a sleeping spot nearby. The absence of spider monkeys west of the road can be explained by the fact that the forest in that area is very dense which decreases visibility. There is also a farm next to this part of the forest which may influence the monkeys' movement in the area. Their presence throughout the rest of the forest is not enough to ascertain whether food resources are clumped or widely spaced. However, the monkeys' consistent presence in the fruit trees around Piro Research Station suggests that those planted trees (i.e. not a natural part of the forest) may be an important source of food for them, at least during certain parts of the year. As described for *A. chamek* in Peru, the monkeys tend to revisit the same trees from day to day (White, 1986). The small feeding groups seen in our study are consistent with Chapman's (1990) findings that larger subgroups incur larger ranging costs because they must travel farther to find large enough food patches to sustain a large group. Since at the time of our study the monkeys around Piro Station relied on lower quality foods such as flowers and leaves, it is likely that they fed in smaller subgroups to reduce ranging costs.

Conclusions

While spider monkeys are largely frugivorous, their diet can vary considerably and can include large amounts of low-quality food such as flowers and leaves. The spider monkeys at Piro Research Station on the Osa Peninsula rely at times on the flowers of the *S. globulifera* tree. Finally, feeding party size may, at least during certain times of the year, be influenced more by food quality than by patch size.

Tables and Figures

TABLE 1. Spider monkey (A. geoffroyi) feeding party size (mean±SD) by food type[1]

Food type	Feeding party size	Number of records
Ripe fruit	3.5±3.0*	6
Unripe fruit	2.2±1.2	6
Leaves	1±0*	8
Flowers	2.3±1.3	11
Ripe and unripe fruit	3	1
Pith of young branch	1	1

"Ripe and unripe fruit" indicates one event when both ripe and unripe fruit were eaten from the same tree by a single feeding party. Asterisk indicates a significant difference at the $p<0.05$ level.

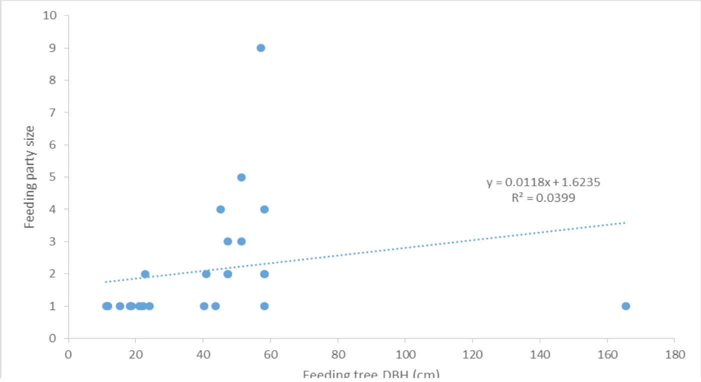

Fig. 1. Feeding party size of the black-handed spider monkey(*A. geoffroyi*) compared to diameter at breast height (DBH) of feeding trees (cm) for all tree species and all food types.

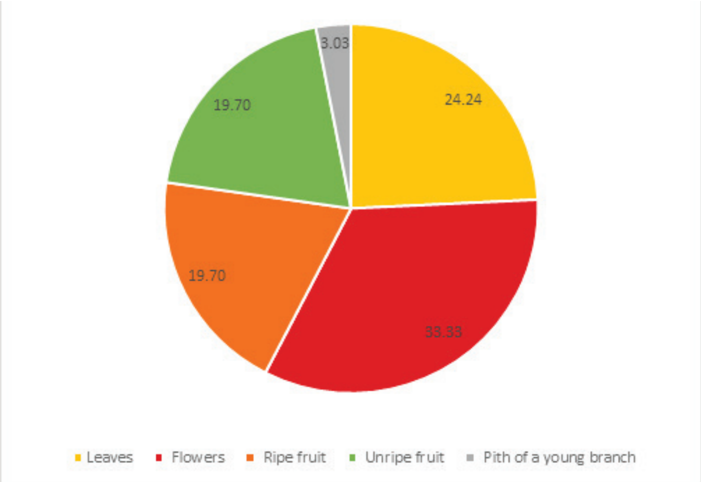

Fig. 2. Diet composition of the black-handed spider monkeys (*A. geoffroyi*) around Piro Research Station from June 28 to July 5, 2015 calculated using frequency. Note: For one feeding event where ripe and unripe fruit were consumed simultaneously, half of that event's frequency weighting was attributed to each separate food type.

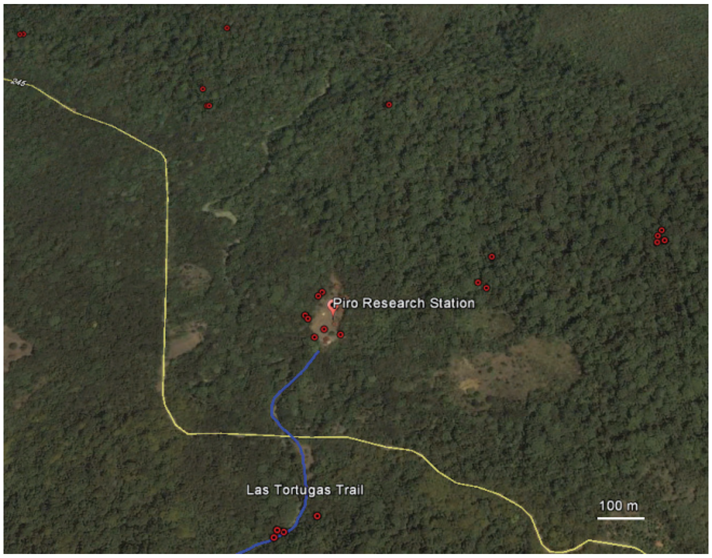

Fig. 3. Map of all spider monkey feeding locations (red dots) recorded around Piro Research Station from June 25 – July 8, 2015. Adapted from Google Earth.

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