# ALTITUDINAL EFFECTS ON THE BEHAVIOR AND MORPHOLOGY OF

# PYGMY TARSIERS (*Tarsius pumilus*) IN CENTRAL SULAWESI, INDONESIA

A Dissertation

by

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# ABSTRACT

Pygmy tarsiers (*Tarsius pumilus*) of Central Sulawesi, Indonesia are the only species of tarsier known to live exclusively at high altitudes.  This study was the first to locate and observe multiple groups of this elusive primate.  This research tested the hypothesis that variation in pygmy tarsier behavior and morphology correlates with measurable ecological differences that occur along an altitudinal gradient.  As a response to decreased resources at higher altitudes and the associated effects on foraging competition and energy intake, pygmy tarsiers were predicted to exhibit lower population density, smaller group sizes, larger home ranges, and reduced sexually selected traits compared to lowland tarsiers.

Six groups containing a total of 22 individuals were observed.  Pygmy tarsiers were only found between 2000 and 2300 m, indicating allopatric separation from lowland tarsiers.  As expected, the observed pygmy tarsiers lived at a lower density than lowland tarsier species, in association with decreased resources at higher altitudes.  The estimated population density of pygmy tarsiers was 92 individuals per 100 ha, with 25 groups per 100 ha. However, contrary to expectation, home range sizes were not significantly larger than lowland tarsier home ranges, and average NPL was smaller than those of lowland tarsiers.  The average home range size for the observed pygmy tarsiers was 2.0 ha, and the average nightly path length (NPL) was 365.36 m.

Pygmy tarsiers exhibited a nonrandom, clumped distribution near forest edges.  While insect abundance and biomass were found to decrease as altitude increased, insect abundance and biomass was higher along anthropogenic edges.  Thus, tarsiers within the study area may mitigate the decreased availability of insects at high altitudes

by remaining close to forest edges, which in turn may be related to smaller than expected home range sizes.  Further, estimates of pygmy tarsier abundance may be inflated because of increased insect abundance along anthropogenic edges.

Contrary to the prediction for smaller group sizes as a response to feeding competition, the observed pygmy tarsiers lived in relatively large groups with multiple adult males.  However, in support of the prediction for energetic constraints on body proportions, the observed pygmy tarsiers did not exhibit sexually selected traits.  The pygmy tarsiers exhibited low sexual dimorphism and small relative testes mass, a trend opposite from lowland tarsier species, which may indicate a constraint on the development of those traits.  Considered together, these results suggest that the observed pygmy tarsiers have adapted to life in an environment with limited resources.  Future studies should explore the possible contributing effects of seasonality and topography.

# DEDICATION

This dissertation is dedicated to my mother and father, Drs. Arunee Grow and John Grow, for all their love and support through the years.  Mom and Dad: you condemned me to become the third Dr. Grow, and for that I am grateful.

# ACKNOWLEDGEMENTS

# NOMENCLATURE

A.S.L.          Above Sea Level

DBH           Diameter at breast height

HA            Hectare

M             Meters

MDE           Mid-domain effect

NPL           Nightly path length (travel distance)

TV            Testicular Volume

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# 1. INTRODUCTION AND LITERATURE REVIEW[*]

## 1.1 RESEARCH OBJECTIVES

Tarsiers, of the family Tarsiidae, are small-bodied (50-150 g), nocturnal primates that are currently distributed across Southeast Asian islands.  There is considerable diversity in behavior and morphology between and within tarsier species.  The goal of the research presented here is to determine the extent that altitude is the driving force behind the unusual behavior and morphology exhibited by a particular tarsier species, pygmy tarsiers (*Tarsius pumilus*), of the upper montane forest of Sulawesi.

Pygmy tarsiers are the only high-altitude species of tarsier, occurring only at altitudes greater than 1800 m above sea level (Musser and Dagosto 1987).  The majority of this project took place from June through September 2010 and January through March 2012 on Mt. Rore Katimbu in Lore Lindu National Park, Central Sulawesi, Indonesia.  This research builds upon a preliminary study conducted May through October 2008, during which the first field observations of this little-known primate species were conducted (Grow and Gursky-Doyen 2010; Gursky-Doyen and Grow 2009).

Compared to lowland tarsiers, pygmy tarsiers exhibit a number of unique characteristics, including extremely small body size (50-60g), variable group composition, a relatively long hindfoot, and a cryptic communication style (Grow and Gursky-Doyen 2010).  These traits may be related to their montane habitat and the

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corresponding reduction in food and tree resources.  Ecological variation along elevational clines is known to associate with variation in primate morphology and behavior, where primates adapt to local conditions along an altitudinal transect.  Thus, pygmy tarsiers are expected to show differences from lowland tarsier species that associate with altitudinal ecology. This research specifically explores the effects on altitude on pygmy tarsier population density, distribution, ranging patterns, and group size and composition. This research also examines the effects of altitude on pygmy tarsier physiology, including body size, limb proportions, and sexually selected traits.

Altitudinal variation in ecology is an important variable in primate evolution. Altitude causes significant effects on primate behavior and morphology (Cui et al. 2006; Ganas et al. 2004; Hanya et al. 2004; Iwamoto and Dunbar 1983; Lehman et al. 2006b; Marshall 2005; Rae et al. 2003).  Observing specialized traits in higher elevation forest allows us to understand how primates respond to different ecological pressures, given that primates at high altitudes are subjected to a different set of ecological conditions than those at lower altitudes.  Climate varies along an elevational gradient, with predictable changes in temperature, precipitation, seasonality, and soil properties (Grubb 1971; Lomolino 2001).  Decreased temperature and increased water content slows the turnover of principal nutrients in soil (Grubb 1971), so overall biomass and productivity is reported to decline at higher altitudes (Vuilleumier and Monasterio 1986). As altitude increases, temperature declines and corresponds to clinal ecological changes (Körner 2007).  Most notably, tree density linearly declines as altitude increases (Körner 2007), an effect that has been documented in pygmy tarsier habitat (Grow and Gursky-Doyen 2010).  At higher altitudes, species diversity also declines, including insect species diversity (Hagvar 1976).

For insectivorous pygmy tarsiers, an altitudinal decline in insect species has implications for their diet, feeding and ranging behaviors, and spatial distribution. Changes in forest structure at higher altitudes, including a lower forest canopy, may further impact habitat usage among pygmy tarsiers. As lowland forest transforms into upper montane forest, trees become shorter, wider, and spaced farther apart (Grubb 1971); this phenomenon has been observed in pygmy tarsier habitat (Grow and Gursky-Doyen 2010). Temperature, forest structure and density, species diversity, and habitat productivity could all affect pygmy tarsier behavioral patterns. This study assessed the behavior and morphology of pygmy tarsiers on Mt. Rore Katimbu in Lore Lindu National Park, Central Sulawesi, in comparison to lowland tarsier species.

## 1.2 TARSIER CLASSIFICATION AND BIOGEOGRAPHY

### 1.2.1 Tarsier Evolution and Phylogeny

As a family, the Tarsiidae exhibit a number of distinguishing derived morphological characteristics. These traits include large eyes with a postorbital plate, a dry rhinarium, cervical vertebrae which allow the head to be turned more than 180 degrees, elongated calcaneus bones of the ankle (the tarsal and navicular bones), a fused tibia and fibula, the presence of grooming claws, a forward placement of the foramen magnum, and one pair of lower incisors (Simons 2003). In terms of behavior, all tarsiers rely on a locomotor method of vertical postures known as vertical clinging and leaping (VCL).

Fossil ancestors of tarsiers are sparse, often with only one specimen representing each species and the relationship to modern tarsiers not well established. They have been found in Asia (China, Thailand) and Africa (Egypt). Fossil tarsiers date back to the Eocene, although since all specimens are incomplete, a fused tibia and

fibula is the only derived feature that has been observed in the fossils (Simons 2003). The oldest known fossil tarsiiform, *Archicebus achilles*, dates to 55 million years ago (Ni et al. 2013). A phylogeny based on an extensive combination of molecular and morphological characters places this fossil as the basal member of the tarsiiform clade. *A. achilles* was probably diurnal, insectivorous, and arboreal, and it possessed a mosaic of anthropoid and tarsiiform features (Ni et al. 2013). Next, *Tarsius eocaenus* (Beard and MacPhee 1994), dating to 40 million years ago in the Middle Eocene, was found in Jiangsu Province, China. Its classification within the genus *Tarsius* was based on only 5 teeth, and has been challenged (Simons 2003). Another study (Dagosto et al. 1996) found a fused tibiofibulae they attribute to *Tarsius eocaneus* in Shanghuang, China, dating to the Middle Eocene. This indicates that a fused tibia and fibula is a very old feature for tarsiers.

Xanthorysis tabrumi (Beard 1998), found in the southern Shanxi Province, China and dating to the Late Middle Eocene, has been suggested as a sister group to tarsiers, which indicates that tarsiers radiated during the Early Paleogene. If this is the case, the Tarsiidae would have longest temporal range of any modern primate family (Simons 2003). A third fossil tarsier has been found outside of Asia. *Afrotarsius chatrathi* (Simons and Bown 1985), comes from the Fayum Province in Egypt and dates to 32 million years ago. It is based on 3 complete and two partial teeth. The most recently dated fossil tarsier, *Tarsius thailandicus* (Ginsburg and Mein 1987), was named from a single isolated molar found in the Lampoon Province of northwestern Thailand, dating to 16-18 million years ago.

Two genera of fossil omomyid tarsiiformes, *Pseudoloris* (Simons 2003) and *Eosimias*, show similarities to tarsiers based on dentition. *Pseudoloris parvulus,* from

France (Simons 2003) and *Pseudoloris pyrenaicus,* a recently found species dating to 34 million years ago in Spain (Minwer Barakat et al. 2010), both date to the Middle Eocene.  Although the connection to tarsiers is not clear, they are interesting tarsier-like specimens found outside of Asia.  *Eosimias sinensis* and *E. centennicus*, respectively found in Jiangsu Province and southern Shanxi Province, China (Beard and MacPhee 1994; Beard et al. 1996), date to the Middle Eocene.  While one author (Beard 1998) suggests these fossils point to an Asian origin for Tarsiidae, another (Simons 2003) argues that Eosimias features are not all consistent with anthropoids.  Thus, the evolution and dispersal patterns of tarsier ancestors are unresolved issues in primatology.

The phylogenetic position of tarsiers in relation to the rest of the order Primates is still unresolved, as they show a mixture of traits with strepsirrhines and haplorhines.  Tarsiers share many traits with anthropoids, including their eye structure (lack of a tapetum lucidum and the presence of a central retinal fovea), postorbital closure, a dry rhinarium, a reduced sense of smell, inability to synthesize vitamin C, middle ear morphology, and the promontory branch of the internal carotid artery supplying blood to the brain (Fleagle 1999; Schwartz 2003).  Tarsiers share some dental synapomorphies with anthropoids in their dentition and even more in the orbit and middle ear (Kay et al. 1997).  Tarsiers also share many anatomical traits with prosmians, including small body size, the presence of grooming claws, and an unfused mandibular symphysis.  Their reproductive anatomy shares traits with anthropoids (hemochorial placental development) as well as prosimians (a bicornuate uterus and the presence of multiple nipples) (Gursky 2002b; Schwartz 2003).  Behaviorally, tarsiers are like prosimians, with their nocturnal and cryptic activities.

Genetic and fossil evidence suggests that tarsiers are a sister group to anthropoids. A maximum parsimony analysis of DNA sequences from multiple primates places tarsiers as a sister group of anthropoids (Meireles et al. 2003). A cladistic analysis of dental, cranial, and postcranial features of living and fossil primates found that the main separation of the living primates is between the two clades, the Strepsirrhine (the Lemuriformes) and Haplorhini (Anthropoidea, including the platyrrhines and catarrhines, and *Tarsius*) (Kay et al. 1997). In this analysis, fossil adapids grouped as a sister to the strepsirrhines, while fossil omomyids grouped with the haplorhines. The fossil Eosimidae grouped with anthropoids. Tarsiers were placed either a sister group to the Eosimidea-Anthropoidea clade, or nested within omomyids. Another analysis similarly groups anthropoids, tarsiers, and omomyids within a clade (Ross et al. 1998). Recent evidence from a new fossil omomyid, *Pseudoloris pyrenaicus*, shows morphological similarities to the modern tarsiers in its dentition (Minwer Barakat et al. 2010), reinforcing the view that there is a strong connection between tarsiers and omomyids. Under this view, the shared common ancestor of anthropoids and tarsiers resembled the omomyids, as a small-bodied insectivorous leaper, although it would have been diurnal unlike typical omomyids; tarsiers then diverged when they specialized in leaping locomotion, became fully carnivorous, and returned to nocturnally (Kay et al. 1997).

However, some question these analyses because they are based primarily on dental features whose evolutionary relationships are not understood (Simons 2003). Although omomyid dental anatomy is similar to modern tarsier dentition, there is no evidence that omomyids shared other tarsier features. If the Tarsiidae did arise from the omomyids then, characters that do not exist in omomyids, such as postorbital

closure, a dry rhinarium, and middle ear morphology, must be considered convergent traits rather than shared, derived anthropoid/tarsier features (Simons 2003).

### 1.2.2 Tarsier Diversity and Distribution

The extant tarsiers have historically been placed into one genus, *Tarsius* (Niemitz 1984b), although a new taxonomy has been proposed to divide the tarsiers into three genera: *Tarsius* (Eastern tarsiers of Sulawesi and surrounding islands), *Cephalopachus* (Western tarsiers of Borneo and Sumatra), and *Carlito* (Philippine tarsiers) (Groves and Shekelle 2010) (Figure 1). Here, classification terminology following Niemitz (1984) is used. Taxonomists recognize as many as eleven distinct tarsier species (Groves and Shekelle 2010). Outside Sulawesi, species include *T. bancanus*, the Bornean tarsier (Horsfield 1821) and *T. syrichta* (Linnaeus 1758), the Philippine tarsier. There are five mainland Sulawesian tarsiers (Figure 2) with distinct distributions that are separated along allopatric or parapatric divisions. *T. spectrum*, the spectral tarsier (Pallas 1778), occurs in northern Sulawesi (Niemitz 1984b), and is argued to be a junior synonym of *T. tarsier* (Brandon-Jones et al. 2004; Groves and Shekelle 2010). *T. lariang*, the Lariang tarsier (Merker and Groves 2006), occurs in Central Sulawesi, southwest of the Palu-Koro faultline (Merker et al. 2009). Dian's tarsier, *T. dianae* (Niemitz et al. 1991), occurs to the east of *T. lariang* in Central Sulawesi, and is argued to be a junior synonym of *T. dentatus* (Brandon-Jones et al. 2004). *T. wallacei* (Merker et al. 2010) has a discontinuous distribution northwest of the Palu-Koro faultline and near Palu. *T. pumilus*, the pygmy tarsier (Miller and Hollister 1921; Musser and Dagosto 1987), is the only tarsier to occupy montane cloud forest in Central Sulawesi. An alternate common name for *T. pumilus* is *mountain tarsier*, which

was proposed to emphasize its unique habitat (Shekelle 2008b). Three additional

species are recognized from nearby Sulawesian islands, including *T. pelengensis*, the

Peleng tarsier (Sody 1949), *T. sangirensis*, the Sangihe tarsier (Meyer 1896), and *T. tumpara* (Shekelle et al. 2008) of Siau island.

**Figure 1. Map of the distribution of tarsier groups. Genera within parentheses are from the revised classification system proposed by Groves and Shekelle (2010).**
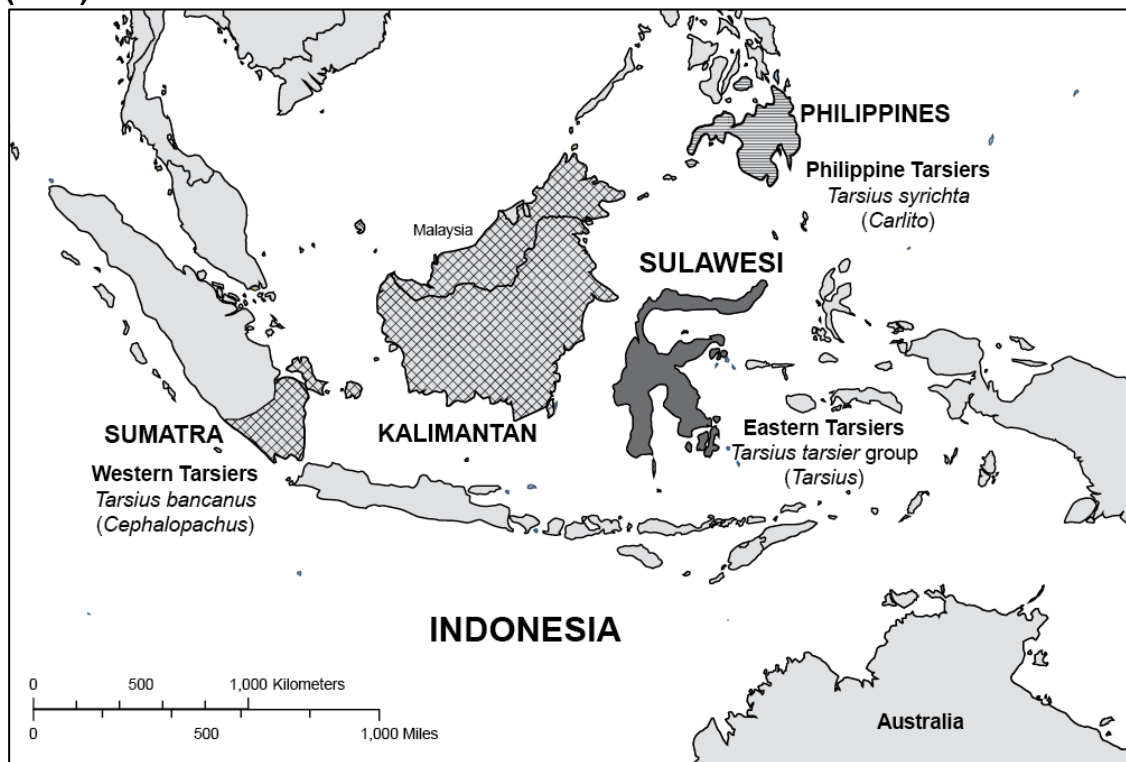


### 1.2.3 Sulawesian Tarsier Biogeography

Tarsiers occupy three distinct biogeographic regions, with Western tarsiers in

the Sundaland islands, Philippine tarsiers from Greater Mindanao, and Eastern tarsiers

from Sulawesi and surrounding islands (Shekelle 2008a). Genetic evidence suggests

that the Sulawesian tarsiers radiated in response to Pleistocene changes in sea level and plate tectonics (Merker et al. 2009), and species boundaries seem to correspond to tectonic activity. Although fossil evidence for Sulawesian tarsier evolution is limited, biogeographical analysis gives information on how their current distribution reflects their past radiations. The biota of Sulawesi arrived by a limited number of possible routes. The fossil tarsiid *Tarsius thailandicus* (Ginsburg and Mein 1987) gives some evidence to the route from Thailand, Sumatrai, Java, and the Lesser Sunda Islands, although no evidence for tarsier habitation on Java has been found (Shekelle 2003).

Sulawesi is located within a biogeographic region called Wallacea, an area of biotic transition between Asia and Australia (Shekelle 2003). Small fragments of land from Asia and Australia aggregated to form Sulawesi during the Pleistocene (Shekelle 2003). The resultant landmass is relatively large, ranking as the eleventh largest island in the world (Shekelle 2003), with a high degree of endemism. The island is home to fewer than expected species of non-mammalian fauna, and more than expected species of mammals (Whitten et al. 2002). The mammalian composition indicates repeated colonizations and radiations by mammals (Shekelle 2003). Although the timing and migration path of the first tarsiers to colonize Sulawesi is unknown, their migration is thought to have occurred before Sulawesi converged into a single landmass (Shekelle 2008a). Thus, the parapatrically separated populations may have began as allopatric populations, isolated across smaller islands, but were pushed together on Sulwesi by plate tectonics (Shekelle 2008a). As a result, Sulawesian tarsier body size evolution is not straightforward.

Tarsiers may represent products of the "island rule," which refers to the negative relationship between the size of island taxa and their mainland counterparts; larger

mammals evolve to be smaller and small mammals evolve to be larger on islands (Foster 1964; Meiri et al. 2004). Generally, the island rule appears supported in primates, especially in terms of body mass (Welch 2009). Under this rule, insular carnivores tend to reduce body size while other taxa tend to increase body size, resulting in insular dwarfism and gigantism compared to mainland taxa (Lomolino 2005). The mechanisms involved in the island rule may vary between species, but the selective pressures are primarily competitive release in an isolated area, resource limitations, diminished dispersal ability, reduced predation pressure, and intraspecific and interspecific competition (Lomolino 2005; Meiri et al. 2004). On small islands with constrained land area, resource limitations may be more important influencers of body size than predation or interspecific interactions (Heaney 1978), as may be the case with pygmy tarsiers. If smaller body size is ancestral for tarsiers, then lowland tarsiers would be island giants, whereas if larger body size is ancestral, then pygmy tarsiers are true pygmies (phyletic dwarfs) (Shekelle 2008b).

### 1.2.4 History of Tarsius pumilus

Historically, *Tarsius pumilus* was known only from a handful of museum specimens. The holotype (USNM 219454; Table 1) was collected by H.C. Raven at 1800 m at Mt. Rano Rano (1 degree 30' S, 120 28' E; Figure 2) on Dec 31, 1917. The species was first described based upon this specimen, as well as two specimens from Gimpu (Miller and Hollister 1921). Musser and Dagosto (1987) confirmed the species status of *T. pumilus* based on the holotype, but found that the Gimpu specimens were actually juvenile *T. tarsier* (*spectrum*) that were incorrectly classified as *Tarsius pumilus*. They also found that G. Heinrich had independently collected a female adult *T. pumilus*

specimen from 2200 m in Latimojong (AMNH 196477; 3 30' S, 120 05' E; Figure 2) in the northern part of the southwestern peninsula of Sulawesi (Musser and Dagosto 1987).  Although this specimen had been misclassified as *T. spectrum*, Musser and Dagosto (1987) found that its morphology corresponded to the *T. pumilus* holotype.

**Table 1. *Tarsius pumilus* museum specimens.**

| Specimen | Altitude (m) | Location | Collector | Year | Citation |
|---|---|---|---|---|---|
| USNM 219454 (holotype) | 1800 | Mt. Rano Rano, Central Sulawesi | H.C. Raven | 1917 | (Miller and Hollister 1921) |
| AMNH 196477 | 2200 | Latimojong mountains, middle-South Sulawesi | G. Heinrich | 1930 | (Musser and Dagosto 1987) |
| MZB 22593 | 2200 | Mt Rore Katimbu, Central Sulawesi | I. Maryanto, M. Yani | 2000 | (Maryanto and Yani 2004) |

Musser and Dagosto (1987) recognized pygmy tarsiers as a distinct species based on the following morphological characteristics: extremely small body size (length), elongated lower incisors, laterally compressed claw-like nails on all digits instead of grooming claws on only the second and third digits, and a distinctive pelage. Following these analyses, multiple scientists attempted unsuccessfully to locate a living population of pygmy tarsiers (Shekelle 2008b). In 2000, a small mammal survey in Central Sulawesi accidentally collected a third museum specimen on Mt. Rore Katimbu, indicating the species still existed in the wild (Maryanto and Yani 2004). This specimen weighed 57 g whereas other Sulawesian tarsier species weigh more than 100 g, confirming that pygmy tarsiers have a comparatively small body mass.

**Figure 2. Map of distribution of Sulawesian tarsier species and locations of pygmy tarsier specimens.** Shaded species distributions based on Merker et al. (2010), and locations of *Tarsius pumilus* based on Musser and Dagosto (1987).
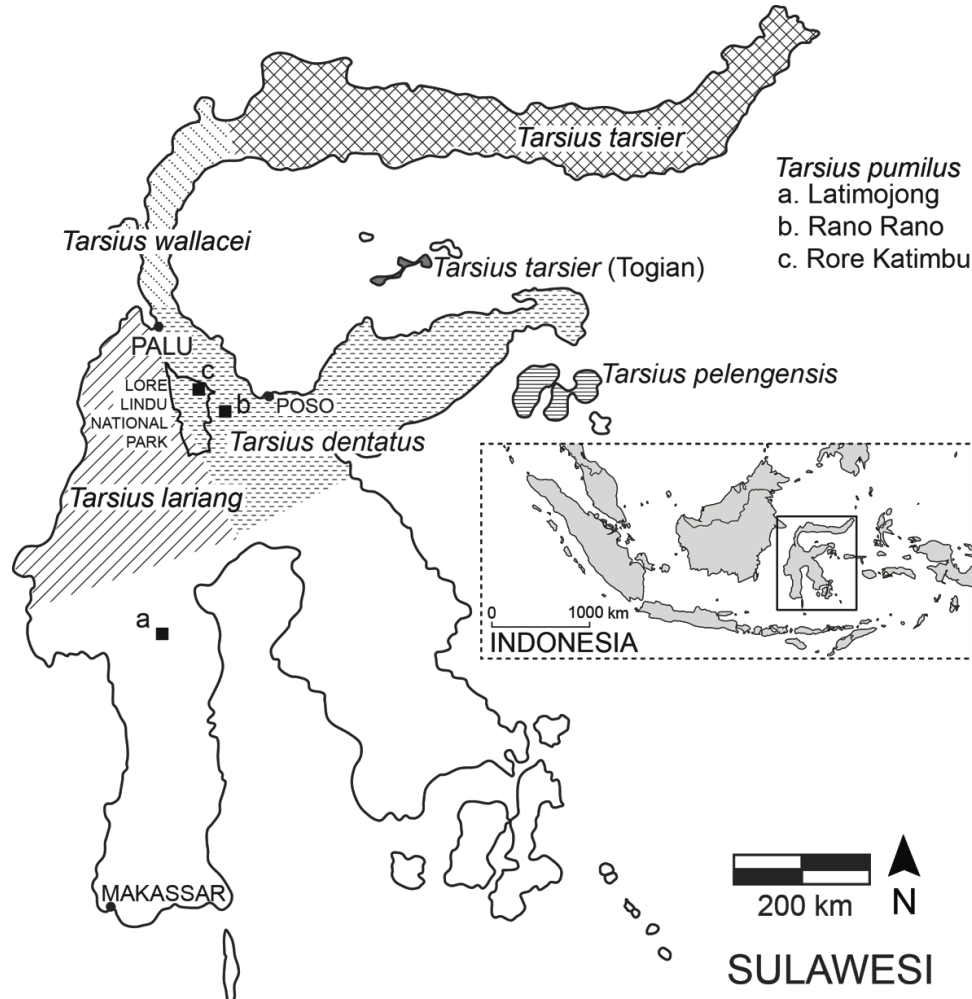


A pilot study that made the first live observations of a group of pygmy tarsiers was conducted at 2100 m on Mt. Rore Katimbu (Grow and Gursky-Doyen 2010). Initial observations suggested pygmy tarsiers differ from the lowland Sulawesian tarsier species in both behavior (habitat usage, larger group composition, and cryptic communication strategies) and morphology (small body size and relatively long hindlimb proportions) (Grow and Gursky-Doyen 2010). Besides small body size, a hallmark

distinguishing characteristic of pygmy tarsiers is their montane habitat.  Unlike all other

tarsier species which occur at lower altitudes, pygmy tarsiers were thought to be

restricted to highland mossy cloud forest, based on the locations the museum

specimens were collected and where initial observations were made (Musser and

Dagosto 1987). Their unusual behavior and morphology may be adaptations to their

high altitude habitat.


## 1.3 ALTITUDINAL VARIATION

### 1.3.1 High Altitude Ecology

Upper montane forest is markedly different from lowland forest, which may

contribute to observed differences between pygmy tarsiers and lowland species.

Climate predictably varies along an elevational gradient (or cline), in terms of

temperature, precipitation, seasonality, and soil properties (Grubb 1971; Lomolino

2001).  A cline is a measurable geographic gradient of characters (Endler 1977).  Clines

occur across geographic areas, with the ecological gradients commonly spanning either

latitude or altitude.    Within these gradients, populations gradually change with the

changing ecological conditions.  Clines can be important in parapatric speciation

(Endler 1977), and an altitudinal cline may be responsible for the pygmy tarsier's status

as a separate species.

In general, as altitude increases, temperature linearly declines (Körner 2007)

and there are a number of clinal ecological changes that occur.  First, tree density

linearly declines as altitude increases (Körner 2007). Second, there is a decrease in

species diversity in both flora and fauna. Although land area reduces as altitude

increases, there is a mean reduction of 40 angiosperm species per 100 m increase,

resulting in a nearly linear negative relationship between species and land area along altitudinal clines (Körner 2007). Insect species diversity similarly declines with altitude (Hagvar 1976). Third, the forest canopy lowers. The change from lowland to upper montane forest includes a decline in biomass disproportionate to a decline in tree height, so trees are shorter yet stockier (Grubb 1971). Fourth, there is an overall reduction in biomass and productivity (Vuilleumier and Monasterio 1986). This decrease in biomass likely is a result of the slow turnover of principal nutrients from the soil (Grubb 1971).

All of these phenomena have been observed in pygmy tarsier habitat (Grow et al. 2013; Grow and Gursky-Doyen 2010). Altitudinal declines in forest and food resources should result in corresponding changes in primate behavior and morphology, with body size responding in particular. Thus, temperature, forest structure and density, species diversity, and habitat productivity should all affect pygmy tarsier traits.

### 1.3.2 Altitudinal Clines in Species Diversity and Abundance

Clinal effects on species diversity and abundance occur along altitudinal gradients, which contributes to the environmental differences and high and low altitudes. There are four well-known hypotheses to explain the causes of elevational gradients in species density and diversity: an elevational area gradient (species area hypothesis), an elevational climate gradient (Massenerhebung effect), geographic isolation of montane populations, and feedback among zonal communities (the mid-domain effect) (Lomolino 2001) (Table 2).

**Table 2.  Predictions of hypotheses applied to elevational gradients of species diversity.**

| Hypothesis | Location of diversity peak | Independent Variable(s) | Prediction |
|---|---|---|---|
| **Mid-domain effect** (Colwell et al. 2004; McCain 2004) | Mid-range altitudes | Interaction between zonal communities | Species diversity peaks at the middle of a geographic range. |
| **Species-area effect** (Terborgh 1973) | Altitude with the largest area | Land area | Species richness varies with the total area of each elevational zone. |
| **Climate (Massenerhebung effect)** | Varies with elevational shifts in climate and environment; depends on the environmental niches of taxa | Climatic and environmental conditions at local elevations | Elevational peaks in species density correspond to local elevational shifts in climate. |
| **Geographic isolation** | Higher altitudes | Species immigration, extinction, and speciation | Immigration rates into elevational zones declines at higher altitudes.  Endemic species peak at higher altitudes. |

*1.3.2.1 The Mid-Domain Effect*

One explanation for altitudinal changes in species diversity is the mid-domain effect (MDE).  The MDE refers to a mid-gradient peak in species richness along a latitudinal or elevational gradient (Zapata et al. 2003).  It is a model used to explain the increase in diversity in the middle of geographic regions, such as between the peak and base of a mountain (Colwell et al. 2004; McCain 2007).  The spatial constraints on a species' range limits diversity on the edges, but diversity increases in the middle due to overlap of species from the surrounding areas (Colwell et al. 2004).  The MDE predicts that the highest degree of species diversity occurs at the elevational midpoint, declining both towards sea level and towards the top of the mountain; this trend should occur regardless of the mountain's height (McCain 2005).

Clines in diversity occur not only at the species level, but also within the genetic diversity of a single species.  The diversity of populations in middle altitudes is a good

sources of information on divergent selection and speciation along an altitudinal cline. In terms of life history traits, populations in middle altitudes are more genetically variable because of the divergence in life history between high and low altitude populations (Orr and Smith 1998). Reproductive isolation between populations at high and low altitudes can explain their behavioral and physiological differences.

Evidence in support of the MDE is mixed. There are two ways of sampling diversity along an elevational gradient; sampling for *gamma* diversity records all instances of taxa along an elevational range, while sampling for *alpha* diversity records species richness in equal sample areas along an elevational transect (Lomolino 2001; McCain 2004). While the MDE has been found for non-mammalian taxa along elevational gradients, these studies sampled for gamma diversity and species richness may be biased by land area (Lomolino 2001; McCain 2004). For example, clear evidence for the MDE was observed in moth (Lepidoptera) species diversity in Costa Rica (Brehm et al. 2007). However, separate studies in the same area did not find support for the MDE among small mammals (McCain 2004; McCain 2007).

While the MDE is an observed phenomenon, it is probably not the primary determinant of diversity. A review of studies testing for the mid-domain effect found that observed and predicted species richness patterns often do not match, and the MDE is not supported (Zapata et al. 2003). Testing of these models is also often problematic, where two-dimensional patterns have been collapsed into one-dimension and data has been spatially autocorrelated (Zapata et al. 2003). Another global analysis of trends in elevational diversity of small mammals indicated a pattern of mid-elevational peaks in species diversity, but the mid-domain effect was not found to explain diversity patterns (McCain 2005). In these studies, diversity peaks were at higher elevations on taller

mountains, indicating that climatic factors produced the effect.  Thus, while the MDE might explain some species richness patterns along gradients, it does not completely explain variation in diversity along a gradient.

*1.3.2.2 Species-Area Effect Hypothesis (Elevational Gradient)*

Related to the MDE is the species area effect hypothesis, which suggests that regions with more land area will have higher species diversity (McCain 2007), with higher speciation rates.   Species richness should vary with the total area of each elevational zone and peak in the zones that have the largest area (Lomolino 2001). This hypothesis predicts that there will be a positive linear relationship in the elevation of a peak in diversity, where species density varies continuously with climatic and environmental variables (Lomolino 2001).   Diversity peaks at different elevations that are optimal for different taxa, but the relative position of peaks in diversity should predictably vary within groups of species that share similar niches (Lomolino 2001). However, land area gradients are not useful in explaining overall species density patterns.  A recent study found that mammalian diversity along elevational gradients are not explained by spatial constraints, and land area is instead a source of error (McCain 2007).

*1.3.2.3 The Massenerhebung Effect of Elevational Vegetation Zones*

The previous explanations of species richness patterns rely on spatial geometry to explain the variation. Studies on area effects generally find that spatial and area constraints influence patterns of species diversity, but do not fully explain observed trends, meaning that these effects are not the primary selective forces involved in

diversity patterns (McCain 2007).  It is an effect that can explain sources of error when other variables are considered.  A more probable explanation of elevational diversity is the "Massenerhebung" effect, which is related to climate (temperature and humidity) rather than purely spatial geometry.

The phenomenon where rain forest divides into distinct regions according to altitude, each with its own plant associations, is termed the Massenerhebung effect (Grubb 1971).  A result of the Massenerhebung effect is the phenomenon where vegetation zones (ecological niches) occur at lower elevations on smaller mountains (Lomolino 2001).  Elevational peaks in species density correspond to elevational shifts in climate.  Under this effect, species diversity varies with local environmental and climatic conditions at different elevations

With this effect, there are three general types of forest on tropical mountains: lowland rain forest, lower montane rain forest, and upper montane rain forest (Grubb 1971).   These forest types correlate with climatological factors, including humidity (fog cover) and temperature.  The effects of temperature on the environment can be direct, such as on rates of photosynthesis, respiration, and cellular development, as well as indirect, such as on rates of mineralization of organic material in the soil (Grubb 1971).

The cause of the Massenerhebung effect is changes in the availability of soil nutrients.  Organic content in soil increases with altitude.  Biomass decreases (e.g. leaf size decreases) at higher altitudes reflect the slow turnover of principal nutrients from the soil (Grubb 1971).  The Massenerhebung effect relates to the mineralization of organic matter to provide nitrogen and phosphorous to plants; at higher altitudes, there is less nitrogen and phosphorous in the soil due to the decrease in temperature and increase in fog, so mineralization is slower (Grubb 1971).  Thus, changes in

mineralization influence forest type and biomass.  Support for the Massenerhebung

effect was produced in a global analysis of small mammals (McCain 2005).  Diversity

peaks were at higher elevations on taller mountains, indicating that climatic factors

produce habitats that correlate with elevation.


*1.3.2.4 Geographic Isolation and the Rescue Hypothesis*

Geographic isolation at higher altitudes can also affect diversity.  High altitude

habitats decline in land area, but also become more isolated from other communities.

Immigration rates are predicted to decline with increasing altitude, with species density

of endemics peaking at intermediate or higher elevations while overall species and

population densities decline at higher elevations (Lomolino 2001).  Since high

elevations also provide geographic isolation, a prerequisite for speciation, speciation

and endemism may increase at higher altitudes (Lomolino 2001).

The "rescue" hypothesis suggests that latitudinal gradients of diversity occur

because of variation in range margins and interactions between species, where

proximity to the range boundaries of other species influences local species richness

(Stevens 1992).  This hypothesis relates to the idea of geographic isolation in montane

environments.  At higher elevations, immigration is less likely, populations are smaller,

and individuals are less likely to be "rescued" by dispersing individuals (Lomolino 2001).

At low latitudes and altitudes, more species occur along the edge of their ranges; even

individuals that are poorly adapted to local conditions can persist because they are near

areas where they be "rescued," inflating species diversity (Stevens 1992).  At higher

altitudes, extinction is more likely.  The rescue hypothesis may drive the distribution of

species ranges across altitudinal and latitudinal gradients in a phenomenon known as Rapoport's Rule.

### 1.3.3 Altitudinal Clines in Range Size

*1.3.3.1 Range Size and Rapoport's Rule of Species Distribution*

While the geographic distribution of the species abundance is well-studied, how the distribution of a species' range size scales with geography is less well-known (Gaston 1996). Rapoport's Rule is related to the area effect hypothesis, and suggests that species ranges increases as distance from the equator increases, or as elevation increases (Rapoport and Bariloche 1982; Stevens 1992). This phenomenon may occur because populations at higher latitudes are subjected to a wider range of annual climatic conditions (more seasonality), which allows them to occupy a wider range of latitudes than low-latitude species (Stevens 1989). Rapoport's rule should also apply to the narrowed range of climatic conditions that occur at higher altitudes (Stevens 1992).

If there is a positive relationship between the range size of a species and altitude (or latitude), then Rapoport's rule predicts that that range size will increase at higher altitudes (Ribas and Schoereder 2006). Thus, species richness should decline on mountains while the altitudinal range of each species increases (Stevens 1992). There is a distinct relationship between the altitudinal range of a species and the number of species that occur in that area (Stevens 1992); low elevation forests have diverse ranges of species that occupy narrow altitudinal ranges.

However, a test of the Rapoport effect in existing literature did not find it to be a widespread ecological phenomenon (Ribas and Schoereder 2006). The application of Rapoports' rule to altitude is also poorly understood (Stevens 1992). Among primates

in the tropics, there is some support for the Rapoport effect (Harcourt 2000), but the adaptability of taxa (such as dietary breadth and body mass) also influences the latitudinal range of species. Especially in primates, the range of a species should relate to a complex set of variables rather than altitude or latitude alone. Beyond range size, these complex variables should also relate to the behavior and habitat usage of a given species.

*1.3.3.2 Body Size Clines*

Clinal changes in the environment can result in changes in an organism's physiology. Declines in resource abundance, including altitudinal declines in resources, can result in decreased body size. Body size clines can occur due to environmental changes that correlate with changes in climate (Blackburn et al. 1999). For example, limited resources can cause latitudinal declines in body size among insects due to temperature, season length, and habitat productivity (Chown and Klok 2003). Body size is an important variable to consider when discussing the behavioral ecology of an organism.

## 1.4 BODY SIZE VARIATION

### 1.4.1 Why Is Body Size Important?

Body size is an important evolutionary trait that affects multiple other aspects of an organism's physiology, behavior, and life history (Jungers 1985). Just as variation in body size is known to occur between human populations based on geographic differences (Perry and Dominy 2009; Shea and Bailey 1996), pygmy tarsier body size also appears to relate to altitudinal geography. The selective pressures involved in

producing pygmy body size and proportions were present in the evolutionary history of pygmy tarsiers, but it is complicated to determine exactly what these pressures were. Since pygmy tarsiers are unique among tarsiers with their high-altitude habitat, it is reasonable to assume that high altitude pressures played an important role in their evolution.

Exploring the high altitude effects on pygmy tarsier body size is significant to understanding tarsier evolutionary relationships. Currently, it is unknown which is the primitive state for Sulawesian tarsiers: the larger body sizes and increased sexual dimorphism of the lowland species or, conversely, the small body sizes and monomorphism of the highland tarsiers (Shekelle 2008b). Understanding whether pygmy tarsier traits are adaptations to high altitude habitat is thus important to understanding the evolutionary history of tarsiers. In response to their resource-constrained habitat, pygmy tarsiers might be phyletic dwarfs like the Callitrichidae, which exhibit reduced body size and derived morphology in response to ecological pressures (Martin 1992). Alternately, since all *Tarsius* fossils are smaller than the extant lowland tarsiers, pygmy tarsiers may represent the ancestral state of Sulawesian tarsiers (Shekelle 2008b).

Environmental selection pressures may have driven the evolution of small body sizes among the Callitrichidae. They are considered phyletic dwarfs among the New World Monkeys, where their reduced body size and special morphological features are derived traits in response to ecological pressures (Ford 1980; Martin 1992). Similarly among humans, it has been hypothesized that pygmy groups experienced selection for size reduction by living in environments with reduced food resources, such as tropical rain forests, where reducing size in turn reduces required caloric intake (Shea and

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Bailey 1996).  It has also been suggested that small body size in human pygmies is a

side-effect of selection for early reproduction under conditions of high mortality,

constraining growth (Migliano et al. 2007; Walker et al. 2006a; Walker et al. 2006b).


### 1.4.2 The Relationship Between Body Size and Abundance

The abundance of a species is typically thought to be constrained by energy

availability (Blackburn and Gaston 1999), as is central to the area effect hypothesis.

The relationship between density and body size adds a level of complexity to the

relationship between land area and diversity.  Animal abundance and body size is

widely thought to negatively correlate, since abundance is limited by the energetic

capacity of the environment (Blackburn and Gaston 1999; Johnson 1999).  The "energy

equivalence rule" explains the relationship between body size and density as the

inverse of the relationship between body size and metabolic rate (White 2007).  Under

this rule, population density scales with body mass as -0.75, which cancels the scaling

of metabolic rate with body mass and results in relatively equivalent rates of energy use

across populations (Johnson 1999).

However, the relationship between body size and abundance is not consistently

supported.  For example, no significant trends in body size and abundance were found

in insects sampled across a latitudinal gradient (Andrew and Hughes 2008).  The

inconsistent trends in body size and abundance may relate to the different forms of this

relationship.  While there are global relationships between the average body size of a

species and its population density, there are multiple distinct forms of this relationship,

including global size-density relationships between species abundance and average

body size, local size-density relationships, and the frequency distribution of body sizes (regardless of species) (White 2007).

Although body size may correlate with abundance, it does not seem to be the primary determinant.  One study found a relationship between local insect species richness and abundance of individuals within each size class, concluding that the relationship between diversity, abundance, and resources is independent of body size (Siemann et al. 1996).  Variation in geographic area and habitat usage has been found as the major explanation for abundance, where body size is a byproduct of this relationship (Blackburn and Gaston 1996).  Similarly, another study found that home range area is a better predictor of geographic area than is body size (Johnson 1999).

### 1.4.3 The Island Rule

The island rule refers to the negative relationship between the size of island taxa and their mainland counterparts, where larger mammals evolve to be smaller and small mammals evolve to be larger on islands (Foster 1964; Meiri et al. 2004).  Under this rule, insular carnivores tend to reduce body size while other taxa tend to increase body size, resulting in insular dwarfism and gigantism compared to mainland taxa (Lomolino 2005).  Body size trends vary between taxa with different resources requirements, such as herbivores and carnivores, or ectotherms and endotherms.  The mechanisms involved in the island rule may vary between species, but the selective pressures are primarily competitive release in an isolated area, resource limitations, diminished dispersal ability, reduced predation pressure, and intraspecific and interspecific competition (Lomolino 2005; Meiri et al. 2004).  Although evidence has been found for the island rule (Lomolino 2005), Meiri et al. (2004) did not find support for the rule in

insular carnivore body mass patterns.  When head, body, and tail length are used as the dependent variables, one study did not find support for the island rule in insular primates (macaques) (Schillaci et al. 2009).  However, the island rule as supported in a cross-species study of primates when body mass and skull length were compared between islands and mainland (Welch 2009).  Generally, the island rule appears supported in primates, especially in terms of body mass.

Ecological pressures such as resource constraints, competition, and predation threats all influence body size, but in different ways on different species that inhabit different land areas (Heaney 1978).  On small islands with constrained land area, resource limitations may be more important influencers of body size, while predation should become more important on medium sized islands; on the largest islands and continents, interspecific competition should be a more primary determinant of body size (Heaney 1978).

Islands provide geographic isolation for the inhabitants, which allows unique courses of evolution to occur (Losos and Ricklefs 2009).  Species diversity is related to the size of the island.  Larger islands have more area for niche spaces, which allows more species to coexist (Losos and Ricklefs 2009).  Rate of speciation is also higher on larger islands, which may relate to the higher biodiversity, as well as the increased ecological complexity on larger, older islands (Losos and Ricklefs 2009).

The island rule can also apply to high altitude ecology.  Mountains can be considered "islands" in the sense that high altitude populations are geographically separated from lowland populations.  However, there are no discrete boundaries like true islands (Brown 1971), so the degree of isolation should not be as strong.  Brown (1971) examined the island effect on small mammals that live in isolated mountaintops

and found that diversity is low at high altitudes because extinctions are not replaced by colonizations, due to geographic isolation. The island effect may thus operate on pygmy tarsiers twofold, due to their high altitude island environment.

### 1.4.4 Bergmann's and Allen's Rules

There are a number of well-studied climatic effects on body size that are generated from clinal geographic change, including a clinal increase in altitude. Bergmann's and Allen's rules relate body size to temperature, and are the most predominantly tested hypotheses of geographic variation in body size. However, a number of studies indicate that the interaction of multiple environmental and life history variables, including lifespan, food size, seasonality, moisture, and temperature, explains geographic body size variation (Chown and Klok 2003; Stillwell et al. 2007). Correspondingly, the body proportions of pygmy tarsiers should be influenced by a more complex set of processes. Alternate hypotheses to body size clines that focus on resource availability probably explain pygmy tarsier body size, but Bergmann's rule will be discussed first.

#### 1.4.4.1 Predictions of Bergmann's Rule and Corollaries

It is well-established that the morphology of endothermic species varies with climate. In particular, Bergmann's rule says that body size of endotherms increases with decreasing temperature along a climatic gradient (Bergmann 1847). Although the rule is most often applied to warm-blooded animals (endothermic homeotherms with a stable, internally controlled body temperature), Blackburn et al. (1999) note that it is also applicable to poikilotherms, including ectothermic fish, amphibians, and reptiles.

Although Mayr classically defined Bergmann's rule as an observable trend that can be empirically supported or refuted, regardless of which causal factors produce the trend (Mayr 1956), Bergmann originally hypothesized that thermoregulation is the mechanism behind body size clines. Thus, although the term "Bergmann's rule" is often used simply to describe body size clines, even if the cause is not thoroughly explored, this paper uses the term to specifically refer to clines where temperature is the causal variable. Explanations for body size clines where thermoregulation is not the main cause are considered alternative hypotheses to Bergmann.

The original formulation of the hypothesis explains the relationship between climate and body size as an adaptation to temperature, where animals in colder climates have larger bodies to decrease heat loss. As a result, the ratio of surface area to volume reduces in colder climates. In endotherms, heat loss and production is relative to surface area, so larger animals produce more heat and lose relatively less heat (Meiri and Dayan 2003). In small animals, changes in body size will have a more significant effect on heat loss (Ashton 2002a), so smaller animals should be affected by Bergman's rule more closely than larger ones. The thermoregulatory hypothesis of Bergmann's rule predicts that (a) along a climatic gradient, populations in colder regions will have increased body size compared to those in warmer regions (i.e. latitude will positively correlate with body size) and (b) temperature (rather than another climatic or environmental variable) will negatively correlate with body size, and (c) smaller animals will be more strongly correlated with temperature than larger animals.

Bergmann's rule is applicable both within and between species, although the original formulation of the rule only refers to interspecific variation. According to the translation (James 1970), Bergmann postulated that smaller species within a genus

occur in warmer climates.  Despite this, the phenomenon is applicable to intraspecific

variation (Blackburn et al. 1999).  Although much literature discusses Bergmann's rule

in terms of both interspecific and intraspecific variation, there is a corollary to

Bergmann's rule that specifically considers interspecific variation.  Rensch's rule

(Rensch 1938; Schillaci et al. 2009) hypothesizes that intraspecific size variation occurs

along climatic clines, following the same patterns as Bergmann's rule.  Thus,

'Bergmann's rule' will be used to discuss interspecific clines in body size while

'Rensch's rule' will be applied to intraspecific clines (even if a cited study refers only to

Bergmann's rule).  Rensch's rule predicts that (a) intraspecific populations in colder

regions will have increased body size compared to those in warmer regions, (b)

temperature correlates with body size, and (c) smaller animals more strongly correlate

with temperature.

Another corollary to Bergmann's rule is Allen's rule, which similarly hypothesizes

that clinal variation in body proportions relates to thermoregulation.  Allen's rule says

that appendage proportions (such as limbs, tails, and ears) will decrease with

decreasing temperature (Allen 1877), since larger bodies and shorter extremities have a

reduced ratio of surface area to volume, resulting in less heat loss (Rensch 1938).

However, framing Bergmann's rule in terms of the size of body parts rather than body

mass does not take into account changes in body shape that can occur with changes in

body mass (Blackburn et al. 1999).  Since Blackburn et al. (1999) suggest using body

mass as the only dependent variable in clinal studies in order to avoid allometric

complications, support for Allen's rule will only be discussed briefly.  Allen's rule predicts

that (a) populations in colder regions will have relatively shorter extremities than those

in warmer climates, (b) temperature will negatively correlate with body proportions, and (c) smaller animals more strongly correlate with temperature.

*1.4.4.2 Support for Bergmann's Rule and Corollaries*

Bergmann's rule and corollaries are considered supported if more than 50% of populations studied follow the rule, although this benchmark is generous (Blackburn et al. 1999). The first prediction of Bergmann's rule and its corollaries, that populations in colder regions will be larger (or have smaller appendages), can be empirically observed regardless of the cause. An evaluation of the literature suggests that the phenomenon of Bergmann's rule, with larger bodied populations in colder climates, generally holds true, but the original hypothesis explaining this observation (heat conservation) does not hold true. In other words, the first prediction is often upheld, while the second prediction receives less support, indicating that a variable other than temperature causes body size clines. Even with support of these two predictions, a correlation with temperature does not prove that body size clines are thermoregulatory. A third prediction, that animals in colder regions experience less heat loss than those in warmer regions, clarifies the thermoregulatory cause of body size. Although the relationship between body size and heat loss is well-known, this third prediction has not been tested directly.

Between species, support for the first two predictions of Bergmann's rule has been found along latitudinal clines in large-scale studies of endothermic species, including birds (James 1970; Mayr 1970) and mammals (Ashton et al. 2000; Blackburn and Hawkins 2004). Bergmann's rule tend to be more strongly supported in birds than mammals (Mayr 1970; Meiri and Dayan 2003). In these studies, body size increases

with increasing latitude, and temperature negatively correlates with both body size and latitude.

Opposite results were found in another study (McNab 1971), which concluded Bergmann's rule did not hold in a cross-species analysis of North American mammals. This analysis found that less than half of mammal species had a positive relationship between body size and latitude, and that the strength of Bergmann's rule is dependent on latitude. However, there may have been methodological problems with these analyses (Ashton et al. 2000). Further, McNab explained the results by noting that larger animals actually lose more energy than smaller organisms (McNab 1971). Contrary to this suggestion, Meiri (2003) notes that even though larger animals require and spend more energy than smaller ones, the larger ones still acquire more energy overall.

Support for Rensch's rule of within-species variation has been observed within species of multiple taxa (James 1970). Support for the first two predictions of Rensch's rule has been found in cross-species analyses of birds (Ashton 2002a; Salomon 2002) and mammals (Rensch 1938; Yom-Tov and Geffen 2006), as well as insects (Chown and Gaston 1999; Stillwell et al. 2007). Moreover, support for the first two predictions of both Rensch's rule and Allen's rule has been found in short-nosed fruit bats (*Cynopterus sphinx*) (Storz et al. 2001) as well as western bird species (Salomon 2002).

*1.4.4.3 Evidence for Bergmann's Rule and Corollaries Among Primates*

Numerous studies have shown support for these principles among humans. In a cross-cultural study, it has been established that there is a relationship between body weight and climate (Roberts 1953). Support for Rensch's rule has been observed in

humans, with clinal variation in the height and weight of Chinese humans (Floyd 2008); children in southern provinces were found to be shorter and weigh less than children in the north, even after age and socioeconomics had been controlled for.  Support for Allen's rule has also been found in human subjects.  People at higher altitudes in the Andes have shorter limbs than those at lower altitudes (Weinstein 2005).  In this study, limb length did not differ along latitudinal gradients, but only differed along altitudinal gradients.   Allen's rule has also been supported in human ancestors.  For example, Neanderthals that inhabited glacial Europe had extremely cold-adapted body proportions (Trinkaus 1981).

The relationship between body size and climate may at least partially explain the evolution of human pygmy body size in hot climates.  Compared to average sized humans, pygmy body proportions have a low height to weight ratio.  These proportions decrease the ratio of volume to surface area and increases efficiency at dissipating heat, as predicted by Allen's rule (Hiernaux 1977; Shea and Bailey 1996).  In addition to dissipating heat more efficiently, smaller body sizes may also generate less heat during physical activity (Cavalli-Sforza 1986).  However, the evolution of the human pygmy phenotype appears to be more complex than simply a thermoregulatory adaptation (discussed in a later section).

Evidence for Bergmann's rule and its corollaries among non-human primates is mixed, although there have been few studies.  A comprehensive study of the order Primates found that Bergman's rule is supported within all primate taxa (Harcourt and Schreier 2009), where median body mass increases with latitude.  Studies that focused on small-bodied prosimians found support for Rensch's rule, including slow lorises (*Nycticebus coucang*) (Ravosa 1998) and gray mouse lemurs (*Microcebus murinus*)

(Lahann et al. 2006), where body mass within each species latitudinally increases with decreasing temperatures. In contrast, Bergmann's rule was not supported at all in vervet monkeys (*Cercopithecus aethiops*) (Cardini 2007). Within these cercopithecines, clinal variation in skull size and shape conformed to a longitudinal (west to east) gradient rather than latitudinal, and rainfall rather than temperature affected skull size (Cardini 2007).

A similar relationship between rainfall and size was found in insular long-tailed macaques (*Macaca fascicularis*) in Southeast Asia (Schillaci et al. 2009). Although Allen's rule was not supported among these macaques, the first prediction of Rensch's rule was supported in this study; increasing latitude positively correlated with skull length. In contrast, the prediction that temperature correlates with body size was not supported in this study; increasing latitude does not correlate with increasing temperature within the Southeast Asian latitudinal range (Schillaci et al. 2009). The authors found that another climatic factor, rainfall, was highly correlated with latitude in this region, and that it held more explanatory power for skull size than temperature. Moreover, while altitude strongly correlated with temperature and rainfall, it did not have a significant affect on morphology. The authors suggest that ecological factors other than temperature are behind latitudinal phenotypic variation within this species (Schillaci et al. 2009).

It is apparent that variables besides temperature affect body size clines. Other climatic or environmental variables that correlate with ecogeographic clines can select for body size shifts. For example, pygmy slow lorises (*N. pygmaeus*) follow the opposite of Rensch's rule and have smaller skull sizes in more northern locations (Ravosa 1998). This observation may be caused by character displacement, where pygmy slow lorises

evolved a separate niche from the sympatric slow lorises; further analysis of their skull revealed their maxillomandibular proportions were reorganized, which is linked to both small body size and a dietary shift to insectivory (Ravosa 1998).

However, the applicability of the preceding primate studies to Bergmann's rule may be problematic.  The assumption that skull size correlates with body mass is invoked in some of the studies (Ravosa 1998; Schillaci et al. 2009), which may confound the results.  Studies that use proxies for body size, including morphological traits that correlate with body size (such as teeth size or wing length), do not accurately assess clinal changes in body mass, since these traits can be influenced by selective forces besides those that drive Bergmann's rule (Meiri and Dayan 2003).  Regardless, variation in primate body size clearly occurs along ecogeographic clines; the question remains of why these clines occur.  Evaluation of the third prediction of Bergmann's rule (smaller animals correlate with temperature more than larger ones) would clarify whether temperature is in fact the driving force.

*1.4.4.4 Application to Altitudinal Gradients*

Altitudinal gradients are less studied than longitudinal clines, and no study has examined primate body size along altitudinal gradients.  Bergmann's rule was originally formulated in terms of latitudinal variation in climate, but similar body mass clines occur along other geographic gradients, such as longitude or altitude (Blackburn et al. 1999). In the absence of alternative selective factors, the same predictions should hold for colder climates at higher altitudes.

However, altitudinal body size patterns often do not mirror latitudinal patterns (Dillon et al. 2006).  Altitude should introduce different variables than latitude and the

mechanisms driving body size may differ between altitudinal and latitudinal body size clines.  While higher altitudes have lower temperatures, shorter growing seasons, and decreased diversity as in higher latitudes, there is also a lower oxygen concentration at high altitudes (Dillon et al. 2006; Liao et al. 2006; Ma et al. 2009).

   While Bergmann's rule is generally supported across latitudinal gradients, both endotherms and ectotherms at high altitudes conform to the converse.  Insect species at high altitudes tend to decrease in body size (Dillon et al. 2006).  Similarly, intraspecific body size of amphibians declines along an altitudinal gradient (Ma et al. 2009).  Among mammals, there is a significant negative relationship between calf body mass and altitude among large bodied moose (Ericsson et al. 2002; Hjeljord and Histol 1999), as well as small-bodied pikas (Liao et al. 2006).

   Given that the interaction between multiple environmental variables explains geographic body size variation (Chown and Klok 2003; Stillwell et al. 2007), altitudinal body size clines appear to be affected by more than just temperature.  Among ectotherms, conformity to Bergmann's rule along altitudinal lines is dependent on lifespans, seasonality and latitude.  As previously noted, the interaction of latitude and altitude produces differences in seasonality.  Altitudinal effects of seasonality differs according to latitude, where high-altitude seasonality is more pronounced at higher latitudes (Körner 2007).  Regions with increasing seasonality at higher altitudes should also have more constraints on body size at higher altitudes.  In accordance, intraspecific body size of weevils increases with altitude in an aseasonal location, but the opposite occurs in a seasonal location (Chown and Klok 2003).  This study suggests that Bergmann's rule is applicable to ectotherms in aseasonal environments, while the opposite occurs in more seasonal environments.  The interaction of another

variable, lifespan, further affects this relationship.  Insects with longer lives tend to show a negative relationship between body size and latitude (increasing seasonality), while insects with shorter lives have a positive relationship (Chown and Gaston 1999).  When generation length comprises a large proportion of growing season length, then seasonal food shortages are more important.

Endotherms, which have long lifespans, should show a similar negative relationship between body size and altitude, where resource availability becomes especially important.  Endotherms at higher altitudes have increased energetic demands due to the colder environment, and smaller body size at higher altitudes may be a response to low oxygen pressure and low temperature (Liao et al. 2006).  Moreover, growing season tends to be shorter at higher altitudes, constraining the length of the developmental period even though high quality food resources are available during this time (Ericsson et al. 2002).  Among moose, when altitude is controlled for, growing season length is still a significant explanatory variable for offspring body mass (Ericsson et al. 2002).

Therefore, even though the general trend of Bergmann's rule holds true, there are a substantial number of deviations, suggesting there is variation in the causal factors.   Altitudinal body mass gradients exhibit the opposite effect of latitudinal clines because of altitudinal effects on habitat productivity.  Deviations from Bergmann's rule along latitudinal clines may have similar causes.

*1.4.4.5 The Thermoregulation Explanation for Bergmann's Rule*

The third prediction of Bergmann's rule, that smaller mammals conform to the rule more than larger ones, implies that body size clines are driven by heat

conservation. An increase in body size gives smaller mammals greater changes in heat conservation than a similar increase in size would give to larger animals (Ashton et al. 2000). In addition, larger animals can thermoregulate with fewer costs (such as increasing fur length without it becoming heavy). This prediction is unsupported since Bergmann's rule does not decline in strength with increasing body size (Ashton et al. 2000).

The relationship between body size and adherence to Bergmann's rule appears to be opposite from predicted. The smallest bodied mammals (in body mass categories below 500g) do not conform to Rensch's rule (Meiri and Dayan 2003). The rule is not valid at all for Rodentia, the largest mammalian order. Meiri (2003) suggests many of these species thermoregulate by behavioral means, such as burrowing or going into seasonal torpor. Among primates, neither the largest nor the smallest forms exhibit Bergmann's effect, perhaps because primates are so restricted to tropical environments (Harcourt and Schreier 2009). Moreover, neither the largest nor the smallest bodied primates are found in the highest latitudes, which suggests that in colder climates, the largest forms cannot obtain enough energy while the smallest cannot thermoregulate (Blackburn and Hawkins 2004). If Bergmann's rule is not applicable to small mammals that are more affected by thermoregulatory issues, then temperature cannot be the primary causal variable.

# Table 3.  Predictions of hypotheses related to body size clines.

| Rule | Explanatory Mechanism | Hypothesis | Independent Variable | Dependent Variable | Predictions |
|------|----------------------|-----------|---------------------|-------------------|-------------|
| **Bergmann's Rule** (1847)<br><br>**Rensch** (1938) | Thermoregulation: heat conservation at low temperatures | Body size will increase as temperature decreases, in order to reduce heat loss. | Temperature | Body Size (interspecific)<br><br>Body Size (intraspecific) | (a) Populations in colder regions have increased body size.<br>(b) Temperature negatively correlates with body size.<br>(c) Smaller animals more strongly correlate with temperature. |
| **Heat Dissipation Hypothesis** | Thermoregulation: heat dissipation at high temperatures | Body size will decrease as temperature increases, in order to maximize heat loss. | Temperature | Body Size | (a) and (b) as above.<br>(c) Larger animals correlate more strongly with temperature. |
| **Dispersal Hypothesis** | Dispersal ability | Geographic clines are a byproduct of dispersal range, where smaller organisms have smaller ranges and have not spread to higher latitudes or altitudes. | Body size | Dispersal range | Organisms with smaller body sizes have reduced dispersal capability. |
| **Converse of Bergmann's Rule** | Resource availability | Body size will increase in areas with more productivity.<br><br>(Body size decreases as resource availability decreases.) | Habitat productivity (Rainfall, biomass) | Body size | (a) Body size is proportional to food productivity<br>(b) Body sizes are larger in environments with greater productivity.<br>(c) In drier areas, body size is influenced more by rainfall. |
| **Starvation Resistance (Seasonality) Hypothesis** | Seasonality | Body size increases as seasonality increases | Seasonal abundance of food | Body size | (a) Body size is proportional to degree of seasonality.<br>(b) Body sizes are larger in more seasonal environments.<br>(c) Larger bodies have proportionally larger fat stores.<br>(d) Organisms are smaller in aseaonal areas compared to those in seasonal areas, and vice versa. |
| **Allen** (1877) | Thermoregulation (heat conservation) | Appendage length will decrease as temperature decreases, in order to conserve heat. | Temperature | Appendage size | (a) Populations in colder regions will have relatively shorter extremities than those in warmer climates.<br>b) Temperature will negatively correlate with body proportions.<br>(c) Smaller animals more strongly correlate with temperature. |

In addition to the lack of support for the third prediction, the thermoregulation explanation cannot account for the presence of body size clines in ectotherms (Ashton 2002a).  Support for Bergmann's rule has been found in ectotherms, including salamanders (Ashton 2002b).  Since ectotherms such as amphibians do not produce internal heat, heat conservation alone cannot explain body size clines (Ashton 2002a).  Although a contradictory study of multiple amphibian species found no relationship between body size and temperature (Adams and Church 2008), the fact that some ectotherms follow the rule suggests temperature cannot be the main causal variable.

Other studies have supporting results.  Most studies indicate that a combination of climatic factors rather than just temperature alone is responsible for body size clines.  For example, while Bergmann's rule was supported among North American birds, size varied with both temperature and humidity (James 1970).  The intraspecific version of the rule has similar results.  For example, body size among American robins (*Turdus migratorius*) varies according to both temperature and humidity (James 1991).  Among bats, in addition to temperature, other climatic variables correlate with body size clines, including humidity and seasonality (Storz et al. 2001).  The body mass patterns of insects have been attributed to latitudinal clines of interactions between temperature, habitat stability, season length, and life history timing (Chown and Gaston 1999).  These results are evidence that Bergmann's effect is not caused temperature alone, and is therefore not driven by the need for heat conservation.  James (1970) proposes that a revised formulation of Bergmann's rule is:  "Intraspecific size variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions."

*1.4.4.6 Alternative Mechanisms Behind Body Size Clines*

Although Bergmann originally explained body size clines as a function of thermoregulatory mechanisms, namely heat conservation, the literature supports alternative explanations (Table 3).  Alternative hypotheses explaining body size clines include heat dissipation (McNab 1971), migration ability (Cushman et al. 1993), starvation resistance (Blackburn et al. 1999; Cushman et al. 1993), and clinal variation in resource availability/seasonality (McNab 1971).

*1.4.4.7 The Heat Dissipation Hypothesis*

Rather than large body size being an adaptation for energy conservation in cooler climates, small body size may be an adaptation to heat dissipation in high temperatures (Lahann et al. 2006; McNab 1971).  According to this hypothesis, the need for heat dissipation explains body size clines.  This hypothesis has similar predictions to the original predictions of Bergmann's rule, except that it predicts larger animals (rather than smaller ones) will correlate more strongly with temperature.  Meiri (2003) found stronger support for Rensch's rule in larger mammals, which is consistent with larger mammals undergoing selection for smaller size.  However, the fact that multiple other variables have been found to correlate with body size, this explanation is just as incomplete as Bergmann's formulation.

*1.4.4.8 The Dispersal Hypothesis*

The dispersal hypothesis suggests body size clines are not directly selected for, but are a byproduct of differential migration abilities for organisms of different sizes. The hypothesis predicts that smaller body sizes have lower migration ability, meaning

they cannot disperse to higher latitudes or altitudes (Blackburn et al. 1999). This prediction has little empirical support. Among ants, dispersal ability is not dependent on size (Cushman et al. 1993). Even small species of birds can migrate long distances (Blackburn et al. 1999).

*1.4.4.9 The Starvation Resistance (Seasonality) Hypothesis*

The starvation resistance hypothesis suggests that larger body sizes are favorable in seasonal or resource poor environments, since large animals can store more fat to subsist on during times of seasonal scarcity (Ashton et al. 2000). This hypothesis predicts that a) body size is proportional to degree of seasonality, b) body sizes will be larger in more seasonal environments (higher latitudes, or lower altitudes), c) larger bodies are more able to withstand declines in food, and d) organisms are smaller in areas that are aseaonal compared to those in a seasonal areas, while individuals in cooler, aseasonal climates are smaller than those in warmer, seasonal areas (Ashton et al. 2000).

The first two predictions are well-supported between species. Small-bodied animal species in areas with lower biomass are larger than individuals of the same species within areas of higher biomass (Blackburn and Hawkins 2004). Resource availability in terms of plant biomass is an important source of variation in body mass for small-bodied mammals (Blackburn and Hawkins 2004). Support for this hypothesis is primarily among endotherms (Ashton 2002a), but it has also been supported among insects (Chown and Gaston 1999); for example, ant body size increases with increasing latitude (Cushman et al. 1993).

Evidence for the second prediction of the starvation resistance hypothesis, where body size increases with seasonality, shows the interesting result that body sizes peak at mid-latitudes, and not at the highest latitudes as Bergmann's rule would predict. Among large mammals, body size has been found to increase with latitude to a point, decreasing at the highest latitudes, so that larger body sizes occur in mid-range latitudes while smaller ones occur on the periphery (Geist 1987). This observation suggests body sizes are more affected by annual productivity and seasonality, rather than purely temperature.

The third prediction for the starvation resistance hypothesis, that larger-bodied animals are more resistant to starvation than smaller ones, has less support. Although larger animals can build larger fat stores (Dunbrack and Ramsay 1993), larger animals do not always have an advantage in energy storage and conservation due to allometric effects. While larger mammals have certain metabolic advantages during seasonal food shortages, smaller mammals are better able to engage in behavioral responses such as seasonal torpor, food caching, and exploiting microhabitats (Dunbrack and Ramsay 1993). Animals of different body sizes may make use of different strategies to adjust to seasonal decreases in food, meaning that seasonality should not directly select for a certain body size (Dunbrack and Ramsay 1993).

Considering the availability of behavioral strategies for energy conservation to alleviate seasonal stress, the starvation resistance explanation may not be the most likely (Blackburn et al. 1999; Dunbrack and Ramsay 1993). Although Chown and Klok (2003) found that seasonality is important to body size clines, they argue that differences in developmental sensitivity to temperature, rather than resistance to seasonal decreases in resources, drive body size clines. In the absence of seasonal

food shortages, growth and development is more sensitive to temperature, and body size increases with altitude; in colder and more seasonal environments, body size is constrained. This idea is related to the resource availability hypothesis for body size clines.

*1.4.4.10 The Resource Availability Hypothesis*

The resource availability hypothesis considers the productivity of a region (availability of food resources) as the strongest correlate to body size. While body size clines undoubtedly relate to abiotic climatic variables, they are often influenced by biotic factors, including habitat productivity and diet. Since production is determined primarily by precipitation (Yom-Tov and Geffen 2006), body size is explained by the interaction of rainfall with other environmental factors. McNab (1971) concludes that most mammals do not follow Bergmann's rule, but those that do are driven by variation in resources instead of temperature. This study found that latitudinal variation in carnivore body size relates to latitudinal differences in food availability and the size of prey.

The productivity hypothesis predicts that a) body size is proportional to food productivity, b) body sizes will be larger in environments with greater productivity, and c) in drier areas, mammalian body size is influenced more by rainfall since production is low (Yom-Tov and Geffen 2006). Support for this hypothesis has been found in vervet monkeys (Cardini 2007). Rainfall, which primarily correlates with habitat productivity, and seasonality were the primary determinants of skull size. This hypothesis is also supported by the negative correlation between latitude and body size in shrews (Ochocinska and Taylor 2003), where colder climates select for smaller body sizes that

require less food.  This explanation is applicable to altitudinal body size clines and the

size reduction observed in pygmy tarsiers (discussed below).


*1.4.4.11 The Converse of Bergmann's Rule*

The converse of Bergmann's rule, where body size is inversely correlated with

temperature and decreases at higher latitudes and altitudes, is associated with declines

in resource availability.  This occurrence is an extension of the resource availability

hypothesis, where the independent variable is again seasonal abundance of resources.

Here, even if decreases in temperature selects for larger body sizes, feeding on poor

quality resources in colder environments can lead to small body sizes (Chown and

Gaston 1999).

While the converse of Bergmann's rule is generally supported among

ectotherms (such as insects and amphibians) along an altitudinal gradient (Chown and

Klok 2003; Dillon et al. 2006; Ma et al. 2009), there is mixed support along a latitudinal

gradient.  Although one study concludes that no latitudinal evidence for Bergmann's rule

exists for insects (Loder 1997), insect body size has been found to generally decline

with increasing latitude (Mousseau 1997).  The converse of Bergmann's rule also

occurs among small-bodied primates (Ravosa 1998) and small-bodied shrews

(Ochocinska and Taylor 2003)

Latitudinal declines in body size are associated with increasingly limited

resources (Chown and Klok 2003), where decreased temperatures correlate with

decrease habitat productivity and changes in season length (Blanckenhorn and Demont

2004).  Body size declines associate with declines in temperature and habitat

productivity along both latitudinal and altitudinal clines.

### *1.4.5 Taxonomic Level of Clinal Variation*

The taxonomic level of clinal variation is important to understanding its causes. Intraspecific and interspecific clines in body size are caused by different mechanisms (Blackburn et al. 1999; Chown and Gaston 1999). For example, intraspecific variation in body size can reflect changes in the availability of a specific resource, where it is scarcer in cooler climates. On the other hand, interspecific variation might reflect differences in resource usage, geographic variation in overall resources (Blackburn et al. 1999), and phylogenetic differences. Moreover, body size variance will always be greater between species than within species (Blackburn et al. 1999). Thus, although Bergmann's rule is applicable both within and between species, the explanation for the observed body size clines may be different.

The taxonomic level of clines is also important to understanding where taxonomic breaks occur. Salomon (2002) proposes that a broken cline is evidence of speciation. Under this theory, clines occur in stages. First, the cline is smooth (no subspecies or variants). Next, the cline is stepped, with steeper clines between variants than within variants. Finally, the cline is broken, and speciation occurs. For example, support for Bergmann's and Allen's rules was found within two species of related birds, but not between them, indicating they are separate species (Salomon 2002). If the rules were supported between species, generating a smooth cline with no marked divisions, then that would indicate continuity between the populations. Among tarsier populations in Central Sulawesi, if there is a break in the cline between high and low altitude populations or if the clines do not fall into the same line, that is further evidence for the species classification of pygmy tarsiers.

### 1.4.6 Are Body Size Clines Adaptive?

Most explanations for body size clines present body size as adaptive.  In order to body sizes to be adaptive both within and between species, population differences along latitudinal or altitudinal gradients must be genetic (Stillwell 2010).  Alternatively, non-genetic sources of variation (phenotypic plasticity) can contribute to body size variation.  Body size might also be a byproduct of another trait that is selected for, or geographic clines may reflect non-adaptive side effects of species distributions (as in the dispersal hypothesis).

## 1.5 ALTITUDINAL EFFECTS ON PRIMATES

### 1.5.1 Spatial and Temporal Variation in Primate Behavior and Morphology

Interspecific and intraspecific variation in primate behavior and morphology often corresponds to variation in environmental selective pressures (van Schaik 1989), including food resource availability.  In a cross-species comparison, variability in primate diet and range usage associated with variation in food abundance, distribution, and quality (Clutton-Brock et al. 1977).  Primate sociality and grouping patterns also vary with food distribution.  For example, among mouse lemurs, females that feed upon dispersed insects exhibit more dispersed social relationships than females that feed on patchy fruit resources (Dammhahn and Kappeler 2009).  Factors other than food availability, including the distribution of sleep sites and risks of predation and infanticide, also affect primate social behavior and habitat usage.  For example, woodland and savanna baboons aggregate at sleeping sites that are inaccessible to predators, generating larger group sizes than macaques, which live in rain forests that contain evenly distributed sleeping sites (Hamilton 1982).  Threat of predation may also impact

sleep site selection. Sifakas select lower daytime resting sites, possibly in response to diurnal avian predators, while they choose higher sleep sites in the nighttime when the predator threat is mammalian (Wright 1998). In terms of social affiliation within groups, risk of infanticide has been suggested as an important selection pressure in the evolution of male and female associations (Van Schaik and Kappeler 1997).

Besides the more well-studied spatial and temporal variability that affects primate behavior and morphology, ecological variation along elevational clines can also associate with variation in morphology and behavior, where organisms adapt to local conditions along an altitudinal transect (Körner 2007). Under the theoretical premise that spatial distribution of resources is a primary determinant of primate behavior patterns (Clutton-Brock et al. 1977; Janson 2000; van Schaik 1989), altitudinal changes in ecology are expected to have behavioral and morphological consequences among pygmy tarsiers. The following section discusses research that supports the premise that variation in pygmy tarsier behavior and morphology is a reflection of variation in habitat along an altitudinal gradient.

### 1.5.2 Foraging Behavior

An altitudinal decline in resource abundance can affect a primate's diet, specifically with regards to consuming a greater proportion of lower quality foods or decreasing dietary diversity (Ganas et al. 2004; Hanya et al. 2003). For example, among mountain gorillas, groups at higher altitudes consume fewer plant and fruit species than groups at lower altitudes, corresponding to a decrease in plant species diversity as elevation increases (Ganas et al. 2004). Primates at higher altitudes also consume a greater proportion of lower quality foods, as observed among gibbons

(Caldecott 1980), as well as increase the proportion of time spent feeding, as observed among gelada baboons (Iwamoto and Dunbar 1983).  Altitude can influence behaviors such as sleeping site selection.  For example, high altitude black and white snub-nosed monkeys select relatively lower altitude sleeping sites during winter, as a thermoregulatory adaptation (Cui et al. 2006).  Altitude also results in decreased primate abundance.  A decline in food availability at higher elevations is associated with declines in group density among Japanese macaques (Hanya et al. 2004) and red colobus monkeys (Marshall 2005), as well as lemur species diversity (Lehman *et al.* 2006).  Finally, the colder climates found at higher elevations are also associated with morphological adaptations.  Japanese macaques in colder climates have larger nasal cavities and smaller maxillary sinus volumes for improved cold-weather respiration (Rae et al. 2003).

Altitudinal decreases in resource availability may also influence pygmy tarsier foraging behavior.  Since insects are the primary food for tarsiers, altitudinal declines in insect size and abundance influence pygmy tarsier feeding patterns.  There are known spatial shifts in insect availability in Central Sulawesi (Merker 2006) that extend along an altitudinal gradient.  Insect diversity declines at higher altitudes due to declines in plant species diversity and reduced habitat area (Lawton et al. 1987). Insect body size also decreases along a cline as temperature and habitat productivity decrease (Chown and Klok 2003).  With a decline in both insect size and diversity at higher altitudes, pygmy tarsier diet may be constrained at high altitudes.  Thus, pygmy tarsiers may consume a greater proportion of smaller insects and have a less varied diet at increasingly higher altitudes.

In addition to altitudinal differences in resource availability, altitudinal changes in climate may affect the foraging strategies of pygmy tarsiers. At lower temperatures, mammals must maintain their body temperature by either decreasing energy expenditure or increasing energy intake (Kleiber and Rogers 1961). Adjustments in time spent foraging may be due to thermoregulation or resource availability. For example, baboons at high altitudes increase time spent feeding and decrease resting time in response to the altitudinal clinal decrease in temperature, increased energetic demands, and decreased food resource availability (Iwamoto and Dunbar 1983). As a result of their highland environment, pygmy tarsiers are subject to the same increase in energetic requirements and decrease in habitat quality, and may exhibit a similar pattern of increasing proportion of time spent feeding at increasingly higher altitudes. These patterns are also expected among tarsiers in the lowland forests of Sulawesi.

Among lowland Sulawesian tarsiers, temporal and spatial variability in food distribution is also associated with intraspecific differences in behavior. For example, spectral tarsiers modify their behavior with seasonal changes, increasing home ranges and travel distances during the dry season when prey abundance is low (Gursky 2000b). Likewise, the variability in spectral tarsiers mating systems is associated with sleeping tree availability. Groups with large strangling fig trees are more likely to be polygynous than groups with small or non-fig sleeping trees (Gursky-Doyen 2010). Similarly, Dian's tarsiers have been observed to modify their ranging and foraging patterns according to the amount of habitat disturbance, by increasing their nightly travel distances (Merker 2006). Dian's tarsiers also reduce group size in disturbed, less productive habitats (Merker et al. 2005).

### 1.5.3 Ranging Patterns

Interspecific and intraspecific differences in home range size and nightly travel distances may reflect temporal or spatial differences in habitat productivity. For example, squirrel monkey groups increase intergroup and intragroup distances as well as daily travel distances when foraging during seasonal periods of low resource availability (Boinski, 2008). Similarly, spectral tarsiers (*T. tarsier*) increase their range size, nightly distance traveled, as well as the distance between group members when foraging, in response to temporal decreases in resource abundance (Gursky 2000b; Gursky 2002a). Home range variation in *T. dianae* is related to spatial differences in habitat quality that result from human activity (Merker 2006). Dian's tarsiers were found to occupy a greater percentage of their home range on a nightly basis in more disturbed and less productive habitats (Merker 2006). Due to decreasing resources at higher altitudes, it is predicted that at higher altitudes, pygmy tarsiers will exhibit larger overall home range size and larger nightly ranging distances than lowland tarsiers, as well as increased distances between group members and groups, and less home range overlap between group members.

### 1.5.4 Habitat Usage

Characteristics of sleeping sites and site selection behaviors also vary with altitude (Cui et al. 2006), especially in terms of tree size. Data from the pilot study in pygmy tarsier habitat shows that as altitude increased, tree height slightly dropped, while the average diameter at breast height of the tree trunks slightly increased (Grow and Gursky-Doyen 2010). Therefore, sleeping site availability is a resource that is expected to vary according to altitude. The pilot study indicated that pygmy tarsier

groups sleep in trees that represent the largest trees available at that altitude in terms of both diameter and height (Grow and Gursky-Doyen 2010).  Spectral, Dian's, and Philippines tarsiers similarly select large trees (Dagosto et al. 2001; Gursky 1997; Merker 2003).  As spectral tarsiers usually select trees of a diameter that represent less than 1% of available trees (Gursky 2007) and large trees are even rarer at high altitudes, pygmy tarsiers may be further constrained in sleeping site options.  Pygmy tarsiers at higher altitudes are expected to choose sleep trees that are large for their altitude, but relatively smaller and shorter than those that pygmy tarsiers select at relatively lower altitudes.  This prediction should be applicable across lowland Sulawesian tarsier species, and pygmy tarsiers may sleep in smaller trees than those of the lowland tarsier species.

Sleeping site characteristics other than tree size may also vary with altitude.  For example, some primates are known to select sites that provide the most thermoregulatory advantages.  Grey mouse lemurs seek thermally insulated sleeping sites, with decreased entrance size and increased wall thickness (Radespiel et al. 1998).   Pygmy tarsiers at higher altitudes may select sleeping sites with increased thermoregulatory function, with thicker insulation.

Behaviors within sleeping sites may also vary with altitude.  In particular, huddling at shared sleeping sites functions as a behavioral means of thermoregulation, especially for small-bodied primates (Kappeler 1998).  Small-bodied tamarins huddle at nighttime sleeping sites to conserve body heat (Heymann 1995).  Tamarins have also been observed to delay leaving the sleeping site in response to colder weather (Smith et al. 2007), indicating the thermoregulatory advantages of huddling may influence the amount of time spent at the sleeping site.  Tarsiers may exhibit similar responses to

altitudinal changes in climate.  While *T. bancanus* and *T. syrichta* do not sleep as a

group at shared sleeping sites (Crompton and Andau 1987; Niemitz 1977), all the

Sulawesian tarsiers have been observed to sleep in groups  (Grow and Gursky-Doyen

2010) Gursky 1995; Merker 2006; Driller et al. 2009).  A primary factor that is

associated with increasing altitude is decreased temperature (Körner 2007). In

Sulawesi, temperature declines 0.6°C per 100 m altitude, and at higher altitudes the

daily temperature range is greater, fluctuating as much as 15 to 20°C (Whitten et al.

2002).  As pygmy tarsiers live in a colder climate than the majority of the Sulawesian

tarsiers, groups at higher altitudes may be expected to spend more time huddling with

group members while at sleeping sites.


### 1.5.5 Population Density, Group Size, and Group Composition

Primate density and diversity declines at higher elevations.  A decline in food

availability at higher elevations is associated with declines in group density among

Japanese macaques (Hanya et al. 2004) and red colobus monkeys (Marshall 2005), as

well as lemur species diversity (Lehman 2006).  Mountain baboons decrease their

population density and group sizes at higher altitude, as well as increase spacing

between adults (Byrne et al. 1993).  Byrne et al. (1993) compared similarly sized groups

at low and high altitudes and found that they had similar foraging efficiency and similarly

low contest competition.  The authors argue that foraging efficiency is maintained at

higher altitudes through lower population density, decreasing competition.  Pygmy

tarsiers are thus expected to live at a lower density than lowland tarsiers.

Food resource availability is also known to influence grouping patterns among

primates (van Schaik 1989).  Multiple primates are known to reduce group size when

there is reduced resource availability.   Spider monkeys and chimpanzees both alter

group size according to food distribution (Chapman et al. 1995).  Food resources can

also affect group composition.  For example, the sex composition of groups of spider

monkeys and chimpanzees may vary with resource distribution and density (Chapman

et al. 1995).  Finally, group densities of primates also relates to spatial decreases in

resource availability, including altitudinal declines in resources.  Group densities of

Japanese macaques are known to be lower at higher altitudes, corresponding to a

decline in annual food abundance.

　　　　The influence of ecological variation in food resources extends to tarsier

grouping associations.  Among the Sulawesian tarsiers specifically, there is both

interspecific and intraspecific variability in social structure, group size, and group

composition (Driller et al. 2009; Gursky 1997; Gursky 2000c; MacKinnon and

MacKinnon 1980; Merker 2006; Merker and Groves 2006) (Table 4).  In terms of group

size, the Sulawesi tarsiers generally sleep in small family groups that share the same

sleep tree, with variation due to ecological variability.  For example, group size among

*T. dianae* decreases in increasingly disturbed habitats (Merker et al. 2005). This

suggests that Dian's tarsiers modulate their group size in response to resource

availability.  Similarly, Driller et al. (2009) suggest small group sizes among *both T.*

*dianae* and *T. lariang* may be an adaptation to low habitat quality, where the smaller

groups reduce feeding competition. If grouping patterns among pygmy tarsiers are a

reflection of forest density, then altitudinal changes in forest density may be an

important variable to pygmy tarsier grouping behavior.  Specifically, if group size is

constrained by tree availability, then pygmy tarsiers are expected to live in smaller

groups as altitude increases.

In addition to resource availability, predation risk can influence the composition of individuals sharing a sleeping site (Anderson 1998).  For instance, although grey mouse lemurs forage solitarily, females form sleeping site associations to minimize the risk of raptor predation (Radespiel et al. 1998).   The threat of predation also affects on the number of males in a group, where additional males can provide predator protection.  For example, in response to higher risks of predation, cercopithecoid primates increase group size, with a disproportionate increase in the number of males (Hill and Lee 1998).  Among red colobus monkeys, an increase in the number of males in a group is associated with a decrease in predation success (Stanford 2002).  Among lemurs, more adult males in a group may be selected for as a means of predator detection (Kappeler 1997a).  While nocturnal primates often use cryptic defense against predators (Clutton-Brock and Harvey 1977; Stanford 2002), spectral tarsiers also use noncryptic anti-predator strategies in the presence of predators including alarm calling and mobbing  (Gursky 2003; Gursky 2005).  In fact, spectral tarsier adult males were more likely to initiate snake mobbing and mob for longer periods of time than females or subadults (Gursky 2005).  Adult males from neighboring groups also participated in mobbing events (Gursky 2005).  These observations indicate that the presence of adult males is important to predator defense among tarsiers, and multiple males may associate in response to predation threats.

Pygmy tarsier sleeping site associations may similarly be influenced by risk of predation.  The threat of avian predation appears to be significant for pygmy tarsiers, as one predation event and several attempts by raptors occurred during the pilot study.  Pygmy tarsiers at higher altitudes occupy forest with less canopy cover and may experience a higher risk of detection by predators.  Additionally, if pygmy tarsiers select

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sleeping sites based primarily on thermoregulatory properties, then they may face the

tradeoff of less protection against predators.  In the pilot study, a group of at least four

pygmy tarsiers was observed (Grow and Gursky-Doyen 2010), including two adult

males and one adult female.  Since it is unusual among tarsiers for multiple adult males

to live in the same group, pygmy tarsier group composition may be influenced by the

threat of predation.  Pygmy tarsiers are expected to have more males per group at

higher altitudes, increasing the chances of predator detection and deterrence at less

protected sleeping sites.


### 1.5.6 Communication Strategies

Variation in habitat structure affects sound transmission and how animals

vocalize (Marten and Marler 1977), including altitudinal variation in habitat.  Variation in

habitat structure may influence communication style among primates, especially with

regards to sound degradation (reverberation), attenuation, and ambient noise (Waser

and Brown 1986).  For example, pygmy marmoset populations adjust vocalizations to

local habitat acoustics (de la Torre and Snowdon 2002).  Population differences in calls

of Japanese macaque have also been found to differ with habitat differences in sound

attenuation (Sugiura et al. 2006).  Variation in tarsier vocalizations may also relate to

habitat variation (Hauser 1993; Nietsch 1999).  Pygmy tarsiers possess reduced

auditory bullae compared to the lowland species (Musser and Dagosto 1987), which

may be a morphological adaptation to sound attenuation in moss forest (Shekelle

2008b).  In primates, middle ear cavity volume associates with sensitivity to hearing

low-frequency sounds (Coleman and Colbert 2010).  A reduced middle ear in pygmy

tarsiers may reflect a decreased need for hearing lower frequency sounds.  Further,

their habitat may have corresponding influences on communication behavior. Moss coverage, humidity, and precipitation increase with altitude on Mt. Rore Katimbu, all of which impact sounds transmission by increasing increase ambient noise and sound attenuation.

In addition to habitat structure, predation risk also affects primate vocalization behavior, especially when returning to sleeping sites. Tamarins decrease vocalizations and become quietly vigilant as they return to their sleeping sites (Heymann 1995). All the lowland Sulawesi tarsier species engage in vocal duet choruses each dawn when returning to their shared sleeping site (Table 4) (Gursky 1997; Gursky 2000a; MacKinnon and MacKinnon 1980; Merker 2006; Niemitz 1984a; Nietsch 1999). In contrast, pygmy tarsiers were never heard vocalizing when returning to their shared sleeping site (Grow and Gursky-Doyen 2010). Initial observations confirmed prior surveys that did not detect these behaviors (Shekelle 2008b). If detection by predators is a greater threat at higher altitudes, pygmy tarsiers may use more cryptic communication strategies, especially near their sleeping site, such as ultrasonic vocalizations or engaging in vocalizations less frequently. In response to both decreased sound transmission and increased risk of exposure to predators at higher altitudes, pygmy tarsiers are expected to engage in vocalizations audible to humans less frequently. Initial observations show that pygmy tarsiers vocalize primarily in the ultrasonic frequency.

Scentmarking is another important behavior that tarsiers use to communicate. For example, *T. tarsier* scentmarks throughout the periphery of territories (Gursky 1997; MacKinnon and MacKinnon 1980). Variation in tarsier scentmarking can be due to environmental variation. For example, scentmarks for *T. tumpara* were found to fade

much quicker than those of other tarsier species, which might be a behavioral adaptation to avoid predators (Shekelle et al. 2008). Unlike all known tarsier species, pygmy tarsier scentmarks were rarely detected during the pilot study (Grow and Gursky-Doyen 2010). The substrates available to pygmy tarsiers are increasingly covered with moss at higher altitudes, which may affect their ability to deposit scentmarks. Humidity at higher altitudes may also diminish transmission of scentmarks, reducing the benefits of engaging in this behavior. It is therefore expected that as altitude increases, and rainfall and moss cover increase, the frequency that pygmy tarsiers scentmark will decrease.

### 1.5.7 Tarsius pumilus Morphology

*1.5.7.1 Body Size*

It has been hypothesized that the relatively small body size of *T. pumilus* is an adaptation to a colder, less productive environment (Musser and Dagosto 1987). The small body size and long limb proportions of pygmy tarsiers produce increased surface area relative to body mass, resulting in heat loss, the opposite of predictions for Bergmann's and Allen's rules. If larger insects are less abundant at higher altitudes, it is possible that pygmy tarsiers consume smaller and fewer insects with lower overall biomass, constraining their body size. The number of invertebrate species, the main food source of tarsiers, is known to decline with altitude (Whitten et al. 2002). Pygmy tarsiers are therefore expected to experience an altitudinal decline in food resources that corresponds to altitudinal declines in body size. As predation risk may be high for pygmy tarsiers, an altitudinal increase in mortality may further contribute to small body size.

Body proportions among pygmy tarsiers may also correlate with altitude declines in resource abundance. Tarsiers are anatomically adapted for leaping, but there is variation in the degree of specialization (Dagosto et al. 2001). *T. bancanus* are the most specialized for leaping (Crompton and Andau 1986; Niemitz 1977; Niemitz 1979), 1985a). It exhibits the longest hindlimb proportions of all tarsiers and uses vertical supports the most (Crompton and Andau 1986). In comparison, *T. spectrum* and *T. dianae* exhibit the shortest proportions and the least specialization (Dagosto et al. 2001). Smaller-bodied leapers maximize leap distances through additional body proportion adaptations, including longer relative tail lengths to increase leap force and adjust body position mid-leap (Demes et al. 1996). In the pilot study, pygmy tarsiers were found to have long hindlimb and tail proportions relative to their total body size as compared to *T. dianae* and *T. spectrum* (Grow and Gursky-Doyen 2010). Therefore, *T. pumilus* body proportions suggest this species may leap more than do the lower altitude Sulawesian species. These proportions may reflect the altitudinal distribution of substrates. Tree density steadily declines as altitude increases, which may result in increasingly greater leaping distances between trees, generating selection pressure for comparatively longer hindlimb lengths. Pygmy tarsiers are thus expected to exhibit longer hindlimbs and leaping distances as tree density declines at higher altitudes.

*1.5.7.2 Sexual Dimorphism*

Sexual dimorphism may decrease at higher altitudes due to resource limitations. Among birds, interspecific degree of sexual dimorphism negatively correlates with altitude (Badyaev 1997), which is suggested to be related to the increased cost of maintenance at higher altitudes. Primates at higher altitudes may be expected to follow

similar patterns of reduced body size and reduced sexual dimorphism. In higher quality

habitats, sexual dimorphism of body size increases among gelada baboons (Popp

1983). Popp (1983) provides a life history explanation for reduced body size in geladas:

in resource poor environments, baboons have higher costs for foraging, but in richer

habitats they can devote more energy to growth and reproduction (such an enhanced

male-male competition through larger body size). Along the same lines, the lack of

sexual dimorphism has been suggested as a produce of low resource availability in

Madagascar (Pochron and Wright 2002). Among the Malagasy lemurs, body sizes may

be limited by the low amount of plant resources and the unpredictable climate (Wright

1999). Environmental constraints limit body size, but larger testes volume offsets this,

emphasizing sperm competition. Primates at high altitudes should experience size

reduction in accordance with these trends, with corresponding effects on their life

history.

Given these observations, pygmy tarsiers are expected to have low sexual

dimorphism but large relative testes size. Initial observations of *T. pumilus* indicate that

the species has low sexual dimorphism and lives in multi-male, multi-female groups

(Grow and Gursky-Doyen 2010). Given their group composition, pygmy tarsiers are

expected to have a more polygynous, multi-male mating system than the lowland

Sulawesian tarsier species.


*1.5.7.3 Locomotor Adaptations*

Claw-like nails serve as locomotor adaptations for small-bodied arboreal

primates. The claws of callitrichids are considered adaptations that allow these dwarfed

primates to cling to large tree branches and trunks, whereas their hands may be too

small to sufficiently grasp these substrates (Martin 1992). The average weight of Callitrichidae species ranges between 110 to 560g (Martin 1992), significantly larger than pygmy tarsiers. Given that pygmy tarsiers are very small, their claw-like nails may serve a similar purpose. Claws may also facilitate clinging to slippery moss-covered substrates. Since moss cover increases with altitude, pygmy tarsier claw-like nails are expected to be longer than those of tarsiers at lower altitudes.

## 1.6 RESEARCH QUESTION

This study will answer the research question: how does altitude affect pygmy tarsier behavior and morphology? It is hypothesized that the behavior and morphology of pygmy tarsiers are adaptations to a high altitude environment. To test this hypothesis, this study investigates whether behavioral and morphological variation within pygmy tarsiers corresponds to altitudinal ecological variation. Variation in pygmy tarsier behavior and morphology are predicted to be correlated with measurable ecological changes that occur on an altitudinal gradient (Figure 3).

**Figure 3. Hypothesis and alternative hypothesis for the causes of pygmy tarsier traits.**

*(a) Hypothesis:* Variation in tarsiers is due to altitudinal ecological gradients.
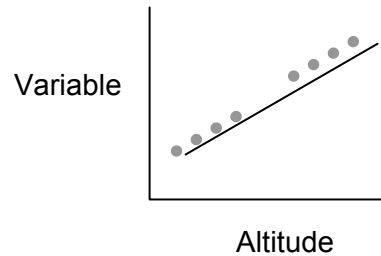
Variable

Altitude

*(b) Alternative Hypothesis:* Variation in tarsiers is due to variables other than altitude, and changes do not occur along a cline.
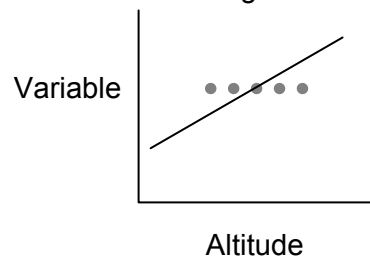
Variable

Altitude

The null hypothesis is that variation in pygmy tarsier behavior and morphology will not be correlated with measurable clinal ecological differences that occur on an altitudinal gradient. The alternative hypothesis is that variation in pygmy tarsier behavior and morphology will be correlated with measurable clinal ecological differences that occur on an altitudinal gradient.

### 1.6.1 Predictions

Under the hypothesis that variation in tarsiers is due to altitudinal ecological gradients, compared to lowland tarsiers, pygmy tarsiers should exhibit behavioral differences that correspond to the environment at higher altitudes. Predictions for this study follow.

*Foraging.* As altitude increases, pygmy tarsiers will (a) consume a greater proportion of smaller insects, (b) consume fewer types of insects, and (c) spend more time foraging.

*Ranging.* As altitude increases, pygmy tarsiers will (a) use larger home ranges, (b) travel longer distances each night, (c) maintain greater distances between groups, (d) exhibit greater distances between group members when foraging, and (e) demonstrate less overlap of individual home ranges.

*Habitat Usage.* As altitude increases, pygmy tarsiers will (a) select a greater proportion of sleeping trees of smaller dimensions (height, dbh), (b) select sleeping trees with more thermoregulatory benefits, and (c) spend more time huddling close to group members at their sleeping site.

*Group Size and Composition.* As altitude increases, (a) pygmy tarsiers will live in smaller groups and (b) a greater proportion of adult males will live in the group.

*Morphology.* As altitude increases, pygmy tarsiers will (a) demonstrate a reduction in body size that correlates with a reduction in food resources, (b) possess longer hindlimbs with respect to total body length, and (c) leap longer distances as they travel.

In order to address these various predictions, altitudinal effects on the population density and distribution of pygmy tarsiers will be discussed first, as well as their group composition and habitat associations. Next, ranging patterns will be examined. Finally, pygmy tarsier morphological traits will be discussed in relation to environmental characteristics.

**Table 4. Multi-species comparison of tarsier ecology, behavior, and morphology. Male and female values are combined unless otherwise noted. Means are given unless a range of values is otherwise noted. n/a indicates the data are not available in published literature.**

| | *Tarsius pumilus* | *T. spectrum* | *T. dianae* | *T. lariang* | *T. syrichta* | *T. bancanus* |
|---|---|---|---|---|---|---|
| Altitude (m asl) | 2100 [e] | 0 (sea level) [g] | 1000 [s] | 500 [u] | 100-200 [r] | 0 (sea level) [a] |
| Distribution | Central Sulawesi | Northern Sulawesi | Western Central Sulawesi | Central Sulawesi [u] | Philippines | Borneo |
| ***Morphology*** | | | | | | |
| Weight (g) | 55 [e] | Female 108.2 [g] Male 125.8 [g] | Female 113 [k] Male 132 [k] | Female 108.7 [u] Male 111 [u] | Female 120 [q] Male 135.5 [q] | Female 116.9 [p] Male 127.8 [p] |
| Sexual Dimorphism (body weight) | No [e] | Yes [j] | Yes [k] | n/a | Yes [r] | No [t] |
| Head & Body Length (mm) | 80 [e] | 127.8 [o] | 163.15 [k] | Skull 38.35 [d] | 127.3 [o] | 132.2 [o] |
| Femur/Thigh Length (mm) | Thigh 49.39 [e] | Femur 49-53 [b] | Thigh Female 55.5 [k] Male 60.5 [k] | n/a | Femur 56.9 [b] | Femur 64 [b] |
| ***Social Organization*** | | | | | | |
| Group Size | 4 [e] | 2-6 [f] | 3.2 - 5.2 [n] | 2-4 [d] | 2-4 [a] | 2 [q] |
| Typical Group Composition | Varied [e] | Family group (adult male, adult female, offspring) [f] | Family group [n] | Family group [d] | Adult male, 1-2 females, & offspring [r] | Solitary, male range overlaps multiple female ranges [a] (and pair bonded [q]) |
| Primary Social/ Mating System | Pairs and Multimale-multifemale [e] | Pair-bonded with facultative polygyny [f, m] | Pair-bonded w/ facultative polygyny [n] | Monogamous [d] | Polygynous [r] | Noyau [a] |
| Sleep in groups? | Yes [e] | Yes [f] | Yes [n] | Yes [d] | No [p] | No [a] |

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**Table 4 Continued.**

| | *Tarsius pumilus* | *T. spectrum* | *T. dianae* | *T. lariang* | *T. syrichta* | *T. bancanus* |
|---|---|---|---|---|---|---|
| ***Sleeping Site*** | | | | | | |
| Sleeping site | Nest in large trees [e] | Nest in large trees (*Ficus*) [j] | Nest in large trees (*Ficus*) [m] | Nest in large trees [d] | Variable (ground, vines, tree trunks, branches) [c] | Vine tangles and platforms [a] |
| Sleeping site location | Periphery of range [e] | Center of range [J] | Periphery of range [n] | n/a | Periphery of range [b] | Periphery of range [a] |
| Sleeping Tree Size DBH(cm)/ Height(m) | 28.40/15.4 [e] | 287/20.79 [J] | Strangling figs or dense undergrowth [m] | n/a | n/a / 7.53 [c] | Vine tangles on 50-90° supports [a] |
| Sleeping Site Height | Canopy level [e] | Near canopy level [j] | 5-10 m [v] | n/a | Ground – 5m [r] (usually < 1m [b]) | 3.5-5 m [a] |
| Sleeping site Fidelity (One dedicated site?) | Yes [e] | Yes [J] | Yes [s] | Yes [d] | No [b, c] | No [a] |
| ***Ranging*** | | | | | | |
| Home Range (ha) | Female 1.77 [e] Male 2.75 | Female 2.3 [h] Male 3.1 [h] | Female 1.58 [n] Male 1.77 [n] | n/a | Female 2.45 [r] Male 6.45 [r] | 4.5-11.25 [a] |
| Nightly Path Length (m) | Female 392.29 [e] Male 318.25 | Female 447.68 [f] Male 760.62 [f] | 905–1,263 [n] | n/a | Female 1119 [r] Male 1636 [r] | Female 1448.1 [a] Male 2081.6 [a] |
| Territorial? | n/a | Yes [g] | Yes [n] | Yes [d] | Yes [r] | Yes [a] |
| % Range Occupied Nightly | n/a | n/a | 25-48% [n] | n/a | Female 6-57% [r] Male 3-74% [r] | Females 66-100% [a] Males 50-75% [a] |
| Leap Distances | 1.24 [e] | 1.4 [l] | n/a | n/a | 1.2 [2] | 1.2 [a] |

**References** a. Crompton and Andau 1987; b. Dagosto et al. 2001; c. Dagosto and Gebo 1998; d. Driller et al. 2009; e. observations from this study; f. Gursky 1995; g. Gursky 1997; h. Gursky 1998; i. Gursky 2007a; j. Gursky 2007b; k. Gursky personal observation; l. Mackinnon and Mackinnon 1980; m. Merker et al. 2005; n. Merker 2006; o. Musser and Dagosto 1987; p. Niemitz 1977; q. Niemitz 1985; r. Neri-Arboleda et al. 2002; s. Tremble et al. 1993; t. Wright et al. 2003; u. Merker and Groves 2006 v. Merker 2003

## 2. METHODS

### 2.1 RESEARCH PERMISSIONS

This research followed ethical standards approved by the Texas A&M University Institutional Animal Care and Use Committee (Animal Use Protocol #2007-8 and 2011-47) and adhered to all Indonesian legal requirements for foreign researchers, with sponsorship from the Indonesian Ministry of Research and Technology (RISTEK), the Directorate General of Forestry (PHKA), and Tadulako University (Palu, Sulawesi, Indonesia).

### 2.2 STUDY SITE

Field observations were conducted in the mid and upper montane rain forest of Mt. Rore Katimbu, alternatively spelled Rorekautimbu or Rorekatimbu (S 01° 16.8', E 120° 18.5') (Figure 4).  The mountain spans 1800-2400 m in elevation and is located within Lore Lindu National Park, Central Sulawesi, Indonesia.  A trail bisects the study area, creating a channel of anthropogenic edges along either side.

In Central Sulawesi, between 1900 and 2000 m vegetation abruptly changes to be dominated by the moss-covered conifers of upper montane forest, and above 2000 the canopy lowers in height and becomes more discontinuous, resulting in denser undergrowth (Whitten et al. 2002).  Lore Lindu National Park, established in 1993, encompasses approximately 217,000 ha of protected forest (Pangau-Adam 2003).  The park contains steep topography, and elevations higher than 1500m comprise 20% of park (approximately 45,300 ha) (Latifah 2005).  Mt Rore Katimbu consists of primary

forest that contains both old-growth and disturbed forest.  Two primate genera, *Macaca* (macaques) and *Tarsius* (Eastern tarsiers), occur within Lore Lindu National Park.

**Figure 4.  Map of the study area on Mt Rore Katimbu in Lore Lindu National Park, Sulawesi (Indonesia).**
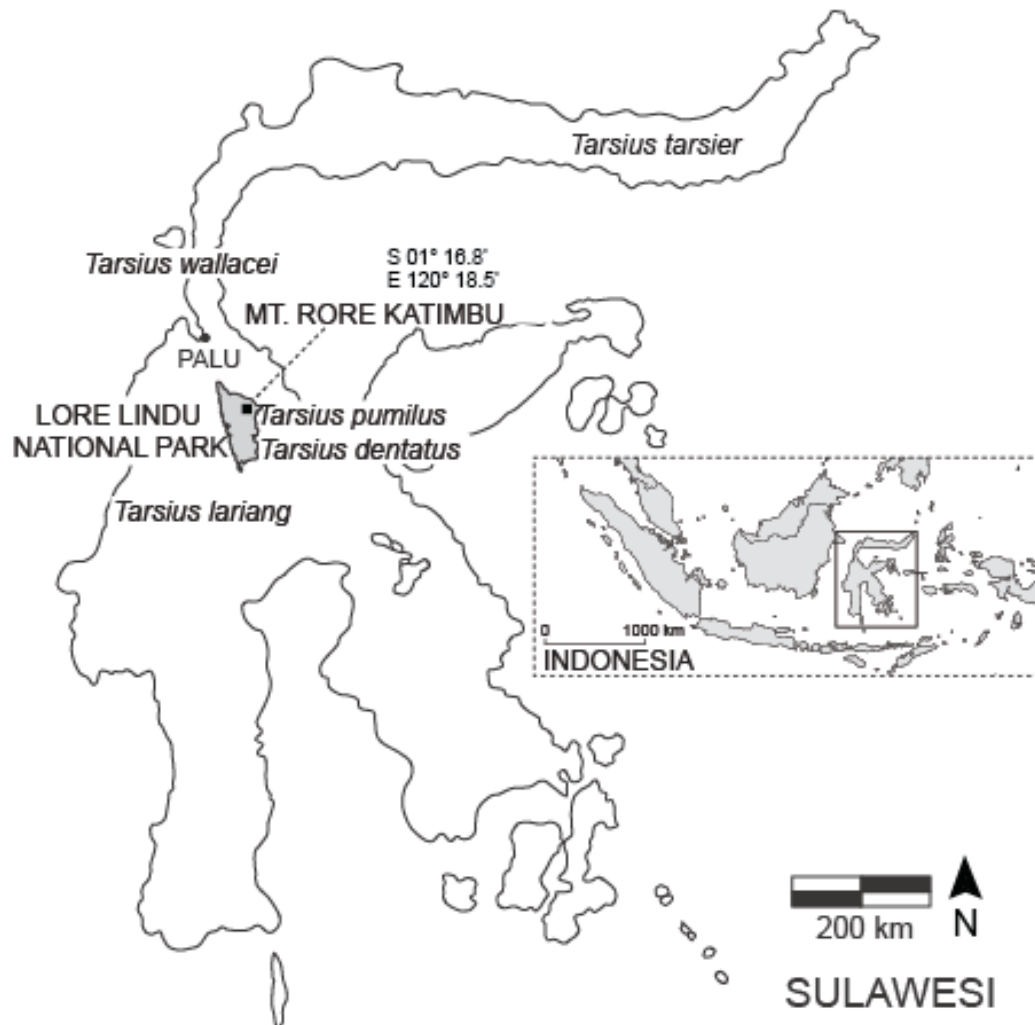


With a highest peak over 2400m, Mt. Rore Katimbu is the tallest mountain within Lore Lindu (Pangau-Adam 2003).  Mt. Rore Katimbu is one of the few mountains with an easily accessible summit, due to a defunct 5 km logging road that has degenerated

into a trail used mainly by pedestrians, motorcycles, and off-road vehicle traffic. During this study, motorcycle traffic occurred on a daily basis, often with large groups of individuals traveling together to harvest forest resources near the mountain summit.

Within Lore Lindu National Park, rainfall is evenly distributed throughout the year, averaging 3000 mm per year (Schweithelm et al. 1992). While there is no clear wet or dry season in Central Sulawesi, rain falls heaviest during the monsoon period between November and April (Pangau-Adam 2003). Seasonality does not usually change with altitude in the tropics (Körner 2007), so although the highlands receive more rain, seasonal changes do not differ between the highland and lowland habitats.

Three species of tarsier live within the boundaries of the national park: the Lariang tarsier (*T. lariang*) and Dian's tarsier (*T. dianae*) at lower altitudes, and pygmy tarsiers in the upper montane forest. While the lower montane forest of Mt. Rore Katimbu (below 1500 m) is dominated by large, buttressed trees, especially oaks, trees gradually become shorter and thinner at higher elevations (Whitten et al. 2002). Between 1900 and 2000 m vegetation changes abruptly to be dominated by the moss-covered conifers of upper montane forest, and above 2000 m the canopy lowers in height and becomes more discontinuous, resulting in denser undergrowth (Whitten et al. 2002). Predators of tarsiers are present in this area, including diurnal forest raptors, which are the predominant birds of prey in Central Sulawesi (Thiollay and Rahman 2002) and are among the most common predators of tarsiers (Gursky 2002a).

Base camp was established at 2120 m, near the top of Mt. Rore Katimbu (01° 17′32.4″S and 120°18′21.8″E). The road divides the east and west sides of the mountain, and is often narrower than 10 m in width, with frequent canopy continuity overhead. The mountain comprises mid-montane (above 1800 a.s.l.) and upper

montane (above 2100 a.s.l.) forest with low-level fragmentation stemming from past

logging and current small-scale exploitation.  Forest edges, defined as the area

immediately preceding the change to open habitat, occurred within 10 m of the road.

## 2.3 SAMPLING

Tarsier and ecological surveys were conducted during June 2007, August

through September of 2008, June through September of 2010, and January through

February 2012.  Within a 1.2 square kilometer area bisected by the road, 24 one-

hectare quadrats were established on the east and west sides of the mountain.

Sampling took place at six 100 m altitudinal increments between 1800 and 2300 m, with

elevation measured by a GPS receiver (Garmin) and digital altimeter (Suunto).  The

slope of the mountain is not uniform, with a steeper slope at higher altitudes; lower

altitudes thus encompass more land area and a greater proportion of quadrats.  In order

to account for seasonal or temporal variation, data collection was rotated between each

of the altitudinal intervals on a weekly basis.

### 2.3.1 Tarsier Capture Methods

Direct observation of pygmy tarsiers is difficult because they are small-bodied

and engage in cryptic nocturnal behavior, with no audible vocalizations.  The tarsiers

were sampled by capturing them with mistnets (Avinet 4-shelf nylon; 6 and 10 m

length), supplemented with visual identification of noncaptured individuals.  Mistnetting

is a standard method to capture lowland Sulawesian tarsier species (Fogden 1974;

Gursky 1995; MacKinnon and MacKinnon 1980; Merker 2006) and was previously used

to successfully capture pygmy tarsiers (Grow and Gursky-Doyen 2010).  Each night,

nets were positioned at a single altitudinal interval (5 nets per quadrat), rotating

between altitudes each week.  Nets were opened at dusk, checked hourly, and closed

at dawn.  Within each quadrat, nets were selectively placed in vegetation that pygmy

tarsiers are known to use as forage habitat, including areas with dense accumulations

of lianas, small trees, and undergrowth.

Immediately after capture, the tarsier was placed in a fabric holding bag and

weighed with a digital scale (Ohaus).  A radio transmitter (Wildlife Materials Inc. and

Lotek Wireless; 151 Mhz frequency) weighing 2-3 grams and less than 2 inches in

length (less than 5% of adult body weight) was glued to the lower back fur of all adults;

these transmitters adhere for less than one month.  Two Lotek Pip Ag386 backpack

tags with temperature sensing weighed 2.6g, and two Lotek Pip Ag393 tags with activity

sensing weighed 2.67g.  All captured individuals were released within one hour.  During

daytime, a waterproof radio receiver (Wildlife Materials Inc.) and a three-element Yagi

antenna were then used to locate tagged individuals in sleeping trees.  This allowed

observation of the group members associated with the sleeping site.

### 2.3.2 Morphological Data Collection and Sample Collection

For all captured individuals, standard external morphometric measurements

were taken with digital calipers (Table 5; Figure 5).  These measurements include:

weight, ear length and width, head length and width, upper and lower hindlimb length,

upper and lower forelimb lengths, foot lengths, third toe length, tail length, testes length

and width, and total body length.

**Table 5. Recording parameters for external measurements of tarsiers.**

| Variable | Recording Parameter |
|---|---|
| Forelimb | Axillary region to the tip of the third longest digit (excluding the nail), with all joints extended |
| Hindlimb | Groin to the end of the longest (fourth) digit, with all joints extended |
| Thigh | Groin to center of the knee, along femur (upper hindlimb) |
| Hindfoot | Proximal end of tarsal bone to distal end of longest (fourth) digit |
| Upper arm | Axillary region to elbow, along humerus |
| Forearm | Elbow to tip of longest digit, excluding nail |
| Tail | Ventral side of tail from base (perianal region) to tip |
| Body | Base of head to base of tail, along dorsal side |

**Figure 5. Diagram of external measurements for live tarsiers.**
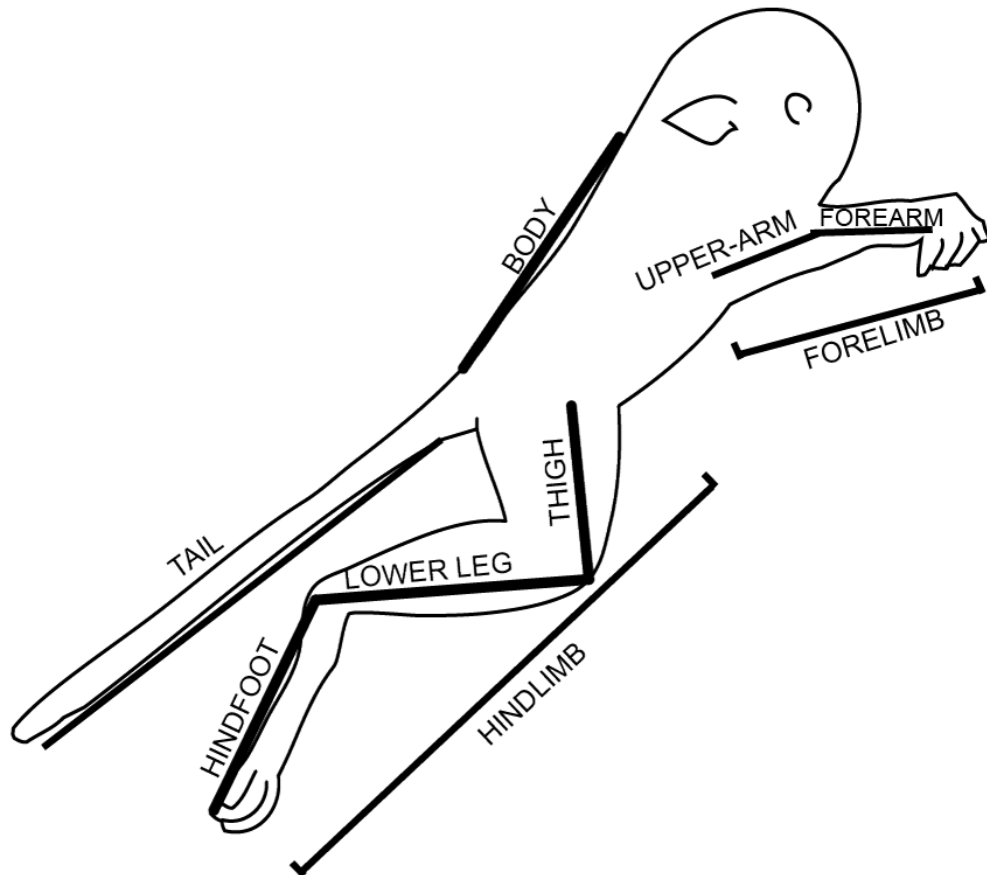
Hair and fecal samples were also taken.  Blood samples were taken from the tail of all captured individuals and stored on Qiagen FTA Spot Cards.  In some instances, small ear biopsies (2 mm$^2$) were taken from sterilized areas and stored in 70% ethanol.

All samples were stored in a refrigerated locker at Bogor Agricultural University in Java, Indonesia.  In 2012, the PI extracted DNA from these samples in collaboration with Stefan Merker (Evolutionary Ecology Group, Goethe University Frankfurt, Germany) using a DNeasy Blood and Tissue Kit (QIAGEN).  The samples were then whole genome amplified (WGA) using a GenomiPhi DNA Amplification Kit. A CITES export permit was received in May 2013, and the twelve WGA products were shipped to Germany at Goethe University Frankfurt, where they currently reside.

### 2.3.3 Group Demographics

Sex and age of identified tarsiers were determined by visual observation using age categories based on weight, dentition, and reproductive condition.  The reproductive status of females (pregnant, not pregnant, or lactating) was assessed by palpation.  Broad age classes are as follows: infant (inability to leap, body size half that of adults), subadult (<50g; testes not descended in males), adult (>50g, testes descended in males or nipples distended in females), and old adult (>50g, teeth show signs of decay and wear).

Group demographics were assessed by determining the size and sex composition of each group, number of individuals per group, total number of groups, and distances between groups.  Groups were defined as the set of individuals who share a sleeping site (Gursky 1995); the number of individuals observed leaving or entering the sleeping site determines group size.  The sex of all captured individuals

was determined, while sex remains unknown for those observed but not captured at the sleeping site.

### 2.3.4 Ecological Surveys

Ecological data was collected at each altitudinal interval, with elevation measured with an altimeter.  At each altitudinal interval, forest composition was assessed within two 20 m$^2$ vegetation plots on either side of the road.  Taking into account the amount of shrubs that occur along forest edges, plots began 10 m from the middle of the road. Within each plot, all trees were counted and identified when possible.  For each tree, height (m), dbh (m), and basal area (m$^2$) were measured (Brower et al. 1990), and degree of moss cover was estimated (categories 25% or less, 25-50%, 50-75%, and 75-100%).  Along 100 m transects within each plot, the degree of canopy cover at 10 m intervals was measured by recording the intensity of daylight (lux) with a digital light meter (Nikon).  The measurements for sleeping trees and the height of the sleeping site relative to the tree were also recorded.

Airborne insects were sampled with malaise traps established for one week per altitudinal interval on the east and west sides of the mountain, as well as in the road. Larger insects were identified to order, measured and weighed, and stored in 70% ethanol.  The total biomass from each sample location was determined by the dry weight of those specimens.

### 2.3.5 Behavioral Data Collection

Tarsiers were observed for a period of 80 nights. Locational data was collected on ranging and travel patterns, including nearest neighbor distances, with the

assistance of radio telemetry, tape measures, a GPS, a compass, and flagging tape. Behavioral focal follows were conducted with standardized sampling methods (Altmann 1974; Martin and Bateson 1993). Follows also included continuous *ad libitum* collection of all-occurrences data on vocalizations, scentmarking, and intragroup or intergroup encounters.

Data on ranging patterns include home range size (ha), the altitudinal range of each group, proximity between group members and between groups, as well as sleep tree diameter, height, and species, its occupancy duration, and times when the tree was entered and exited. Data on travel patterns include nightly travel distance, travel height, substrate usage, and leaping distances. Data on substrate usage was also collected for each tree the tarsiers were found to occupy. This includes tree species, diameter and height, the percent of moss cover on the tree, the support type used (tree trunk, tree branch, tree buttress, undergrowth, vine, ground), support diameter and height from ground, and the substrate's orientation (vertical (80-90), angled (45-80), horizontal (45), or sloping (10-45)). Posturing and substrate data was collected using previously outlined definitions (Crompton and Andau 1987), and leaping distance between substrates was recorded. Sleep tree height was estimated with a clinometer and DBH will be measured (Brower et al. 1990), and the height of the sleep hole relative to the tree was also recorded.

## 2.4 DATA ANALYSIS

### 2.4.1 Estimation of Population Density and Distribution

The population density of pygmy tarsiers was estimated using the quadrat census method of fixed point counts (National Research Council Committee on

Nonhuman Primates 1981), based on captures within the 24 one-hectare quadrats on either side of the road.  Density was estimated (number of individuals per square kilometer) by dividing the number of observed individuals by the total sample area, using the equation $D_i = n_i/A$, where $n_i$ is the number of individuals counted and $A$ is the total area (Brower et al. 1990).   Because a variety of fauna were captured in the mistnets, the relative species density (proportion of all captured species) of pygmy tarsiers was calculated with the equation $RD_i = D_i/\sum D$) (Brower et al. 1990).  In order to quantify the spatial distribution of pygmy tarsier groups Morisita's Index of Dispersion, $I_d = n * [(\sum X^2 - N)/N(N-1)]$ was calculated, where $n$ is number of plots, $N$ is the number individuals in all n plots, and $X$ is the number of individuals per plot (Brower et al. 1990). Under this index, $I_d = 1.0$ indicates a random dispersion, $I_d = 0$ indicates a perfectly uniform dispersion, and $I_d > 1.0$ indicates a patchy distribution; the maximum aggregation of individuals in one plot occurs when $I_d = n$ (the number of plots sampled).

### 2.4.2 Ecological Assessments

Statistical calculations were conducted using the SPSS 16.0 and JMP 10 software packages.  To determine differences in forest composition (tree density, size, basal area, and moss coverage) according to altitude or side of road, Student's $t$-tests and Pearson's chi-square tests were conducted.  Where appropriate, differences between means were compared with one-way analysis of variance (ANOVA), followed by the Tukey-Kramer multiple comparisons test or an unpaired $t$-test.

Pearson's chi-square tests were conducted to determine whether insect biomass and frequencies differ with distance to road and altitude.  Due to small sample sizes and the violation of the normality assumption, the Wilcoxon signed-rank test (non-

parametric alternative to Student's *t*-test) was used to compare sleeping trees to available trees.

### 2.4.3 Home Range Calculation

Home range, the area used by tarsiers, was calculated for all radiotracked individuals.  Garmin BaseCamp 4.0.1.0 was used to download spatial movements recorded with GPS, as well as to visualize and measure nightly distances.  For each focal individual, minimum home range size based on all known focal sightings (Bearder and Martin 1979) was estimated using the minimum convex polygon (MCP) method (White and Garrott 1990).

The software package BIOTAS 2.0a (Ecological Software Solutions LLC) was used to calculate MCP.  Because the 100% MCP estimator is sensitive to sample size, data area curves were calculated to explore sample size effects.  Home ranges are only reported for individuals with a sufficient number of location points to accurately calculate home range.  This number was established by creating individual sample size area curves using BIOTAS 2.0a, to ensure an asymptote had been reached prior to estimating home range (Haines et al. 2006).  The degree of spatial overlap between individual home ranges was assessed by the Schluter multivariate test for significant associations between points , where the null hypothesis is that there is no association. This analysis is performed on a grid of square quadrats and compares the densities of points for each individual in each quadrat.

### 2.4.4 Nightly Path Length Calculation

The distance traveled on a nightly basis, nightly path length (NPL), was calculated for radiotagged individuals.  NPL is determined by adding together the consecutive distances (measured with an electronic rangefinder and tape measures) between locations obtained from radiotracking during 12-hour shifts. Nightly path length (NPL) was estimated as both a rate per hour, and as a total length.  Locations were sampled every 15 minutes, and coordinates were recorded using a GPS receiver.  In the event that the focal tarsier's location could not be discerned at a 15-minute interval, the distance between the next available point and the last known location was used in the calculation of total NPL.  The NPL of all individuals started and ended at the sleeping site.

### 2.4.5 Limb Proportion Comparisons

An interspecific comparison of tarsier limb proportions was conducted based on right external measurements of live tarsiers.  Data (n=58) include Sulawesian tarsiers: *Tarsius pumilus* (n=17), *T. spectrum* (n=12; Gursky 1997), and *T. wallacei* (n=10; Merker et al. 2010), as well as the Philippine tarsier (Bohol), *T. syrichta* (n=19).  Linear characters were standardized by $\log_{10}$ transformation or scaling the variable by the cube root of body mass. Discriminant function analysis was performed on standardized linear variables in order to distinguish between pygmy tarsiers and lowland tarsiers. Canonical discriminant analysis generated linear functions that predicted group membership according to species and geographic location, using a step-wise variable selection procedure. Linear regressions of log-transformed mass and limb

measurements were compared between pygmy tarsiers and lowland tarsier species grouped together.

### *2.4.6 Morphometric Analysis*

*2.4.6.1 Testes Size Comparisons*

**2.4.6.1.1 Datasets**

Body weights and testes measurements of adult wild tarsiers come from a combination of unpublished and published values. Wild tarsier weights include: *Tarsius pumilus* (N=17) (this study); *Tarsius dianae* (N=44) (Tremble et al. 1993, n=6; Merker 2003, n=29; Shekelle 2003, n=7; Gursky 1997, n=2); *Tarsius spectrum* (N=42) (Gursky 1997, n=21, Shekelle 2003); *Tarsius bancanus* (N=12) (Wright et al. 1987); *Tarsius syrichta* (N=10) (Neri-Arboleda 2002, n=10); *Tarsius lariang* (N=8) (Merker and Groves 2006); and *Tarsius wallacei* (N=8) (Merker et al. 2010). Testes measurements include *T. pumilus* (N=6) (Grow unpublished data), *T. spectrum* (N=9) (Gursky 1997), and *T syrichta* (N=7) (Gursky unpublished data). Data for other primate species are taken from Harcourt et al. (1995). Because primate testes volume can vary according to breeding season, testes volumes were taken during a breeding season, as determined by the presence of pregnant females.

**2.4.6.1.2 Testes Measurements and Analyses**

Testicular volume (TV) was calculated from length and width measurements using the equation for a regular ellipsoid: $TV = (\pi W^2 * L) / 6$ (Bercovitch 1996, Dixson et al. 1980, Kappeler 1997). Testes weight was calculated from volume using the formula:

Testes weight = TV*2*1.1, where 1.1 is the conversion factor for calculating weight of body tissue (Harcourt et al. 1995).

Gonad mass as a proportion of body mass ('gonadosomatic index' or GSI) is a measure of sperm competition. High GSI indicates sperm competition is occurring (Pochron and Wright 2002, Wright et al. 2003). In order to compare relative testes size between species, a linear regression of log transformed male testes mass (Harcourt et al. 1981) controls for body size. Species located above the regression line (high GSI) undergo sperm competition, and have relatively larger testicles than expected from body size (Harcourt et al. 1981, Kappeler 1997). Species below the regression line experience less sperm competition, and therefore should have fewer breeding males. Degree of sexual dimorphism was assessed by male weight as a percentage of female weight, calculated with the equation: Average male weight / Average female weight X 100 (Kappeler 1991).

*2.4.6.2 Body Proportions*

An allometric analysis of pygmy tarsier limb proportions compared to other tarsier species was conducted based on standard external measurements of live tarsiers. Data (n=58) include Sulawesian tarsiers: *Tarsius pumilus* (n=17), *T. spectrum* (n=12) (Gursky 1997), and *T. wallacei* (n=10) (Merker et al. 2010), as well as the Philippine tarsier (Bohol), *T. syrichta* (n=19). Linear characters were standardized by log transformation or scaling the variable by the cube root of body mass. To test the hypothesis that pygmy tarsiers have distinct body proportions from other species, canonical discriminant analysis was performed (JMP 10.0.0, SAS Institute Inc.; SPSS

21.0.0, IBM) on scaled linear characters to generate linear functions that predict group membership according to "pygmy" status, species, and geographic location.

# 3. POPULATION DENSITY, DISTRIBUTION, GROUP COMPOSITION, AND HABITAT ASSOCIATIONS OF *TARSIUS PUMILUS*[*]

## 3.1 BACKGROUND

### 3.1.1 Altitudinal Effects on Primate Density and Distribution

Altitudinal changes correspond to shifts in ecology that are important to primate evolution.  The specialized traits of high-altitude primates allow us to understand how primates respond to ecological pressures in a range of environments, in terms of both intraspecific behavioral plasticity and interspecific variation.  Habitat productivity declines at higher altitudes, and primates are affected by the decrease in foraging efficiency in multiple ways, including decreased dietary diversity, decreased dietary quality, and reduced body size.  In terms of dietary diversity, groups of mountain gorillas (*Gorilla beringei beringei*) at higher altitudes consume fewer plant and fruit species than do groups at lower altitudes, which corresponds to a decrease in plant species diversity at higher elevations (Ganas et al. 2004).  Primates at higher altitudes also consume a greater proportion of lower quality foods, as observed among gibbons (*Hylobates lar*) (Caldecott 1980).  At higher altitudes, primates have also been observed to increase the proportion of time spent feeding, as observed among gelada baboons (*Theropithecus gelada*) (Iwamoto & Dunbar 1983).  Decreased foraging efficiency at higher altitudes may relate to reduced body size, as indicated by the smaller average body mass in high-altitude male geladas (Popp 1983).

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[*] The data reported in this section are reprinted with permission from "Altitude and Forest Edges Influence the Density and Distribution of Pygmy Tarsiers (*Tarsius pumilus*)" by Nanda Grow et al., 2013 in the *American Journal of Primatology*, Volume 75, pp. 464-477, Copyright 2013 Wiley Periodicals LLC.

Primates can mitigate the effects of altitude on foraging efficiency and competition through population size and distribution. In particular, increased scramble competition at higher altitudes can lead to decreased population density (Byrne et al. 1993). Primate abundance is known to decline at higher altitudes, as has been documented among Japanese macaques (*Macaca fuscata*) and red colobus monkeys (*Procolobus gordonorum*) (Hanya et al. 2004; Marshall 2005). In this section, I explore the effects of altitudinal ecology on the population density and distribution of pygmy tarsiers at altitudes at 2000 m and above.

A number of studies have found variation in primate densities and distributions is associated with foraging pressures at higher altitudes, including increased home range sizes, decreased group sizes, and decreased density (Table 6). Primates can adjust to altitudinal effects on foraging competition in two ways: reduce direct contest competition by living in smaller groups, or reduce overall scramble competition by living at a lower population density (Byrne et al. 1993). Mountain-dwelling baboons (*Papio ursinus*) were found to live at a lower population density at high altitudes, with no difference in contest competition (displacements) or nutritional intake between high and low altitude populations (Byrne et al. 1993); the baboons were not observed to use discrete food patches at any altitude. The effect of direct of indirect competition at higher altitudes may relate to the spatial and temporal distribution of food resources. For example, frugivorous *Ateles* spp. have smaller foraging groups at higher altitudes (Shanee 2009), and *Ateles* is known to engage in fission-fusion foraging patterns to minimize feeding competition when ripe fruit is rare and widely dispersed (Norconk and Kinzey 1994). Given the assumption of decreased resource availability in higher altitudes, it was predicted that pygmy tarsiers would exhibit lower population density than lowland

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Sulawesian tarsiers.  It was also predicted that pygmy tarsiers would maintain smaller groups than lowland tarsiers.

**Table 6.  Summary of previous studies that explored the effects of altitude on foraging patterns among primates.**  High-altitude adaptations include a decrease in population density (scramble competition), decreased group size (contest competition), and an increase in home range size at higher altitudes.  Mean values are given; refer to original publications for sample sizes and definitions of "high" and "low" altitude in each study.

| High Altitude Adaptation | Species | High Altitude | Low Altitude | References |
|---|---|---|---|---|
| Smaller population density (scramble competition) | Mountain baboons *Papio ursinus* | 0.95 individuals/km$^2$ | 1.87 individuals/km$^2$ | Byrne et al.1993 |
| | Bornean white-bearded gibbons *Hylobates abibarbis* | 0.44 individuals/km$^2$ | 4.20 individuals/km$^2$ | Marshall 2009 |
| | Red colobus *Procolobus gordonorum* | 0.24-0.48 groups/km | 0.70-0.88 groups/km | Marshall et al. 2005 |
| | Japanese macaques *Macaca fuscata* | 0.21 groups/hour | 0.41 groups/hour | Hanya et al. 2004 |
| Increased home range size (foraging efficiency) | Javan gibbons *Hylobates moloch* | 37 ha | 17 ha | Kim et al. 2011; Kappeler 1984 |
| Smaller foraging groups (contest competition) | Nilgiri langur *Semnopithecus johnii* | 4.25 individuals/group | 6.50 individuals/group among lower elevation Hanuman langurs (*S. entellus*) | Kumara & Singh 2004 |
| | Japanese macaques *Macaca fuscata* | 13.60 individuals/group | 21.70 individuals/group | Hanya et al. 2004 |
| | Spider monkeys *Ateles* spp. | Group size decreases 1 individual per 100 m increase in altitude | | Shanee 2009 |
| | Mountain baboons *Papio cynocephalus ursinus* | Troops at high altitudes divide into increasingly smaller and unsustainable groups | | Henzi et al. 1990 |

Another variable that influences primate density and dispersion is the distribution of forest edges.  Forest fragmentation causes edge effects, where environmental

continuity is disrupted and the ratio of the forest perimeter to the total forest area increases (Bogaert et al. 1999). Forest boundaries possess attributes of a microhabitat, with distinctive vegetation structure, resource availability, and animal abundance in comparison to the forest interior (Kremsater and Bunnell 1999). Tree height declines along forest edges, and shrubby vegetation increases (Kremsater and Bunnell 1999).

According to socioecological theory, the distribution of resources influences the distribution and social behavior of primate populations (Vogel and Janson 2011). By extension, the distribution and density of primates is affected by microhabitat variation, including the availability and distribution of forest edges. In general, with a lower canopy, forest edges offer increased insect biomass (Malcolm 1994) and increased light penetration for nighttime navigation (Kremsater and Bunnell 1999), making edges ideal foraging habitat for nocturnal, insectivorous primates.

### 3.1.2 Responses to Forest Edges

Primates with different diets should respond to forest edges differently. Because certain types of insect prey are more abundant near forest margins, insectivores can benefit from remaining near edges and therefore may be more "tolerant" of forest edges than primates that do not consume insects (Lehman et al. 2006a). For example, frugivorous greater dwarf lemurs (*Cheirogaleus major*) exhibit a negative edge effect and reduced densities near forest edges (Lehman 2006). On the other hand, Geoffroy's marmoset (*Callithrix geoffroyi*) was found to occupy forest edges where their primary food resources, gums and insects, were more abundant (Passamani and Rylands 2000). The marmosets fed on gums 68.6% of the time, most heavily from lianas, and fed on invertebrates 14.6% of the time (Passamani 2000); both of these food sources

favor areas with increased light exposure and are more abundant along forest edges (Passamani and Rylands 2000). Similarly, in southeastern Madagascar omnivorous grey mouse lemurs (*Microcebus rufus*) that consume insect prey have been observed to range closer to forest edges than less insectivorous lemurs, including *Propithecus diadema edwardsi*, *Lepilemur microdon*, and *Eulemur fulvus rufus* (Lehman et al. 2006a). In western Madagascar, although the abundance of arboreal, nocturnal airborne insects did not differ between forest edges and the interior, lesser mouse lemurs (*Microcebus murinus*) were observed to have a biased distribution near forest edges where a preferred insect food source, Homopteran secretions, were more abundant (Corbin and Schmid 1995).

The insects exploited by tarsiers may exhibit a positive edge effect. Tarsiers only consume arthropods (Gursky 1997; MacKinnon and MacKinnon 1980; Niemitz 1984a). Spectral tarsiers have been observed to consume primarily Lepidoptera (31.58% of diet) and Orthoptera (23.60%), along with Hymenoptera (13.24%), Isoptera (13.08%), and Coleoptera (11.32%), where most of these prey were obtained from leaves (46.3%) or the air (34.8%) (Gursky 2000b). Flying arthropods, especially Coleoptera, have been found to have a significant edge preference in pine forest, and the total abundance of arthropods was found to decline as distance from edge increased (Jokimaki 1998). Although we lack data on the diet of pygmy tarsier, their diet is assumed to be similar to that of all other tarsier species.

Edges are known to influence the distribution of fauna in Central Sulawesi; for example, avian diversity is greater along anthropogenic edges within Morowali Nature Reserve (Alvard and Winarni 1999). At high altitudes in Central Sulawesi, major sources of anthropogenic edges are rudimentary roads. Roads are a significant source

of forest fragmentation, and create more than 1.5 times the amount of edge habitat as clearcuts do (Reed et al. 1996). Road edges exploited by pygmy tarsiers are characterized by low-level disturbance. In many cases, these illegal logging roads were used decades earlier, and are now pedestrian and motorcycle paths that are used daily, along with the occasional all-terrain vehicle. Considering the effects of altitude and forest edges on both insect availability and primate density, pygmy tarsiers might use road edges as a means of compensating for reduced food availability at higher altitudes. Due to this potential increase in food resources along anthropogenic forest edges, it was predicted that pygmy tarsiers would exhibit higher abundance near anthropogenic edges.

In this section, the abundance and spatial dispersion of pygmy tarsiers is discussed. Initial results suggest that pygmy tarsiers appear to live at lower density than lowland Sulawesian tarsier species (Grow and Gursky-Doyen 2010), with a nonrandom distribution near forest edges. Their ranging activity and sleeping site selection may be influenced by food availability near anthropogenic edges, resulting in higher than expected abundance.

## 3.2 RESULTS

### 3.2.1 Population Density and Distribution

Within the 1.2 km$^2$ sample area, six groups were observed with a total of 22 individuals. Based on the number of observed individuals in 24 1-ha plots, the mean number of individuals per hectare was 0.9167 individuals, with 0.25 groups per ha. The estimated population density was 92 individuals per 100 ha.

The mean group size was 3.60 individuals, and group size ranged from two to five individuals. Group composition was variable (Table 7). All groups contained an infant, a juvenile, or a lactating or pregnant female. A greater proportion of adult females than adult males were observed (Figure 6). The average distance between sleeping sites of neighboring groups was approximately 165 m, with six identified sleeping trees for four of six groups (some groups alternated trees, and the sleeping trees for two groups could not be located).

**Table 7. Group composition and altitudinal distribution for *Tarsius pumilus* on Mt. Rore Katimbu; question marks indicate unknown age or sex.**

| Group | n | Altitude | Sex | Age | Reproductive Condition |
|-------|---|----------|--------|-------------|------------------------|
| 1 | 4 | 2250 | Male | Subadult | |
| | | | Male | Subadult | |
| | | | Female | Adult | Not pregnant/lactating |
| | | | ? | ? | |
| 2 | 4 | 2300 | Female | Adult | Not pregnant/lactating |
| | | | Female | Adult | Not pregnant/lactating |
| | | | Male | Subadult | |
| | | | ? | Juvenile | |
| 3 | 3 | 2100 | Male | Older Adult | |
| | | | Female | Adult | Lactating |
| | | | ? | Infant | |
| 4 | 5 | 2100 | Male | Subadult | |
| | | | Male | Subadult | |
| | | | Male | Adult | |
| | | | Male | Adult | |
| | | | Female | Adult | Lactating |
| 5 | 2 | 2150 | Female | Adult | Pregnant |
| | | | Male | Adult | |
| 6 | 4 | 2000 | Female | Adult | Lactating |
| | | | Male | Adult | |
| | | | ? | Adult | |
| | | | | Infant | |

**Figure 6.  Age and sex demographics for *Tarsius pumilus* on Mt. Rore Katimbu.**
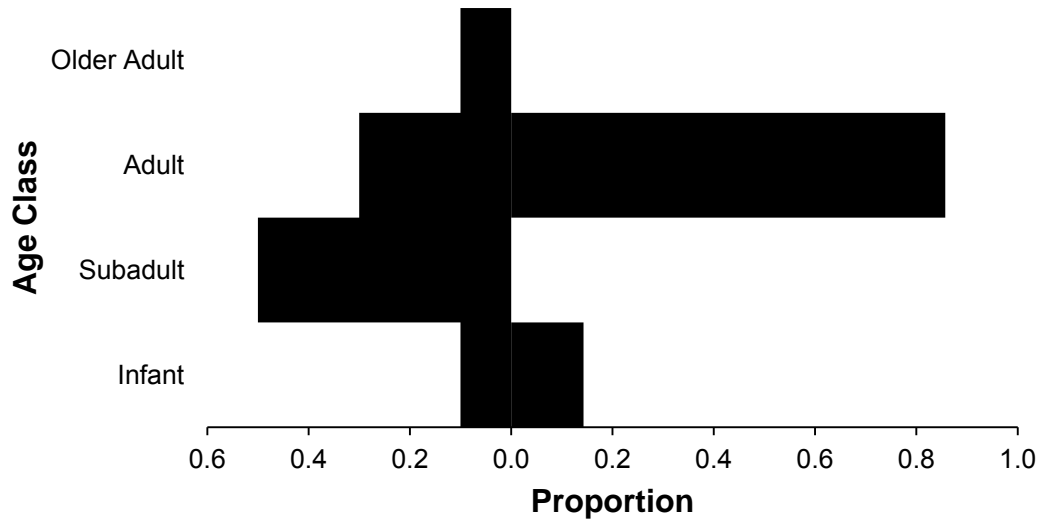


### 3.2.2 Spatial Distribution of Groups

Pygmy tarsiers were not randomly distributed throughout the sample area. Morisita's index of dispersion is $I_d$ = 2.55 (N=22 tarsiers, n=24 plots), indicated a tendency toward an aggregated, non-random distribution.  A comparison of observed and Poisson probabilities for the number of individuals in a plot shows that capture locations for pygmy tarsiers were clumped by the forest edge (Figures 7, 8).  The tarsiers were observed to remain near the edge when foraging and their sleeping trees were similarly located along edges; five out of six identified sleeping trees were located 35 m or less from an edge (Table 8). A Chi-square test for random dispersion also shows that dispersion is significantly different from random ($X^2_{0.05,19}$ = 30.144).

**Figure 7. Spatial and altitudinal distribution of pygmy tarsier individuals across the study area on Mt. Rore Katimbu, Lore Lindu National Park, Sulawesi, based on approximated capture locations from mistnets.** Pentagons indicate primary sleeping trees for four groups, ♀ indicates a female individual, ♂ indicates a male individual, and question marks (?) indicate observed individuals of unknown sex.
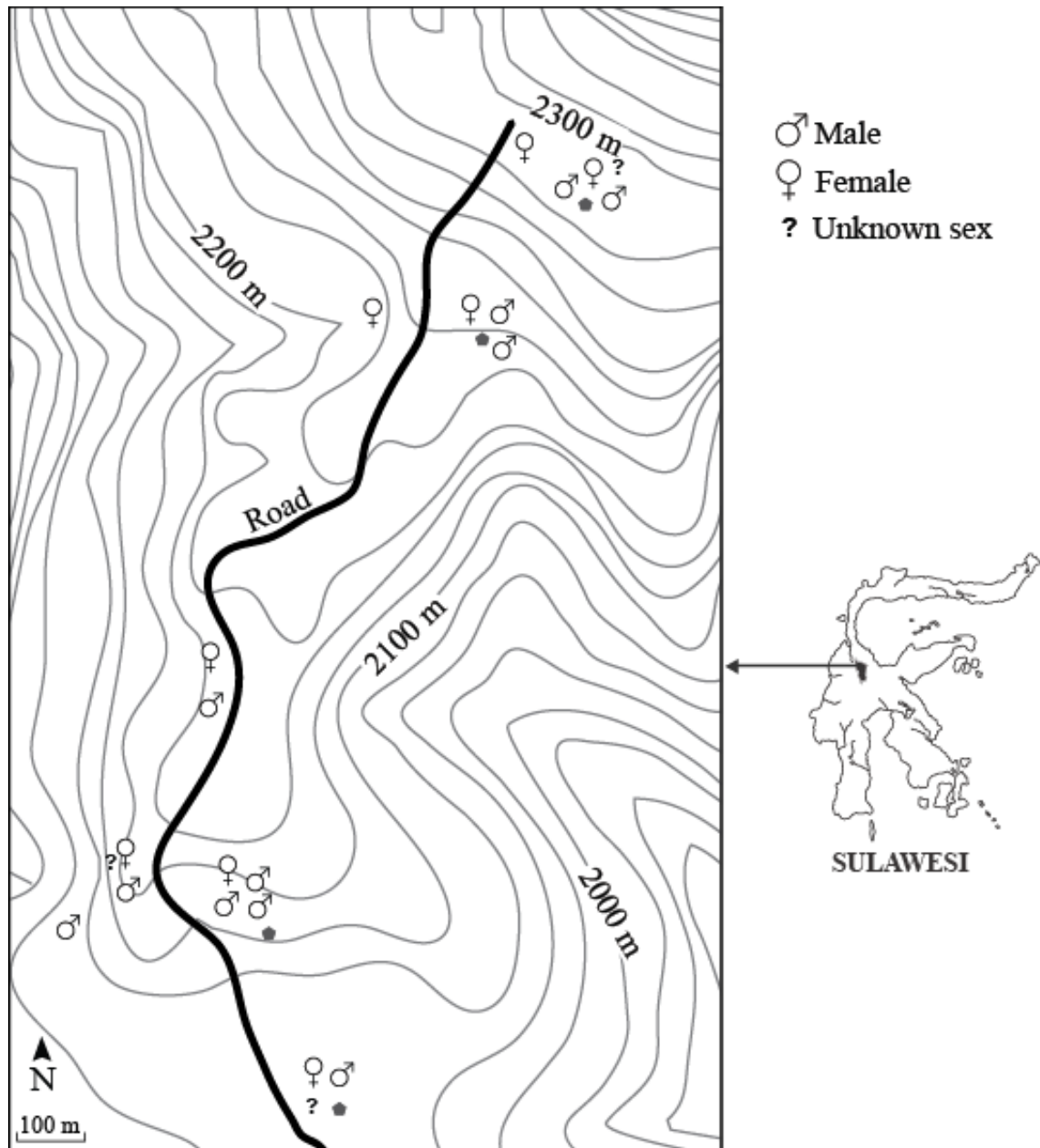
**Figure 8.  Observed and random probabilities of number of individuals in a plot.**
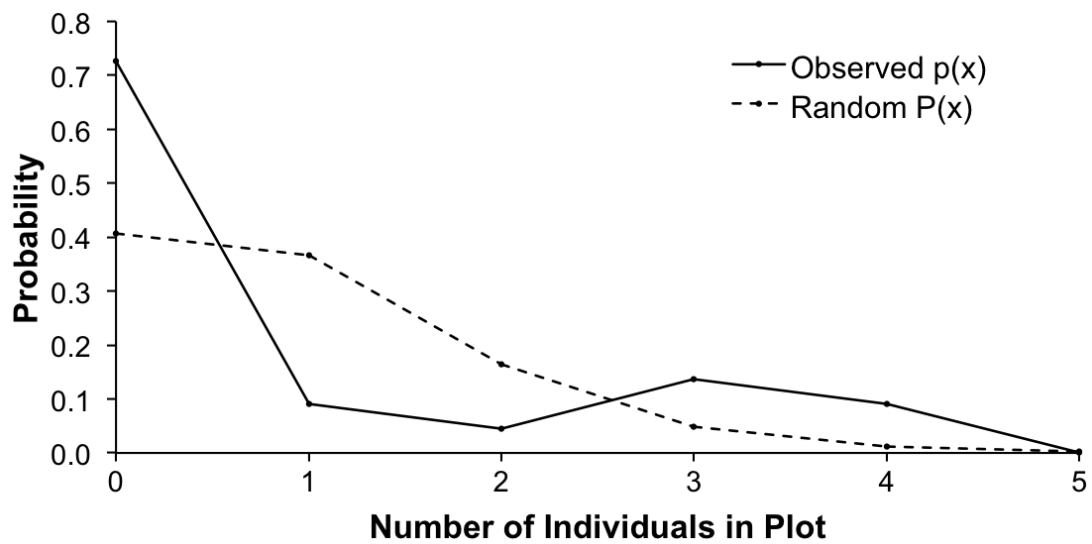


**Table 8.  Sleeping tree size and shortest distance to road for all located sleeping trees.**

| Group | Altitude | Height (m) | DBH (cm) | Distance to road (m) |
|-------|----------|------------|----------|----------------------|
| 1 | 2200 | 15 | 26.75 | 30 |
| 2 | 2300 | 25 | 37.58 | 157 |
| 2 | 2300 | 12 | 7.64 | 164 |
| 4 | 2100 | 20 | 22.29 | 35 |
| 6 | 2000 | 5 | 47.77 | 20 |
| 6 | 2000 | 19 | 86.94 | 110 |
| 6 | 2000 | 25 | 92.68 | 40 |

### 3.2.3 Ecological Data

The average daily precipitation at the study site was 9.64 mm, with no significant difference between altitudes.  Daily precipitation during the January-March research period (the "wetter" season) was higher than during the June-September period (10.86mm compared to 8.43mm).  At 2200m, the average daily temperature during the wetter season was 60.98 while the average daily temperature during the drier season was 65.49.  Besides tarsiers, 84 individuals representing at least 15 species were also live-captured in the nets (57 birds and 27 bats; Table 9).  Of these individuals, 84% were insectivorous.

**Table 9.  List of captured and released fauna at the study site.**

| Latin Name | Common Name | N | Diet |
|---|---|---|---|
| **Birds** | | | |
| *Eumyias panayensis* | Island Flycatcher | 5 | Insectivore |
| *Myza celebensis* | Lesser Sulawesi Honeyeater | 14 | Nectar |
| *Cyornis rufigastra* | Mangrove Blue Flycatcher | 4 | Insectivore |
| *Trichastoma celebense* | Sulawesi Babbler | 3 | Insectivore |
| *Cyornis hoevelli* | Blue Fronted Flycatcher | 10 | Insectivore |
| *Nectarinia jugularis* | Olive-Backed Sunbird | 1 | Nectar, insects |
| *Myza sarasinorum* | Greater Sulawesi Honeyeater | 3 | Nectar |
| *Pachycephala sulfuriventer* | Sulphur-vented Whistler | 2 | Insects, small animals |
| *Gerygone sulphurea* | Golden-Bellied Gerygone | 3 | Insectivore |
| *Rhipidura teysmanni* | Rusty-bellied Fantail | 6 | Insects, small animals |
| *Phylloscopus sarasinorum* | Sulawesi Leaf Warbler | 1 | Insectivore |
| *Accipter nanus* | Small Sparrowhawk | 1 | Carnivore |
| *Coracornis raveni* | Maroon-Backed Whistler | 1 | Insectivore |
| unknown | | 3 | unknown |
| | **Total** | 57 | |
| **Bats** | | | |
| Megaderma *spp.* | | 27 | Insectivore |
| | **Total Captured** | 84 | |

### 3.2.4 Forest Structure

Forest structure differs within the high-altitude range that tarsiers occupy. Twelve 20 by 20 m vegetation plots revealed that tree density (number per plot) varied

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by altitude, with higher density at lower altitudes (N=2343; Figure 9).  The low density at

1900 m corresponds to increased anthropogenic disturbance at that altitude.  Tree size

(the ratio of DBH to height) was significantly different between altitudes (Student's $t$-test:

α=0.05; $t$=1.961, $p$<0.001), with trees of the largest DBH and shortest stature occurring

at higher altitudes.  Forest composition varied with altitude in terms of vegetation

density, tree height (F=61.524, $p$<0.001) (Figure 10), basal area (F=4.543, $p$=0.0035),

and moss coverage (Pearson's chi square: $X^2$ = 608.982, df=9.0, $p$<0.0001).  There was

no significant difference between tree height, DBH, or basal area between the west and

east sides of the mountain at any altitude (Tukey-Kramer: α=0.05; q*=1.961), but moss

coverage was significantly different when all altitudes were pooled ($X^2$ = 119.989,

df=3.0, $p$<0.0001).

**Figure 9.  Tree density per 800 m$^2$ according to altitude and mountain slope.**
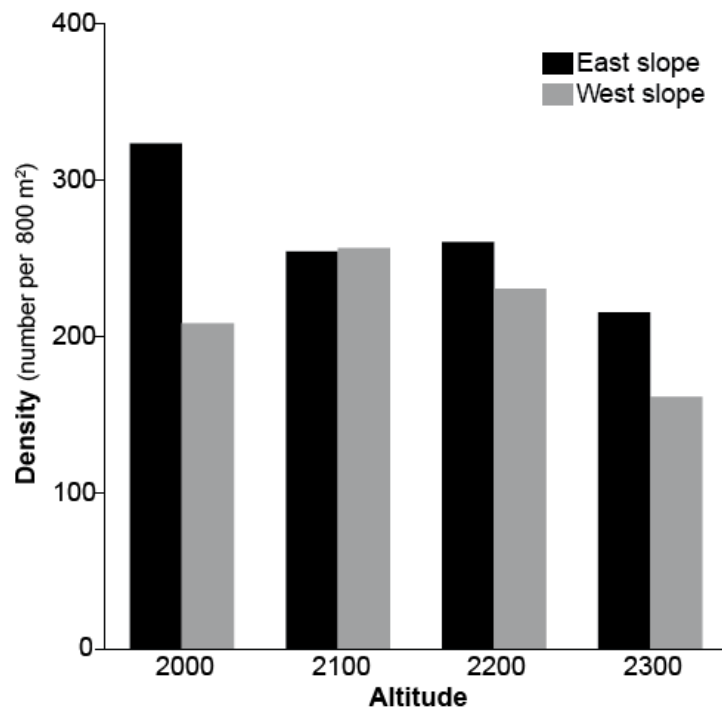
**Figure 10. Tree diameter at breast height (DBH) (m) according to altitude, measured in two 20 m by 20 m vegetation plots at each altitudinal interval (N=2343). Dashed line indicates grand mean.**
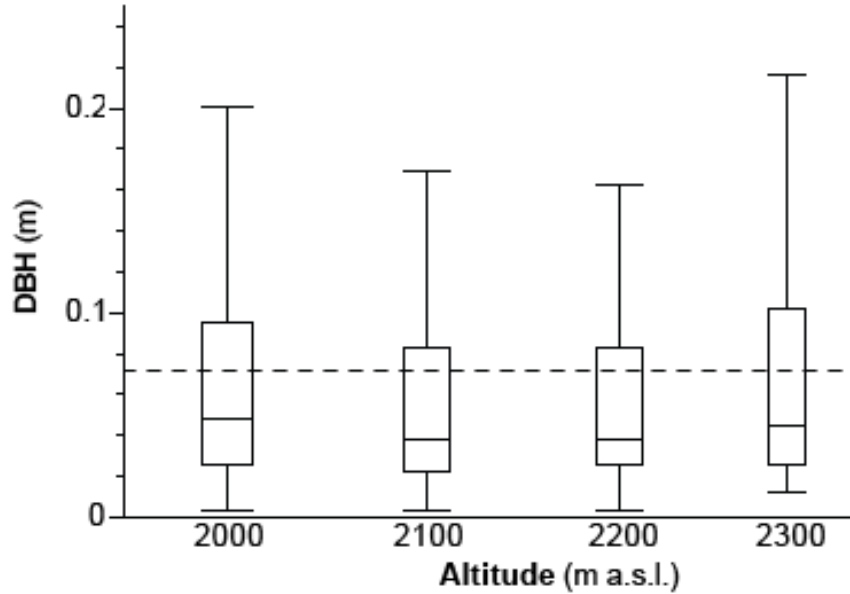


Vegetation plots indicated that mean tree height decreases at higher altitudes (Figure 11). Mean tree height is significantly different between all pairs of altitudes (Kruskal-Wallis: $q^*$=1.9599, α= 0.05, $p < 0.0001$), except for 2000-2200m, and 2100-2300m. Conversely, the basal area of trees increases at higher altitudes, where total basal area is larger at the highest altitudes sampled (Figure 12). Mean basal area of sampled trees was significantly different between altitudes, where the highest altitudinal interval (2300m) is significantly different from the lowest altitudinal interval (2000m) (Student's $t$-test: $t$=1.96121, α= 0.05, $p$=0.00283) and the next lowest altitude (2100m) ($p$=0.00216). Based on vegetation plots, the estimated total basal area per 1-ha at 2000, 2100, 2200, and 2300m a.s.l. is 47.01, 47.52, 63.19, and 65.38 $m^2$, respectively.

**Figure 11.  Boxplots of tree heights at the study site according to altitude, measured in two 20 m by 20 m vegetation plots at each altitudinal interval (N=2343).  Dotted line indicates grand mean.**
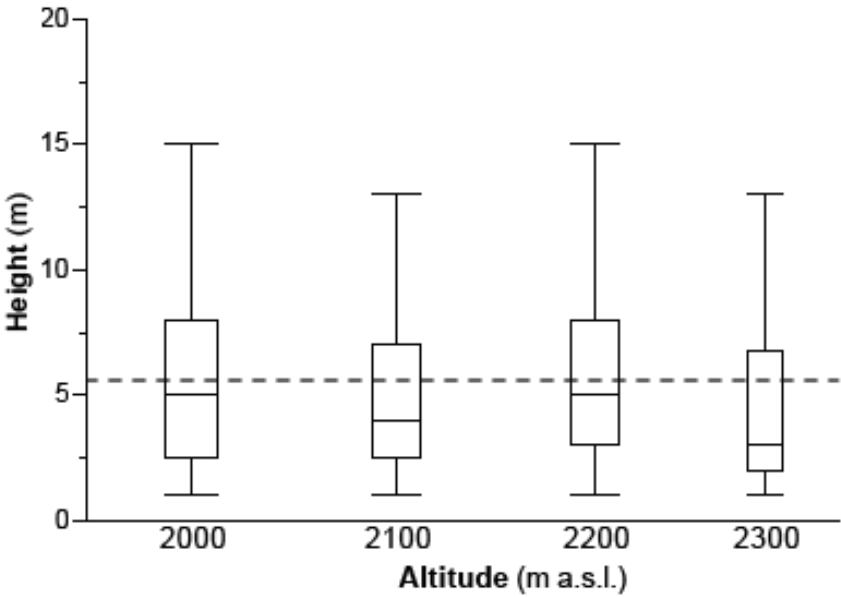


**Figure 12.  Total basal area of trees within 20m by 20m vegetation plots at each altitude.**
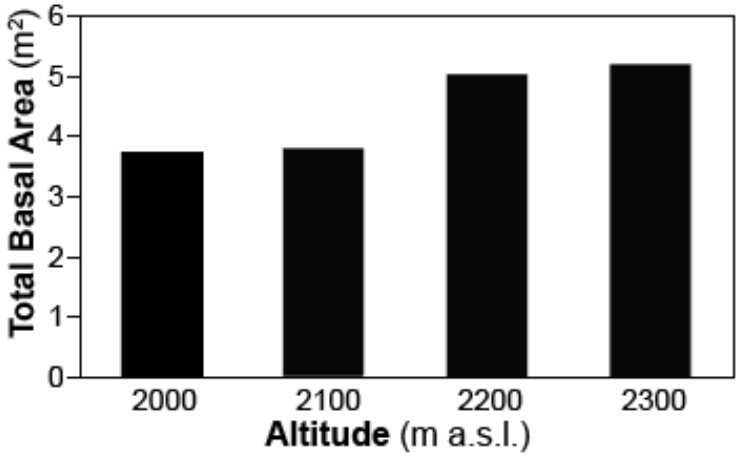
**Figure 13. Linear regressions of tree height plotted against basal area for each altitude. Open circles indicate sleeping trees.**
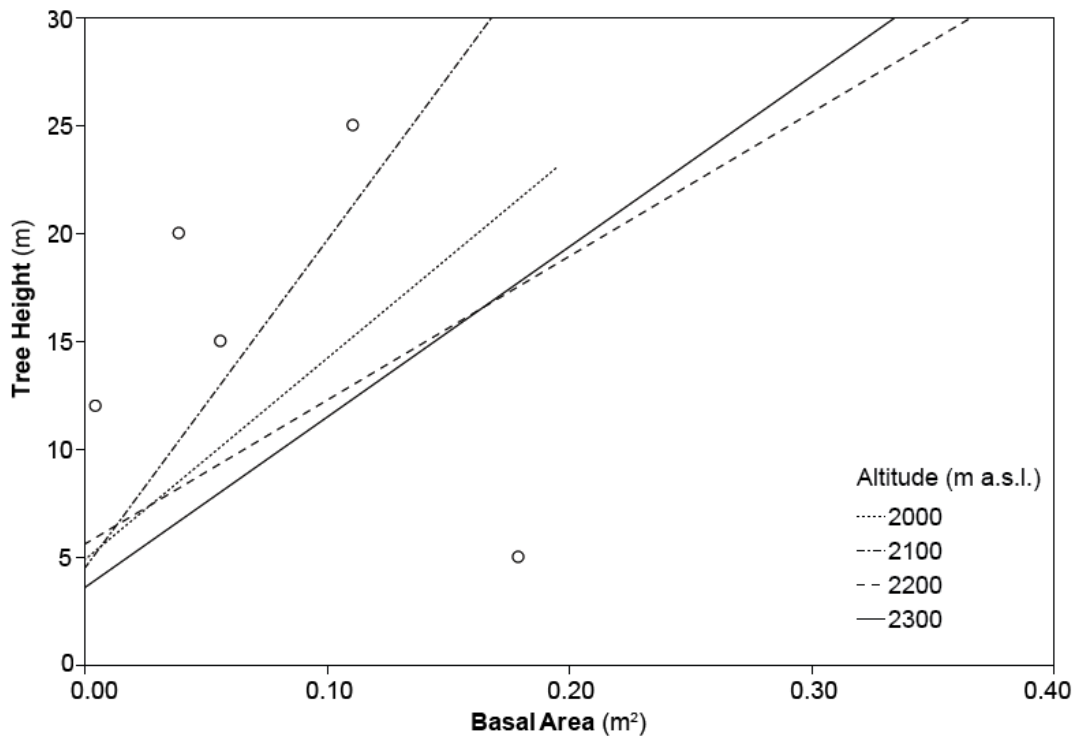


### 3.2.5 Sleeping Trees

In a plot of basal area against tree height, four out of five of the sleeping trees fell above the regression lines (Figure 13), indicating taller than average height. All sleeping trees were located less than 170m from the logging road (Table 10). There was no difference in luminous intensity recorded at each altitude (Wilcoxon: $X^2$=3.4046, df=3, $p$=0.3333), but pygmy tarsiers were found to select trees that allowed less light through (and hence provided more canopy cover) than most sampled trees (Figure 14). The average amount of luminous intensity underneath sleeping trees, recorded at the base of each tree, is 514.6 lux (n=6), while the average luminous intensity along transects at all altitudes is 1113.152 lux (n=66). The very small sample of sleeping trees limits statistical testing, but the difference in canopy cover between the samples of

sleep trees and available trees approaches significance (Wilcoxon: $X^2$ = 3.411, α= 0.05,

df=1, *p*=.0647).  Two evergreen trees used by pygmy tarsiers as sleeping sites were

identified from the Fagaceae family, including *Castanopsis acuminatissima* (white oak)

and *Lithocarpus havilandii*.  One sleeping tree was dead, indicating that even dead

trees are an important resource for tarsiers and should be included in vegetation

analyses.

**Table 10.  Characteristics of sleeping sites for *Tarsius pumilus*.**

| Group | Sleeping Tree Height (m) | Basal Area (m$^2$) | Light (lux) | Sleeping site height |
|---|---|---|---|---|
| 1 | 15 | 5.62 | 557 | Canopy |
| 2 | 25 | 11.09 | 728 | 15m |
| 2 | 12 | 0.46 | 746 | Canopy |
| 4 | 20 | 3.90 | 282 | 15m |
| 6 | 5 (stump) | 17.91 | 360 | Ground/root system |
| 6 | 19 | 59.34 | 260 | Canopy |
| 6 | 25 | 67.42 | 200 | Canopy |

**Figure 14.  One-way analysis of light intensity (lux) at base of trees, with sleeping trees compared to available trees sampled along transects.**
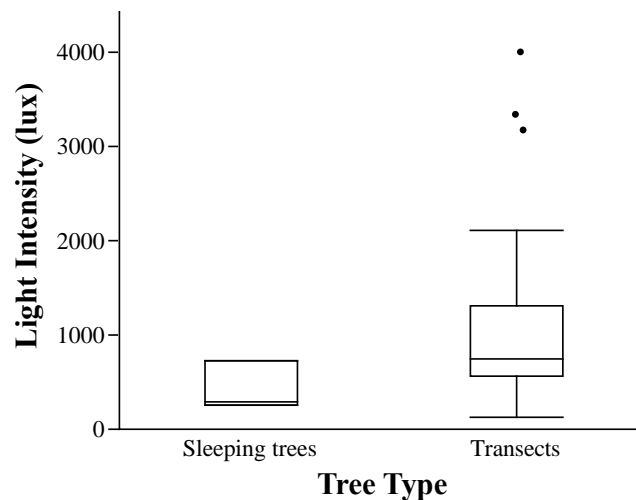
### 3.2.6 Insect Distribution

Total dry weight (g) of airborne nocturnal insects, number of specimens, and number of orders represented declined at higher altitudes (n=1027). At altitudes 2000-2300 m**,** total biomass (interior and edge combined) decreased with increasing altitude (Figure 15), and insect biomass was greater at forest edges than within the forest interior (Figure 16). These effects were not observed at altitudes 1800-1900 m. Controlling for altitude, insect biomass significantly differed with respect to distance from the forest edge, with higher biomass along the edge compared to 100m within the forest (Kruskal-Wallis: $X^2$ = 358.663, df=1.0, *p*<0.0001).

**Figure 15. Airborne nocturnal insect diversity and biomass (g) by altitude, including samples from both forest edge and interior.**
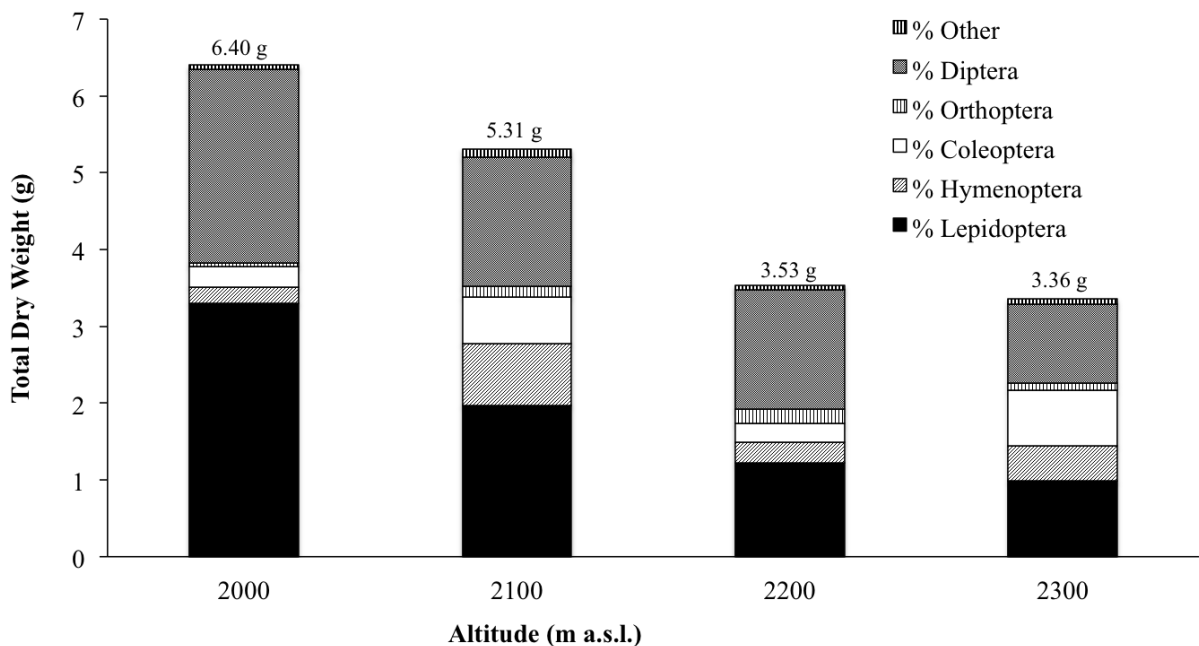
**Figure 16. Comparison of total biomass (g) of sampled nocturnal airborne insects in forest interior and along edge at 100-m altitudinal intervals.**
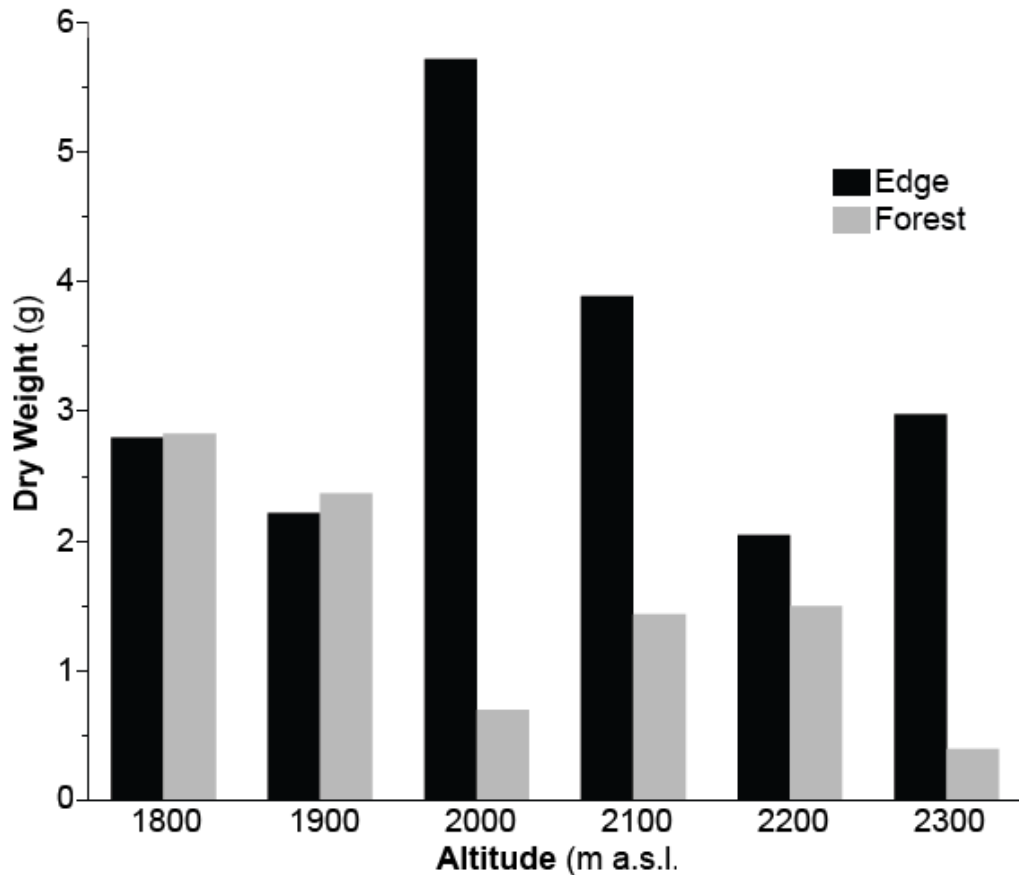


Although insect biomass differed with respect to distance from the edge, insect abundance (number of individuals) did not differ significantly (Kruskal-Wallis: $X^2$ =1.125, df=1.0, $p$=0.289; Figure 17).  Increased insect biomass near the forest edge was explained by an increased number of airborne insects that exceeded 5 mm in length. The proportion of insects of the Orders Lepidoptera and Orthoptera captured in traps combined (insect taxa preferred by lowland tarsier species (Gursky, 2000) was significantly higher along edges than within the forest (Pearson's chi square: $X^2$=4.500, df=1, $p$=0.034; Figure 18).  Across all altitudes, there was no difference in insect

abundance between the field seasons (June-September 2010 and January-March 2012) (Student's t-test: α=0.05; $t$=0.348, $p$=0.755).

**Figure 17. Airborne insect biomass (upper) and abundance (lower) by location: forest edge (along road) or 100 m within forest.**
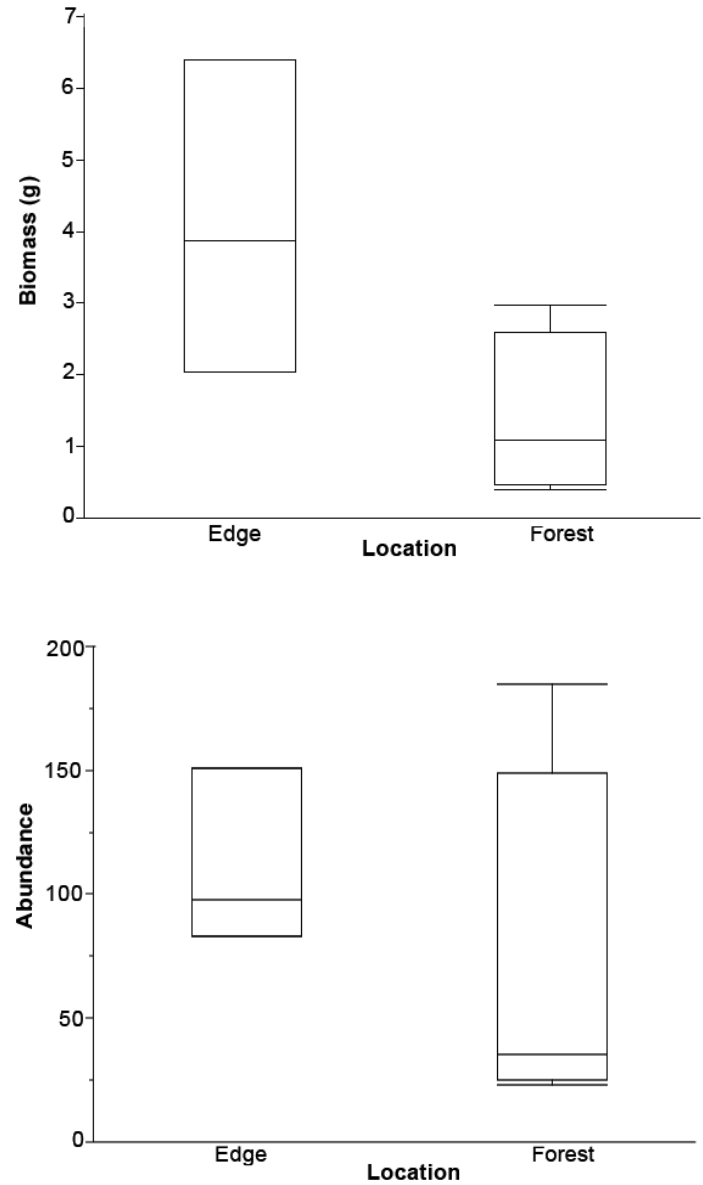
**Figure 18. Proportion of airborne insects (Lepidoptera and Orthoptera) along edges compared to 100 m in forest, across all altitudes. Dashed line indicates grand mean.**
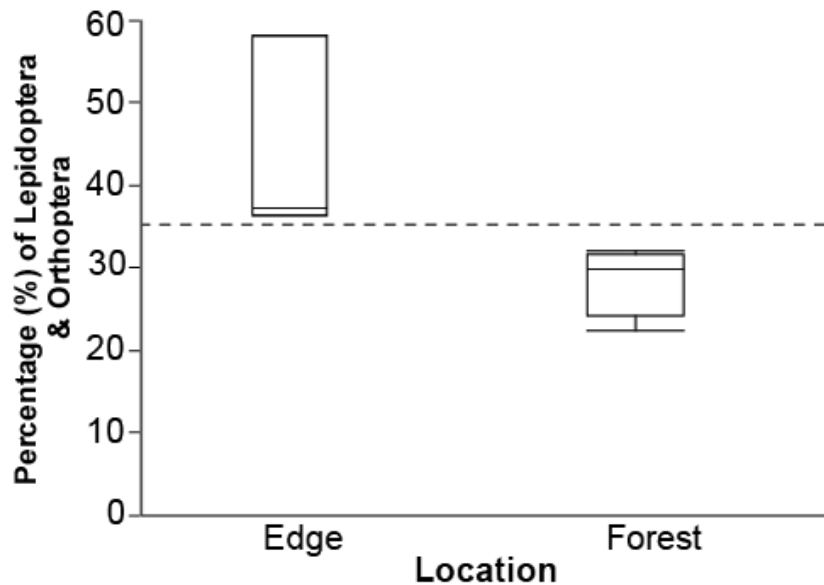


## 3.3 DISCUSSION

### *3.3.1 Pygmy Tarsier Distribution Patterns*

Pygmy tarsier dispersion and density is affected by forest composition, structure, and resource availability. These results suggest that the distribution of pygmy tarsiers is biased towards forest edges, where a higher biomass of larger insects was observed, especially airborne insects such as Lepidoptera that other tarsier species are known to prefer (Gursky 2000b). Insect availability was negatively related to altitude and positively associated with anthropogenic edges. The distribution of pygmy tarsiers found in this study indicates that pygmy tarsiers use anthropogenic edges to compensate for reduced insect resources at high altitudes.

While it is likely that pygmy tarsiers modify their behavior according to time of year, seasonal effects probably did not have a significant influence on the results of this

study.  First, Central Sulawesi is typically described as aseasonal in terms of rainfall and temperature.  Within Lore Lindu National Park, rainfall is evenly distributed throughout the year (Schweithelm et al. 1992).  There is no clear wet or dry season in Central Sulawesi, although rain falls heaviest during the monsoon period between November and April (Pangau-Adam 2003).  Second, this study encompassed two field seasons, one of which covered the wetter season.  There was no significant difference in insect abundance between the two field seasons, indicating pygmy tarsiers may not experience marked seasonal changes in insect availability across the year.

Pygmy tarsiers live at a lower density than reported for lowland Sulawesian species (Table 11).  Lower density is expected because higher altitude ecology is associated with reduced primate abundance (Byrne et al. 1987; Hanya et al. 2004; Marshall 2005).  Contrary to expectations, however, high altitude pygmy tarsiers exhibit group sizes (mean of 3.6 individuals) that are comparable to lowland Sulawesian tarsier species (2-6 individuals) (Table 12) (Driller et al. 2009; Gursky 1995; Merker 2006). However, unusually, two groups contained multiple adult males and females. This suggests that aspects of social organization, including intrasexual tolerance, aggression, and mating competition may play a greater role in determining tarsier group size than feeding competition.  These results further may be influenced by the time of the study; all groups contained an infant, a juvenile, or a lactating or pregnant female, indicating that the study occurred during a birthing season for pygmy tarsiers.

The uneven sex ratio between adult males and females has a number of possible explanations, including a higher male mortality, where a lower percentage of male subadults survive into adulthood.  One source of mortality is predation. The small

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sparrowhawk (*Accipter nanus*) is a known predator of tarsiers, and was captured less than 10m from where a tarsier was captured.

**Table 11.  Comparison of estimated population densities within genus *Tarsius*.**

| Species | Common Name | Location | Habitat | Estimated Population Density |
|---|---|---|---|---|
| *Tarsius dianae* | Dian's tarsier | Central Sulawesi | Lowland rain forest | 45-268 individuals/km$^2$ (Merker et al. 2005) |
| *Tarsius spectrum* | Spectral tarsier | Northern Sulawesi | Lowland rain forest | 156 individuals/km$^2$ (Gursky 1998) |
| *Tarsius pumilus* | Pygmy tarsier | Central Sulawesi | Highland cloud forest | 92 individuals/km$^2$ |
| *Tarsius syrichta* | Philippine tarsier | Philippines | Lowland rain forest | 57 individuals/km$^2$ (Neri-Arboleda et al. 2002) |

**Table 12.  Comparison of group sizes (number of individuals per group) for *Tarsius*.**

| Species | Group Size | Reference |
|---|---|---|
| *Tarsius pumilus* | 2-5 | |
| *T. spectrum* | 2-6 | Gursky 1995 |
| *T. dianae* | 3.2-5.2 | Merker 2006 |
| *T. lariang* | 2-4 | Driller et al. 2009 |
| *T. syrichta* | 2-4 | Crompton & Andau 1987 |
| *T. bancanus* | 2 | Niemitz 1985 |

The estimate of pygmy tarsier abundance may be influenced by their attraction to anthropogenic edges, where insect availability may influence their ranging patterns and sleeping site locations.  The proximity of all known sleep trees to the road suggests that edges also influence sleeping site selection; pygmy tarsiers select larger trees (a mean height of 15.40 m compared to a mean height of 5.57 m for all sampled trees) as their sleep trees (as well as dead and decaying trees). Although pygmy tarsier densities are lower than those of lowland tarsiers, these results might be overestimates because of anthropogenic edge effects,

Anthropogenic edges can affect the abundance and distribution of insect prey, influencing where insectivores forage. Forest edges have been to found serve as high quality food patches for insectivorous primate species. Primates are more abundant along forest edges where primary resources are more abundant (Passamani and Rylands 2000), and insectivorous primates range closer to edges (Lehman et al. 2006a). For example, saddle backed tamarins (*Saguinus fuscicollis*) incorporate a large proportion of insects in their diet, which may relate to their preference of foraging in secondary forest and forest edges (Yoneda 1984). Insectivores also are known to use forest edges to obtain preferred foods; bat species that specialize on Lepidoptera forage along forest edges rather than interiors, where prey abundance of dipterans, homopterans, and lepidopterans was found to be higher (Morris et al. 2010). Pygmy tarsiers may similarly forage near forest edges to obtain preferred food items. In this study, the proportion of Lepidoptera and Orthoptera present in malaise traps combined was found to be greater near forest edges. However, the proportion of these insects declined at higher altitudes at both edges and interior capture locations. Spectral tarsiers (*T. tarsier*) eat a greater proportion of Orthoptera (grasshoppers, crickets) and Lepidoptera (moths, butterflies) during times of high seasonal resource abundance, where consumption of Orthoptera increased 84% and consumption of Lepidoptera increased 64% during the wet season (Gursky 2000b). In this study, a greater proportion of larger bodied insects occurred along forest edges. Since biomass, but not total abundance, of airborne insects increases near forest edges, pygmy tarsiers may seek these larger airborne insects as a food source. Although the sample of food and habitat availability was limited, insect diversity and abundance was found to decline

significantly at higher altitudes, suggesting that pygmy tarsiers use forest edges to increase access to food items.

Pollen records indicate that Central Sulawesi has experienced marked anthropogenic landscape modification for the past 2,000 years (Kirleis et al. 2011a). However, tarsiers are able to sustain their population in the face of limited forest disturbance; lowland Dian's tarsiers (*T. dianae*) have the highest density (268 individuals/ha) in undisturbed forest, but still have relatively high density (187 individuals/ha) in slightly disturbed forest (Merker et al. 2005). Although population density and home range size are inversely correlated in primate species such as howler monkeys (*Alouatta seniculus*) (Crockett and Eisenberg 1987) and indris (*Indri indri*) (Glessner and Britt 2005), Dian's tarsiers experience smaller home range size (1.58 ha) in undisturbed forest where population density is high than in heavily disturbed forest where population density is low (45 individuals/ha) (Merker et al. 2005). In slightly disturbed forest, pygmy tarsiers may modify their ranging locations to exploit newly available forage habitat along edges, as seen in nocturnal lemur species (Lehman 2006).

### 3.3.2 Invertebrate Edge Effects

As vegetation density and distribution shifts near forest edges, the availability of both diurnal and nocturnal invertebrate prey also changes. At the study site, the secondary vegetation of forest edges was found to be associated with increased insect biomass and abundance for understory nocturnal insects. There are several reasons why nocturnal insects may prefer forest edges.

A primary reason is that nocturnal insects may be attracted to increased light penetration near forest edges. Light-attracted species tend to replace typical understory species at edges (Kremsater and Bunnell 1999). Nocturnal arthropods have evolved sensitive visual systems that allow them to navigate in low levels of light (Warrant and Dacke 2010). At night, arthropods use light to receive celestial and terrestrial cues for visual orientation, including spatial landmarks and the moon cycle (Warrant and Dacke 2010). Access to the open night sky, especially as a backdrop for visual contrasts, is thus important for nighttime navigation among insects (Warrant and Dacke 2010).

Arthropod abundance also correlates with vegetation structure, and diurnal species that prefer complex, shrubby habitat increase in abundance along forest edges (Kremsater and Bunnell 1999). The increase in dead or fallen trees along edges provides suitable habitat for both diurnal and nocturnal invertebrates (Kremsater and Bunnell 1999). Vegetation that consists of a high proportion of small trees and shrubs, such as within small forest patches, was positively correlated with the abundance of large and small diurnal arthropods (Jokimaki 1998). Similarly, forest edges consist of secondary vegetation. Although the undergrowth tends to be denser in upper montane forest (Whitten et al. 2002), insects such as dipterans, homopterans, and lepidopterans may prefer growth along edges (Morris et al. 2010).

Wind is another important variable that is affected by forest edges (Chen et al. 1995) and influences the dispersal of both diurnal and nocturnal flying insects (Whitaker et al. 2000). Clear cutting trees results in increased wind velocity within the clearing and can lead to increased insect abundance along altered forest edges (Whitaker et al. 2000). This effect has been found to be greater among larger bodied insects (>10 mm),

which are more abundant along edges (Whitaker et al. 2000); smaller insects can be blown farther and higher than larger ones.  Thus, wind may also affect the size distribution of invertebrates along forest edges.  Larger, and therefore higher quality, insects (>3 mm) have been found in relatively greater abundance along forest edges (Fowler et al. 1993).  This current study is consistent with this finding.  Size effects may also relate to taxonomic differences in response to edges.  For example, Cicadellidae and Isoptera (a preferred food of lowland tarsiers) are found along edges (Fowler et al. 1993), while pollinators such as bees and wasps respond negatively to the presence of edges (Brown and Hutchings 1997).

### 3.3.3 Altitude Effects

In Central Sulawesi, tropical mountains experience a linear increase in species diversity; plant species diversity (angiosperms, ferns, and conifers) is highest in upper montane forest (2400 m) and lowest at low to mid-montane elevations, where tropical Fagaceae contributes the majority of the biomass (Culmsee et al. 2010).  The extension of low diversity to mid-level altitudes may potentially serve as an isolating mechanism between lowland and highland populations.  In this study, pygmy tarsiers were not located below 1900 m.  With an exclusively high-altitude range, pygmy tarsiers may prefer forest edges in response to limitations in the availability of preferred insect foods of tarsiers, including Lepidoptera and Orthoptera.  As pygmy tarsiers were not found to live in smaller groups than lowland tarsiers, but were found to live at a lower density, the effects of scramble competition for these resources may be significant.

This study provides evidence that the high altitude ecology of pygmy tarsiers, including cooler temperatures, reduced tree density, shorter tree height, decreased

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plant species diversity, and a reduction in the availability of insect resources, are likely

to influence pygmy tarsier behavior and evolution.  One explanation of the small body

size of pygmy tarsiers is that it is a primitive trait for all tarsiers (Shekelle 2008b).  This

study gives some support to an alternate hypothesis that small body size is a derived

condition related to reduced resource availability at higher altitudes (Musser and

Dagosto 1987).


### 3.3.4 Negative Edge Effects

Primates experience a threshold to habitat disturbance (Lehman et al. 2006b).

Thus, although slightly disturbed habitat is suitable for *T. dianae*, the largest home

ranges are found in heavily disturbed forest (Merker 2006; Merker et al. 2005). It is

important to note that although tarsiers may respond positively to forest edges, edges

may have an overall negative impact on their survival.  The interior-to-edge ratio can

indicate the extent of disturbance present in habitat fragments (Bogaert et al. 1999).  At

this study site, pygmy tarsiers experience a channel of disturbance from the 5 km

logging road, leaving a relatively high interior-to edge ratio.  However, the level of edge

effect will increase as human disturbance increases over time.  Roads also cause

changes in erosion patterns, noise level, and pollutants (Coffin 2007).  In this regard, it

is important compare the effects of natural edges to anthropogenic edges on primate

populations.

Primates are more vulnerable to predation in open areas, such as along forest

edges, where the more sparsely distributed vegetation increases their visibility and

accessibility to predators (Isbell, 1994).  Some Indonesian raptors prefer to hunt along

forest edges (Thiollay and Meyburg 1988), and forest raptors in central Sulawesi are

confirmed to occur along forest edges and in more open and disturbed forest (Thiollay and Rahman 2002). Pygmy tarsiers therefore experience a tradeoff of increased predation threat when they occupy forest edges.

### 3.3.5 Habitat Usage

In terms of sleeping sites, pygmy tarsiers appear to prefer trees that allow less light through the canopy and some of the largest trees available as their sleeping sites. Trees in the Fagaceae family might be of particular importance to pygmy tarsiers.  In another study, this family of trees was found to be less species-rich at upper-montane than mid-montane forest, but with a relatively large basal area representing the family (Culmsee 2011).  The same study also found that *Lithocarpus havilanii*, a tree used as a sleeping site by pygmy tarsiers, is the most abundant Fagacea species found in upper-montane forest, but that this species is less prominent in mid-montane forest (Culmsee 2011).

### 3.3.6 Conclusions

Pygmy tarsiers live in upper montane and mid-montane moss forest where total basal area increases at higher altitudes.  Their dispersion and density is associated with resource availability; individuals remain close to forest edges where insects are larger and more abundant.  Pygmy tarsier dispersion along anthropogenic edges appears to be a key factor in their distribution.  This study indicates pygmy tarsiers live at a density lower than lowland Sulawesian tarsiers, possibly in response to living in high-altitude forest.

# 4. ALTITUDINAL RANGE AND RANGING PATTERNS, AND HABITAT ASSOCIATIONS

## 4.1 BACKGROUND

### 4.1.1. Tarsier Biogeography

The distribution of a primate species is related to current ecological conditions and historical dispersal patterns (Lehman and Fleagle 2006). The biogeography of island primates is particularly important to understanding primate distribution patterns. As Charles Darwin observed (Darwin 1845), islands are a good means to explore adaptation, speciation, and radiations because of their small land area, distinctive boundaries, relative geographic isolation, and unique dispersal and diversification potential for colonizing fauna (Losos and Ricklefs 2009). Given that tarsiers probably originated in Asia in the Middle Eocene (Beard 1998; Fleagle and Gilbert 2006) and are currently distributed across southeast Asian islands, tarsier diversity holds particular importance for understanding primate distribution patterns. This section examines how the ranging patterns and elevational distribution of high-altitude pygmy tarsiers compare to those of lowland tarsier species.

Tarsiers exhibit geographic distributions that closely relate to their taxonomic distinctions; all tarsier taxa exhibit complete allopatric separation or parapatric (adjacent) species ranges, while no species are sympatric (Shekelle 2008a). Elevation factors into the allopatric separation of the species, and pygmy tarsiers are the only highland form to occur in Sulawesi (Grow et al. 2013; Musser and Dagosto 1987).

The taxonomic diversity of tarsiers is greater in Sulawesi than any other island on which

they occur (Merker et al. 2009) (although this may reflect a lack of tarsier research

outside of Sulawesi), and their diversity corresponds to geographic variation.

One factor that affects the current geographic distribution of Sulawesian tarsier

species is the movement of Ice Age landmasses.  Tarsiers exhibit species distribution

patterns that correspond to past plate tectonic and glacial activity (Merker et al. 2009).

DNA evidence and vocalization patterns indicate that two parapatric tarsier species in

central Sulawesi, Dian's tarsier and the Lariang tarsier, split 1.4 mya, with their

distribution reflecting a split between the species along a faultline (Merker et al. 2009).

Although the timing and migration path of the first tarsiers to colonize Sulawesi is

unknown, their migration is thought to have occurred before Sulawesi converged into a

single landmass (Shekelle 2008a), during the Miocene (Merker et al. 2009).  Thus, the

currently parapatrically separated tarsier populations may have began as allopatric

populations, isolated across smaller islands, but may have been pushed together on

Sulawesi by plate tectonics (Shekelle 2008a).

These prior colonization events are likely related to the current altitudinal

geographic distribution of Sulawesian tarsier species.  Tarsiers exhibit geographic

distributions that closely relate to their taxonomic distinctions; all tarsier taxa exhibit

complete allopatric separation or parapatric (adjacent) species ranges, while no species

are sympatric (Shekelle 2008a).  Elevation factors into the allopatric separation of the

species.  Sulawesi is mountainous, and the montane zone from 1000 to 2400 m covers

approximately 20% of land on the island (Culmsee 2011).  *Tarsius pumilus* is the only

species of tarsier to live above 1500 m (Table 13), and have only been found at

altitudes above 1800 m a.s.l. (Grow et al. 2013; Musser and Dagosto 1987).  In

comparison, Dian's tarsier occurs in the same central Sulawesi region and has been

studied at approximately 700 m (Merker et al. 2005) up to 1100 m (Merker 2003).


**Table 13. Altitudinal ranges for tarsier species based on locations of study sites.**

| Species | Altitudinal Range | References |
|---|---|---|
| *Tarsius pumilus* | 1800-2200 m | Musser & Dagosto 1987 (derived from documentation on specimens) |
| *Tarsius dentatus* (*T. dianae*) | 0-1400 | Shekelle et al. 1997, Merker 2003, MacKinnon & MacKinnon 1980 |
| *Tarsius lariang* | 500 | Merker & Groves 2006 |
| *Tarsius tarsier* (*T. spectrum*) | 0-1400 | Nietsch 1999, Gursky 1995 |
| *Tarsius wallacei* | 500 | Merker et al. 2010 |
| *Tarsius bancanus* | 0 - 1200 | Crompton & Andau 1987 |
| *Tarsius syrichta* | 69-200 | Neri-Arboleda et al. 2002 |


### *4.1.2 Altitudinal Range of Species Distributions*

The number of species that occur in an area further affects the altitudinal range

of a species.  Lower elevation forests include a more diverse range of taxa that occupy

narrow altitudinal ranges, while mountains show a decline in species richness but an

increase in the altitudinal range of each species (Stevens 1992).  This idea, known as

Rapoport's Rule, was originally developed to suggest that species ranges increase with

latitude, as distance from the equator increases (Rapoport and Bariloche 1982), but has

also been found to apply to increases in elevation (Stevens 1992).  As a consequence

of the Rapoport effect, the elevational distribution of primates may positively correlate

with altitude.  For example, groups of chacma baboons (*Papio ursinus*) at high altitudes

occupy altitudes from 2000 to 3000 m, while those at lower altitudes occupy a narrower range from 1600 to 2000 m (Whiten et al. 1987).

A large altitudinal niche may be explained by local ecological conditions, higher ecological tolerance levels, and by spatial constraints. With linear increases in elevation, measurable ecological changes occur, including decreases in temperature, reduced species diversity, and changes in forest structure (Körner 2007). All of these variables may influence primate elevational distribution patterns. First, primate altitudinal ranges are known to correspond to altitudinal changes in food resources. For example, black-and-white snub nosed monkeys (*Rhinopithecus bieti*) of the highly seasonal Tibetan plateau have been found to use higher elevations during the winter, where sunlight availability is higher (Quan et al. 2011) and there is greater access to lichens, an important fallback food (Grueter et al. 2012). Another explanation for increased ranges is that higher altitude species may be more broadly adapted to a range of climatic conditions, such as decreases in temperature, while lower altitude species have more narrow climatic tolerances (Stevens 1992). Finally, the availability of land area can explain the altitudinal range of species. For example, it has been proposed that the lemurs of Madagascar exhibit broad elevational ranges, and high species diversity at mid-range altitudes, because of the relative lack of lowland habitat (Goodman and Ganzhorn 2004). Thus, altitudinal variation in ecological conditions may affect the altitudinal ranges of tarsier species.

### 4.1.3 Altitude and Ranging Behaviors

Altitude may also positively correlate with the home range sizes of individuals within a species. Home range is related to the diversity and abundance of resources in

a given area, and biomass declines at higher altitudes (Körner 2007). Intraspecific altitudinal variation in home range size is seen among primates, with larger home ranges at higher altitudes. For example, rhesus monkeys (*Macaca mulatta)* occupy a wide range of environments, and have larger mean home ranges in mountainous regions of China (16 km$^2$) (Wenyuan et al. 1993) and Pakistan (8 km$^2$) (Richard and Richard 1985) than in lowland China (0.37 km$^2$; Southwick et al. 1996). Similarly, larger group home ranges have been observed among chacma baboons (*Papio ursinus*) at high altitudes, in comparison to those at lower altitudes (Whiten et al. 1987). Tarsiers specifically are known to alter their home range sizes in response to spatial and temporal variation food availability. Spectral tarsiers increase home ranges during the dry season when insect availability is low (Gursky 2000b), while Dian's tarsiers occupy a greater percentage of their home range on a nightly basis in disturbed and less productive habitats (Merker 2006). Compared to lowland tarsiers, little is known about pygmy tarsier ranging behavior and habitat usage.

### 4.1.4 Hypotheses

This section reports results from surveys and observations conducted from May through October 2008, June to September 2010, and January to March 2012. This study seeks to a) assess the altitudinal range of pygmy tarsiers, and determine if there is overlap with lowland tarsier species; b) describe the ranging patterns of pygmy tarsiers; and c) compare home range sizes of pygmy tarsiers to lowland Sulawesian tarsiers. Given that species ranges should increase as elevation increases (Stevens 1992) and tarsier food resources decline at higher altitudes (Grow et al. 2013), I hypothesized that pygmy tarsiers would have a larger altitudinal range than lowland

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tarsiers.  Further, given that an altitudinal reduction in resources has been observed in pygmy tarsier habitat (Grow et al. 2013), I hypothesized that pygmy tarsiers would have relatively large home ranges.

## 4.2 RESULTS

### 4.2.1 Altitudinal Distribution

Over the course of this research, six groups (22 individuals) were observed on Mt. Rore Katimbu.  The altitudinal distribution of observed groups ranged from 2000-2300 m.  Although altitudes 1800-2300 m were sampled, no pygmy tarsiers were found below 2000 m. Groups tended to be large; three groups of four individuals were found at 2000, 2250, and 2300 m, while a group of five individuals was found at 2100 m. Within the study area, adult tarsiers were radiotracked; they did not make audible vocalizations as moved throughout their ranges, but were recorded to communicate at higher frequencies.

### 4.2.2 Ranging Patterns

To test for the effects of sample size, sample size area curves were compared (Figure 19).  Based on the curves that reached a plateau, only four out of 13 adult individuals were sufficiently radiotracked allowing for home range estimation.  From this sample, the average home range size for pygmy tarsiers is 2.0 ha, with an average of 1.77 ha for the three females, compared to 2.75 ha for the one male (Table 14).  The home ranges of the male (ID 250) and female (ID 115) from Group 6 exhibit a high degree of overlap (Figure 20).  The intersecting area of overlap is 1.993 ha, with a perimeter of 537.36 m.

**Figure 19. Sample size area curves for four radiotracked individuals, as indicated by group, sex, and radio ID.**
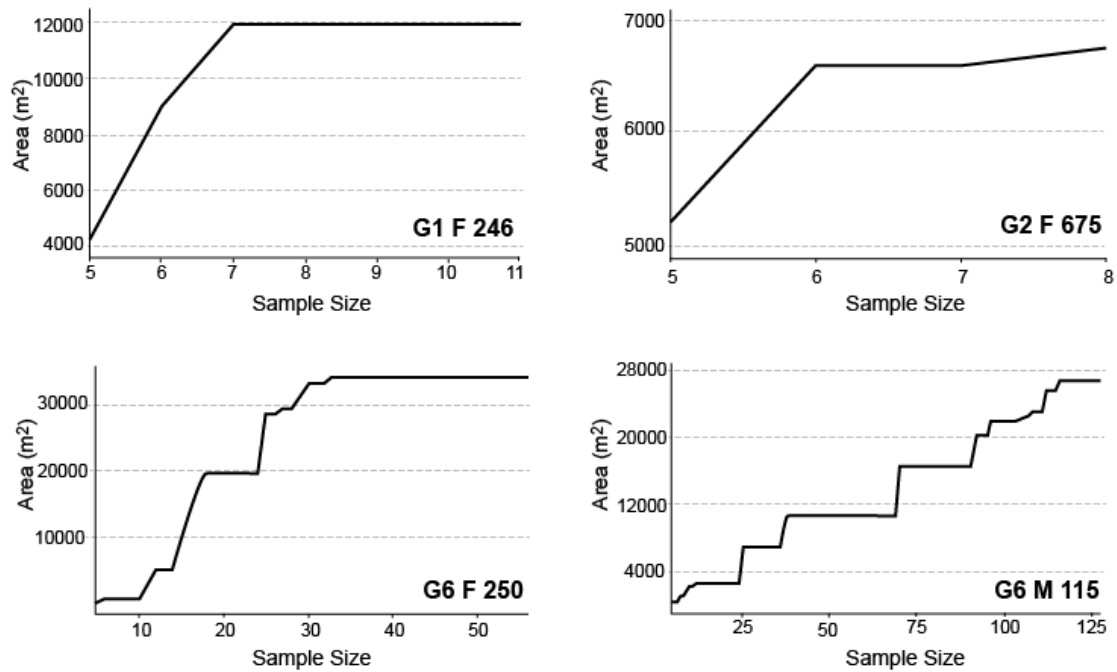


**Table 14. Home range sizes for each of the radiotracked adult pygmy tarsiers at the study site.**

| Radio ID | Age & Sex | Altitude | Data Points | Home Range (ha) |
|---|---|---|---|---|
| 115 | Adult Male | 2000 | 129 | 2.75 |
| 250 | Adult Female | 2000 | 57 | 3.43 |
| 675 | Adult Female | 2300 | 9 | 0.68 |
| 246 | Adult Female | 2250 | 12 | 1.19 |

**Figure 20. Home ranges for individuals in groups 1,2, and 6. Numbers indicate group.**
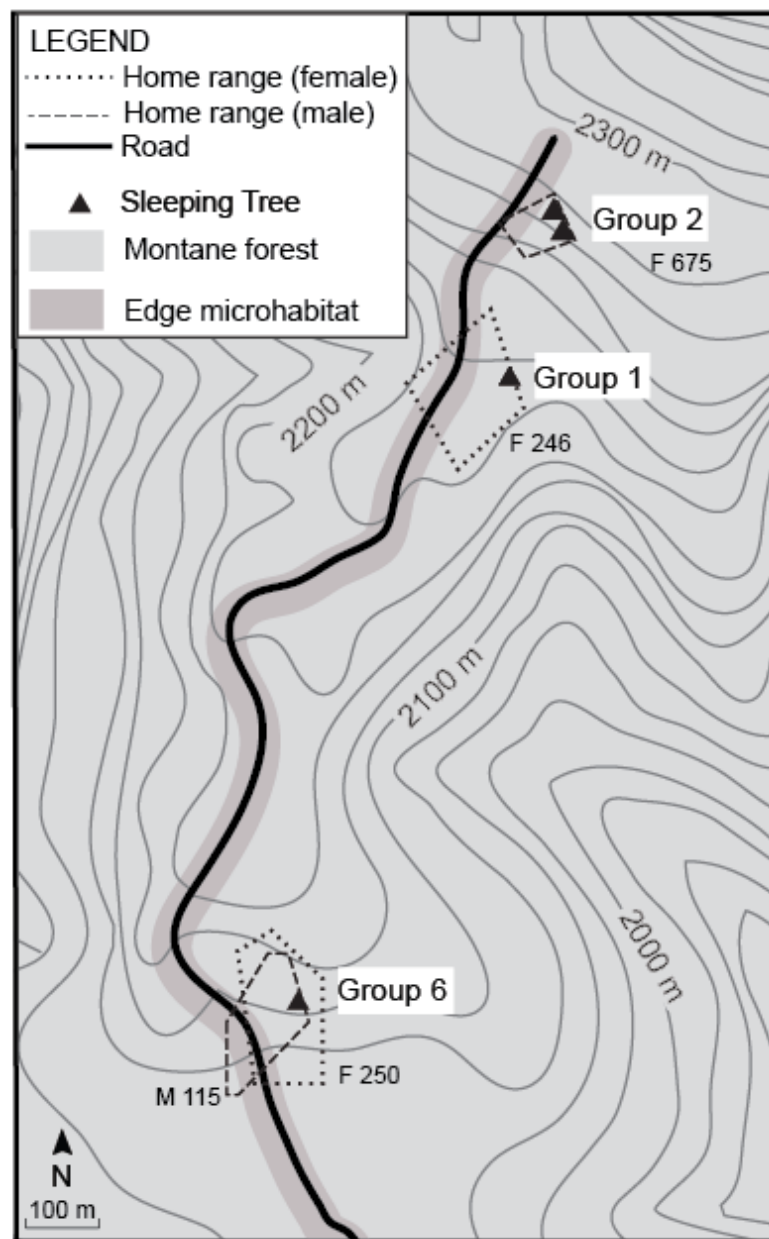
The Schluter test for multivariate association rejected the null hypothesis of no association (n=432 sampling units, variance ratio=1.155, W=498.99, *p*-value=0.001), indicating the locations of the male and female were associated. The average nightly path length (NPL) for adult pygmy tarsiers is 365.36 m (Table 15). The average NPL for females is 392.29 m (7 nights; 3 females), while the average for the one male is 318.25 m (4 nights).

**Table 15. Travel distances and altitudinal ranges for radiotracked adult pygmy tarsiers during 12-hour night shifts.** Listed here are nightly travel distance (NPL), the minimum and maximum altitude at which locational points were recorded, and the number of data points per night.

| Date | Group | ID | Sex | NPL (m) | Min Altitude | Max Altitude | Data Points |
|------|-------|-----|--------|---------|--------------|--------------|-------------|
| 8/23/08 | 1 | 246 | Female | 547 | 2250 | 2266 | 8 |
| 8/26/08 | 1 | 246 | Female | 204 | 2250 | 2266 | 6 |
| 7/16/10 | 2 | 675 | Female | 436 | 2221 | 2242 | 9 |
| 2/9/12 | 6 | 250 | Female | 330 | 2018 | 2038 | 9 |
| 2/10/12 | 6 | 250 | Female | 479 | 2003 | 2032 | 12 |
| 2/12/12 | 6 | 250 | Female | 520 | 1996 | 2027 | 23 |
| 2/13/12 | 6 | 250 | Female | 230 | 2014 | 2022 | 12 |
| 2/24/12 | 6 | 115 | Male | 318 | 1986 | 2018 | 23 |
| 2/25/12 | 6 | 115 | Male | 236 | 2018 | 2024 | 45 |
| 2/26/12 | 6 | 115 | Male | 235 | 2018 | 2028 | 22 |
| 2/28/12 | 6 | 115 | Male | 484 | 1998 | 2028 | 39 |

**4.3 DISCUSSION**

Results indicate that lowland and highland tarsier species experience an altitudinal separation. Pygmy tarsiers are allopatrically separated from lowland tarsier species in Sulawesi, including *Tarsius dianae* that occurs and low and mid altitudes in central Sulawesi (Table 16). This finding is in alignment with the observation that all other tarsier taxa that are allopatric or parapatric, but not sympatric (Shekelle 2008a).

The specialized diet of tarsiers may relate to this observation, given that tarsiers are entirely faunivorous and feed primarily on airborne insect prey.

**Table 16. Comparison of altitudinal range, nightly path length, and home range size for tarsier species. Values are averages for females (F) and males (M).**

| Species | Altitudinal Range (m a.s.l.) | Nightly Path Length (m) | Home Range (ha) |
|---|---|---|---|
| *Tarsius pumilus* | 2000-2300 | F 392 <br> M 318 | F 1.77 <br> M 2.75 |
| *Tarsius dentatus* <br> (*T. dianae*) | 0[a] <br> 650-990[b] <br> 0-1400[c] | F 945 <br> M 905[b, d] <br> (25-48% of range[e]) | F 1.58 <br> M 1.77[d, f] |
| *Tarsius lariang* | 500[g] | n/a | n/a |
| *Tarsius tarsier* <br> (*T. spectrum*) | 0-500[h] <br> 0-1400[i] | F 447.68 <br> M 760.62[i] | F 2.3 <br> M 3.1[j] |
| *Tarsius wallacei* | 500[k] | n/a | n/a |
| *Tarsius bancanus* | 0[k] - 1200[l] | F 1448.1 (66-100%) <br> M 2081.6 (50-75%)[m] | F 7 <br> M 10[m] |
| *Tarsius syrichta* | 69-200[n,o] | F 1119 (6-57%) <br> M 1636 (3-74%)[o] | M 6.45 <br> F 2.45[o] |

a. Shekelle et al. 1997, b. Merker 2003, c. MacKinnon & MacKinnon 1980, d. Merker 2010, e. Merker et al. 2005, f. Merker 2006, g. Merker & Groves 2006, h. Nietsch 1999, i. Gursky 1995, j. Gursky 1998, k. Merker et al. 2010, l. Crompton and Andau 1987, m. Gorog and Sinaga 2008, n. Rehakova-Petru et al. 2012, o. Neri-Arboleda et al. 2002

This study did not encounter pygmy tarsiers below 2000 m on Mt. Rore Katimbu, despite numerous surveys at lower altitudes, although a pygmy tarsier specimen was previously recorded at 1800 m (Musser and Dagosto 1987); it is possible that this measurement is inaccurate, as it was taken over 70 years ago. Lowland Sulawesian tarsier species occur up to approximately 1000 m (Merker 2003) and have been reported as high as 1400 m (MacKinnon and MacKinnon 1980). The only other tarsiers that have been found above 1000 m were observed in Kalimantan (Borneo), where tarsiers have been captured above 1200 m (Gorog and Sinaga 2008); however, this is not common. Even with these lowland species extending as high as 1400 m, there is still a clear 400 m separation between lowland and pygmy tarsiers.

Pygmy tarsiers were found at 2000-2300 m and do not occupy a wider

elevational range than lowland tarsiers, as was predicted by Rapoport's rule. (This

elevational range is also narrower than expected based on previous reports of

specimens collected below 2000 m.) However, the Rapoport effect is not a universal

phenomenon. For example, a cross-species analysis of the latitudinal and altitudinal

ranges of Andean passerine birds found that neither latitude nor altitude could explain

spatial variation in ranges sizes (Ruggiero and Lawton 2008). The ecological variation

between the lowlands and highlands of Sulawesi may be a significant factor in

determining the altitudinal niches of Sulawesian tarsier species. Forest at high altitudes

in Sulawesi exhibits a marked reduction in food resources for tarsiers, with insect size

and abundance decreasing at progressively higher altitudes (Grow et al. 2013). With a

wide altitudinal gap between pygmy tarsiers and lowland tarsiers, pygmy tarsiers may

be specifically adapted to occupy a narrow high-altitude range. Pygmy tarsiers also

exhibit adaptations to this altitudinal decrease in resource, and bias their spatial

positions near forest edges, where insects are found in greater abundance (Grow et al.

2013). Meanwhile, lowland tarsiers may represent species with broad niches, or

tolerance to a range of conditions, that occupy wider ranges.

Differentiation between lowland and highland forms of taxa, with high-altitude

dwarfing, is seen in other Sulawesian taxa. The smaller mountain anoa (*Bubalus

quarlesi*) occurs at higher elevations while the larger lowland anoa (*Bubalus

depressicornis)* inhabits lower elevations, although it has been suggested that the two

forms may reflect clinal altitudinal variation in body size within one species of anoa

(Burton et al. 2005; Whitten et al. 2002). One isolating mechanism between low-altitude

and high-altitude populations might be differences in plant diversity at low, middle, and high altitudes.

In some cases, species diversity along altitudinal gradients peaks in the middle, an occurrence known as the mid-domain effect. The mid-domain effect is thought to occur because of spatial constraints of species' ranges, where more overlap occurs at mid-range elevations on a mountain (McCain 2007). This phenomenon does not universally describe all gradients of phylogenetic diversity (Zapata et al. 2003). Previous studies in the mountains of Sulawesi have found an opposite effect, where plant species diversity increases with increasing altitude; it is highest in upper montane forest at 2400 m a.s.l., while it is lowest at low and mid-montane elevations (Culmsee et al. 2010). Although anthropogenic influences may affect this observation, lower plant diversity at lower altitudes may also relate to the wider altitudinal range of lowland tarsiers.

Pygmy tarsier home ranges are comparable to, or relatively larger than, those of lowland tarsiers, although interpretation of these results is limited by a small sample size. One female (#250) of Group 6 had a relatively large home range size, with an area curve that reached an asymptote based on a large number of data points. The full home ranges of two additional females may not have been fully tracked, if their area curves have only reached local plateaus and not yet their respective asymptotes. Thus, the home ranges of females #246 and #685 may be larger than estimated. If this is the case, pygmy tarsier home ranges could very well be larger than lowland tarsier ranges. Compared to the home ranges of tarsiers in the Philippines and Borneo, all Sulawesian tarsier home ranges are much smaller, which may relate to differences in habitat or

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anthropogenic disturbance.  Larger home ranges are beneficial in habitats where food is scattered or limited (Altmann 1974).

While pygmy tarsier home ranges and area are larger, their nightly path length is shorter, indicating that pygmy tarsiers do not utilize a large proportion of their home range on a nightly basis.  On different nights, pygmy tarsiers use different parts of their home range.  The relatively small nightly path length of pygmy tarsiers is unexpected, given that nightly travel distances are known to increase in habitats with lower productivity.  For example, spectral tarsiers (*Tarsius spectrum*) increase home range sizes and travel distances during the dry season when prey abundance is low (Gursky 2000b).  Similarly, Dian's tarsiers (*Tarsius dianae*) have been observed to increase their nightly travel distances in more disturbed forest (Merker 2006). One explanation for the short nightly travel distances of pygmy tarsiers is their biased distribution near anthropogenic forest edges (Grow et al. 2013), where insects are more abundant, lessening the need to increase foraging area.

A possible confounding variable is seasonal changes in resources.  However, there is no clear seasonality in Central Sulawesi in terms of rainfall (Schweithelm et al. 1992), and tropical montane forest exhibits less seasonality than temperate forest.  This study sampled during both the monsoon period between November and April (Pangau-Adam 2003), and during the dryer months of the summer, thereby reducing the potential effect of seasonality.

A final important variable that affects the ranging patterns of all Sulawesian tarsiers is habitat disturbance.  Forest that is unaltered by human activity is quickly disappearing from Central Sulawesi.  As Merker et al. (2004) observed, in 2001 there was no pristine forest below 950 m, although only three years earlier he observed

pristine forest at 700-750 m.  Because of the rapid rate of habitat loss in the region, care

must be taken to determine how human habitat disturbance affect tarsier populations.

As human activity encroaches on high-altitude forest in the region, highland tarsiers

may have further challenges to face in the future.

# 5. *Tarsius pumilus* BODY PROPORTIONS

## 5.1 BACKGROUND

This section examines altitudinal effects on the physiology of primates.  First, this section explores whether two sexually selected traits, sexual dimorphism of body mass and testes volume, match allometric and behavioral expectations for pygmy tarsiers. Next, the consequences of small body size in pygmy tarsiers is discussed, as well as the allometric implications of their limb proportions.

### *5.1.1 Altitudinal Effects on Sexually Selected Traits*

*5.1.1.1 Sexual Dimorphism and Mating System*

Sexual dimorphism of body size and relative testes size correlate with primate mating systems.  In polygynous mating systems with one breeding male, sexual dimorphism of body size increases, emphasizing contest competition (Figure 21).  In systems with multiple breeding males (multimale and dispersed mating systems), testes size increases in association with higher sperm competition (Harcourt 1997; Harcourt et al. 1981; Harcourt 1995; Møller 1988).  Pygmy tarsiers were observed to sleep in groups with more than one adult male, indicating they should experience more sperm competition (have larger relative testes size) than lowland populations where adult males do not associate.

**Figure 21. Expectations for mating system based on sexually selected traits (sexual dimorphism of body size and relative testes size).**
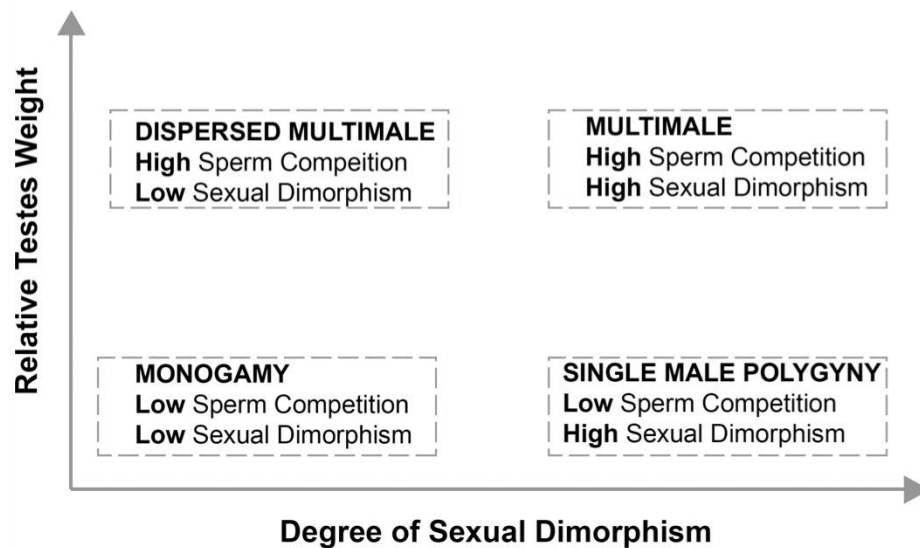


Sexual selection theory predicts that sexual dimorphism and testes size will correlate with mating system. Since male reproductive fitness is limited by access to females, males generally undergo stronger sexual selection than females (Bateman 1948). Intrasexual competition can be precopulatory (contest competition) or postcopulatory (sperm competition). According to classic precopulatory sexual selection theory (Darwin 1871), male competition leads to intrasexual selection for increased agonistic ability, including larger body size and secondary sexual characteristics. Using sexual dimorphism as a proxy of intersexual competition, the degree of sexual dimorphism in a species should correlate with mating system (Plavcan 2001a). Thus, among primates, larger body mass differences between males and females should associate with stronger male-male competition, indicating a more polygynous mating system (Plavcan 2001b; Wright et al. 2003).

The prediction that sexual dimorphism increases in polygynous mating systems, especially those with one breeding male, is supported in primates. Polygynous haplorhines are more sexually dimorphic than monogamous species (Clutton-Brock et al. 1977). Moreover, single-male species had relatively smaller testes combined with sexual dimorphism (Harcourt et al. 1981). The prediction that testes are larger in polygynous mating systems, especially those with multiple breeding males, is also supported. Larger testes relative to body size measures degree of sperm competition, and associates with a polygynous mating system in primates (Harcourt 1997; Harcourt et al. 1981; Harcourt 1995). In primate species where there are multiple breeding males, testes size increases (Harcourt et al. 1995; Møller 1988). In multimale mating systems, relative testes size increases, but sexual dimorphism is not as pronounced as in mating systems with one breeding male (Harcourt et al. 1981; Kappeler 1997b)). Testes size is also relatively large among prosimians with nongregarious mating systems, such as the noyau (dispersed) system seen in mouse lemurs, pottos, and some galagos, where females in estrus mate with multiple males (Dixson 1987).

*5.1.1.2 Sperm Competition and Mating System*

Postcopulatory sexual selection can occur in the form of sperm competition, where sperm compete to fertilize eggs (Parker 1970). Sperm competition associates with larger testes relative to body size, and indicates a multi-male mating system (Harvey and Harcourt 1984). Postcopulatory sperm plugs are another effect of sperm competition, where the plugs keep ejaculate within the vaginal canal (Dixson and Anderson 2001). Sperm competition should be most important in mating systems that include multiple breeding males (Harcourt et al. 1981).

The predictions that body size and testes size associate with higher fertility have support among multimale primates.  Primates with larger testes produce a higher volume of ejaculate, higher sperm counts, and have higher sperm motility (Møller 1988).  Among rhesus macaques, testes size associates with successful fertilizations, as well as body size and rank (Bercovitch 1996).  Although testes size in baboons is relatively high (Harcourt et al. 1995), savanna baboon (*Papio cynocephalus*) body size and testes size were not found to associate with intraspecific differences in volume of male ejaculation (Bercovitch 1989).  However, quality of ejaculate may be the most important benefit, given that primates with larger testes produce not only a higher volume of ejaculate, but higher quality sperm as well (Møller 1988).

Although body size influences testes size, under sperm competition body size alone should not be able to predict testes volume (Pochron and Wright 2002).  The size of testes in primates is influenced by mating system and other variables beyond body size (Kenagy and Trombulak 1986).  Similarly, allometry alone cannot account for sexual dimorphism in primates (Gaulin and Sailer 1984).

While breeding season seems to not affect testes size among even seasonally breeding primates (Harcourt et al. 1995), there is evidence that breeding season is important to sperm competition in lemurs.  Among sifakas, while there is a positive relationship between body size and testes size during the non-breeding seasons, there is no relationship during the breeding season, during which smaller males grow larger testes comparable to those among larger males (Pochron and Wright 2002).  Phillippine tarsiers (*Tarsius syrichta*) exhibit a similar relationship (Wright et al. 2003).

Although haplorhine primates (humans, apes, monkeys, and tarsiers) usually conform to sexual selection theory, with high sexual dimorphism, strepsirrhine primates tend to exhibit less dimorphism and often monomorphic body size (Plavcan 2001b). Polygynous lemurs do not exhibit sexual dimorphism (Kappeler 1997a; Wright 1999). Both strepsirrhines and tarsiers have only a slight difference in the degree of sexual dimorphism between monogamous and non monogamous species (Kappeler 1990). Moreover, strepsirrhine primates often do not exhibit the typical signs of sperm competition (enlarged testes). Kappeler tested the predictions of sperm competition among strepsirrhine primates and found that multi-male species did not have significantly larger testes than those in solitary or monogamous species (Kappeler 1997a). However, lemurs engage in other forms of sperm competition, such as copulatory plugs and the displacement of previous plugs as seen in *Lemur catta* (Parga 2003).

Although phylogenetic history and body size play a role in determining strepsirrhine testes size, environmental factors may also affect sexually selected traits in lemurs (Kappeler 1997a). A comparison of testes size to body weight in sifakas (*Propithecus diadema edwardsi*) found a mix of sexually selected traits: while sifakas do not exhibit sexual dimorphism, they exhibit high sperm competition (Pochron and Wright 2002). A lack of sexual dimorphism usually indicates monogamous mating patterns, but sifakas exhibit breeding patterns with significant deviations from monogamy (Pochron and Wright 2002). The lack of sexual dimorphism thus might be attributed to resource availability in Madagascar (Pochron and Wright 2002). Among the Malagasy lemurs, body sizes may be limited by the low amount of plant resources and the unpredictable

climate (Wright 1999).  Thus, environmental constraints limit body size, but larger testes volume offsets this, emphasizing sperm competition.


*5.1.1.3 Sexual Dimorphism at Higher Altitudes*

Sexual dimorphism may decrease at higher altitudes due to resource limitations. The lack of sexual dimorphism has been suggested as a product of low resource availability in Madagascar (Pochron and Wright 2002).  Among the Malagasy lemurs, body sizes may be limited by the low amount of plant resources and the unpredictable climate (Wright 1999).  Thus, environmental constraints limit body size, but larger testes volume offsets this, emphasizing sperm competition.

Primates at higher altitudes may be expected to follow the same pattern. Primates at high altitudes experience size reduction in accordance with these trends, which has corresponding effects on their life history.  Male gelada baboons (*Papio anubis*) adjust body size to their environment by increasing body size and degree of sexual dimorphism at sites with higher rainfall (Popp 1983).  Males (but not females) also reduce body size in high altitude habitats, even with a high amount of rainfall; this size reduction has been explained as a response to the decline in plant species and food availability at higher elevations (Popp 1983).  Popp (1983) provides a life history explanation for reduced body size in geladas: in resource poor environments, baboons have higher costs for foraging, but in richer habitats they can devote more energy to growth and reproduction (such an enhanced male-male competition through larger body size).

Thus, pygmy tarsiers are expected to have low sexual dimorphism but large relative testes size.  Initial observations of *T. pumilus* indicates the species have low

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sexual dimorphism and live in multi-male, multi-female groups (Grow and Gursky-

Doyen 2010).  Given their group composition, pygmy tarsiers are expected to have a

more polygynous, multi-male mating system than the lowland Sulawesian tarsier

species.


***5.1.2 Altitudinal Effects on Body Proportions***

*5.1.2.1 Body Size*

      Declines in resource abundance, including altitudinal declines in resources, can

result in decreased body size.  Body size clines can occur due to environmental

changes that correlate with changes in climate (Blackburn et al. 1999).  For example,

limited resources can cause latitudinal declines in body size among insects due to

temperature, season length, and habitat productivity (Chown and Klok 2003).  Similar

environmental constraints may have driven the evolution of small body sizes among the

Callitrichidae (marmosets and tamarins) (Ford 1980; Leutenegger 1980; Martin 1992).

These primates are unique in that they experience multiple births (twinning) in addition

to small body size.  Twinning is a presumably derived characteristic that evolved from

single-birthing ancestors, given that callitrichines share reproductive traits with primates

that give single births, including a unicornuate uterus and the number of nipples

reduced to a single pectoral pair (Leutenegger 1980). The evolution of apparently

monogamous mating systems among callitrichines may relate to both body size

constraints and the need for paternal investment (Leutenegger 1980).  Since even a

single neonate is relatively large compared to maternal size (Leutenegger 1973),

reducing the percentage of viable births, multiple offspring may offset these risks.

Moreover, a high reproductive burden (high litter to maternal weight ratio) selects for

more parental investment, since female callitrichines are unable to raise multiple offspring alone. As callitrichines do not exhibit sexual dimorphism (Sussman and Garber 1987), they fit the model of monogamy, but most of the Callitrichidae have larger than expected testes volume (Harcourt et al. 1995).

Along the same lines, it has been hypothesized that the relatively small body size of *T. pumilus* is an adaptation to a colder, less productive environment (Musser and Dagosto 1987). Their body size and limb proportions are not likely to be thermoregulatory adaptations. Their small body size and long limb proportions produce increased surface area relative to body mass, resulting in heat loss, the opposite of predictions for Bergmann's and Allen's rules. If larger insects are less abundant at higher altitudes, it is possible that pygmy tarsiers consume smaller and fewer insects with lower overall biomass, constraining their body size. The number of invertebrate species, the main food source of tarsiers, is known to decline with altitude (Whitten et al. 2002). Pygmy tarsiers are therefore expected to experience an altitudinal decline in food resources that corresponds to altitudinal declines in body size. As predation risk may be high for pygmy tarsiers, an altitudinal increase in mortality may further contribute to small body size.

*5.1.2.2 Limb Proportions*

Dwarfed lineages may exhibit allometric patterns opposite from interspecific trends, with a mixture of ancestral and derived traits (Hanken and Wake 1993). Morphometric measurements were used to explore whether the highland pygmy tarsier has dwarfed over time, and to determine if there are interspecific differences in limb

proportions among tarsiers. Pygmy tarsiers were hypothesized to exhibit distinct limb proportions compared to interspecific trends among lowland tarsier species.

Pygmy tarsier body proportions may be affected by resource limitations at higher altitudes.  Given that there is more spacing between trees at higher altitudes (Körner 2007), pygmy tarsiers may have relatively long hindlimb and tail lengths for their body size (Grow and Gursky-Doyen 2010) as a reflection of greater leaping distances. Longer limb proportions and relative tail lengths are adaptations to greater leaping distances in leaping primates (Demes et al. 1996).


## 5.2 RESULTS

### 5.2.1  Sexually Selected Traits

Although *Tarsius pumilus* clearly exhibits reduced body size (Figure 22), they do not show significant body mass differences between the sexes (Kruskal-Wallis: $\alpha$=0.05; $Z$=0; $p$=1; Table 17, Figure 23). Pygmy tarsiers show a pattern of low sexual dimorphism similar to *T. bancanus*, *T. tarsier*, and *T. lariang*.  *T. tarsier* and *T. lariang* are monogamous (Driller et al. 2009; Gursky 1997; Merker et al. 2005), while the Philippine tarsier, *T. syrichta*, is the most dimorphic (p<0.0186), and accordingly follows a polygynous mating pattern with multiple breeding males (Neri-Arboleda et al. 2002).

**Figure 22. Tarsier body mass (g) by species and sex (N=118).**
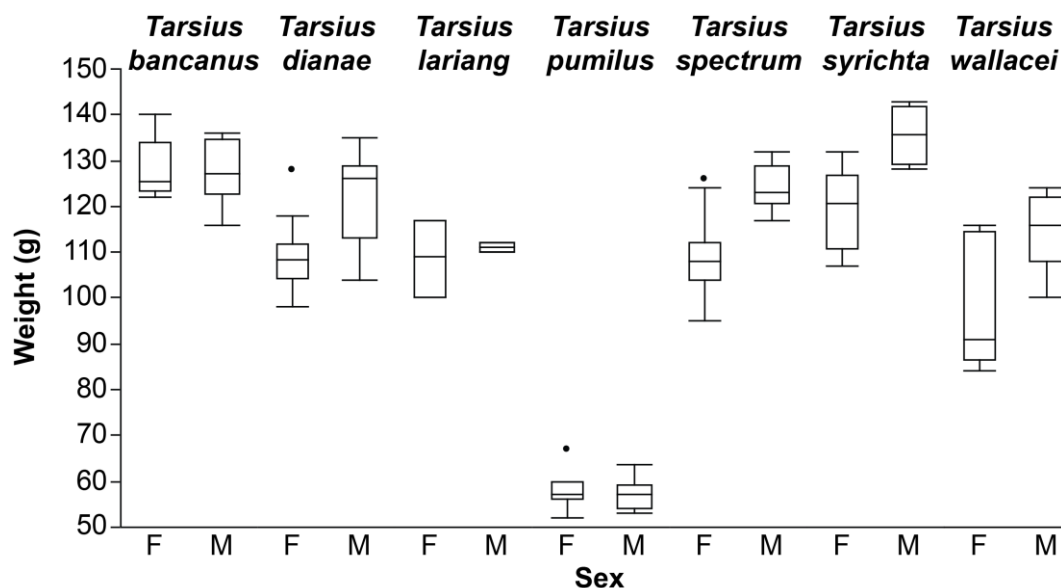


**Table 17. Kruskal-Wallis test (α=0.05) for difference between male and female weights for tarsier species.**

| Species | Z | *p*-value | N male/female | Sexual Dimorphism |
|---|---|---|---|---|
| Tarsius bancanus | 0.2410 | 0.8095 | 6 / 6 | No significant difference |
| Tarsius dianae | 3.4704 | 0.0005 | 11 / 24 | Significant sexual dimorphism |
| Tarsius lariang | 0.2887 | 0.7728 | 2 / 3 | No significant difference |
| Tarsius pumilus | 0.0000 | 1.0000 | 6 / 6 | No significant difference |
| Tarsius spectrum | 4.0034 | *p* < 0.0001 | 10 / 23 | Significant sexual dimorphism |
| Tarsius syrichta | 2.2454 | 0.0247 | 4 / 6 | Significant sexual dimorphism |
| Tarsius wallacei | 1.9033 | 0.0570 | 5 / 5 | Approaching significance |

**Figure 23. Degree of sexual dimorphism plotted against average body weight for tarsier species.**
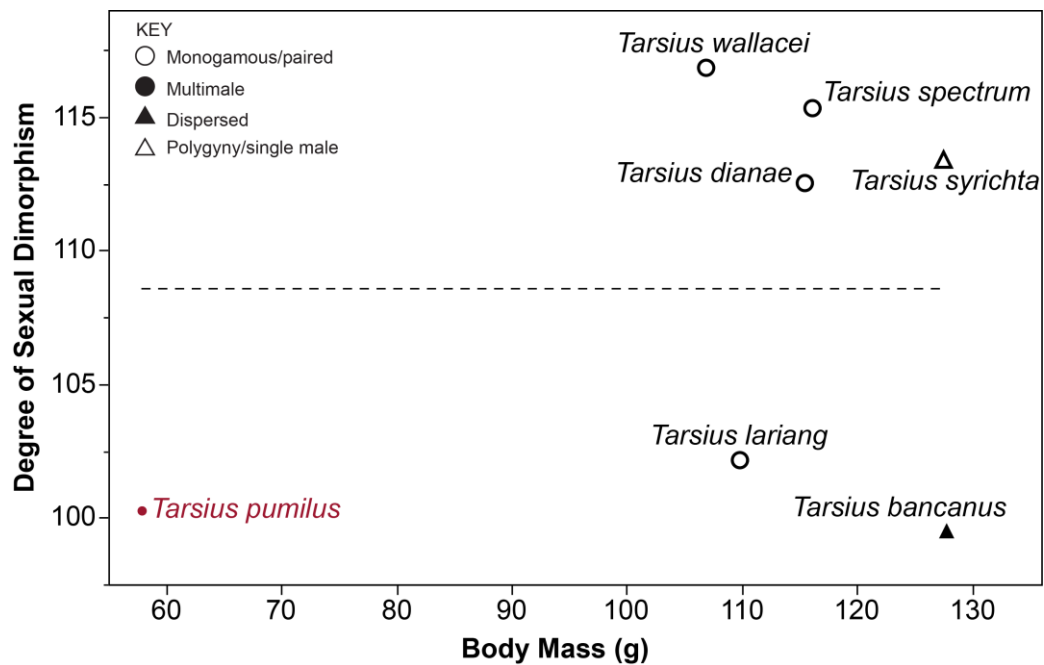


Compared to the other tarsier species, pygmy tarsiers have relatively smaller testes volume (Figure 24), indicating less sperm competition. As indicated in Figure 24, primates with multiple breeding males are predicted to fall above the regression line (closed symbols), with relatively larger testes weight for their body mass. Primates with a single breeding male (open symbols) are predicted to fall below the regression line. Unlike most primates, small-bodied nocturnal primates do not fit well the relationship between testes mass and mating system; species below the regression with relatively small testes tend to have multiple breeding males.

**Figure 24. Primate testes weight (g) in relation to body weight (g) using log$_{10}$ transformed data (averages).** Closed symbols indicate mating systems with multiple males, while open symbols indicate those with one breeding male.
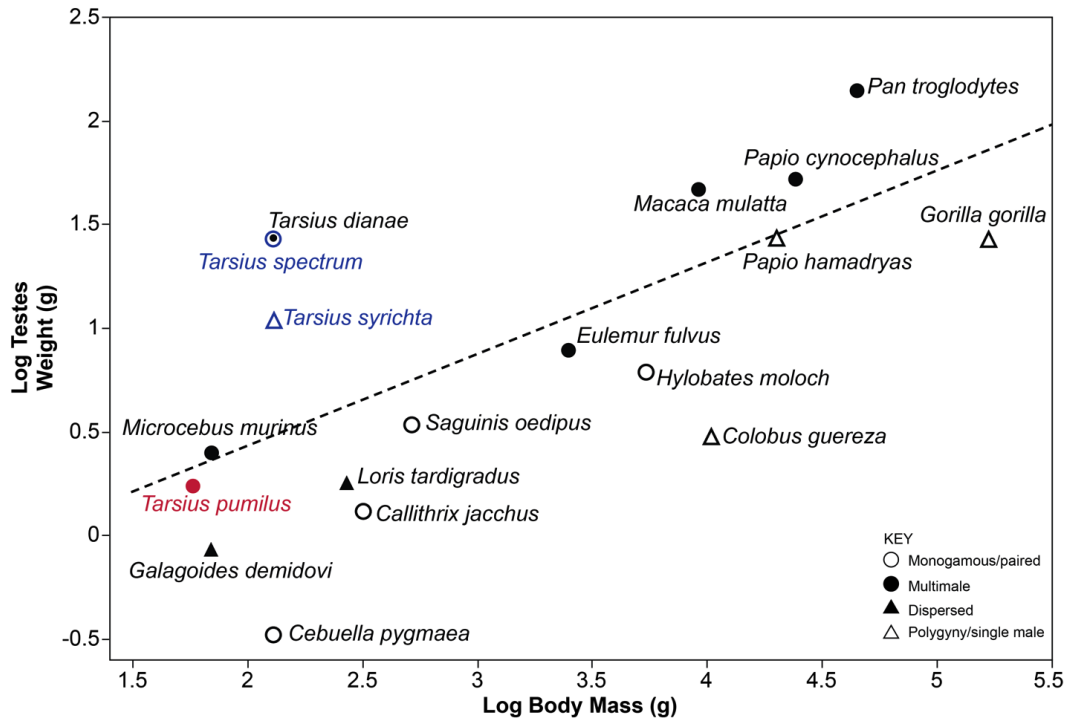


Compared to primates in general, tarsiers trend towards larger testes for their body size (above the regression line). In contrast, *Tarsius pumilus* falls below the regression line, indicating smaller testes size and less sperm competition. Tarsiers and multi-male primates tend to have larger testes than average (respective average residuals of 0.9350 and 0.2552), while *Tarsius pumilus* an average testes size (residual of 0.0301; Table 18). Compared to other tarsier species, *Tarsius pumilus* exhibits both low sexual dimorphism and low sperm competition, traits that usually associate with paired/monogamous systems (Figure 25).

**Table 18.  Mean residual values for monogamous primate species, multi-male primates, tarsiers (average of non-pygmies), and *Tarsius pumilus*, as taken from regression in Figure 24.**

|  | Monogamous Primates | Multi-Male Primates | *Tarsius* | *Tarsius pumilus* |
|---|---|---|---|---|
| Residual Value | -0.5654 | 0.2552 | 0.9350 | 0.0301 |

**Figure 25.  Degree of sexual dimorphism (average male weight / female weight x 100) plotted against relative testes mass (average testes mass / average body mass) (N=58).**
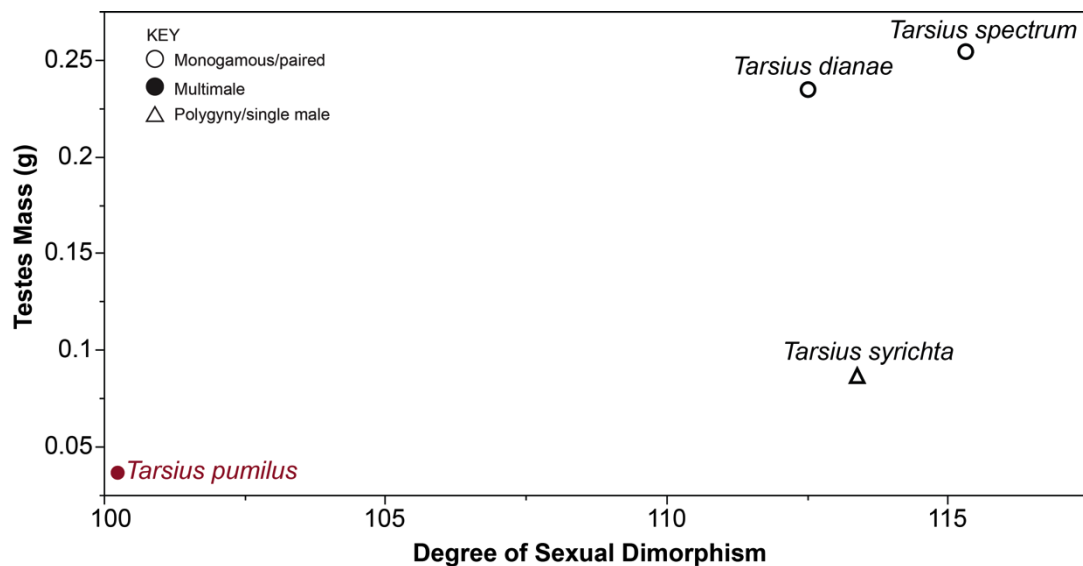


### 5.2.2 Body Proportions

Discriminant function analyses using stepwise variable selection procedures were applied to the live external measurements of pygmy tarsiers and lowland tarsier species.  Results showed clear separation.  Variables included in the analysis are body length (BODY), forelimb length (FORELIMB), hindlimb length (HINDLIMB), upper leg length (THIGH), foot length (HINDFOOT), upper arm length (UPPER-ARM), and forearm length (FOREARM), all size standardized.  Variables also included approximations of the Intermembral Index (INTERMEM; [(UPPER-ARM + FOREARM) x

100] / [THIGH +LOWER LEG]), Crural Index (CRUR; [UPPER LEG x 100] / THIGH, and Brachial Index (BRACH; LOWER ARM x 1000] / UPPER ARM).

*5.2.2.1 Canonical Discriminant Analysis: Species*

A canonical plot derived from canonical discriminant analysis reveals that limb lengths accurately distinguish between tarsier species, where 94.83% classify correctly using cross-validation (Figure 26).  A stepwise variable-selection procedure selected FOREARM, HINDLIMB, THIGH, and HINDFOOT as good candidates for discrimination. The first axis (Canonical1) explained 75.09% of the variation.  Standardized canonical coefficients were largest for FOREARM (1.039) and HINDLIMB (0.49). The second axis (Canonical2) explained 24.85% of the variation. Standardized coefficients were largest for HINDLIMB (-1.35), THIGH (1.27), and HINDFOOT (0.45).

*5.2.2.2 Canonical Discriminant Analysis: Geographic Location*

A stepwise variable selection procedure was also applied to a canonical discriminant analysis of tarsier geographic locations (Philippines, Central Sulawesi, and Northern Sulawesi ).  In the canonical plot discriminating between geographic locations, 91.23% classified correctly. Pygmy tarsiers overlap with *T. wallacei* in Central Sulawesi (Figure 27).  Standardized coefficients for Canonical1 (81.63% of variation) were largest for CRUR (3.77), THIGH (3.16), and LOWER LEG (-1.64), while THIGH (4.9), CRUR (3.89), LOWER LEG (-2.19), and UPPER ARM (-1.09) were largest for Canonical2 (18.37% of variation).

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**Figure 26.  Canonical plot of limb proportions by tarsier species, using size standardized variables.  Circles indicate 95% confidence ellipses for group means.**
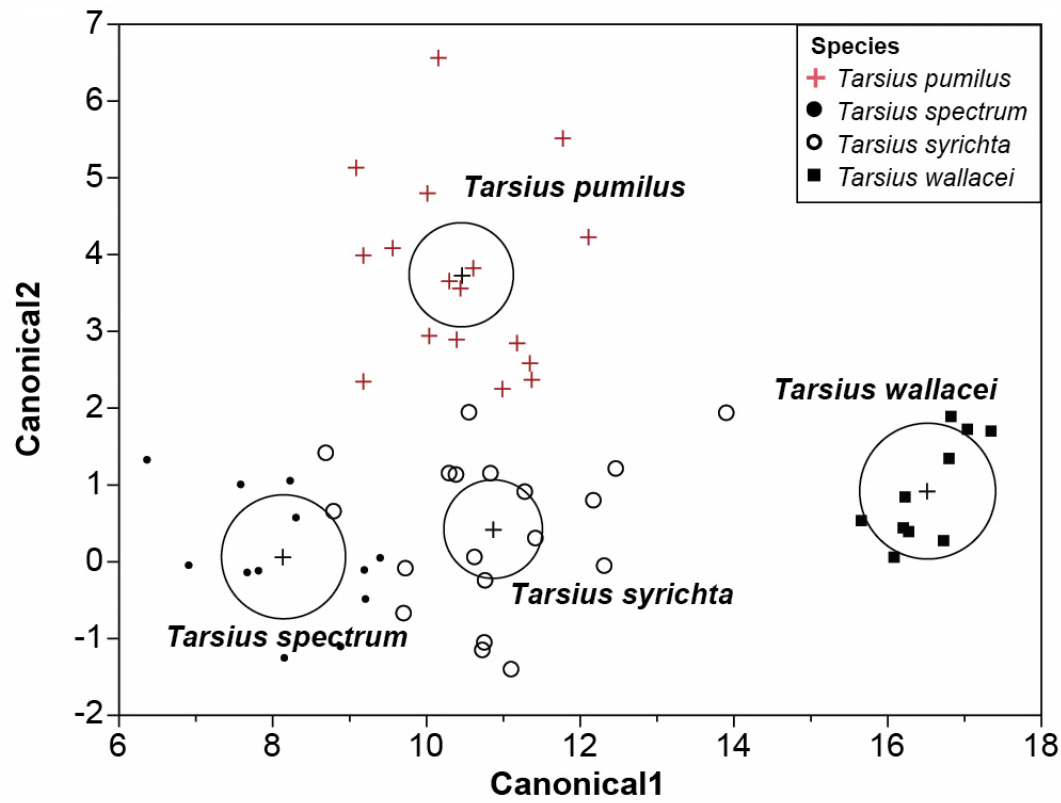
**Figure 27.  Canonical plot of tarsier limb lengths by geographic location.**
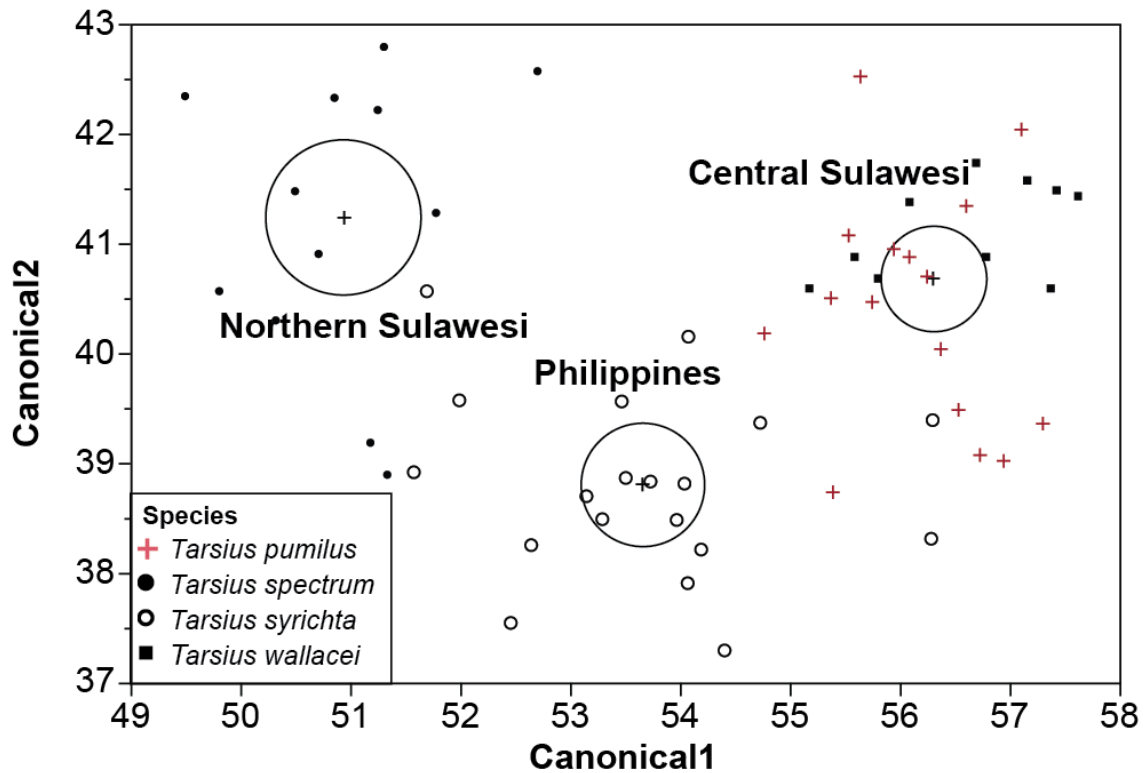


*5.2.2.3 Discriminant Function Analysis: Highland vs. Lowland*

Group membership in lowland tarsiers (*T. spectrum, T. wallacei, T. syrichta*) versus highland pygmy tarsiers (*T. pumilus*) is accurately predicted by limb proportions, controlling for body size.  A stepwise discriminant analysis classified 91.38% of individuals correctly as "pygmy" versus "non-pygmy" (Wilks' Lambda=0.49, $p < 0.0001$). Philippine tarsiers were the only species to misclassify as pygmy tarsiers.  Pygmy tarsiers are distinguished primarily by FOREARM (-10.35), THIGH (5.92) and INTERMEM (forelimb relative to hindlimb length) (9.44).

*5.2.2.4 Regressions*

Among lowland tarsiers, a positive relationship exists between hindlimb length and body mass (Figure 28; upper graph).  Among pygmy tarsiers, a stronger positive relationship exists, with a steeper slope (lower graph). No significant relationships occurred between any other variable.  Pygmy tarsiers have comparatively longer hindfoot and thigh lengths (Figure 29). Pygmy tarsier hindfoot lengths are significantly different than non-pygmy species (Student's *t*-test: *t*=-3.710, *p*-value=0.0014).

**Figure 28.  Regressions of log hindlimb lengths plotted against log body mass.**
Pygmy tarsiers are shown in the right graph (red plus signs) while lowland tarsiers are shown in the left graph (squares: *Tarsius wallacei*; closed circles: *Tarsius spectrum*; open circles: *Tarsius syrichta*).
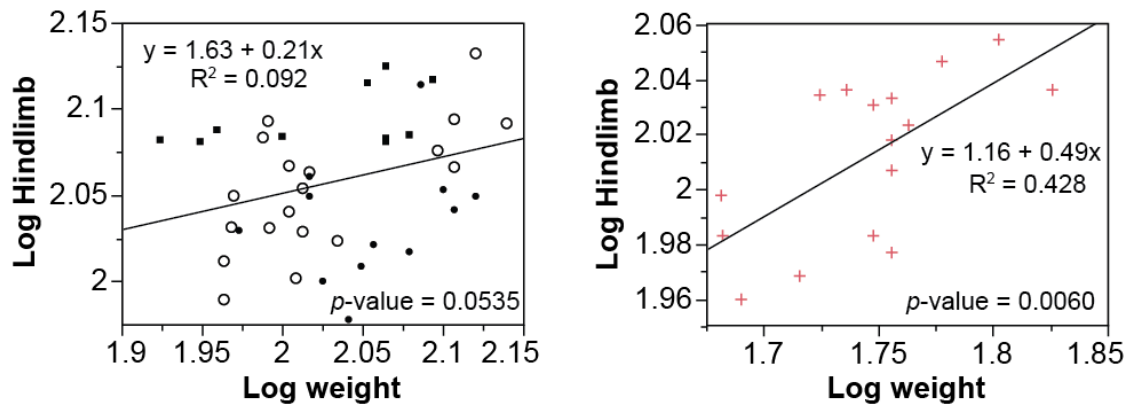
**Figure 29. Boxplots of size standardized hindfoot and thigh lengths.**
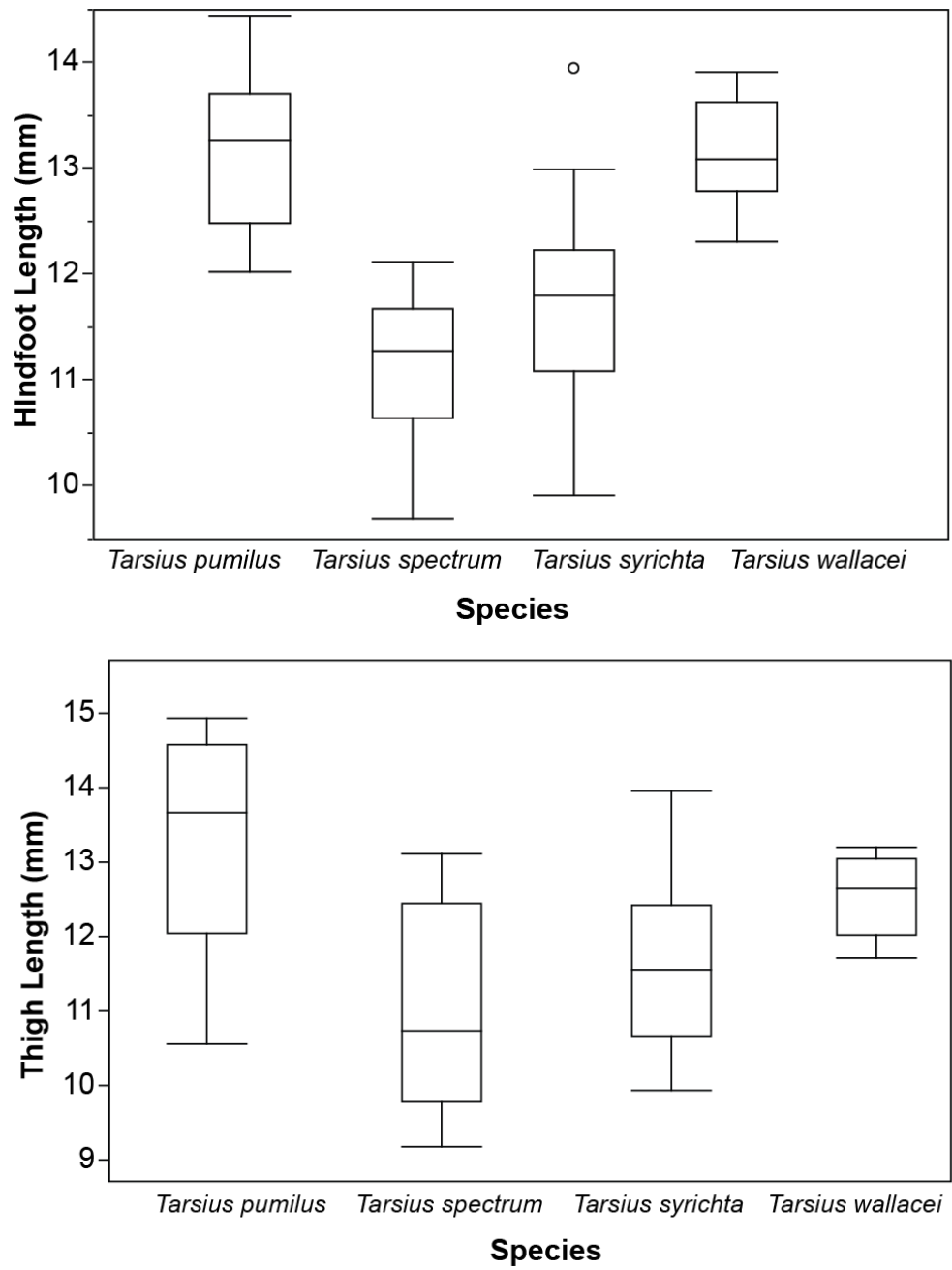
**5.3 DISCUSSION**

*5.3.1 Sexually Selected Traits*

Results indicate pygmy tarsiers should have a more monogamous mating pattern, because of their low sexual dimorphism and smaller relative testes size. Because of their observed multi-male, multi-female grouping patterns, pygmy tarsiers were expected to have relatively larger testes and a more polygynous mating system. However, while *Tarsius* and multi-male primates tend to have larger testes than average, the testes of *Tarsius pumilus* are average, contrary to expectations to undergo selection from sperm competition in their multi-male groups. Interestingly, as shown in Figure 24, pygmy tarsiers appear to fit near nocturnal primates below the regression line that have a dispersed or noyau mating system, where male home ranges overlap multiple females. While their mating system remains unclear, these analyses show that their pattern of sexual dimorphism and testes size is distinctive among tarsiers.

*Tarsius pumilus* body measurements point to a monogamous mating system. Their low sexual dimorphism and sperm competition fit the expectations for phyletic dwarves, and sexual dimorphism of body size may be constrained in their resource-limited habitat. Pygmy tarsiers may experience less sexual selection pressures than lowland tarsier species in association with high altitude constraints. Production and maintenance costs of sexually selected traits are higher in harsher environment. For example, interspecific sexual dimorphism has been shown to decrease at higher altitudes among birds (Badyaev 1997).

Tarsiers tend to have relatively large testes and do not appear to conform to expectations for sexual dimorphism based on their observed mating systems (Table 19). The Phillippine tarsier (*Tarsius syrichta*) exhibits sexual dimorphism (Wright et al.

2003) a polygynous mating system (Neri-Arboleda et al. 2002). The Bornean tarsier, *T. bancanus*, does not exhibit any sexual dimorphism (Wright et al. 2003) and has a dispersed mating system, where male's range overlaps the ranges of multiple females (Crompton and Andau 1987). The Sulawesian tarsiers are primarily monogamous, with facultative polygyny, and are sexually dimorphic (Gursky 1997; Gursky 2007; Merker 2006). *T. spectrum* and *T. dianae* exhibit moderate sexual dimorphism of body size and relatively large testes size, somewhat contrary to their observed monogamous mating patterns.

**Table 19. Comparison of tarsier grouping patterns, sexual dimorphism, and relative testes size, with expectations for mating systems.**

|  | *Tarsius syrichta* | *T. bancanus* | *T. dianae* *T. lariang* *T. spectrum* | *T. pumilus* |
|---|---|---|---|---|
| Group composition | One male, multiple females | Multimale-multifemale (nongregarious) | One male, one female | Multimale-multifemale or one male, one female |
| Sexual dimorphism | High | Low | Higher | Lower |
| Sperm competition | Medium | Higher | High | Lower |
| Predicted mating system | Polygyny | Polygyny (more breeding males) | Multimale | Monogamy |
| Observed mating system | Polygyny | Dispersed | Monogamy; some polygyny | Multimale and paired |

Pygmy tarsiers live at high altitudes in groups with multiple adult males, but generally do not exhibit sexually selected traits. Contrary to expectations based on large and low sexual dimorphism do not conform to expectations from the group composition of pygmy tarsiers. These results suggest a monogamous mating system among pygmy tarsiers, and may indicate these tarsiers experience less sexual selection

pressures than lowland tarsier species in association with high altitude constraints. These results may be complicated by temporal changes in testes size, since mating season and seasonal effects are unknown in pygmy tarsiers.

### 5.3.2 Body Proportions

A primary driver of the small body size of pygmy tarsiers may be limited food resources. Among humans, it has been hypothesized that pygmy groups experienced selection for size reduction by living in environments with reduced food resources, such as tropical rain forests, where reducing size in turn reduces required caloric intake (Shea and Bailey 1996). It has alternately been suggested that small body size in human pygmies is a side-effect of selection for early reproduction under conditions of high mortality, constraining growth (Migliano et al. 2007; Walker et al. 2006b). Recent evidence supports the hypothesis for the evolution of human pygmy body proportions that links life history traits to the evolution of these growth patterns (Bailey 1991; Migliano et al. 2007; Stock and Migliano 2009; Walker et al. 2006b). In particular, a high mortality rate drives an early onset of reproduction, which has the side effect of constraining the period of growth. In other words, pygmy body size is the result of selection for higher fertility early in life, and constrained body size is effectively a byproduct of a reduced growth period. Selection may favor earlier reproduction among populations with high morality; if these populations experienced delayed reproduction, there would be a greater chance of dying before reproducing. Independently analyzed cross-cultural data suggest all pygmies have high mortality, fast development, and early ages of first reproduction (Migliano et al. 2007; Perry and Dominy 2009; Walker et al. 2006b). These ideas may be equally applicable to pygmy tarsiers. As predation risk

may be high for pygmy tarsiers, an increase in mortality at higher altitudes may further contribute to small body size.

Based on discriminant analyses, body proportions hold phylogenetic significance for tarsier species. This study found that limb proportions are an accurate means to discriminate between species and geographic location. Previously, tarsier species have been classified based on skull and body length (Dagosto et al. 2003), as well as tail tuft lengths (Merker et al. 2010).

Pygmy tarsiers classify correctly according to geography, separate from Northern Sulawesian tarsiers. Pygmy tarsiers classify near other Central Sulawesian tarsiers primarily by the ratio of upper to lower leg (an approximation for the crural index). Pygmy tarsiers have relatively long hindlimbs due to elongated thigh and foot lengths – indicating elongated femora and tarsal bones – and moderately long forearms. In comparison, *T. wallacei* in Central Sulawesi have relatively long forearms for their body length.

Among prosimians, there is a weak negative relationship between the crural index (ratio of lower leg to upper leg, or the tibia to the femur and body size (Anemone, 2003). A high crural index is better for longer leaping distances. A higher crural index in smaller-sized pygmy tarsiers indicates their limbs may be scaling allometrically.

Pygmy tarsiers also exhibit limb proportions that are distinctive from lowland tarsiers as a group, controlling for body size. The body proportions of pygmy tarsiers may be adaptations to energetic constraints in a montane environment. Further studies are necessary to explore the evolution of body proportions among tarsiers. Larger sample sizes will clarify if tarsier limb proportions aside from hindlimb length also result in significant regressions against body size.

Body size diversity within primate families is an important means of exploring the effects of geographic and environmental variation.  Reduced body size can be adaptive and evolve from direct selection for smaller body size, or it can indirectly result from selection for a related trait that produces smaller body size, such as life history traits (Hanken and Wake 1993).  Declines in resource abundance, including geographical declines in resources, can result in decreased body size.  These selection pressures may have driven the evolution of small body sizes among the Callitrichidae. Ford (1980) suggests that dwarfism is adaptive, and proposes multiple reasons, including predation pressures, resource limitations, interspecific competition for resources, climatic pressures, and character displacement (filling a previously unfilled body size niche).

# 6. CONCLUSIONS

## 6.1 SUMMARY OF RESULTS

Although altitude is known to have significant effects on primate behavioral and morphological variation (Cui et al. 2006; Ganas et al. 2004; Hanya et al. 2004; Iwamoto and Dunbar 1983; Lehman et al. 2006b; Marshall 2005; Rae et al. 2003), altitudinal variation in tarsiers had not yet been explored despite the unusually wide altitudinal range utilized by the genus. This study represents the first study of altitudinal differences in tarsier populations, as well as the first to observe multiple groups *Tarsius pumilus.* Results show that: a) pygmy tarsiers live at low population density; b) pygmy tarsiers were found to have a non-random distribution near forest edges; c) pygmy tarsiers do not appear to have larger home ranges or longer nightly travel distances than lowland tarsiers; d) pygmy tarsiers exhibit a lack of sexually selected traits in conjunction with small body size; and e) pygmy tarsier limb proportions are relatively long, and accurately discriminate them from lowland tarsier species.

### 6.1.1 Population and Distribution of Groups

In summary, the estimated population density of the observed pygmy tarsiers is 92 individuals per 100 ha. Within the study area, pygmy tarsiers live at a lower density than lowland Sulawesian tarsier species, which is associated with decreased resources at higher altitudes. The abundance and spatial dispersion of pygmy tarsiers differs compared to the lowland tarsiers, and may be affected by high altitude variables.

Forest structure differs within the high-altitude range (2000 to 2400 m) that pygmy tarsiers occupy, where tree density and size decrease with increasing altitudes.

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In this area, pygmy tarsiers exhibited a nonrandom, clumped distribution near forest edges. While insect abundance and biomass decreases as altitude increases, insect abundance and biomass is higher along anthropogenic edges at all altitudes. Thus, estimates of pygmy tarsier abundance may be higher than expected because of increased insect abundance along anthropogenic edges. Pygmy tarsiers may respond the decreased availability of insects at high altitudes by foraging close to forest edges.

### 6.1.2 Ranging

Contrary to hypotheses, home range sizes of pygmy tarsiers were not significantly larger than lowland tarsier home ranges, and average NPL was smaller than those of lowland tarsiers. Although these results are limited by the small sample size of focal individuals, the relatively small NPL of pygmy tarsiers may be explained by their biased distribution near forest edges, which mitigates the need to increase foraging area.

### 6.1.3 Body Size and Proportions

Pygmy tarsiers live at high altitudes in groups with multiple adult males, but generally do not exhibit sexually selected traits. Members of the species were observed to sleep in groups with more than one adult male, indicating they should experience more sperm competition than lowland populations where adult males do not associate. Contrary to expectations, pygmy tarsiers exhibit low sexual dimorphism and sperm competition, suggesting that they evolved in a low quality environment where sexually selected traits are constrained.

Tarsier species can be accurately distinguished based on forearm and hindlimb proportions, controlling for body weight. Tarsiers accurately discriminate based on geographic location, based on thigh, lower leg, and forearm proportions. Pygmy tarsiers exhibit relatively long hindlimb proportions for their body size. However, further research is necessary to clarify if pygmy tarsiers have undergone an evolutionary size reduction.

## 6.2 CONCLUSIONS

*"Tarsiers are astonishingly deliberate and stupid-appearing in behavior, so much so that it seems a miracle that they can survive." (Davis 1962)*

Although natural historians such as Davis (1962) have underappreciated the survivability of tarsiers, as Jablonski has noted, tarsiers are in fact well adapted to their dietary niche, which has allowed them to persist since the Middle Eocene (Jablonski 2003). Tarsiers are quick, effective hunters, engaging in energetically costly leaps between trees in order to capture their prey. This research indicates that tarsiers are remarkably have adapted to any environment they are encountered in, even in the seemingly perilous forests on mountaintops. Pygmy tarsiers, the only high altitude Sulawesian species of tarsier, exhibit differences in their population, behavior, and anatomy from lowland tarsiers that coincide with environmental differences. Despite their seemingly harsh montane habitat, they have endured since tarsiers first populated the region and shown a remarkable ability to survive.

Despite their proven ability to survive under changing conditions, pygmy tarsiers have a number of more recent habitat threats. Although higher altitudes are somewhat

more protected from human activity, the forest in the study area is clearly secondary disturbed forest. Remains from the illegal logging activities that occurred in the 1970's can be found throughout the mountain. The logging road up Mt. Rore Katimbu, although now inaccessible by vehicles, is the primary threat to this particular location. It makes the mountain a particularly popular location for campers, tourists, motorcyclists, and occasional hunters. Individuals regularly enter the forest to cull resources, particularly damar gum from Dipterocarpaceae trees, and often deforest new growth trees to make trails or build fires. The large trees that produce damar are tapped, which does not kill them, but requires daily visits to tapped trees to harvest the resource. Although the montane rainforest in Lore Lindu National Park has preserved 90% of its canopy cover, residents of villages located within and near the park continue to extract resources and modify the landscape. The increasing population density of humans in national park regions brings increasing threat to forest (Kirleis et al. 2011b).

Further, the amount of available habitat for pygmy tarsiers is severely constrained. In Lore Lindu National Park, elevations higher than 1500m characterize only 20% of the park (approximately 45,300 ha) (Latifah 2005). Given that pygmy tarsiers have not been observed below 2000m and not all of those elevations harbor suitable habitat, they will inhabit only a fraction of that area. Pygmy tarsiers (*Tarsius pumilus*) are currently on the list of the world's twenty-five most endangered primates, published by the Primate Specialist Group of the IUCN Species Survival Commission (Mittermeier et al. 2012). Thus, understanding pygmy tarsier population structure, behavior, and habitat usage are all crucial to addressing the conservation needs of the species.

In general, primates are highly adaptable animals that have undergone multiple radiations across a variety of habitats.  High altitude populations are presented with a particular set of challenges, to which they have developed unique and interesting solutions.  Primates living at living altitudes are demonstrative of the flexibility and resiliency of the order, and yet questions of altitude are often overlooked in primate studies - perhaps because of the remoteness of primate populations and the difficulty in establishing field studies.  However, more and more primates may be forced into higher altitudes as lower-altitude habitat diminishes with anthropogenic changes.  Studying high altitude primates is instructive of how primates have adapted to different altitudes in the past, and how they continue to do so in the future.

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# APPENDIX A

## FIGURES

*A-1. A female Tarsius pumilus individual.*

*A-2. A male T. pumilus individual.*

*A-3. A T. pumilus sleeping tree at 2100m in altitude.*

*A-4. The sleeping site of T. pumilus near the top of the sleeping tree.*

# APPENDIX B

## TABLES

*B-1. External morphometric measurements for captured Tarsius pumilus individuals. Empty cells indicate missing values.*

*All lengths in millimeters (mm) and all weights in grams (g).*

|  | Group 1 | | | Group 2 | | | Group 3 | | Group 4 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Altitude | 2200 | 2200 | 2200 | 2300 | 2300 | 2300 | 2100 | 2100 | 2100 | 2100 | 2100 | 2100 | 2100 |
| Age Class | Adult | Subadult | Subadult | Adult | Subadult | Adult | Adult | Adult | Subadult | Subadult | Adult | Adult | Adult |
| Sex | Female | Male | Male | Female | Male | Female | Male | Female | Male | Male | Male | Female | Male |
| Weight (g) | 52.00 | 50.10 | 48.10 | 56.00 | 49.00 | 56.00 | 58.00 | 60.00 | 54.50 | 48.00 | 57.00 | 57.00 | 63.50 |
| Ear width (mm) |  | 15.80 | 19.03 | 16.00 | 13.14 | 15.00 | 12.89 | 28.10 | 15.14 | 13.00 | 13.16 | 30.40 | 12.63 |
| Ear length | 14.73 | 20.40 | 19.50 | 22.00 | 18.00 | 21.75 | 19.60 | 20.10 | 21.60 | 23.70 | 21.90 | 25.00 | 22.51 |
| Foot length | 46.00 | 26.10 | 48.88 | 50.00 |  | 46.00 | 48.80 | 49.10 | 51.30 | 52.30 | 52.00 | 48.00 | 51.14 |
| Big toe length | 17.10 | 13.60 | 19.23 | 13.40 | 10.85 | 11.25 | 14.40 | 11.20 | 14.30 | 11.50 | 13.59 | 11.70 | 11.27 |
| Big toe width |  |  |  | 5.30 | 5.38 | 5.40 |  | 4.60 | 4.90 | 5.20 | 5.10 | 5.50 | 5.66 |
| Toe 2 Length |  |  |  | 12.40 | 11.00 | 10.72 | 12.40 | 11.23 | 12.30 | 13.20 | 12.24 | 11.00 | 12.96 |
| Toe 2 Claw Length |  |  |  | 4.90 | 4.15 | 4.70 | 5.50 | 5.07 | 4.86 | 5.00 | 4.40 | 4.00 | 5.12 |
| Toe 3 Length |  |  |  | 10.40 | 10.00 | 13.42 | 11.44 | 11.30 | 14.09 | 14.30 | 14.30 | 14.50 | 13.04 |
| Toe 3 Claw Length |  |  |  | 5.00 | 3.80 | 4.30 | 3.80 | 4.30 | 4.20 | 5.00 | 3.64 | 5.10 | 6.17 |
| Toe 4 Length |  |  |  | 15.60 | 16.60 | 14.20 | 18.65 | 19.20 | 15.84 | 16.92 | 18.30 | 16.80 | 15.37 |

|  | Group 1 | | | Group 2 | | | Group 3 | | Group 4 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sex | Female | Male | Male | Female | Male | Female | Male | Female | Male | Male | Male | Female | Male |
| Toe 4 Claw Length |  |  |  | 3.60 |  | 3.18 | 4.20 | 3.12 | 4.60 | 3.80 | 3.50 | 3.50 | 3.87 |
| Toe 5 Length |  |  |  | 12.30 | 13.08 | 13.00 | 14.04 | 14.30 | 12.00 | 12.50 | 11.40 | 11.90 | 13.34 |
| Toe 5 claw length |  |  |  | 3.15 |  | 3.60 | 4.46 | 3.90 | 2.90 | 3.40 | 3.30 | 3.00 | 3.84 |
| Lower leg length | 37.80 | 31.10 | 45.82 | 52.50 | 52.30 | 52.50 | 56.02 | 53.70 | 57.60 | 48.80 | 56.00 | 53.31 | 53.62 |
| Upper leg length | 55.00 | 42.90 | 50.27 | 54.70 | 38.67 | 43.50 | 49.30 | 57.50 | 50.90 | 50.50 | 45.50 | 54.51 | 59.56 |
| Hindlimb Total Length | 138.80 | 100.10 | 144.97 | 107.20 | 90.97 | 96.00 | 105.32 | 111.20 | 108.50 | 99.30 | 101.50 | 107.82 | 113.18 |
| Tail length | 180.00 | 180.00 | 195.00 | 200.00 | 166.00 | 181.06 | 181.00 | 185.00 | 183.00 | 191.20 | 194.00 | 200.50 | 207.82 |
| Hair tuft length |  |  |  | 122.00 | 116.00 | 110.00 | 116.50 | 102.00 | 112.00 | 102.00 | 114.00 | 118.60 | 125.73 |
| Body length | 80.00 | 111.10 | 97.70 | 86.00 | 80.65 | 61.73 | 68.11 | 82.00 | 62.60 | 60.20 | 54.40 | 71.20 | 70.80 |
| Head width |  |  |  | 33.00 | 36.36 | 47.20 | 32.00 | 28.10 | 33.20 | 31.00 | 31.50 | 30.40 | 33.50 |
| Head length |  |  |  | 33.00 | 25.10 | 40.70 | 32.30 | 33.10 | 35.90 | 30.50 | 30.66 | 30.40 | 31.60 |
| Head and body length |  |  |  | 104.00 | 105.75 | 102.43 | 100.41 | 115.10 | 98.50 | 90.70 | 85.06 | 101.60 | 102.40 |
| Total length (including tail) | 260.00 | 291.10 | 292.70 | 304.00 | 271.75 | 283.49 | 281.41 | 300.10 | 281.50 | 281.90 | 279.06 | 302.10 | 310.22 |
| Hand length | 29.17 | 31.50 | 31.47 | 26.00 |  | 24.90 | 22.20 | 30.00 | 28.40 | 26.80 | 25.75 | 27.60 | 29.53 |
| Thumb width |  |  |  |  |  |  |  |  |  |  |  | 2.30 | 2.75 |
| Thumb length | 12.70 | 11.25 | 16.59 | 10.70 | 9.84 | 13.80 | 9.20 | 11.00 | 9.70 | 13.80 | 13.60 | 13.00 | 10.18 |
| Thumb claw |  |  |  |  |  |  |  |  |  | 2.66 |  | 2.60 | 2.08 |
| Finger 2 |  |  |  | 14.50 | 14.09 | 16.00 | 14.05 | 17.30 | 17.56 | 17.00 | 18.40 | 15.70 | 17.46 |
| Finger 2 claw |  |  |  |  |  |  | 3.63 | 3.25 |  | 3.30 |  | 2.90 | 3.55 |
| Finger 3 |  |  |  | 16.40 | 18.06 | 18.44 | 15.80 | 18.50 | 17.09 | 16.50 | 18.98 | 17.16 | 19.93 |
| Finger 3 claw |  |  |  |  |  |  | 3.95 | 3.30 |  | 4.25 |  | 2.98 | 3.46 |
| Finger 4 |  |  |  | 16.10 | 16.60 | 16.20 | 16.00 | 16.08 | 17.48 | 18.70 | 16.80 | 17.00 | 20.01 |
| Finger 4 claw |  |  |  |  |  |  | 3.85 | 3.20 |  | 3.60 |  | 3.35 | 3.15 |

| | Group 1 | | | Group 2 | | | Group 3 | | Group 4 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sex | Female | Male | Male | Female | Male | Female | Male | Female | Male | Male | Male | Female | Male |
| Finger 5 | | | | 12.70 | 10.88 | 10.90 | 11.00 | 11.33 | 11.80 | 12.50 | 12.26 | 13.40 | 12.64 |
| Finger 5 claw | | | | | | | 3.24 | 2.55 | | 3.15 | | 3.20 | 3.12 |
| Eye width | | | | 13.20 | 11.00 | 12.70 | 13.58 | 14.00 | 15.14 | 12.90 | 11.60 | 11.40 | 14.10 |
| Orbit distance | | | | 8.00 | 5.66 | 5.90 | 6.80 | 6.60 | 8.20 | 6.70 | 6.40 | 5.60 | 6.30 |
| Nose width | | | | 4.20 | 5.12 | 5.50 | 5.56 | 6.70 | 6.86 | 6.90 | 5.40 | 5.30 | 4.50 |
| Nose protrusion | | | | 3.40 | | 6.00 | 3.85 | 4.50 | 4.55 | 4.40 | 4.40 | 4.10 | 4.27 |
| Upper arm length | | 29.30 | 34.65 | 36.00 | | 29.70 | 27.04 | 33.00 | 26.60 | 23.80 | 28.00 | 28.80 | 33.33 |
| Lower arm length | | 27.10 | 34.33 | 36.00 | | 34.40 | 27.00 | 30.50 | 31.90 | 31.60 | 36.70 | 34.00 | 33.41 |
| Testes width | | | | | 5.56 | | 11.70 | | 11.45 | | 8.80 | | 9.15 |
| Testes length | | | | | 11.65 | | 12.60 | | 10.00 | | 12.30 | | 16.84 |
| Foot pad 1 width | | | | | 5.43 | 4.30 | 4.53 | 6.40 | 4.60 | 3.80 | 4.50 | 4.70 | 5.24 |
| Food pad 1 length | | | | | 7.73 | 6.70 | 6.83 | 7.15 | 6.98 | 6.45 | 7.20 | 7.30 | 6.93 |
| Foot pad 2 width | | | | | 4.75 | 3.60 | 4.95 | 5.50 | 4.50 | 3.90 | 3.60 | 4.20 | 4.43 |
| Food pad 2 length | | | | | 5.60 | 6.30 | 6.20 | 3.30 | 5.54 | 5.50 | 5.70 | 5.80 | 6.29 |
| Foot pad 3 width | | | | | 3.60 | 3.00 | 2.66 | 3.05 | 3.70 | 2.80 | 3.00 | 4.05 | 3.12 |
| Foot pad 3 length | | | | | 6.55 | 9.20 | 5.94 | 7.20 | 6.30 | 6.80 | 6.70 | 6.43 | 7.35 |

| | Group 5 | | Group 6 | |
|---|---|---|---|---|
| Altitude | 2150 | 2150 | 2000 | 2000 |
| Age Class | Adult | Adult | Adult | Adult (young) |
| Sex | Female | Male | Female | Male |
| Weight (g) | 67.00 | 57.00 | 57.00 | 53.00 |

*B-1 Continued.*

|  | Group 5 | | Group 6 | |
|---|---|---|---|---|
| **Sex** | Female | Male | Female | Male |
| **Ear width (mm)** | 14.00 | 14.25 | 17.04 | 14.00 |
| **Ear length** | 20.28 | 20.53 | 24.13 | 25.85 |
| **Foot length** | 54.60 | 53.00 | 53.63 | 54.22 |
| **Big toe length** | 15.35 | 15.92 |  | 10.88 |
| **Big toe width** | 6.00 | 2.53 |  | 5.17 |
| **Toe 2 Length** | 14.80 | 13.14 |  | 13.00 |
| **Toe 2 Claw Length** | 4.70 | 4.13 |  | 5.00 |
| **Toe 3 Length** | 15.50 | 12.78 |  | 13.00 |
| **Toe 3 Claw Length** | 4.30 | 3.72 |  | 4.00 |
| **Toe 4 Length** | 17.50 | 16.85 |  | 17.31 |
| **Toe 4 Claw Length** | 3.60 | 3.64 |  |  |
| **Toe 5 Length** | 14.54 | 13.63 |  | 13.47 |
| **Toe 5 claw length** | 3.80 | 2.54 |  |  |
| **Lower leg length** | 55.28 | 52.66 | 52.19 | 52.72 |
| **Upper leg length** | 53.20 | 42.07 | 52.00 | 55.28 |
| **Hindlimb Total Length** | 108.48 | 94.73 | 157.82 | 162.22 |
| **Tail length** | 199.00 | 187.57 | 181.00 | 186.00 |
| **Hair tuft length** | 134.50 | 102.74 | 116.00 | 120.00 |
| **Body length** | 77.15 | 66.40 | 60.77 | 77.00 |
| **Head width** | 33.68 | 34.52 | 20.46 | 25.38 |
| **Head length** | 31.80 | 31.00 | 24.02 | 32.00 |
| **Head and body length** | 108.95 | 97.40 | 84.79 | 109.00 |
| **Total length (including tail)** | 307.95 | 284.97 | 265.79 | 295.00 |

*B-1 Continued.*

|  | Group 5 | | Group 6 | |
| --- | --- | --- | --- | --- |
| Sex | Female | Male | Female | Male |
| **Hand length** | 30.00 |  | 25.18 | 31.15 |
| **Thumb width** |  |  |  |  |
| **Thumb length** | 15.09 | 9.75 | 9.98 | 9.00 |
| **Thumb claw** | 2.09 | 2.60 |  |  |
| **Finger 2** | 17.11 | 15.46 | 13.55 | 12.00 |
| **Finger 2 claw** | 3.37 | 3.70 |  |  |
| **Finger 3** | 18.11 | 17.30 | 16.34 | 20.00 |
| **Finger 3 claw** | 2.94 | 3.80 |  |  |
| **Finger 4** | 17.12 | 16.80 | 14.97 | 20.70 |
| **Finger 4 claw** | 3.14 | 2.82 |  |  |
| **Finger 5** | 14.77 | 13.65 | 11.57 | 12.00 |
| **Finger 5 claw** | 2.45 | 2.52 |  |  |
| **Eye width** | 15.26 | 11.05 | 12.63 | 14.77 |
| **Orbit distance** | 7.15 | 3.42 | 6.09 | 7.00 |
| **Nose width** | 4.00 | 6.18 | 5.04 | 7.00 |
| **Nose protrusion** | 4.52 | 6.03 |  |  |
| **Upper arm length** | 29.71 | 29.45 | 34.41 | 29.18 |
| **Lower arm length** | 34.67 | 34.64 | 35.00 | 32.26 |
| **Testes width** |  | 9.71 |  |  |
| **Testes length** |  | 15.17 |  |  |
| **Foot pad 1 width** | 4.60 |  |  |  |
| **Food pad 1 length** | 7.70 |  |  |  |
| **Foot pad 2 width** | 4.40 |  |  |  |

*B-1 Continued.*

|  | Group 5 | | Group 6 | |
|---|---|---|---|---|
| **Sex** | Female | Male | Female | Male |
| **Food pad 2 length** | 6.18 | | | |
| **Foot pad 3 width** | 3.20 | | | |
| **Foot pad 3 length** | 7.56 | | | |