Evolution of Sexual Size Dimorphism in Squirrels

by

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Abstract

Difference between the sizes of the sexes in a species (sexual size dimorphism SSD) is a common phenomenon, and most mammals are male-biased in size. Female-biased size dimorphism (FBSD) is uncommon in mammals. Flying squirrels exhibit a unique lifestyle (gliding), which could require females to evolve larger size to attain functional or reproductive advantages. In this dissertation I examined the evolution of FBSD in flying squirrels using comparative approaches. I began by examining all squirrels and their patterns of dimorphism to determine if FBSD evolved in association with gliding. FBSD was seen to evolve multiple times across squirrels, and the ancestor to flying squirrels was male-biased, implying that FBSD evolved in association with a gliding lifestyle. An analysis of ecological predictor variables revealed that FBSD was predicted by arboreal habits, nocturnality and tropical latitudes, and that extreme MBSD was predicted by open habitats and sociality. In a second analyses, I examined body size partitioning across two sympatric squirrel communities, temporal and diurnal, in Borneo. Species and sexes partitioned themselves along a non-overlapping size spectrum, implying that species evolved specific sizes to minimize competition. SSD does not seem to enhance partitioning of resources. Finally, I examined patterns of scaling (Rensch's rule) of FBSD across 27 flying squirrel species based on morphometric measurements from museum specimens. Flying squirrels were seen to scale in accordance with Rensch's rule, which predicts that FBSD decreases with increasing body size across related species. Females had relatively longer tails and larger heads than males, indicating that selection for enhanced gliding ability may have resulted in FBSD. Within flying squirrels, small-bodied gliders with reduced patagia had more compensatory morphological adaptations than large bodied gliders with extended patagia. Comparative phylogenetic analyses revealed that patterns of gliding morphostructure and dimorphism are deeply rooted within the phylogenetic history of this tribe.

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Chapter 1

SEXUAL SIZE DIMORPHISM: AN INTRODUCTION

The sexes of sexually reproducing life forms often differ in size, and this dimorphism in size is referred to as sexual size dimorphism (SSD). SSD may be minimal (monomorphism), male-biased, or female-biased. Female-biased size dimorphism (FBSD) is the norm in most plants and ectotherms, while the majority of birds and mammals display male-biased size dimorphism (MBSD) (Fairbairn 1997, Shine 1989). Because FBSD is rare in mammals, it has also been called reversed sexual size dimorphism (from an anthropocentric point of view, MBSD is the norm). In this dissertation I use the notations FBSD and MBSD to denote the two trends in dimorphism.

Species can be sexually dimorphic in specific body parts or in overall body size, and these dimorphisms have usually evolved to confer specific advantages to species' survival. In this dissertation I examine SSD in overall body size, and SSD in overall body size is measured using head and body or total body length in most cases.

How is SSD measured ?

SSD is most commonly expressed as ratios, and the use of ratios *versus* other measures (eg. residuals of regression of one sex over the other) has been widely debated (Ranta *et al.* 1994, Smith 1999). A number of different ratios have been used (a few examples: log means (Log (Male/Female)), Storer's Index (Male-Female/[(Male+Female)/2] (Storer 1966), ((Male-Female)/Female) and ((Male-Female)/Male), and Lovich and Gibbon's (1992) two-step ratio (ratio of larger sex/ smaller sex; and assigned positive when females are larger and negative when males are larger)), though the most common ratio is a simple ratio of the larger sized sex divided by the smaller (Smith 1999). Since most studies examine MBSD, ratios that are most commonly used are Male size/Female size. In this dissertation I explore the evolution and patterns of FBSD and use the ratio Female Size/Male Size for most of the analyses.

What causes SSD ?

The size of specific morphological features as well as overall body size of an organism are often under selection (Andersson 1994) and individuals and sexes derive benefits from evolving either large body sizes or small sizes (Szekely *et al.* 2008). SSD evolves when selective pressures on body size are stronger in one sex than another, of if selective processes push the sexes in opposing directions (Greenwood and Adams 1987, Hedrick and Temeles 1989, Karubian and Swaddle 2001).

Sexual size dimorphism has been the focus of a number of studies, and a recent book compiles studies that explore the enigma of sexual size dimorphism from macro (broad-scale patterns across taxa) and micro (patterns and processes within species) perspectives as well as studies that examine proximate developmental and genetic mechanisms that cause SSD (Fairbairn *et al.* 2008). The evolution of body size dimorphism is traditionally explained by natural selection or sexual selection, and the latter could be either inter-sexual selection (epigamic selection) or intra-sexual selection (Darwin 1871, Trivers 1982).

Most studies of sexual size dimorphism have found evidence in support of sexual selection, and size dimorphism is often related to mating behavior, irrespective of which sex is larger (Amadon 1975). Selection in relation to sex is regarded as more intense in highly polygynous and polygynandrous mating systems and strong sexual dimorphism is to be expected more often in these species (Bjorklund 1991), while monogamous species are typically expected to be monomorphic in body size. Non-sexual natural selection has received much less attention as a explanation for sexual size dimorphism.

1. *Sexual selection*

Theories explaining SSD have largely described it as benefiting traits that increase an individual’s reproductive success, and variants of this are applied to large male size, large female size and small male size (see below and Table 1.1).

1.1. *Large male size*

The evolution of large male size in MBSD has largely been explained by male-male competition for territories or resources, ultimately influencing male reproductive success (Andersson 1994, Weckerly 1998).

1.2 *Large female size*

Explanations for the evolution of larger sized females have been less straightforward and encompass a range of hypotheses from increased foraging efficiency (Reynolds 1972, Snyder and Wiley 1976), behavioural advantages (Andersson and Norberg 1981, Cade 1960, Jehl and Murray 1986, Mueller 1986), and the 'big mother hypothesis' (Myers 1978, Ralls 1976). Ralls (1976) proposed that larger female size conferred increased reproductive advantages

TABLE 1.1: A list of hypotheses explaining the evolution of MBSD and FBSD as conferring behavioural or mating advantages to either sex. All of these hypotheses pertain to increased reproductive success of the sexes.

Hypothesis	Explanation	Reference
Large male size		
Male-male competition	Larger males win more competitions and mates	Anderson and Fedak 1985, Andersson 1994
Increased dominance	Larger males are more dominant and secure more resources and mates	Berry and Shine 1980, Ellis 1995, Andersson 1994
Territory and nest defense	Larger males defend territory and nests better than smaller males	Downhower *et al.* 1983
Large female size		
Increased fecundity	Female fecundity increases with size	Mueller and Meyer 1985, Reynolds 1972, Selander 1972,. Howard, 1988b; Harvey, 1990; Ralls, 1976; Wiklund and Karlsson, 1988

Hypothesis	**Explanation**	**Reference**
Early breeding	Larger females can breed earlier in uncertain environments	Neuhaus *et al.* 2004
Larger offspring/ Egg size hypothesis/ Reproductive effort hypothesis:	Larger females give birth to larger young/ lay larger eggs	Roff 1992, Reynolds 1972, Selander 1972, Mueller and Meyer 1985, see Cabana et al 1982
Larger litters	Larger females give birth to larger litters	Dobson and Michener 2005, see Cabana *et al.* 1982
More frequent litters	Larger females give birth to more frequent litters	Cox *et al.* 2003
Incubation efficiency hypothesis	Larger females for reasons of heat economy incubate more efficiently	Synder and Wiley 1976
Increased foraging efficiency (= Increased food supplementation to young)	Larger females can bring back more food to the nest, and can supplement young better	Reynolds 1972, Snyder and Wiley 1976
Male subordination/ Female dominance	Larger females make the male subordinate, ensuring that the male will provide food. Large females play a part in the maintenance of the pair bond	Anderson and Norberg 1981, Cade 1960, Jehl and Murray 1986, Mueller 1986
Anti-cannibalism	Larger females prevent males from cannibalizing the young, which are guarded by the female	Amadon 1959
Pair formation	Larger females run a lower risk of being imperiled or intimidated during pair formation	Amadon 1959, Mueller 1986
Starvation hypothesis/ Increased reproductive success in uncertain environments	Larger females can cope for longer without food under harsh conditions, and this theory implies that large females will breed earlier than small ones	Lundberg 1986, Koprimaki 1986, Svendsen and White 1997
Follicle protection hypothesis	Larger females run a lower risk of damage the developing eggs during locomotion	Walter 1979

Hypothesis	Explanation	Reference
Female supplementary feeding hypothesis:	Larger females supplement the males foraging from a broader prey size spectrum during the latter half of the breeding period	Reynolds 1972, Snyder and Wiley 1976
Small male size		
Aerodynamic agility	Small males are better at aerodynamic displays and can win contests with other males	Jehl and Murray 1986, Serrano-Meneses and Szekely 2006, Szekely *et al.* 2000, Blomqvist *et al.* 1997
Increased mating success	Mating success increases with decreased male size, particularly if the female is unreceptive	Bisazza and Pilastro 1997
Male territorial defense hypothesis	Smaller, more agile males are favored in territorial defense.	Mueller 1986, Andersson and Norberg 1981
Male energy saving hypothesis	Smaller males expend less energy and can therefore provide more food to the young and family	Reynolds 1972

to females, like increased fecundity (Mueller and Myer 1985, Reynolds 1972, Selander 1972), early breeding (Neuhaus *et al.* 2004), larger young (Roff 1992), larger litters (Dobson and Michener 2005), more frequent litters (Cox *et al.* 2003), and increased reproductive success in uncertain environments (Svendsen and White 1997). The big mother hypothesis is also assumed to have a functional significance–larger female structural size allows for compensation of the weight gained during gestation and lactation (Andersson and Norberg 1981, Myers 1978). See Table 1.1 for details.

1.3 *Small male size*

A number of studies have proposed that selection might confer competitive advantages to smaller male size, such as for agility during aerial courtship displays (Jehl and Murray 1986, Serrano-Meneses and Szekely 2006, Szekely *et al.* 2006), increased territory defense and male reproductive success (See Table 1.1).

2. *Natural selection*

The second explanation for patterns of sexual size dimorphism—natural selection—has received comparatively little attention in research studies, though a recent review evaluates the impact of various environmental and ecological factors (reviewed in Isaac 2005). Explanations for SSD with respect to ecological factors includes partitioning of habitat and resources by the sexes, habitat and microhabitat that species occupy, latitude and seasonality.

Table 1.2: A list of ecological hypotheses explaining the evolution of MBSD and FBSD due to the advantages these confer on a species' survival within its environment.

Theory	Explanation	Reference
Food competition hypotheses	Dimorphism reduces food competition between the sexes	Jehl and Murray 1986, Selander 1966, 1972, Earhart and Johnson 1970, Snyder and Wiley 1976, Schoener 1967, Walker and Rypstra 2002
Thermal stress	MBSD in endotherms can be explained as males can tolerate heat stress better given they have external testes (or near external in birds). Females are more susceptible to heat stress, which could damage fetuses. Smaller size would give females a thermoregulatory advantage, with lower surface to volume ratios	Greenwood and Wheeler 1985
Diel cycle (Diurnality vs. Nocturnality)	Diurnal species are more visually oriented, and sexual selection contests might be more frequent, allowing for evolution of MBSD	Trivers 1972
Habitat occupied	More open habitats might result in patchy resources, allowing for aggregation of females, which in turn leads to male-male competition and MBSD	Jarman 1974, Perez-Barberia *et al.* 2002, Ford 1994
Micro-habitat partitioning	Sexes adapt specifically to their micro-habitats, and SSD is one such adaptation. Eg: More arboreal species are FBSD and more terrestrial species are MBSD as they can display more for mates	Butler *et al.* 2002, Cheverud *et al.* 1985, Leutenegger and Cheverud 1982

Theory	Explanation	Reference
Latitude	Increasing latitude results in increased MBSD. In the tropics, aseasonality results in continuous breeding times and increased variance in male reproductive success (implying FBSD)	Weckerly 1998
Population density	MBSD decreases at high population densities	Isaac and Johnson 2003

Why Squirrels ?

Endotherms like mammals and birds are predominantly male-biased in SSD, though there have been examples of FBSD in several families (eg.: mammals: rabbits, pikas, anteaters, sloths, whales, dolphins; birds: raptors, owls, shorebirds, nightjars). Several isolated instances of species or subfamilies within mammals exhibit FBSD, like chipmunks and flying squirrels within the squirrel family.

Squirrels are an ideal group in which to investigate the effects of natural selection on the evolution of size dimorphism. They belong to a speciose family (Sciuridae; 51 genera, 278 species) that inhabit a wide variety of habitats (open to very dense vegetation) over a range of latitudes (Steppan and Hamm 2006). They occur on 5 continents across a variety of climates (arctic to tropical) and altitudes (sea level to over 5,500 m amsl). Sciuridae are unique in being the only mammalian family containing species exhibiting diverse lifestyles- arboreal, terrestrial, subterranean and gliding. Recent studies propose that the earliest squirrels were arboreal, and that they diversified into a variety of habitats and lifestyles (Steppan *et al.* 2004). Sexual size dimorphism in some species of squirrels was investigated by Schulte-Hostedde (2007), and revealed mixed patterns of size dimorphism among squirrels. However, the species list was not extensive, and covariates of the ecology of species and the phylogenetic relationships between species were not taken into account. Patterns of sexual dimorphism also tend to be phylogenetically conserved throughout lineages, and it is difficult to infer the particular significance of any dimorphism in any species without a comprehensive study of related species.

In this Dissertation

In this dissertation I examine the evolution of sexual size dimorphism patterns in mammals that exhibit a unique life-style—gliding locomotion. Gliding is an uncommon mode of locomotion, and female-biased size dimorphism has been noted in several gliders. In order to explain this, I compare the largest group of gliding mammals, flying squirrels, with their nearest relatives, tree squirrels and ground squirrels. Various hypotheses predict patterns of evolution of SSD across the family (see Tables 1.1, 1.2). I approach the question of the evolution of FBSD in these gliding mammals from a macro-evolutionary viewpoint, examining broad scale patterns within the entire sciurid family, and within sympatric communities of squirrels. Finally, I examine FBSD with a narrower perspective, and examine all flying squirrels for allometry of scaling of SSD across species, but also for evidence for advantages of female size pertaining to functional morphology.

All chapters are written as collaborations with F. Stephen Dobson, and the rest of the dissertation is written in manuscript form in the plural and not in the first person.

Chapter 2: Patterns of sexual size dimorphism in squirrels.

Sexual size dimorphism is a common trait and can be either male-biased or female-biased. Though it is commonly believed that sexual selection as the primary cause for the evolution of sexual size dimorphism, it is also important to consider the influence of ecological and environmental factors. Squirrels are a diverse widely distributed family, and they exhibit various lifestyles and occupy different habitats. In this chapter we examine the evolution of patterns of sexual size dimorphism among squirrels and ecological and environmental factors within a phylogenetic framework in order to arrive at the factors that might affect sexual size dimorphism.

Chapter 3: Community structure and body size relationships of squirrels.

Body sizes of species play an important role in the structuring of communities and the co-occurrence of species. Theory predicts that the number of species found in an environment depends on how species partition themselves (by way of resource utilization, temporal separation, etc.) and we investigate patterns of co-occurrence of squirrels in Southeast Asia.

We test for morphological separation of species as well as the similarity of such patterns across diurnal and nocturnal species.

Chapter 4: Rensch's rule and patterns of size dimorphism in flying squirrels.
The size ratio of the sexes are known to scale allometrically among a group of related species. Males and females (and consequently MBSD and FBSD) scale differently in relation to overall body size, and these patterns have come to be known as Rensch's rule. While there is a lot of evidence in favour of Rensch's rule holding true in cases of male-biased dimorphism, there is mixed evidence in favour of the pattern with respect to female-biased dimorphism. Flying squirrels are an ideal group for such analysis given their diversity and unique life-style. Additionally, we examine the functional significance of large body size in females, in order to determine if FBSD has evolved to confer advantages relative to gliding locomotion.

LITERATURE CITED

Amadon, D. 1975. Why are female birds of prey larger than males ? Raptor research 9: 1-11.

Anderson, S.S. and M.A. Fedak. 1985. Grey seal males: energetic and behavioural links between size and sexual success. Animal Behaviour 33: 829-838.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton.

Andersson, M. and R.Å. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnaean Society 15: 105-130.

Berry, J. F. and R. Shine. 1980. Sexual size dimorphism and sexual selection in turtles (order Testudines). Oecologia 44: 185-191.

Bisazza, A. and A. Pilastro. 1997. Small male mating advantage and reversed size dimorphism in poeciliid fishes. Journal of Fish Biology 50: 397-406.

Bjorklund, M. 1991. Evolution, phylogeny, sexual dimorphism and mating system in the Grackles Quiscalus-Spp Icterinae. Evolution 45(3): 608-621.

Blomqvist, D., O.C. Johansson, U. Unger, M. Larsson, and L.A. Flodin. 1997. Male aerial display and reversed sexual size dimorphism in the dunlin. Animal Behaviour 54: 1291-1299.

Butler, M.A., T.W. Schoener, and J.B. Losos. 2002. The relationship between sexual size dimorphism and habitat use in greater Antillean *Anolis* lizards. Evolution 54(1): 259-272.

Cabana G., A. Frewin, R.H. Peters, and L. Randall. 1982. The effect of sexual size dimorphism on variations in reproductive effort of birds and mammals. American Naturalist 120: 17-25.

Cade, T.J. 1960. Ecology of the peregrine and gryflacon populations in Alaska. University of California Publications in Zoology 63(3): 151-290.

Cheverud, J.M., M.M. Dow, and W. Leutenegger. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. Evolution 39: 1335–1351.

Cox, R.M., S.L. Skelly, and H.B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57: 1653–1669.

Darwin, C. 1871.The descent of man and selection in relation to sex. London: John Murray.

Dobson, F.S., and G.R. Michener. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76: 851-862.

Downhower, J.F., L. Brown, R. Pederson, and G. Staples. 1983. Sexual selection and sexual dimorphism in mottled sculpins. Evolution 37: 96-103.

Earhart, C.M., and N.K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72: 251-264.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethology and Sociobiology 16: 257-333.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28: 659-687.

Fairbairn, D.J., W.U. Blanckenhorn, and T. Székely. 2008. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, USA.

Ford, S.M. 1994. Evolution of sexual dimorphism body weight in platyrrhines. American Journal of Primatology 34: 221–244.

Greenwood, P.J., and J. Adams. 1987. Sexual selection, size dimorphism and a fallacy. Oikos 48: 106-108.

Harvey, A.W. 1990. Sexual differences in contemporary selection acting on size in the hermit crab *Clibanarius digueti*. American Naturalist 136: 292-304.

Hedrick A.V. and E.J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends in Ecology and Evolution 4: 136–138.

Howard, R.D. 1981. Sexual dimorphism in bullfrogs. Ecology 62: 303-310.

Isaac, J.L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review 35 (1): 101-115.

Isaac, J.L. and C.N. Johnson. 2003. Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. Behavioral Ecology 14: 818–822.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48(34): 215-267.

Jehl, J.R., Jr. and B.G. Murray, Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Pp. 1-86 in Current Ornithology, vol. 3 (R. F. Johnston, ed.) Plenum, NY.

Karubian, J. and J.P. Swaddle. 2001. Selection on females can create 'larger males'. Proceedings of the Royal Society Series B-Biological Sciences 268: 725–728.

Leutenegger, W. and J.M. Cheverud. 1982. Correlates of sexual dimorphism in primates: ecological and size variables. International Journal of Primatology 3: 387–402.

Lovich, J.E. and J.W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development and Aging 56(4): 269-81.

Mueller, H.C. 1986. The evolution of reversed sexual size dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin 98: 387-406.

Mueller H.C. and K. Meyer. 1985. The evolution of reversed sexual dimorphism in size. A comparative analysis of the Falconiformes of the western Palearctic. In: Johnston RF (ed) Current ornithology 2. Plenum, New York, pp. 65–101.

Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. American Naturalist 112 (986): 701-712.

Neuhaus P., D.R. Broussard, J.O. Murie, and F.S. Dobson. 2004. Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. Journal of Animal Ecology 73: 36–43.

Pérez-Barbería, F.J., I.J. Gordon, and M. Pagel. 2002. The origins of sexual dimorphism in body size in ungulates. Evolution 56: 1276-1285.

Ralls, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51: 245-276.

Ranta, E., A. Laurila, and J. Elmberg. 1994. Reinventing the Wheel: Analysis of Sexual Dimorphism in Body Size. Oikos 70(3): 313-321.

Reynolds, R.T. 1972. Sexual dimorphism in accipiter hawks: A new hypothesis. Condor 74: 191-197.

Roff, D.A. 1992. The evolution of life histories. Chapman and Hall; New York.

Sanderson, M.J., D. Boss, D. Chen, K.A. Cranston, and A. Wehe. 2008. The PhyLoTA Browser: processing GenBank for molecular phylogenetics research. Systematic biology, 57 (3): 335-346.

Schoener, T.W. 1967. The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus*. Science 155: 474–477.

Schulte-Hostedde, A. 2007. Sexual size dimorphism in rodents, in Wolff, J. O. and Sherman, P. W. (Eds.) Rodent Societies: An ecological and evolutionary perspective. The University of Chicago Press, Chicago. Pp 115-128.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. In B Campbell (ed.), Sexual selection and the descent of man. Chicago: Aldine.

Serrano-Meneses, M.A. and T. Szekely. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. Oikos 113: 385-394.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64: 419-461.

Smith, R.J. 1999. Statistics of sexual size dimorphism. Journal of Human Evolution 36: 423-459.

Snyder, N.F.R. and J.W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monographs 20: 1-96.

Steppan, S.J., B.L. Storz, and R.S. Hoffmann. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Molecular Phylogenetics and Evolution 30: 703-719.

Steppan, S.J. and S.M. Hamm. 2006. Sciuridae. Squirrels. Version 13 May 2006. http://tolweb.org/Sciuridae/16456/2006.05.13 in The Tree of Life Web Project, http://tolweb.org/

Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83: 423-436.

Svendsen. G.E. and M.M. White. 1997. Body mass and first-time reproduction in female chipmunks. Canadian Journal of Zoology 75: 1891-1895.

Székely, T., J.D. Reynolds, and J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. Evolution 54: 1404–1413.

Székely, T., T. Lislevand, and Figuerola. 2008. Sexual size dimorphism in birds. *In* Fairbairn, D.J., W.U. Blanckenhorn, and T. Székely. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, USA

Trivers, R.L. 1972. Parental investment and sexual selection. In B. Campbell (Ed.) Sexual selection and the descent of man. Chicago: Chicago University Press.

Walker, S.E and A.L. Rypstra. Sexual dimorphism and the differential mortality model: is behaviour related to survival? Biological Journal of the Linnean Society: 97–103.

Walter, H. 1979. Eleonora' Falcon: Adaptations to prey and habitat in a social raptor.University of Chicago Press, Chicago, Illinois, USA.

Weckerly, F.W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 77: 33–42.

Wiklund, C. and B. Karlsson. 1988. Sexual size dimorphism in relation to fecundity in some Swedish Satyrid Butterflies. American Naturalist 131: 132-138.

Chapter 2

ORIGINS AND ECOLOGICAL CORRELATES OF SEXUAL SIZE DIMORPHISM IN SQUIRRELS.

INTRODUCTION

Sexual size dimorphism (SSD) is a common morphological pattern within many animal species. Patterns of sexual size dimorphism vary, and while most birds and mammals exhibit male-biased size dimorphism (MBSD), female-biased size dimorphism (FBSD; also called “reversed sexual size dimorphism”) is common in most ectotherms and plants (Fairbairn 1997, Greenwood and Adams 1987, Shine 1989, Weckerly 1998). Patterns of size dimorphism are well documented, and have been a focal area of research since Darwin’s time (Fairbairn 1997, Fairbairn *et al.* 2008). While most mammals exhibit male-biased size dimorphism, predominantly female-biased dimorphism has been recorded in certain Orders like Chiroptera (bats), Lagomorpha (rabbit and pikas), Cetacea (whales, dolphins and porpoises), Xenarthra (sloths, armadillos and anteaters) and Macroscelidea (elephant shrews) (Myers *et al.* 1979, Ralls *et al.* 1977, Lindenfors *et al.* 2008). FBSD has sometimes also been recorded within mostly male-biased Orders. For example, though rodents, the largest mammalian Order, are predominantly male-biased, there are several instances of FBSD in rodent species (Family Muridae: golden spiny mice (Krasnov *et al.* 2008), Family Sciuridae: chipmunks, flying squirrels (Schulte-Hostedde 2007, Hayssen 2008)).

While there are numerous comparative studies of factors that determine SSD, most of these relate patterns to sexual selection, and its fitness and reproductive advantages (Andersson 1994, Fairbairn *et al.* 2008). Few studies have examined the role of ecological factors in shaping SSD (reviewed by Isaac 2005). Comparative approaches have been used to examine the relationship between SSD and predictor traits using methods like phylogenetic independent contrasts (Felsenstein 1985) or generalised least squares (Martins and Hansen 1997) to account for phylogenetic non-independence. However, few studies have reconstructed the evolution of the pattern of SSD across taxa (using methods like ancestral state reconstruction (Cunningham *et al.* 1998). Squirrels are a diverse family of rodents that showcase a variety of lifestyles and habits (Thorington and Farrell 2007), and patterns of sexual size dimorphism have been little explored in this family. In this study, we map the evolution of SSD patterns across the phylogeny and examine ecological variables that might be correlated to patterns of SSD in squirrels.

Phylogeny-based studies of the evolution of characters are now integral to evolutionary biology and such reconstructions enable us to understand underlying selective mechanisms that allow the evolution of specific traits (Weins *et al.* 2007). Ancestral state reconstruction analysis can help in understanding the pattern of character evolution (Cunningham *et al.* 1998) and has increasingly been used in the analysis of traits like plumage patterns and size dimorphism across sexes of related species (Omland and Hofmann 2006). Species evolve patterns of sexual size dimorphism (FBSD or MBSD) in response to specific pressures, traditionally explained as either sexual selection or natural selection (Darwin 1871).

The evolution and causes of SSD have been investigated in macro-analyses of several taxa and species, micro-analyses within species and across populations, and also from the mechanistic, physiological and genetic viewpoints (compilation in Fairbairn *et al.* 2008). Most studies to date explain both MBSD and FBSD in relation to mating strategies and sexual selection (Amadon 1975), with males and females differing in attributes because of the way the two sexes maximize their reproductive success (Katsikaros and Shine 1997). Male size is largely explained by male-male competition for resources and mates (both for large males in MBSD species (Andersson 1994) and small males in FBSD species (Szekely *et al.* 2000)), while large female size in FBSD species is explained by hypotheses pertaining to fecundity selection, functional morphology and behavioral advantages ('big mother hypothesis': Ralls 1976, Myer 1978, Mueller and Meyer 1985, Szekeley *et al.* 2000). In chipmunks (genus *Tamias*) exhibiting FBSD, large female size is maintained by reproductive advantages and increased survival during adverse weather conditions, while male reproductive success was found to be independent of male body size (Schulte-Hostedde *et al.* 2002a, 2000b, Schulte-Hostedde and Millar 2002).

The second explanation for patterns of sexual size dimorphism—natural selection—has received comparatively little attention in research studies, though a recent review compiles various environmental and ecological hypotheses affecting SSD (reviewed in Isaac 2005). Most of these hypotheses relate environmental variables back to the mating system, via resource availability and seasonality. A few of these include habitats occupied (open habitats promote sociality and male displays: Jarman 1974, Perez-Barberia *et al.* 2002), arboreal/terrestrial habits (terrestrial habits promote sociality and male displays: Ford 1995, Leutenegger and Cheverud 1982), diurnal/nocturnal activity (diurnal species have active displays leading to MBSD: Trivers 1972) and latitude occupied (tropical regions are aseasonal, promoting asynchronus breeding and low male reproductive variance; hence FBSD: Weckerly 1998). Ecological lifestyle and diet also impose constraints on an animal's life, and affect various life-history traits (Dobson 2007, Sibley and Brown 2007). A suite of behavioral and social traits accompanies lifestyles, like gliding or living underground. While subterranean mammals typically exhibit polygynous mating systems (Lacey 2000), both female and male-biased dimorphisms have been recorded in this group.

Squirrels are an ideal family in which to investigate the evolution of SSD patterns as well as the effects of natural selection on the evolution of size dimorphism. They belong to a speciose family (Sciuridae; 51 genera, 278 species), display a diversity of ecological habits, and occupy a wide variety of habitats (open to very dense) over a range of latitudes (Steppan and Hamm 2006). Sciurids are unique in being the only mammalian family containing species exhibiting arboreal, terrestrial, subterranean and gliding lifestyles. While sexual size dimorphism has been documented across squirrels (Hayssen 2008a), there have been no attempts to explain the evolution of patterns of dimorphism across the family. FBSD has been documented in several species of squirrels with differing life-histories and ecological habits, and in this study we examine the patterns of evolution of FBSD across squirrels, and correlate this to their ecology.

An analysis of SSD across all mammals suggests that the distribution of SSDs is leptokurtic, with most mammals being almost monomorphic or slightly male-biased, with few mammals evolving FBSD or extreme MBSD (> 10 % difference: Lindenfors *et al.* 2008). Given that rodents in general are monomorphic or only moderately male-biased (1.09: Lindenfors *et al.* 2008), we hypothesize that SSD patterns like FBSD or extreme MBSD evolved within the sciurid family in response to specific ecological and life-history parameters, possibly across multiple lineages of squirrels. In accordance with the principle of parsimony, we predict that the ancestral state of SSD across squirrels is monomorphic, with more derived lineages exhibiting more dimorphic traits (in this case—FBSD or more extreme MBSD). The big mother hypothesis predicts that the large size of females allows females to gain weight without a loss in gliding efficiency. A second prediction specific to flying squirrels concerns their gliding lifestyle—if a gliding lifestyle and the functional constraints on female gliders have caused FBSD to evolve in flying squirrels, we should see a clear switch to FBSD at the base of the flying squirrel tribe, with its ancestor being male-biased in dimorphism.

In this study we also examine causal relationships between ecological parameters and SSD patterns, and hypothesize that FBSD and extreme MBSD evolved in response to lifestyles and ecological parameters of the environments inhabited by squirrels. We outline below several predictions regarding SSD that are based on the theories discussed earlier in this section. We predict that squirrels in conditions that allow for male-male competition (open habitat, terrestrial activity, diurnal activity patterns, seasonal availability of resources, sociality and temperate distribution) should be more male-biased in dimorphism. Concerning FBSD, we predict that squirrels in tropical latitudes with low seasonality (promoting asynchronous breeding) should be female-biased. Regarding lifestyle, we predict that squirrels that exhibit a gliding lifestyle should specifically evolve FBSD, in order to confer advantages of functional morphology to pregnant females.

METHODS

a) Taxonomy of family Sciuridae

The family Sciuridae comprises of approximately 290 species in 57 genera, and they are categorised into five subfamilies (Mercer and Roth 2003, Helgen *et al.* 2005, Thorington and Heaney 2005). Several studies have examined the phylogenetic relationships between squirrels (Arbogast 2007, den Tex *et al.* 2010, Herron *et al.* 2004, Mercer and Roth 2003, Steppen *et al.* 2004, Yu *et al.* 2006), and the three most comprehensive molecular studies (Herron *et al.* 2004, Mercer and Roth 2003, Steppen *et al.*2004) all support the same taxonomic subfamily groupings (outlined below). In this study we followed the taxonomic classification of Thorington and Hoffmann (2005) for the bulk of the sciurids. However, a recent revision of ground squirrels by Helgen *et al.* (2009) advocates the splitting of the ground squirrel genus *Spermophilus* into 9 genera based on genetic studies, and we incorporate this into this study.

The subfamilies Sciurillinae and Ratufinae are monotypic lineages, comprising of one species (*Sciurillus*) and four species in one genus (*Ratufa*) respectively, while the bulk of squirrels are in the other three subfamilies. The subfamily Callosciurinae comprises of Asian tree squirrels in 14 genera (*Callosciurus*, *Glyphotes*, *Menetes*, *Sundasciurus*, *Nannosciurus*, *Reithrosciurus*, *Dremomys*, *Lariscus*, *Prosciurillus*, *Hyosciurus*, *Rubrisciurus*, *Tamiops*, *Exilsciurus*, *Funambulus*), including the diverse Indo-Malayan tree squirrels. The most widespread subfamily is Xerinae, containing two tribes of ground squirrels—the Holarctic Marmotini (genera: *Spermophilus*, *Notocitellus*, *Otospermophilus*, *Callospermophilus*, *Ictidomys*, *Poliocitellus*, *Urocitellus, Xerospermophilus*, *Cynomys*, *Marmota*, *Ammospermophilus*, *Tamias*) and Asian and African Xerini (genera: *Xerus, Spermophilosis*, *Atlantoxerus*); and the African tree squirrels (genera: *Funisciurus*, *Paraxerus*, *Epixerus*, *Protoxerus*, *Heliosciurus*, *Myosciurus*). The last subfamily, Sciurinae, comprises of both tree and flying squirrels in two distinct tribes (Sciurini—new World tree squirrels, and Pteromyini—flying squirrels). Flying squirrels comprise of 15 genera in both the Old and New Worlds (genera: *Aeretes*, *Aeromys*, *Trogopterus*, *Belomys*, *Pteromyscus*, *Eoglaucomys*, *Pteromys*, *Petaurista*, *Eupetaurus*, *Glaucomys*, *Hylopetes*, *Petaurillus*, *Petinomys*, *Iomys*, *Biswamoyopterus*) and are monophyletic in origin. New World tree squirrels occur in 5 genera (*Microsciurus*, *Syntheosciurus*, *Rheithrosciurus*, *Sciurus*, *Tamiasciurus*) and are a sister group to the clade comprising flying squirrels.

b) *Body size data*

Body size data (head and body length, tail length and mass) for males and females of 260 of the 292 species of squirrels (Order Rodentia: Family Sciuridae) were obtained from the literature (sources listed in Appendix I). We augmented a data set collected by Hayssen (2008) that compiled size information from the literature as well as from measurements of over 4000 squirrels in 9 museums. We used head and body length as our indicator of overall size. Head and body length from museum specimens is taken from tags (in both Hayssen's (2008) study and ours) - measured before animal specimens are prepared, and is comparable to data from studies in the field obtained from the literature. If the sexes were not reported separately in Hayssen's (2008) dataset, we collected data on the sexes to augment our dataset. We also gathered data from museums that were not visited by Hayssen (2008): Bombay Natural History Society Museum, Mumbai, India; Zoological Survey of India, Kolkatta, India; Senckenberg Museum of Natural History, Frankfurt, Germany; and Berlin Museum of Natural History, Berlin, Germany. We also examined literature, including the ASM's Mammalian Species Accounts (http://www.science.smith.edu/msi/msiaccounts.html). Body size data were checked against the data we obtained from Hayssen (2008), and when there were conflicts in the trends of dimorphism of species (eg: female-biased vs. male-biased) we cross-checked the literature and used data either from the most comprehensive studies available, or used an average of studies. Examples of this are species like *Marmota monax*, *Marmota caudata* and *Marmota marmota*, where Hayssen's data indicated female-biased dimorphism but several other studies reported male-biased dimorphism. Appendix I is a list of sources for the data, and Appendix II is a list of museum specimens that were examined during this study.

c) *Ecological Data*

We collected ecological information for squirrel species from the literature: lifestyle, strata occupied, habitat occupied, diel cycle, sociality, length of activity cycle through the year, and geographic information. Maximum latitude inhabited and mid latitude of range were recorded for the geographic location of species. We also additional literature, including the ASM's Mammalian Species Accounts (http://www.science.smith.edu/msi/msiaccounts.html) for ecological data.

Lifestyle exhibited by each species was recorded in one of three categories: arboreal (including scansorial (inhabiting both trees and the ground) behaviour and excluding gliding behaviour), gliding, and ground-dwelling. These are three fundamentally different lifestyles, and though gliding squirrels are arboreal, they have distinct body architecture and have evolved under different selection pressures from arboreal squirrels, justifying their separate categorization (Thorington and Ferrell 200). These categorizations are also well supported in the literature (Mercer and Roth 2003, Thorington and Heaney 2005, Thorington and Farrell 2007). However, as strata occupied by squirrels are not automatically reflected in the lifestyle category (eg: some tree squirrels are ground-dwelling), we included a second variable with details of the strata used by squirrels (arboreal vs. terrestrial). Information was obtained from the literature, and squirrels were categorized as arboreal and terrestrial depending on where they spent most time. If squirrels were scansorial (using both arboreal and terrestrial strata), they were placed in a separate category.

Habitat inhabited by squirrels was categorised as forested (including tropical, temperate, deciduous forests) or open (including deserts, plains, steppes, and grasslands). Information on habitat used by squirrels was obtained from the literature (Appendix I), and categories were collapsed into the two above-listed choices. Two measures of period of activity were recorded - a measure of diel activity (diurnal or nocturnal) and a measure of length of activity cycle through the year (species that hibernate vs. species that do not hibernate). Squirrels were also categorised as social or solitary based on information from the literature (Appendix I). All the above variables were coded as discrete characters.

Information of the geographic range occupied by squirrels was obtained by examining maps in the literature (Kingdon 1997, Payne, Philipps and Francis 1985) as well as from online databases and websites. For species in North America the database Natureserve was used (Natureserve Explorer 2009), and for certain species maps were available on the IUCN database (listed in Appendix I). Latitude at the northern and southern ends of a species' range were recorded, and from this the midpoint of the species' range and range of latitude were calculated.

d) *Ratio of dimorphism*

Ratios have typically been used to examine sexual size dimorphism and ratios of the mean of body size of the sexes (Male/Female, or Female/Male) are the most commonly used ratio (reviewed in Smith 1999). Several different ratios have been reported, including log means (Log(Male/Female)), Storer's Index (Male-Female/[(Male+Female)/2] (Storer 1966), ((Male-Female)/Female) and ((Male-Female)/Male), and Lovich and Gibbon's (1992) two-step ratio (ratio of larger sex/ smaller sex; and assigned positive when females are larger and negative when males are larger). Several studies (Smith 1999, Aitchley *et al.* 1976, Ranta *et al.* 1994) reviewed the use of ratios and residuals, and Smith (1999) suggested that a simple log or linear ratios are sufficient for most analyses of SSD. The ratio of dimorphism used in this study was Female size/Male size. These were then recoded as discrete variables of SSD, with ratios greater than 1 indicating FBSD and ratios less than or equal to 1 indicating MBSD.

e) *Phylogeny reconstruction*

Three studies (Roth and Mercer 2003, Steppan *et al.* 2004, Herron *et al.* 2004) provided genera-level phylogenies for the family Sciuridae, while several others provide species-level phylogenies for ground squirrels (Steppan *et al.* 1999, Heron *et al.* 2004) and flying squirrels (Arbogast 2007, Yu *et al.* 2006). For the purpose of this study we reconstructed a genus-level phylogeny of all squirrels, and squirrel sequences were downloaded from the PhyLota database (http://phylota.net/) (Sanderson *et al.* 2008) in clusters (accession numbers of sequences used in this study are in Appendix III). PhyLota compiles searches for different taxa from NCBI Genbank, and organizes them into accumulated files. Searches were for Sciuridae, and clusters of data were downloaded for the single-copy nuclear-encoded gene interphotoreceptor retinoid binding protein (IRBP) exon 1. IRBP is exclusive to the vertebrate genome (Borst et al, 1989) and encodes a 140-kD protein that is involved in vision. IRBP is widely used in the study of mammalian phylogenies (Stanhope *et al.* 1992, DeBry and Sagel 2001, Jansa and Voss 2001), and Springer et al (2001) suggest that nuclear genes like IRBP are potentially more appropriate in the reconstruction of relationships among higher-level taxa. IRBP has also been widely used in rodent phylogenies (DeBry and Sagel 2003, Jansa and Weksler 2004, Weksler 2003), including squirrels (Mercer and Roth 2003,).

Only one sequence per species was retained in the dataset. Sequences were examined visually and the most complete sequence for a genus was retained. We standardised the taxonomy for the dataset by following the classification of Wilson and Reeder 2005, and modified older names of the downloaded sequences to match this taxonomy. Additionally, ground squirrel names were changed to match the new classification laid out by Helgen *et al.* (2009). IRBP sequences were also downloaded for three outgroup species—*Allactaga sibirica* (family Dipodidae), *Glilurulus japonicus* (family Gliridae) and *Aplodontia rufa* (family Aplodontia).

The sequences were aligned with MAFFT (Katoh *et al.* 2005) and the alignment was viewed in Se-AL (http://tree.bio.ed.ac.uk/software/seal/). We then checked for consistent regions with the program Aliscore (Misof and Misof 2009), which identifies ambiguously aligned regions in multiple sequence alignments. Ambiguous regions were removed with Alicut Version 2.2 (Kück P 2010, unpublished. http://utilities.zfmk.de) and then imported into jMODELTEST (Posada 2008, Guindon and Gascuel 2003) to determine the best model of evolution for the dataset. GTR+I+G was chosen as the best model for the gene.

Bayesian tree reconstructions were conducted with MrBayes (Huelsenbeck and Ronquist 2001,Ronquist and Huelsenbeck 2003) on the CIPRES server (Cyberinfrastructure for Phylogenetic Research http://www.phylo.org/). Two replicate searches were performed on the data, and each analysis ran for 6 million generations, with 4 chains (one cold, three heated), using default priors, and sampling every 1000 generations. The first 10,000 trees were discarded as burn-in. We used Tracer v 1.4.1 (Drummond and

Rambaut, 2007) to calculate ESS values and visually inspect files for evolutionary parameters. Convergence of tree topology was assessed using AWTY (Nylander *et al.* 2008).

f) *Phylogenetic signal and Character evolution*

Phylogenetic signal

Species that are related might resemble each other in traits purely as a function of their relationship and shared inheritance, and it is essential to gauge the extent of phylogenetic signal in the trait to be examined before analyses are carried out. If the dataset does not exhibit any phylogenetic signal, comparative methods are not necessary for analysis. There are a number of different methods to assess phylogenetic signal of both discrete and continuous traits. A maximum likelihood based method - Pagel's lambda (Pagel 1999) was used to test for signal in the discrete SSD values. Pagel's Lambda is a tree transformation parameter that has the effect of gradually removing phylogenetic signal and testing the degree to which the trait of interest exhibits phylogenetic signal on trees with and without signal. Pagel's Lambda was calculated using the geiger package (Harmon *et al.* 2008) in R.

Ancestral States of SSD

Ancestral state reconstructions of characters on phylogenies can be done in a number of ways - using parsimony methods (Maddison and Maddison 1992), maximum likelihood methods (Pagel 1999) and Bayesian methods (Pagel *et al.* 2004). Reconstructions can also be performed on a single tree (a tree with branch lengths equal to one, a parsimony tree or maximum likelihood tree) or on a Bayesian posterior sample tree. One of the assumptions of ancestral state reconstruction is that branch lengths carry information on the probability of phenotypic change, implying that states at the end of long branches tend to be less similar than states at the ends of short branches (Cunningham *et al.* 1998, Ekman *et al.* 2008). This assumes a correlation between genetic change and changes in morphology, and there have been arguments for and against this assumption (reviewed by Ekman *et al.* 2008). For this study we used a tree reconstruction based on molecular sequences for analysis (see methods above, part e).

We reconstructed ancestral states of SSD using parsimony as well as maximum likelihood methods in MacClade 4.8 (Maddison and Maddison 2005). Unordered parsimony analysis was performed on the categorical data (coded in two states). When characters are designated as unordered, a change from any state to another is counted as one step (also called Fitch parsimony (Fitch 1971, Maddison and Maddison 2003)). The analysis also calculates metrics for the final cladogram (with character states mapped on it) like length, consistency index and a retention index. Length, or the number of steps, is the number of character changes required to result in the character patterns seen across taxa in the tree. Trees with lower lengths are preferred as they assume fewer homoplasies and are so more parsimonious. Parsimony analysis results in the tree with the most parsimonious length. The Consistency Index (CI) and Retention Index (RI) are measures of the relative homoplasy required by a tree. CI is calculated as the percentage of the number of steps expected given the number of character states in the data divided by the actual number of steps. CI is an indicator of homoplasy, and a CI close to zero implies no homoplasy, while a CI of 1 indicates a lot homoplasy. RI is a measure of the synapomorphy that is expected from the dataset that is retained as synapomorphy in the tree; in other words, it calculates the observed number of steps relative to the number of steps possible (Maddison and Maddison 2003). An RI of zero implies no synapomorphy, while an RI of one indicates high synapomorphy. A random distribution of reconstructed steps was obtained by mapped SSD onto 1000 equally probable trees in MacClade, and the above listed metrics were calculated for these trees. The distribution of metrics (length, CI and RI) from the random trees was then compared to the actual tree to determine whether there was significant phylogenetic inertia in SSD.

Ancestral character states of SSD were also assessed using Maximum Likelihood methods in Mesquite version 2.74 (Maddison and Maddison 2005). Analysis was performed using the maximum credibility tree from the Bayesian analysis, and we used both one-rate (One-parameter Markov k-state model: gains and losses of FBSD occur at the same rate) and two-rate models (Asymmetrical 2-parameter Markov k-state model: gains and losses of FBSD happen at different rates) of evolution. A likelihood ratio test was used to determine the model that best fit the data.

g) *Ecological correlates of sexual size dimorphism*

Patterns of SSD were generated and ANOVAs were used to test for variation of these patterns across genera and subfamilies. Bar charts were used to depict the average SSD ratios across subfamilies and genera. Mosaic displays and four fold plots were used to represent SSD across the categorical ecological variables. A mosaic display depicts the frequencies from the n-way contingency table as nested rectangular regions whose area is proportional to the frequency in a cell or marginal subtable (Friendly 1994). More specifically, they start as a square with a length of 1, and this is split vertically with the widths of the columns being proportional to the probabilities of the first variable. Each of these bars is then split horizontally according to the probabilities of the second categorical variable and any additional variables. The result is stacked rectangles of different sizes within a grid that reflect the combination of variables in the contingency table. Mosaic plots also provide Pearson residuals that measure the departure of each cell from independence, similar to a Chi-square test. Color and shading are used to represent the sign and magnitude of standardized residuals from a specified loglinear model, and residuals less than -2 or greater than 2 signify departure at the 95% significance level (Crawley 2007, Friendly 1994). Fourfold plots allow for a visual display of the association (log odds ratio different from 1) between variables in a contingency table. In four fold plots each cell of the contingency table is shown by a quarter circle, and this area is proportional to the count. Confidence rings for the odds ratios are drawn around each quarter to depict significance for the quarter (Friendly 1994, Crawley 2007). All graphs were created with ggplot2 (Hadley 2009) and R (R Development Core Team 2010).

<u>Logistic Regression Models</u>

Logistic regression models are a kind of Generalized Linear Model (GLM), which allow the use of categorical response variables with non-normal distributions. GLM's also use maximum likelihood methods instead of least squares for estimation of parameters (Quinn and Keough 2002). We used logistic regression to determine whether FBSD or MBSD evolved in relation to ecology using six discrete variables (lifestyle, strata, sociality, habitat, diel activity cycle and annual activity cycle) and three continuous variables (average body size of both sexes, mid-latitude and maximum latitude). The unit of analysis for the logistic regressions was genus, and trait values of species within each genus were averaged to obtain genus-level trait data. The measure of SSD used was a categorical variable (FBSD or MBSD); explained earlier in section c) of Methods. Prior to analyses, the predictor variables were examined for collinearity. All variables were included in the full model, and stepwise logistic regressions were performed. An information-theoretic approach based on Akaike's (1973) Information Criteria (AIC) was used to evaluate the regression models (Burnham and Anderson 2002). All analyses were performed in R (R Development Core Team) and the R package MuMIn (Barton 2009) was used to obtain model averaging scores.

Generalised Estimating Equations

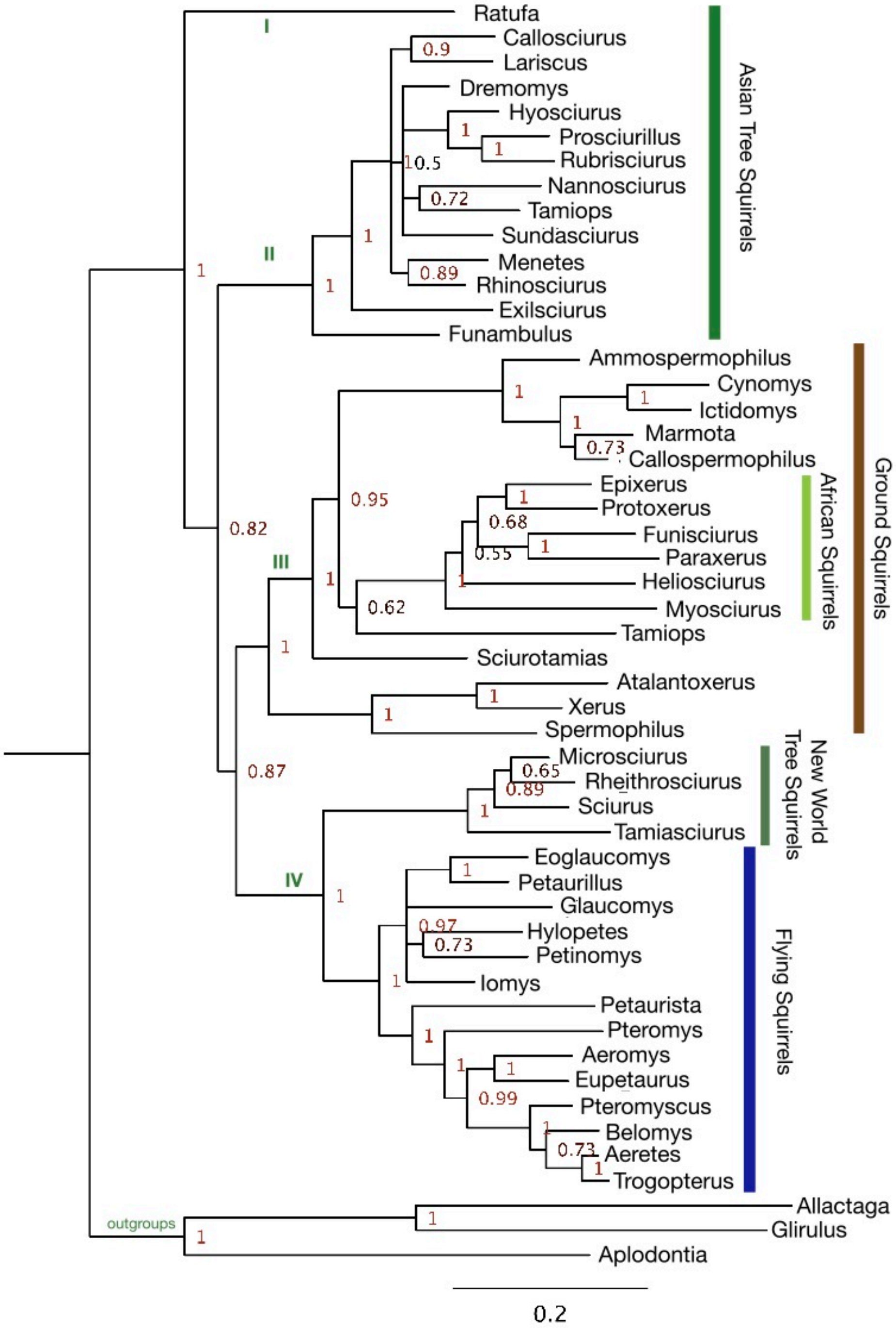
The data were analysed within a phylogenetic framework using Generalised Estimating Equations (GEE) in the package APE (Analysis of Phylogenetics and Evolution) (Paradis *et al.* 2004) in R (R Development Core Team 2011). GEE's are a extension of GLMs to non-normal responses and correlated data (Liang and Zeger 1986, Quinn and Keough 2002), and are advocated as a procedure for analysing comparative data within a phylogenetic framework (Paradis and Claude 2002, Paradis 2006). In GEE’s the dependence among species is taken into account with a correlation matrix. For analysis of SSD and ecological variables, we used a binomial family for the response variable, and used the phylogenetic tree generated from the Bayesian analysis outlined above. Unlike the GLM method, which is based on maximum likelihood, the GEE method is based on quasilikelihood. Therefore, Akaike’s Information Criterion (AIC) is not applicable to GEEs directly, and a Quasilikelihood Information Criterion (QIC) (Pan 2001) is used for model selection.

RESULTS

Tree Reconstruction

The tree topology and clades that resulted from the Bayesian reconstruction were broadly concurrent with published phylogenies of sciurids (Figure 2.1). We recovered the major subfamily clades similar to those outlined in earlier studies (Mercer and Roth 2003). The subfamily Ratufinae was recovered as monophyletic and as outgroup to the three other subfamilies (Callosciurinae, Sciurinae and Xerinae). The genera within each of the subfamilies were also recovered as expected, though within the subfamilies certain clades differed in their placement.

Figure 2.1: Majority rule phylogram of sciurid phylogeny reconstructed (IRBP gene) using Bayesian phylogenetic analyses using a GTR+G+I model of evolution. Posterior probabilities estimated are indicated at nodes. Each genus is represented by one species, and three outgroup taxa are included.



Overall patterns on dimorphism

Average dimorphism across all squirrels was female-biased and the different subfamilies of squirrels did not exhibit different patterns of dimorphism (ANOVA, F = 1.11, p>0.05). While subfamilies Ratufinae, Sciurillinae and Sciurinae exhibited moderate female-biased dimorphism (average ratios of female/male size: 1.022, 1.01 and 1.01 respectively), subfamilies Xerinae and Callosciurinae were moderately male-biased (0.99 and 0.99 respectively) (Figure 2.2). Within subfamilies, there was variation in patterns across genera (Figure 2.3).

FIGURE 2.2: Sexual size dimorphism across squirrel subfamilies. SSD is calculated as Female Head and Body Length/ Male Head and Body Length.

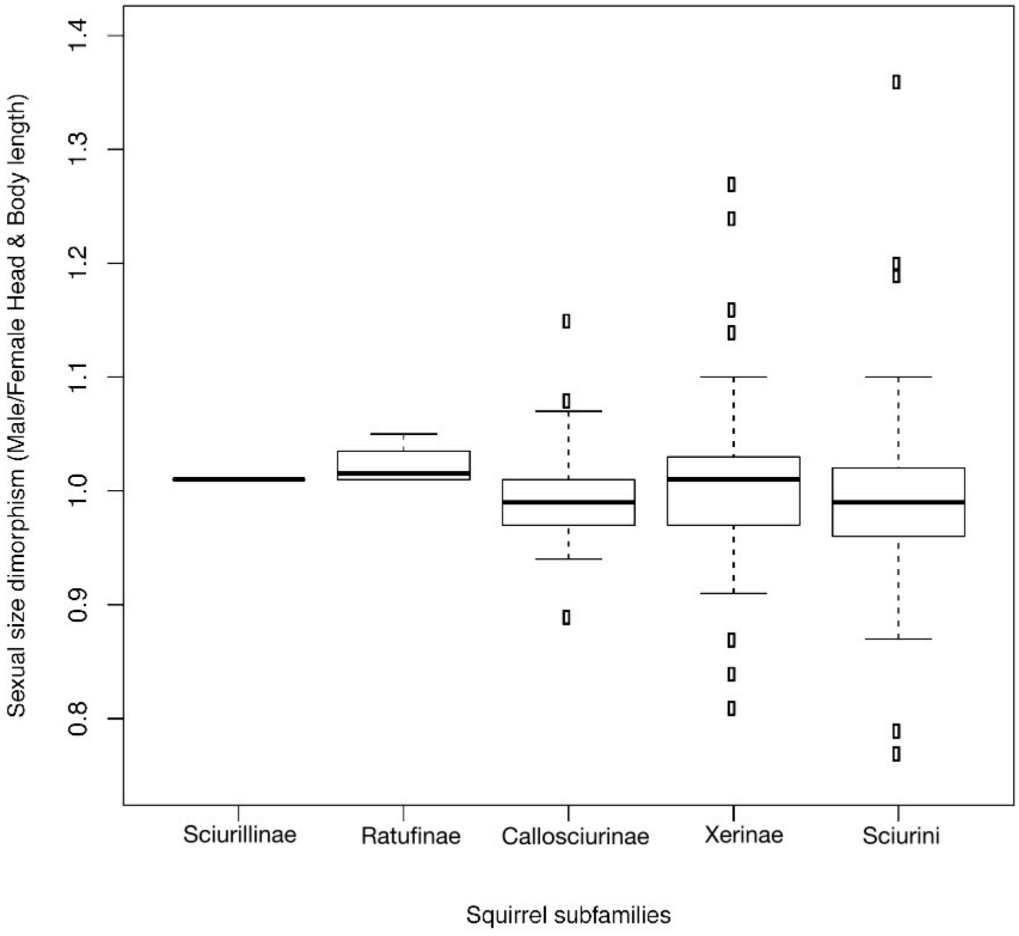
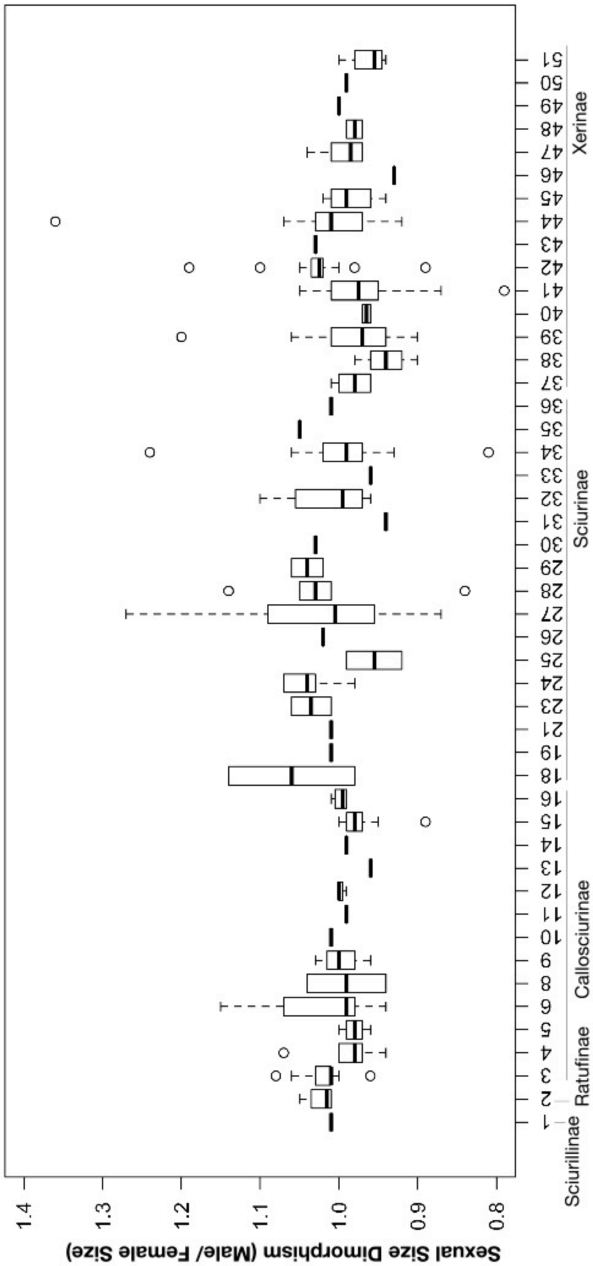


FIGURE 2.3: Sexual size dimorphism across squirrel genera within subfamilies. SSD is calculated as Female Head and Body Length/ Male Head and Body Length.



Genera: 1 Sciurillus, 2 Ratufa, 3 Callosciurus, 4 Dremomys, 5 Exilisciurus, 6 Funambulus, 7 Glyphotes, 8 Hyosciurus, 9 Lariscus, 10 Menetes, 11 Nannosciurus, 12 Prosciurillus, 13 Rhinosciurus, 14 Rubrisciurus, 15 Sundasciurus, 16 Tamiops, 17 Aeretes, 18 Aeromys, 19 Belomys, 20 Biswamoyopterus, 21 Eoglaucomys, 22 Eupetaurus, 23 Glaucomys, 24 Hylopetes, 25 Iomys, 26 Petaurillus, 27 Petaurista, 28 Petinomys, 29 Pteromys , 30 Pteromyscus, 31 Trogopterus, 32 Microsciurus, 33 Rheithrosciurus, 34 Sciurus, 35 Syntheosciurus, 36 Tamaisciurus, 37 Ammospermophilus, 38 Cynomys, 39 Marmota, 40 Sciurotamias, 41 Spermophilus, 42 Tamias, 43 Epixerus, 44 Funisciurus, 45 Heliosciurus, 46 Myosciurus, 47 Paraxerus, 48 Protoxerus, 49 Atlantoxerus, 50 Spermophilopsis, 51 Xerus

Phylogenetic signal and Character evolution

That there was phylogenetic signal in sexual size dimorphism (Log likelihood with phylogeny = -102.2526, Log likelihood without phylogeny = -105.3374, $p < 0.05$).

When ancestral states of SSD were mapped using parsimony methods, FBSD showed few repeats of convergence and reversal within squirrels (Figure 2.4). SSD characters across the tree had low homoplasy, with a CI of 0.09, implying that SSD arose few times and that there was low convergent evolution across the tree for FBSD. The Retention Index was also low (0.37), implying relatively low synapomorphy of FBSD across sciurids. The most parsimonious tree length was 11, and there were 8 parsimonious trees reconstructed with this topology. When we examined the number of gains and losses of SSD states, the majority of states did not change (ie, FBSD stayed FBSD, and MBSD stayed MBSD), and gains of FBSD were more common than losses (Figure 2.4). When SSD was mapped across 1000 random trees, CI was still low, indicating almost no homoplasy, with CI ranging from 0.07-0.079 being most common (in 460 of 1000 trees). The RI calculated from random trees was lower than from the observed tree, being 0.19 in 246 of the trees. The ancestral state for all squirrels was equivocal (Figure 2.4).

The two models of maximum likelihood reconstructions—a single rate vs. different rates of gains and losses of SSD—both resulted in similar outcomes of SSD trait mapping across the phylogeny. The different rates model (asymmetric rate model) was not significantly different from the single rate model ($p>0.05$), though the single rate model (-ln L 28.286) fit marginally better than the different rates model (-ln L 28.012). Both models revealed that the ancestor of all squirrels was more male-biased than female-biased. Though the different rates model assessed the rates of gains and losses of FBSD as marginally different—2.48 (forward rate) and 3.63 (backward rate)—it did not appear that SSD was evolving in any particular direction in squirrels overall. The overall rate of change as assessed by the single rate model as 2.64. Reconstruction of probabilities of ancestral states at nodes revealed that the ancestor to the tribe Pteromyinae was female-biased, but the ancestor to the subfamily Sciurinae is male-biased (Figure 2.5).

FIGURE 2.4: Reconstructed states of sexual size dimorphism (SSD) across squirrel genera. Branch shading reflects the single most parsimonious reconstruction for ancestral SSD patterns; light branches represent MBSD, dark branches represent FBSD, and notched branches signify equivocal reconstruction.

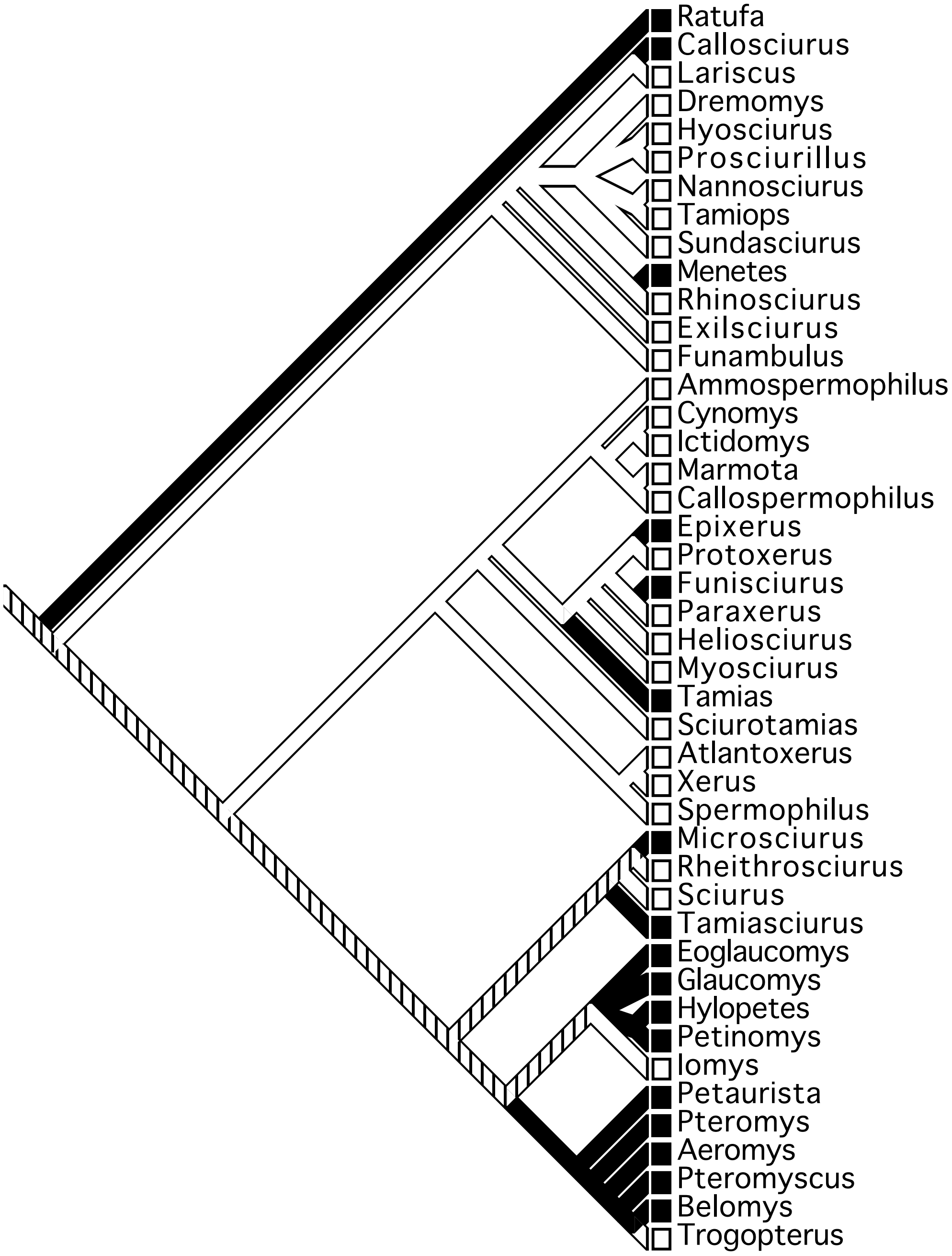
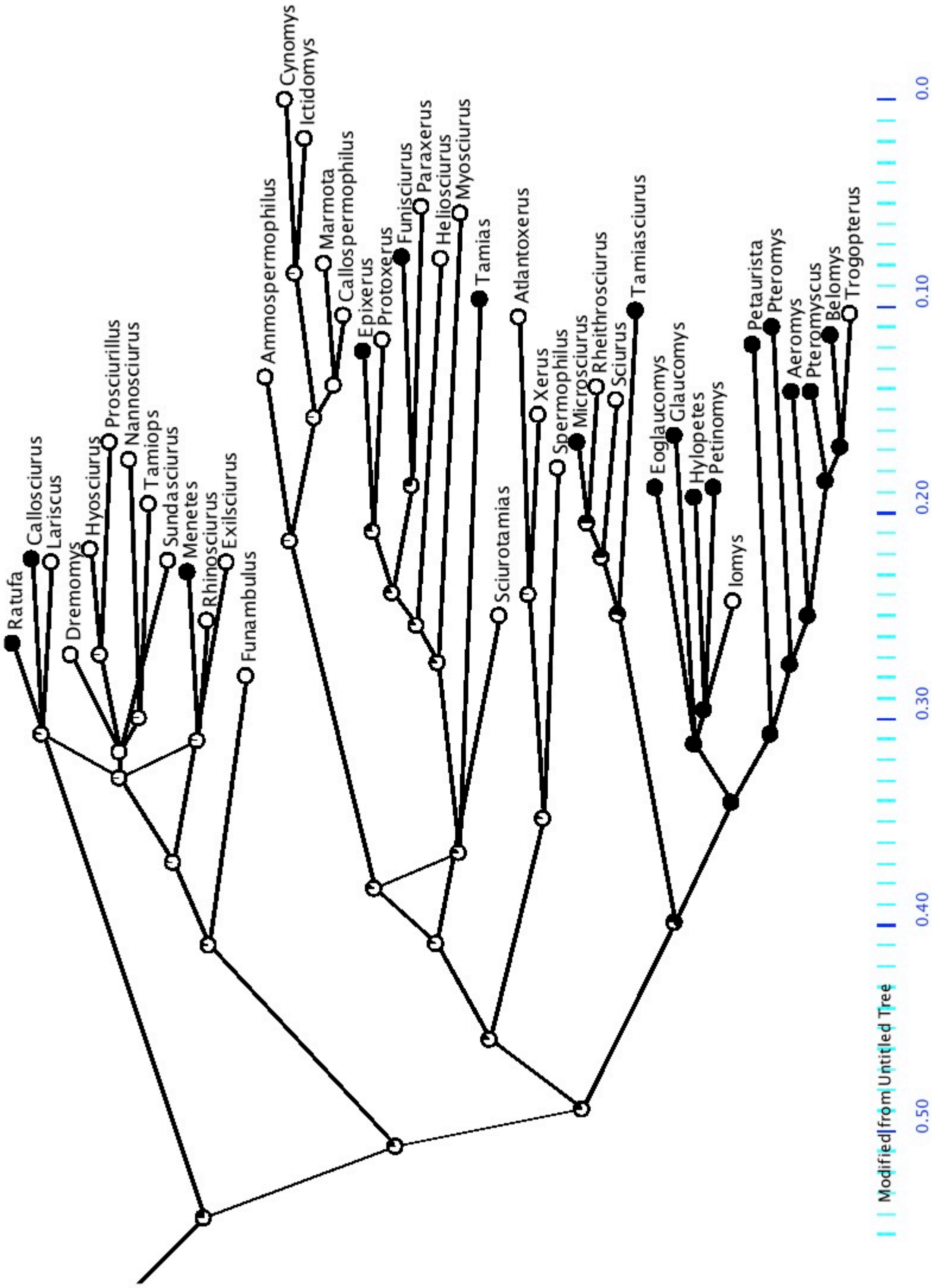


FIGURE 2.5: Reconstructed states of sexual size dimorphism (SSD) across squirrel genera. Pie charts at nodes indicate likelihood-based probability of MBSD (white) versus FBSD (black), using likelihood estimates of transition rates (fixed as equal) between the two states of SSD.



Ecological variables and sexual size dimorphism

Squirrels did not exhibit either pattern of SSD across all categories of ecological variables examined. Mosaic plots and Pearson's comparisons of the patterns of SSD across lifestyle and strata of squirrels revealed that the number of ground squirrels that were social and male-biased was significantly greater than other categories (Figure 2.6, Figure 2.7).

FIGURE 2.6: Mosiac plot of Sexual Size Dimorphism of squirrels in different lifestyles exhibiting different kinds of Sociality. The nested rectangular regions depict the proportional frequency of each category, and the colored rectangles represent departure of the cell from independence (calculated using Pearson's residuals: legend on side of plot).

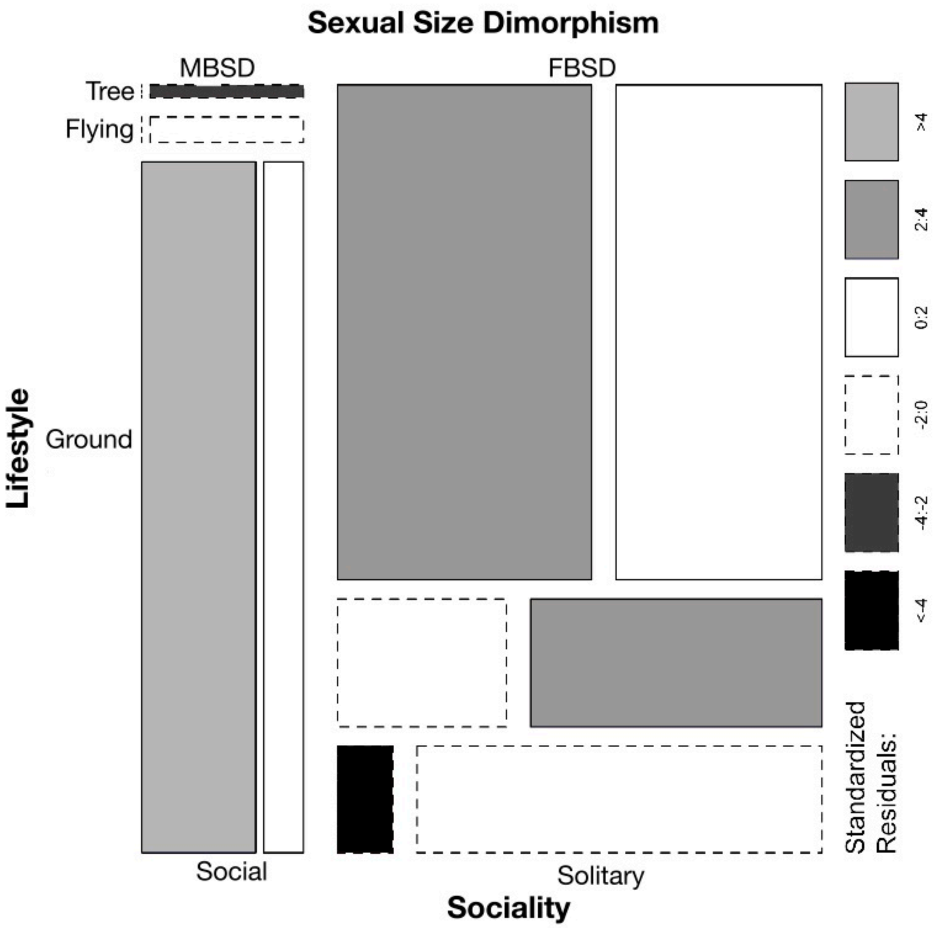
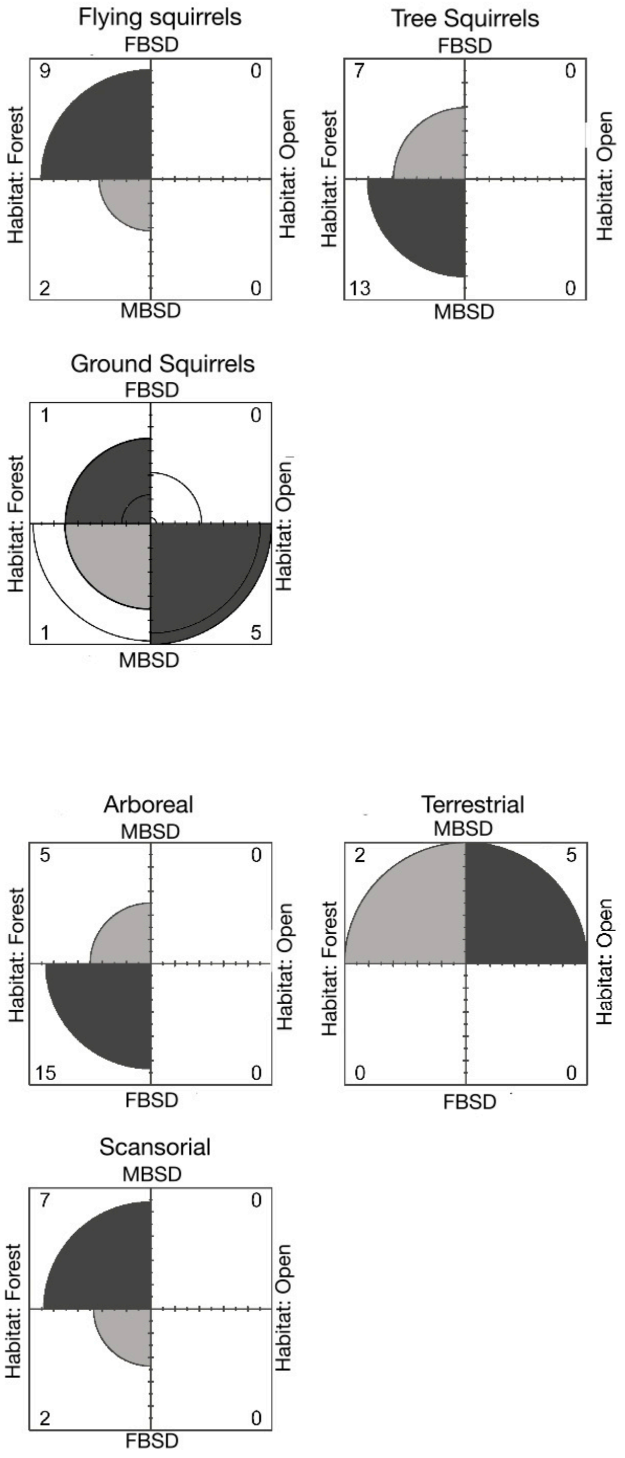


FIGURE 2.7: Four fold plots of FBSD and MBSD across squirrels in differing habitat categories with a) lifestyles and b) strata. Each quarter represents a cell in the contingency table, and confidence rings indicate significance of odds ratio calculations.



The analysis of non-phylogenetically transformed data with logistic regressions suggested that a simple model, one that incorporated strata used by squirrels and mid latitude occupied, had the lowest AIC score and was the best model according to the information theoretic approach (Table 2.1, 2.2). The model contained the two variables that were most important across all the models, being present in 27 of the top models (ranked by AIC score). More complex models contained the variables maximum latitude occupied by squirrels and diel activity; however, these two variables were not important across all models. FBSD was positively associated with both measures of latitude in all the models where these two variables were present, with one exception. In one model, maximum latitude was negatively associated with FBSD in the presence of lifestyle, strata and mid latitude. FBSD was negatively associated with strata in all models where this variable was present, indicating that as FBSD is seen in arboreal squirrels more than in ground squirrels. Squirrels in more tropical latitudes displayed more FBSD and species in more temperate regions exhibited more MBSD.

TABLE 2.1: Correlation table amongst variables used to determine ecological factors responsible for the patterns of SSD seen amongst squirrel genera. Spearman's correlation was used to determine relationships among variables, and significant correlations ($p<0.05$) are marked with an asterisk*.

	Diel Activity	**Strata**	**Annual Activity**	**Habitat**	**Lifestyle**	**Sociality**
Diel Activity	1					
Strata	-0.468*	1				
Annual Activity	-0.180	0.532*	1			
Habitat	-0.277	0.716*	0.669*	1		
Lifestyle	0.247	0.478*	0.525*	0.690*	1	
Sociality	0.163	-0.581*	-0.455*	-0.734*	-0.642*	1

TABLE 2.2: Maximized log-likelihood [log(L)], number of estimable parameters (K), Akaike's Information Criterion correction (AICc), Delta (Δ) AIC and Akaike weights (w_i) for logistic regression models comparing sexual size dimorphism of squirrel genera modeled on ecological characteristics. Models were ranked by Delta (Δ) AIC.

	log(L)	**K**	**AICc**	**Δ AIC**	**w_i**
Strata (-), Mid Latitude (+)	-19.493	3	45.65	0	0.09
Strata (-), Maximum Latitude (+), Mid Latitude (+)	-18.316	4	45.78	0.12	0.08
Strata (-), Diel Activity (+), Mid Latitude (+)	-18.33	4	45.8	0.15	0.08
Strata (-), Annual Activity (+), Habitat (-), Mid Latitude (+)	-17.139	5	46.04	0.39	0.07
Strata (-), Habitat (-), Maximum Latitude (+), Mid Latitude (+)	-17.598	5	46.96	1.31	0.05
Strata (-), Annual Activity (+), Habitat (-), Maximum Latitude (+), Mid Latitude (+)	-16.251	6	47.05	1.39	0.04
Strata (-), Diel Activity (+), Annual Activity (+), Habitat (-), Mid Latitude (+)	-16.488	6	47.52	1.87	0.04
Strata (-), Annual Activity (+), Mid Latitude (+)	-19.197	4	47.54	1.88	0.04
Strata (-), Maximum Latitude (+), Mid Latitude (+), Sociality (+)	-17.952	5	47.67	2.02	0.03
Strata (-), Body Size (-), Maximum Latitude (+), Mid Latitude (+)	-17.953	5	47.67	2.02	0.03
Strata (-), Diel Activity (+), Maximum Latitude (+), Mid Latitude (+)	-18.06	5	47.89	2.23	0.03
Strata (-), Habitat (-), Mid Latitude (+)	-19.394	4	47.93	2.28	0.03
Strata (-), Diel Activity (+), Annual Activity (+), Mid Latitude (+)	-18.084	5	47.93	2.28	0.03
Strata (-), Body Size (-), Diel Activity (+), Mid Latitude (+)	-18.102	5	47.97	2.32	0.03
Strata (-), Maximum Latitude (+), Mid Latitude (+)	-19.415	4	47.97	2.32	0.03
Strata (-), Mid Latitude (+), Sociality (+)	-19.418	4	47.98	2.33	0.03

Strata (-), Body Size (-), Mid Latitude (+)	-19.451	4	48.05	2.39	0.03
Strata (-), Diel Activity (+), Habitat (-), Mid Latitude (+)	-18.223	5	48.21	2.56	0.03
Strata (-), Diel Activity (+), Mid Latitude (+), Sociality (+)	-18.248	5	48.26	2.61	0.02
Strata (-), Annual Activity (+), Maximum Latitude (+), Mid Latitude (+)	-18.265	5	48.3	2.64	0.02
Strata (-), Diel Activity (+), Maximum Latitude (+), Mid Latitude (+)	-18.298	5	48.36	2.71	0.02
Strata (-), Lifestyle (+), Maximum Latitude (-), Mid Latitude (+)	-18.315	5	48.4	2.74	0.02
Diel Activity (+), Habitat (-), Mid Latitude (+)	-19.735	5	48.61	2.96	0.02
Strata (-), Annual Activity (+), Habitat (-), Maximum Latitude (+), Mid Latitude (+)	-17.087	4	48.72	3.07	0.02
Strata (-), Body Size (-), Annual Activity (+), Habitat (-), Mid Latitude (+)	-17.113	6	48.77	3.12	0.02
Strata (-), Annual Activity (+), Habitat (-), Mid Latitude (+), Sociality (+)	-17.133	6	48.81	3.16	0.02
Strata (-), Body Size (-), Habitat (-), Maximum Latitude (+), Mid Latitude (+)	-17.396	6	49.34	3.69	0.01
Strata (-), Habitat (-), Maximum Latitude (+), Mid Latitude (+), Sociality (+)	-17.409	6	49.36	3.71	0.01
Diel Activity (+), Annual Activity (+), Habitat (-), Mid Latitude (+)	-18.878	5	49.52	3.87	0.01

The analysis of ecological data after controlling for phylogeny using generalized estimating equations suggested that a simple model with diel activity had the lowest QIC score, followed closely by a model with sociality explaining SSD (Table 2.3). More complex models, such as one with both diel activity and sociality had even lower QIC scores, being fourth in the list of top models. As in the logistic regression models, the GEE models indicated that FBSD was positively associated with a nocturnal lifestyle. MBSD seemed to be more positively associated with species that were social, while FBSD was associated with solitary species (Table 2.4).

TABLE 2.3: Quasilikelihood Information Criterion correction (QIC) and Estimate Scale Parameter for GEE models comparing sexual size dimorphism of squirrel genera modeled on ecological characteristics. Models were ranked by QIC.

Model	QIC	Estimated scale parameter
Diel Activity	62.03617	0.559934
Sociality	62.82404	0.6109819
Lifestyle	66.35828	0.5870187
Sociality, Diel Activity	66.49974	0.5928212
Sociality, Lifestyle	72.01136	0.6745285

TABLE 2.4: Details of the top two GEE regression models modeling sexual size dimorphism of squirrel genera on ecological characteristics. The models were selected according to the QIC values - refer Table 3 for details.

	Estimate	S.E.	t	Pr(T >|t|)
SSD ~ Sociality				
(Intercept)	-0.8483251	0.7497751	-1.131439	0.2770303
Sociality: Solitary	0.8843858	0.8698625	1.016696	0.3266842
SSD ~ Diel Activity				
(Intercept)	-0.4321266	0.4265557	-1.01306	0.3283571
Diel Activity: Nocturnality	0.7049998	0.9169155	0.768882	0.4548414

DISCUSSION

We found several lines of evidence to suggest that FBSD and pronounced MBSD evolved in squirrels in response to specific ecological conditions. The distribution of sexual size dimorphism was leptokurtic, with most genera exhibiting moderate male-biased dimorphism, and only few exhibiting FBSD or extreme MBSD. This mirrored the patterns found in mammals overall (Linderfors *et al.* 2008), indicating that FBSD and pronounced MBSD possibly evolved under select circumstances. Some genera of tree and ground squirrels (*Callosciurus*, *Tamias*) and all flying squirrels (Tribe Pteromyini) exhibited FBSD, while several marmots and ground squirrel genera displayed extreme MBSD.

Reconstruction of the ancestral state of SSD of all squirrels revealed that male-biased sexual size dimorphism was the most probable ancestral state of all squirrels and that FBSD has evolved more than once across multiple lineages. We found some support for the hypothesis that FBSD evolved in concordance with a gliding lifestyle: the tribe of flying squirrels show a distinct shift towards FBSD, with their nearest ancestor and the ancestor to their subfamily (subfamily Sciurini) being male-biased. FBSD also evolved in the ground-dwelling chipmunks of the genus *Tamias*, while all other ground squirrels evolved pronounced MBSD.

Of the ecological variables examined, we find that diel cycle, sociality, latitude and strata were predictors of SSD patterns as predicted. Trivers (1972) predicted that diurnal, active and visually oriented species might exhibit selection for larger males, but this hypothesis had not been tested (Isaac 2005). We find that diurnal squirrels tended to be male-biased in dimorphism, and nocturnal species were female-biased. Both diurnal tree squirrels and ground squirrels were moderately male-biased, with the most pronounced male-biased dimorphism occurring in ground squirrels. Ground squirrels and marmots live in open habitats with good visibility, and males are known to defend territories, which enhances reproductive success of males (Armitage 2009). Flying squirrels are almost exclusively nocturnal (Thorington and Farrell 2007, Nandini and Sinha 2009), and were largely female-biased in dimorphism. Nocturnal activity possibly reduces visual interactions, and maintenance of territories and securing mates might be through other forms of communication such as calls (R. Nandini personal observation, LM Gilley personal communication) and mating chases (R. Nandini personal observation) rather than visual displays.

Sociality was also seen to play a role in determining SSD of species, and more social species exhibited more MBSD than solitary species. Within ground squirrels (subfamily Xerinae), the more social species displayed MBSD while solitary species like chipmunks were female-biased in dimorphism. In species that live in social groups, males might evolve larger body size for territory defense or male-male competition for mates (Jarman 2008). In solitary species like chipmunks where males are the smaller sex, these pressures might be absent. Schulte-Hostedde and colleagues (2002) examined male running speed (as a surrogate for agility) and body size and they found that running speed did not influence male reproductive success. They suggest that there might be fitness advantages conferred on females for larger body size, especially in adverse environmental (eg. climatic) conditions (Levenson 1990, Schulte-Hostedde *et al.* 2002).

Prior to accounting for phylogenetic relatedness, we found evidence in favor of latitude occupied by squirrels and SSD, and strata occupied by squirrels and SSD patterns. While latitude and strata occupied were not as important after incorporating phylogeny, we still found them to contribute to the explanations of SSD patterns. Squirrels that were closer to the tropics were FBSD while those in higher latitudes exhibited MBSD. The effect of increasing body size with latitude (Bergmann's rule) has been linked to increased sexual size dimorphism, as larger overall body size has been shown to be linked with higher levels of polygyny (Loisson *et al.* 1999). While most studies find evidence of Bergmann's rule, they report confounding trends with size dimorphism, and explain their results as an artifact of the seasonality of climates, its effect on resource availability and consequently mating systems (Storz *et al.* 2001, Quinn *et al.* 1996, Isaac and Johnson 2003, Weckerly 1998).

Strata occupied also influenced SSD patterns, and, as predicted, arboreal squirrels exhibited FBSD while more terrestrial species exhibited MBSD. The ancestors to the arboreal tribes Pteromyinae (flying squirrels) and the Sciurini (tree squirrels) were likely primarily female-biased. Arboreal environments are three-dimensional, and large female size might have evolved to confer advantages of functional significance as climbing and leaping might impose constraints on females while they are pregnant, and larger mothers might be better mothers (Myers 1978, Ralls 1977). Following this assumption, female gliding squirrels should be even larger relative to males than female tree squirrels, as excess weight will affect gliding performance more severely than climbing or running performance. In accordance with this, our data show that flying squirrels display the most strongly female-biased dimorphism patterns of all squirrels. Another possibility for reaching the same SD patterns would be if arboreal males evolved to be smaller sized to enable more aerodynamic displays for sexual selection. While there are no studies examining the role of male agility in reproductive success, squirrels are known to be very agile and acrobatic, which could be important in displays or scramble-competition (Szekeley *et al.* 2000).

The trend of male-biased dimorphism in terrestrial squirrels was also seen in squirrels that are actually tree squirrels, but spend a large part of their time on the ground. This is highlighted in the Callosciurine tree squirrels, where most basal species in the group are male-biased. Some examples of this are squirrels of the genera *Hyosciurus* (long-nosed squirrels that live mostly in grasslands), *Lariscus* (striped ground squirrels), *Menetes* (ground squirrels that live in Asian rainforests), *Nannosciurus* (pygmy squirrel in rainforests), and *Rhinosciurus* (shrew-faced pygmy squirrel) (Medway 1965). All these squirrels are small bodied, and live in tropical habitats and forest understory areas. The most derived genus of this subfamily, tree squirrels of the genus *Callosciurus*, show a significant reversal to female-biased dimorphism. During the course of this study, based on the data collected, *Callosciurus* seems to be the most arboreal of the squirrels in this subfamily.

This study, spread across a large taxonomic canvas, has been able to reconstruct the significance of various ecological traits in the evolution of species and entire groups of squirrels. SSD patterns have possibly evolved in response to factors in the ecological habitat inhabited by squirrels, which in turn have possibly dictated mating systems and strategies for reproductive success employed by the sexes. FBSD has evolved in squirrels in response to specific pressures like a gliding lifestyle, and MBSD is more pronounced in diurnal terrestrial species.

LITERATURE CITED

Amadon, D. 1975. Why are female birds of prey larger than males ? Raptor research 9: 1-11.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton.

Andersson, M. and R.Å. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnaean Society 15:105-130.

Arbogast, B.S. 2007. A brief history of the New World flying squirrels: Phylogeny, biogeography and conservation genetics. Special Feature Article, Journal of Mammalogy 88: 840-849.

Barton, K. 2009. MuMIn: multi-model inference. In: R package version 0.12.0. http://r-forge.r-project.org/projects/mumin/

Bjorklund, M. 1991. Evolution, phylogeny, sexual dimorphism and mating system in the Grackles Quiscalus-Spp Icterinae. Evolution 45(3): 608-621.

Blomqvist, D., O.C. Johansson, U. Unger, M. Larsson, and L.A. Flodin. 1997. Male aerial display and reversed sexual size dimorphism in the dunlin. Animal Behaviour 54:1291-1299.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed.

Butler, M.A., T.W. Schoener, and J.B. Losos. 2002. The relationship between sexual size dimorphism and habitat use in greater Antillean *Anolis* lizards. Evolution 54(1): 259-272.

Cade, T.J. 1960. Ecology of the peregrine and gryflacon populations in Alaska. University of California Publications in Zoology 63(3): 151-290.

Cheverud, J.M., M.M. Dow, and W. Leutenegger. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. Evolution 39:1335–1351.

Cox, R.M., S.L. Skelly, and H.B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653–1669.

Cunningham, C.W., K.E. Omland, and T.H. Oakley. 1998. Reconstructing ancestral character states: a critical reappraisal. Trends in Ecology and Evolution 13(9): 361-366.

Darwin, C. 1871.The descent of man and selection in relation to sex. London: John Murray.

DeBry, R.W. and R.M. Sagel. 2001. Phylogeny of Rodentia (Mammalia) Inferred from the Nuclear-Encoded Gene IRBP. Molecular Phylogenetics and Evolution 19: 290-301.

den Tex, Robert-Jan, Thorington, Richard W., Jr., Maldonado, Jesus E. and Leonard, Jennifer A. 2010. Speciation dynamics in the SE Asian tropics: putting a time perspective on the phylogeny and biogeography of Sundaland tree squirrels, *Sundasciurus*. Molecular Phylogenetics and Evolution 55: 711-720.

Dobson, F.S. 2007. A life-style view of life-history evolution. Proceedings of the National Academy of Sciences, in press.

Dobson, F.S. and G.R. Michener. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76:851-862.

Drummond, A. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: ARTN 214.

Ekman S., H. Andersen, and M. Wedin. 2008. The limitations of ancestral state reconstruction and the evolution of the ascus in the Lecanorales (Lichenized Ascomycota). Systematic Biology 57 (1): 141-156.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28: 659-687.

Fairbairn, D.J., W.U. Blanckenhorn, and T. Székely. 2008. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, USA.

Ford, S.M. 1994. Evolution of sexual dimorphism body weight in platyrrhines. American Journal of Primatology 34:221–244.

Friendly, M. 1994. Mosaic displays for n-way contingency tables. Journal of the American Statistical Association 89: 190-200.

Friendly, M. 1994. A fourfold display for 2 by 2 by k tables. Technical Report 217, York University, Psychology Department, http://www.math.yorku.ca/SCS/Papers/4fold/4fold.ps.gz

Garland, T., Jr., A.F. Bennett, and E.L. Rezende. 2005. Phylogenetic approaches in comparative physiology. Journal of Experimental Biology 208:3015-3035.

Garland, T., Jr., P.H. Harvey, and A.R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-42.

Garland, T., Jr., P.E. Midford, and A.R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39:374-388.

Greenwood, P.J. and J. Adams. 1987. Sexual selection, size dimorphism and a fallacy. Oikos 48: 106-108.

Guindon S. and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52: 696-704.

Harmon, L.J., J.T. Weir, C.D. Brock, R.E. Glor, and W. Challenger. 2009. GEIGER: investigating evolutionary radiations. Bioinformatics 24 (1): 129-131.

Hedrick A.V. and E.J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends in Ecology and Evolution 4:136–138.

Herron M.D., T.A. Castoe, and C.L. Parkinson. 2004. Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilu*s). Molecular Phylogenetics and Evolution 31:1015-1030.

Huelsenbeck, J.P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754-755.

Isaac, J.L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review 35 (1): 101-115.

Isaac, J.L. and C.N. Johnson. 2003. Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. Behavioral Ecology 14: 818–822.

Jansa, S.A. and R.S. Voss. 2000. Phylogenetic studies on didelphid marsupials I. Introduction and preliminary results from nuclear IRBP gene sequences. Journal of Mammalian Evolution 7: 43–77.

Jansa, S.A. and M. Weksler. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. Molecular Phylogenetics and Evolution, 31: 256-276.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48(34):215-267.

Jehl, J.R., Jr. and B.G. Murray, Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Pp. 1-86 in Current Ornithology, vol. 3 (R. F. Johnston, ed.) Plenum, NY.

Karubian, J. and J.P. Swaddle. 2001. Selection on females can create 'larger males'. Proceedings of the Royal Society Series B-Biological Sciences 268: 725–728.

Katsikaros, K. and R. Shine. 1997. Sexual dimorphism in the tusked frog, *Adelotus brevis* (Anura: Mypobatrachidae): the roles of natural and sexual selection. Biological Journal of the Linnean Society, 60: 39-51.

Katoh, K., Kuma, K., Toh, H. and T. Miyata. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Research 33:511-518.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London and New York.

Krasnov, B.R., Morand, S., Hawlena, H., Khokhlova, I.S., and G.I. Shenbrot. 2008. Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. Oecologia 146: 209-217.

Lacey, E.M. 2000. Spatial and social systems of subterranean rodents. pp.257-300 In Life Underground: the biology of subterranean rodents, Ed. Lacey, E. A, Patton, J. L. and Cameron, G. N. The University of Chicago Press Ltd., Chicago.

Leutenegger, W. and J.M. Cheverud. 1982. Correlates of sexual dimorphism in primates: ecological and size variables. International Journal of Primatology 3:387–402.

Liang, K.Y. and S.L. Zeger. 1986. Longitudinal data analysis using generalized linear models, Biometrika 73: 13–22.

Loison, A., J.-M. Gaillard, C. Pèlabon, and N.G. Yoccoz. 1999. What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research 1:611–633.

Lovich, J.E. and J.W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development and Aging 56(4):269-81.

Maddison, W.P. and D.R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution. Version 3.0, Sinauer Associated Press, .

Mercer, J.M. and V.L. Roth. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568-1572.

Mueller, H.C. 1986. The evolution of reversed sexual size dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin 98:387-406.

Mueller H.C. and K. Meyer. 1985. The evolution of reversed sexual dimorphism in size. A comparative analysis of the Falconiformes of the western Palearctic. In: Johnston RF (ed) Current ornithology 2. Plenum, New York, pp. 65–101.

Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. American Naturalist 112 (986):701-712.

Natureserve. 2011. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.0. NatureServe, Arlington, VA. U.S.A. Available http://www.natureserve.org/explorer. (Accessed: <date>)

Neuhaus P., D.R. Broussard, J.O. Murie, and F.S. Dobson. 2004. Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. Journal of Animal Ecology 73:36–43.

Nylander, J.A.A., J.C. Wilgenbusch, D.L. Warren, and D.L. Swofford. 2008 AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24: 581-583.

Omland, K.E. and C.M. Hofmann. 2006. Adding color to the past: ancestral state reconstruction of bird coloration. In G. E. Hill and K. J. McGraw eds. Bird Coloration Volume 2: Function and Evolution Harvard University Press. Pp. 417-454.

Oshida, T., R. Masuda, and M.C. Yoshida. 1996. Phylogenetic relationships among Japanese species of the family Sciuridae (Mammalia, Rodentia), inferred from nucleotide sequences of mitochondrial 12s ribosomal RNA genes. Zoological Science 13:615-520.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology 48(3):612–622.

Pagel, M., A. Meade, and D. Barker. 2004. Bayesian estimation of ancestral character states on phylogenies. Systematic Biology 53 (5): 673-684.

Paradis, E. 2006. Analysis of Phylogenetics And Evolution With R. Springer-Verlag, New York USA.

Paradis, E. and J. Claude. 2002. Analysis of comparative data using Generalized Estimating Equations. Journal of Theoretical Biology 218: 175–185.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289-290.

Payne, J., C.M. Francis, and K.Philips (1985). A field guide to mammals of Borneo. The Sabah Society and World Wild Fund, Kota Kinabalu, Malaysia.

Pérez-Barbería, F.J., I.J. Gordon, and M. Pagel. 2002. The origins of sexual dimorphism in body size in ungulates. Evolution 56:1276-1285.

Posada D. 2008. jModelTest: Phylogenetic Model Averaging. Molecular Biology and Evolution 25: 1253-1256.

Post, E., R. Langvatn, M.C. Forchhammer, and N.C. Stenseth. 1999. Environmental variation shapes sexual dimorphism in red deer. Proceedings of the National Academy of Sciences 96: 4467-4471.

Quin, D.G., A.P. Smith, and T.W. Norton. 1996 Eco-geographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). Australian Journal of Zoology 44:19–45.

Quinn, G. and M. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ralls, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51: 245-276.

Ranta, E., A. Laurila, and J. Elmberg. 1994. Reinventing the Wheel: Analysis of Sexual Dimorphism in Body Size. Oikos 70(3): 313-321.

Reynolds, R.T. 1972. Sexual dimorphism in accipiter hawks: A new hypothesis. Condor 74: 191-197.

Roff, D.A. 1992. The evolution of life histories. Chapman and Hall; New York.

Sanderson, M.J., D. Boss, D. Chen, K.A. Cranston, and A. Wehe. 2008. The PhyLoTA Browser: processing GenBank for molecular phylogenetics research. Systematic biology, 57, 3: 335-346.

Ronquist, F. and J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. In B Campbell (ed.), Sexual selection and the descent of man. Chicago: Aldine.

Serrano-Meneses, M.A. and T. Szekely. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. Oikos 113:385-394.

Schulte-Hostedde, A.E. And J.S. Millar. 2001. Measuring sexual size dimorphism in the yellow-pine chipmunk (Tamias amoenus). Canadian Journal of Zoology, 78, 728–733.

Schulte-Hostedde, A.E., J.S. Millar, and G.J. Hickling. 2001. Sexual dimorphism in body composition of small mammals. Canadian Journal of Zoology, 79, 1016–1020.

Schlute-Hostedde, A. 2007. Sexual size dimorphism in rodents, in Wolff, J. O. and Sherman, P. W. (Eds.) Rodent Societies: An ecological and evolutionary perspective. The University of Chicago Press, Chicago. Pp 115-128.

Shine, R. 1979. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419-461.

Sibley, R.M. and J.H. Brown. 2007. Effects of body size and lifestyle on evolution of mammal life histories. Proceedings of the National Academy of Sciences, in press.

Smith, R.J. 1999. Statistics of sexual size dimorphism. Journal of Human Evolution 36: 423-459.

Snyder, N.F.R. and J.W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monographs 20: 1-96.

Springer, M.S., R.W. DeBry, C. Douady, H.M. Armine, O. Madsen, W.W. de Jong and M.J. Stanhope. 2001. Mitochondrial versus nuclear gene sequences in deep-level mammalian phylogeny reconstruction. Molecular Biology and Evolution 18(2): 132-143.

Stanhope, M.J., J. Czelusniak, J-S Si, J. Nickerson, and M. Goodman. 1992. A molecular perspective on mammalian evolution from the gene encoding interphotoreceptor retinoid binding protein, with convincing evidence for bat monophyly. Molecular Phylogenetics and Evolution 1: 148-160.

Steppan, S.J., B.L. Storz, and R.S. Hoffmann. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Molecular Phylogenetics and Evolution 30:703-719.

Steppan, S.J., M.R. Akhkverdyan, E.A. Lyapunova, D.G. Fraser, N.N. Vorontsov, R.S. Hoffmann, and M.J. Braun. 1999. Molecular phylogeny of the marmots (Rodentia: Sciuridae): tests of evolutionary and biogeographic hypotheses. Systematic Biology 48:715–734.

Steppan, S.J. and S.M. Hamm. 2006. Sciuridae. Squirrels. Version 13 May 2006. http://tolweb.org/Sciuridae/16456/2006.05.13 in The Tree of Life Web Project, http://tolweb.org/

Storz, J.F., J Balasingh, H.R. Bhat, P.T. Nathan, D.P.S. Doss, A.A. Prakash, and T.H. Kunz. 2001. Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). Biological Journal of the Linnaean Society 72: 17–31.

Svendsen. G.E. and M.M. White. 1997. Body mass and first-time reproduction in female chipmunks. Canadian Journal of Zoology 75:1891-1895.

Székely, T., J.D. Reynolds, and J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. Evolution 54 :1404–1413.

Székely, T., R.P. Freckleton, and J.D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. Proceedings of the National Academy of Sciences 101:12224–12227.

Tamura, N., Hayashi, F., and K. Miyashita. 1988. Dominance hierarchy and mating behavior of the Formosan Squirrel, *Callosciurus erythraeus thaiwanensis*. Journal of Mammalogy 69(2): 320-331.

Thorington, R.W.Jr., and R.S. Hoffmann. 2005. Family Sciuridae, pp. 754. In D.E. Wilson and D.M. Reeder (eds.), Mammal Species of the World. Smithsonian Institution Press, Washington, D. C.

Trivers, R.L. 1972. Parental investment and sexual selection. In B. Campbell (Ed.) Sexual selection and the descent of man. Chicago: Chicago University Press.

Weckerly, F.W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 77:33–42.

Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae:Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29: 331-349.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer New York.

Yu, F., F. Yu, J. Pang, C.W. Kilpatrik, P.M. McGuire, Y. Wang, S. Lu, and C.A. Woods. 2006. Phylogeny and biogeography of the *Petaurista philippensis* complex (Rodentia: Sciuridae), inter- and intraspecific relationships inferred from molecular and morphometric analysis. Molecular Phylogenetics and Evolution 38(3): 755-766.

Chapter 3

CHARACTER DISPLACEMENT IN SPECIES AND SEXES OF SYMPATRIC SQUIRRELS

INTRODUCTION

The structure and mechanisms underlying the co-existence of sympatric species within communities have received much attention (Brown and Wilson 1956, Cody and Diamond 1975, MacArthur 1972). Sympatric species that are similar in form are placed into “guilds” by ecologists to reflect their similarity in resource use and in niche occupation (Brown and Wilson 1956). A fundamental question about guilds is how such similar species can coexist in nature, since their similarity is thought to engender interspecific competition. Such species, however, are known to promote co-existence and reduce competition via differences in the way in which their similar resources are used. Some of the ways species partition resources are the use of space, resources or time of activity. Squirrels comprise a speciose guild that are key components of tropical rainforests in Southeast Asia, and in this study we examine temporal separation between two sympatric guilds of squirrels in Southeast Asia. Further, we investigate morphological separation within each of these guilds.

Morphological differences associated with resource use (eg. body size, size of trophic apparatus) between closely related co-occurring species have long been considered indirect evidence for competition (Dayan et al. 1989, 1990, Greene 1987, Hutchinson 1959, MacArthur 1958, Schoener 1974, Simberloff and Boecklen 1981, Weins 1982). Hutchinson (1959) proposed a body-size “rule”, which predicted that sympatric, similar species would be regularly spaced along a size sequence, separated by an average size ratio of 1.3 (usually 1.1 to 1.4; subsequently dubbed the ‘Hutchinsonian ratio’) in linear measurements. Brown and Wilson (1956) further suggested that species differences were accentuated in the zones of sympatry and weakened in other areas of a species' range, and termed this ‘character displacement'. Strong et al. (1979) predicted that community-wide character displacement was another pattern resulting from competition, which expressed itself as equal-size ratios between co-existing species (overdispersion of species sizes). Studies have found evidence for patterns of Hutchinson's rule and character displacement in a variety of taxa, like birds (Schoener 1984), carnivores (Dayan et al. 1989) and rodents (Ben-Moshe et al. 2001, Dayan and Simberloff 1994). In addition to partitioning of species along the size spectrum to reduce competition, sexes within a species might exhibit size dimorphism, allowing them to act like morphospecies and partition resources (Dayan and Simberloff 1998, 2005). Sexes of species are also seen to partition along the size spectrum in order to reduce competition, and this has received much attention with carnivores (reviewed in Dayan and Simberloff 2005).

Ecological character displacement caused by inter-specific competition is also known to result in species occupying more distinct niches. Interspecific competition can result in sympatric species occupying different microhabitats,as seen with reptiles (strata and substrate)(Schoener 1974, Schoener 1970, Alatalo and Moreno 1987). Temporal separation is another way that species can reduce overlap, and can involve partitioning of resources between different times of the day, or between day and night, or even between different times of year and can complement separation by food or habitat. It has been suggested that predators are more likely to partition themselves by day and night than herbivores or omnivores as the latter depend on resources that are not usually replenished within a 24 hr cycle (Schoener 1974, Gutman and Dayan 2005). Also, it has been argued that closely related species, which are prime candidates for competition, are usually evolutionarily constrained to being active during the same part of the diel cycle (Kronfeld-Schor et al. 2001, Kronfeld-Schor and Dayan 2003). Temporal partitioning has not been extensively studied (Kronfeld-Schor and Dayan 2003), though such studies have examined a number of taxa including ants (Albrecht and Gotelli 2001), spiders (Gertsch and Reichert 1976), rodents (Gutman and Dayan 2005) and bats (Adams and Thibault 2006). Squirrels are a unique family of mammals in which sympatric species occupy the same spatial niches with different temporal cycles. Tree squirrels are diurnal while flying squirrels are nocturnal, and in Asian forests many species of each of these assemblages are sympatric in tropical forests (Thorington and Ferrell 2007). Both these assemblages exhibit a considerable range of body sizes, and provide an ideal system to examine character displacement in two sympatric temporally separated communities that occupy the same niche.

Squirrels are distributed worldwide but reach their highest diversity in Southeast Asia (Koprowski and Nandini 2008), and the Sunda shelf and Malay peninsula are particularly diverse, with up to 46 species of tree and flying squirrels occurring in this region (Corbett and Hill 1992, den Tex et al. 2010). Mercer and Roth (2003) attribute the explosive diversification of squirrels on the Sunda shelf islands to changes in sea-level in the pre-pleistocene era. Adaptive radiation has been described in explosive radiation events, where divergence by species in particular traits allow them better exploit differing ecological opportunities (Schluter 2000, Glor 2010). Signatures of adaptive radiations might be retained in morphological traits, as seen in cetaceans (Slater et al. 2010). Given that both the diurnal tree squirrel and nocturnal flying squirrel assemblages are most diverse in Southeast Asia (Koprowski and Nandini 2008), we hypothesize that squirrel species within each of these assemblages partition along a size spectrum, allowing them to exploit different resources within the same habitat. Additionally, the sexes of squirrels are known to be dimorphic in size to varying degrees (see Chapter 2 in this dissertation), and we further hypothesise that the same pattern will be seen when the sexes are examined as morphospecies. We use body size as an indirect measure of competition, assuming that body size will dictate niches used (eg: larger flying squirrels use larger tree hollows; Nandini and Sinha 2009) as well as resources consumed (Brown and Wilson 1956). Many studies of niche partitioning in mammals use tooth size as a measure of diet breadth and food consumed (Dayan and Simberloff 2005). However, in several studies of mammals, tooth size has found to scale isometrically with body size (Creighton 1980), and we use body size as the measure of interest in this study given the rarity of museum collections from Southeast Asia for several species.

METHODS

Study species and location

Squirrels belong to the rodent family Sciuridae, and are widely distributed, being especially speciose in the tropical forests of Southeast Asia (Koprowski and Nandini 2007). Squirrels occur as three major body forms—tree squirrels, flying squirrels and ground squirrels, and both tree and flying squirrels reach their maximum diversity in the forests of Southeast Asia (Corbett and Hill 1992, Koprowski and Nandini 2008). Both tree and flying squirrels occupy various vertical strata of the forest, and feed predominantly on leaves, bark, fruits, flowers, seeds, fungi, lichen and arthropods. Tree squirrels are known to nest in dreys or in hollows of trees, while flying squirrels are known to rest primarily in tree hollows, though there have been some observations of flying squirrels nesting in dreys. However, despite their similar habits, tree squirrels are diurnal, while flying squirrels are nocturnal, and it has been hypothesised that this partitioning of time allows so many species to co-exist in the same region.

For this study we investigate patterns of body size separation of squirrels on Borneo, as reliable occurrence records and size data are available for this island. The island is very rich in biodiversity (McKinnon et al. 1998) and consists of a variety of rainforests covering a wide range of altitudes (Payne and Francis 1985). Borneo is the world's third largest island, and is located at the centre of the maritime region and is politically divided between Malaysia, Indonesia and Brunei. There are 34 species of squirrels recorded from Borneo (Corbett and Hill 1992), and of these, 14 are nocturnal flying squirrels (4 endemic to Borneo) and 20 are diurnal tree squirrels. Each of these assemblages spans more than an order of magnitude, within flying squirrels varying in weight from 80 gm (*Hylopetes spadiceus*) to 2.9kg (*Petaurista petaurista*), and tree squirrels varying from 60 gm (*Exilisciurus exilis*) to 2.0 kg (*Ratufa affinis*). All flying squirrels belong to Subfamily Sciurinae, tribe Pteromyini, and are believed to have radiated in Southeast Asia around 18 mya (Mercer and Roth 2003). The majority of tree squirrels found in Southeast Asia belong to the subfamily Callosciurinae, and all radiated in Southeast Asia around 11 mya (Mercer and Roth 2003). The monotypic genus *Rheithrosciurus* belongs to the predominantly New World subfamily Sciurinae, and possibly entered Southeast Asia at a much later date. The largest squirrel in the diurnal assemblage, the giant squirrel *Ratufa* belongs to one of the oldest squirrel lineages—the subfamily Ratufinae. From natural history accounts of species (Harrison 1956, Banks 1931, Chasen 1940, Hill 1960, Medway 1965, Medway 1969, Payne and Francis 1998) and some focused biological studies, we know that species of both the diurnal and nocturnal assemblages partition resources along the forest strata, with a few species using the lower strata of the forest and the ground, and some species being almost wholly arboreal. While there are some tree squirrels that are almost exclusively ground-dwelling (Harrison 1956), there are no flying squirrels that occupy this habitat dimension. The diurnal tree squirrel assemblage comprises of squirrels that are both arboreal and terrestrial in nature, and the genus *Hyosciurus* is mostly terrestrial, inhabiting grasslands (Hayssen 2008). The genera *Lariscus* and *Menetes* are predominantly ground dwelling in rainforests (Hayssen 2008).

Body size information

Total body length was used as a measure of body size, as it is less variable within and among individuals than body mass. An analysis across squirrels reveals that lifestyles and ecological variables predict patterns of sexual size dimorphism, and squirrels exhibit both male and female-biased size dimorphism (see Chapter II for details). Flying squirrels are predominantly female-biased in size, while tree squirrels are predominantly male-biased in size. However, some genera of tree squirrels in Southeast Asia are female-biased, including some species on Borneo. Given that any one sex was not larger across all species in this analysis, we used a body size value averaged across both sexes as the species value for analysis. Body size data for flying squirrels and tree squirrels was obtained from the literature and guide books (Harrison 1956, Chasen 1940, Payne and Francis 1985).

For the morphospecies analysis, we used body size information (Head and Body length) from the literature for each sex of all the species that occurred on Borneo. The sources for the data are listed in Appendix I. We did not manage to obtain data for both sexes of two squirrel species in the diurnal assemblage—*Lariscus hosei* and *Glyphotes simus*, and these species were treated as monomorphic for the analysis.

Analysis

There are two main ways that questions of size overlap are addressed: testing for a minimum size ratio between any pair of related species in a guild, and determining that the size ratio between adjacent size-ranked species pairs is larger than expected (Dayan and Simberloff 1998, Gotelli and Entsinger 2001).

Hutchinson (1959) observed that there was a minimum size ratio (larger species/

smaller species) between any two potentially competing species that allowed then to co-exist together. In his examination of 13 species, he found this to be 1.3, and several other species have found similar ratios (see review by Dayan and Simberloff 1998). If the observed ratio in the data is less than the putative ratio, the claim is falsified. We test whether there is a minimum ratio operating amongst sympatric squirrel species or morphospecies that allows them to co-exist, and use the null model program Ecosim's (Gotelli and Entsinger 2001) Size Overlap module to do this. We analysed tree squirrels and flying squirrels separately to test for signals in these two groups. Data for tree and flying squirrels entered in a matrix that was then shuffled to produce random patterns that could be expected in the absence of competitive interactions. The Size overlap module of EcoSim also allows for determining whether the minimum segment length is larger than what would be expected by chance. The minimum segment length is the smallest segment length of any pair of species in the dataset. In a structured assemblage, this should be larger than expected by chance. EcoSim constructs random assemblages based on the observed data, and we specified a log uniform distribution for the data with user-defined limits to the dataset. The minimum and maximum body sizes for both assemblages were determined based on our knowledge of squirrel species found elsewhere in Southeast Asia and their known maximum and minimum body sizes. 5000 random distributions were generated and the minimum segment length generated from the empirical data and the simulated data were compared. If the observed minimum was significantly larger than 95 % of the simulated values, we concluded that competition structured the community assemblage (Gotelli and Entsinger 2001).

The second way to examine the question of character displacement is to test for variance between ratios of adjacent species along a size spectrum. If character displacement is operating, the assumption is that there must be even spacing of these species along a spectrum. Statistical procedures commonly used to test for this are the Variance test (Poole and Rathcke 1979) and the Barton-David test (Barton and David 1956, Dayan et al. 1998) among others (Roth 1981, Irwin 1955). We used the Size Overlap module of EcoSim (Gotelli and Entsinger 2001) to test for variance in segment length, which measures the tendency for even spacing of adjacent size-ranked species or morphospecies in the community. Segment length is calculated as the difference between the body size of two consecutive species in a size-ranked continuum (ordered smallest to largest). A structured assemblage would have a smaller variance than an unstructured assemblage. Further options chosen were logarithmic transformation with no rounding, with all species in the dataset included in the source pool with colonisation rates set to 1.0, giving each species an equal probability of colonisation. We generated 5000 random distributions and compared variance in segment length between the observed and simulated datasets. Variance in segment length tests the prediction that species should be regularly spaced if competition influences the phenotype, and we assumed this occurred if the observed variance was significantly less than 95% of the simulated values (Gotelli and Entsinger 2001).

We also used Barton and David's statistic (Barton and David 1956) to test for the constancy of size ratios between adjacent species. The Barton-David test (B-D test) has been widely used to detect whether any two points are too close together on a line, and tests if this ratio is too small to have been expected by chance alone. We follow the procedure outlined by Simberloff and Boecklen (1988) and Dayan et al. (1999). Log-transformed size values of species are ordered from smallest to largest, and the difference between the logs of two species is the log of the ratio of two species adjacent in ranking. These segments are then ordered in increasing order, from g_1 to g_n. Three statistics $G_{1,n}$ (ratio of smallest to largest size ratio), $G_{1, n-1}$ (ratio of smallest to second largest size ratio) and $G_{2, n}$ (ratio of second smallest to largest ratio) were calculated. Probability values were calculated from Barton and David (1959). Even though the B-D test is described as more of a descriptive statistic of patterns rather than a rigorous statistical test (Dayan et al. 1992), its use is justified because it is accurate (Boecklen and NeSmith 1985) and it has been used in numerous other studies on character displacement, particularly in mammals, and thus facilitates comparisons (Dayan et al. 1989a, b, 1990, 1992, Dayan and Simberloff 1994). All three above described statistics were applied to the species assemblages, and we tested the morphospecies assemblages for constancy in minimum segment length and variance in segment length.

RESULTS

Species partitioning

The two assemblages examined—nocturnal flying squirrels and diurnal tree squirrels spanned similar ranges of body size, and their distributions were not significantly different (KS test, D=0.3786, p-value>0.05.) Flying squirrels ranged in body length from 70 mm to 400 mm while tree squirrels ranged in size from to 74mm to 350 mm. Figures 3.1 a and b depict the distribution of body sizes for flying and tree squirrels, and species both assemblages seem to partition themselves in a linear non-overlapping order. The distributions of the sizes of flying and tree squirrels are not normally distributed, and there are more large species than medium-sized species.(Figure 3.2 a and b).

Minimum segment length ratios for both tree and flying squirrels were not significantly different from simulated values. For the nocturnal flying squirrels, though the observed mean minimum segment length was greater than that for the simulated data, this was not significant (Standardised Effect Size=-0.83, p>0.05, Table 3.1). Similarly, for tree squirrels, the mean minimum segment length for the observed data was greater than the simulated data, this was not significant (Standardised Effect Size=-0.63, p> 0.05, Table 3.1).

TABLE 3.1: Values of observed and simulated values of minimum-segment length and variance in segment length of squirrel species arranged in order of ascending size. * indicates significance in the case when variance in segment length of observed assemblage > simulated assemblages.

	Minimum Segment Length		**Variance in Segment Length**	
	Observed	**Simulated**	**Observed**	**Simulated**
Flying squirrels	0.001	0.0003	**0.001***	0.0001
Tree squirrels	0.001	0.001	**0.002***	0.0003

For nocturnal flying squirrels, the variance in segment length ratios was significantly smaller than that expected by chance. Mean variance in segment length of nocturnal flying squirrels was greater for the observed assemblage than the simulated assemblage, and the size overlap of observed was significantly less than the expected (Standard effect size=-1.40, p< 0.05, Table 1), implying some community structure (Figure 3.3a). The same trend was reflected for diurnal tree squirrels also, and again, the variance in segment length ratios for this assemblage was significantly smaller than expected by chance. The size overlap of observed was significantly less than the expected (Standard effect size=-1.151 , $p<0.05$), implying some community structure (Figure 3.3.b, Table 3.1). The Barton-David test shows no equality of ratios among species of flying squirrels (all ratios had $p>0.05$) or tree squirrels. Only one of the ratios for tree squirrels showed any equality (Table 3.2).

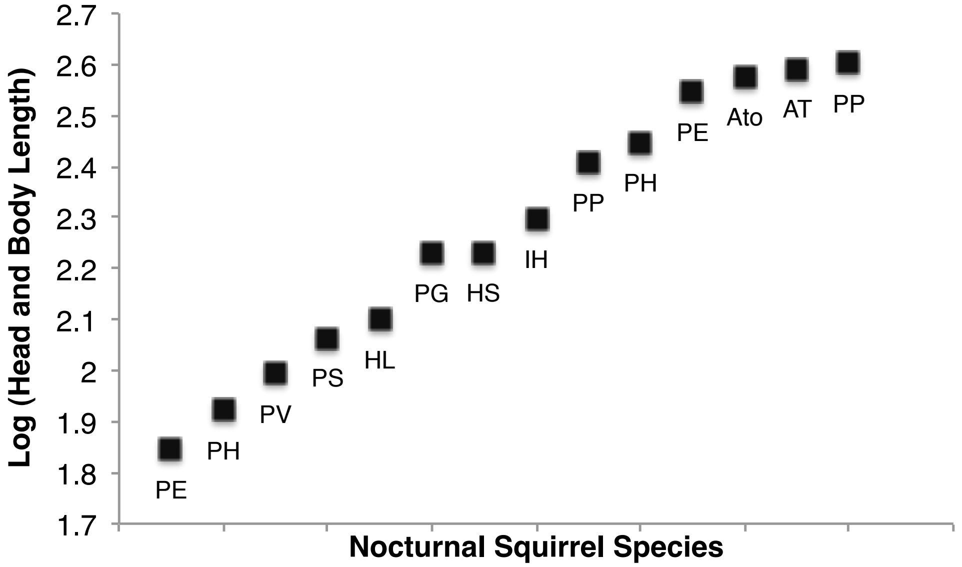
TABLE 3.2: Results of the Barton-David test comparing size ratios of adjacent-sized species of flying squirrels and tree squirrels in Borneo. Refer section c of Methods for details of the test.

	Statistic	**Value**	**Probability**
Flying squirrels	$G_{1,13}$	7.336	ns
	$G_{1,12}$	4.830	ns
	$G_{2,13}$	6.873	ns
Tree squirrels	$G_{1,20}$	0.067	0.05
	$G_{1, 19}$	6.383	ns
	$G_{2, 20}$	0.428	ns

Size ratios between adjacent species in both the assemblages were similar to other studies on mammals: and the mean size ratio of nocturnal flying squirrels was 1.14, with the smallest ratio between any two flying squirrels was 1.002, and the largest was 1.34. Diurnal tree squirrels spanned a larger continuum of ratios. This assemblage had a mean ratio of 1.093, and a minimum of 1.004 and a maximum of 1.49. When the two distributions were compared, there did not seem to be any significant differences in the ratios (Wilcoxon test, W=168, $p > 0.05$, Figure 3.4).

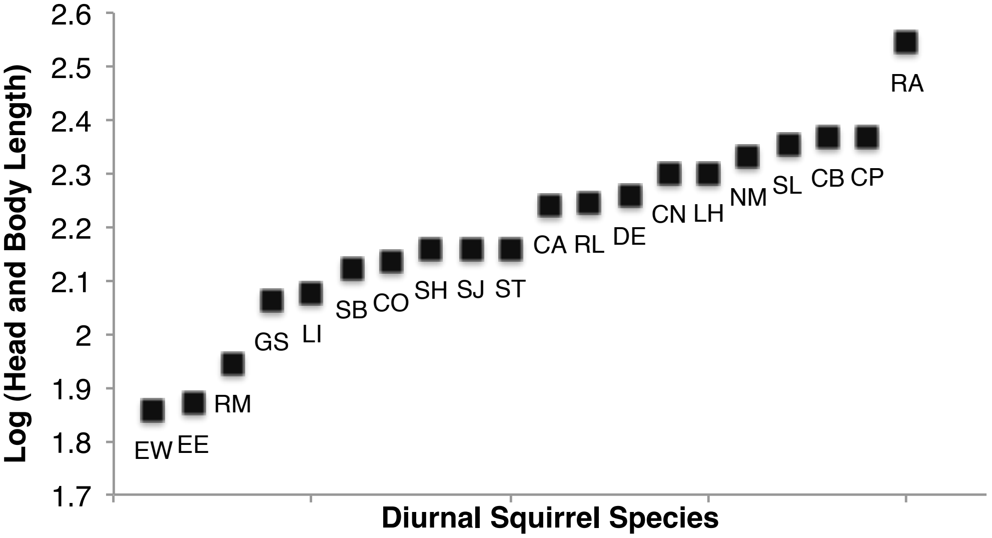
FIGURE 3.1: Distribution of Head and body length of species of squirrels in Borneo. a: species of nocturnal flying squirrels, b: species of diurnal tree squirrels.

a)



PE: Petaurillus emiliae, PH: Petaurillus hosei, PV: Petinomys vordermanni, PS: Petinomys setosus, HL: Hylopetes lepidus, PG: Petinomys genibarbis, HS: Hylopetes spadiceus, IH: Iomys horsfieldi, PP: Pteromyscus pulverulentus, PH: Petinomys hageni, PE: Petaurista elegans, ATo: Aeromys thomasi, AT: Aeromys tephromelas, PP: Petaurista petaurista

b)



EW: Exilisciurus whiteheadi, EE: Exilisciurus exilis, RH: Rheithrosciurus macrotis, GH: Glyphotes simus, LI: Lariscus insignis, SB: Sundasciurus brookei, CO: Callosciurus orestes, SH: Sundasciurus hippurus, SJ: Sundasciurus jentinki, ST: Sundasciurus tenuis, CA: Callosciurus adamsi, RL: Rhinosciurus laticaudatus, DE: Dremomys everetti, CN: Callosciurus notatus, LH: Lariscus hosei, NM: Nannosciurus melanotis, SL:Sundasciurus lowii, CB: Callosciurus baluensis, CP: Callosciurus prevostii, RA: Ratufa affinis

FIGURE 3.2: Frequency distribution of Head and body length of species and morphospecies of squirrels in Borneo. a: species of nocturnal flying squirrels, b: species of diurnal tree squirrels, c: morphospecies of nocturnal flying squirrels, d: morphospecies of diurnal tree squirrels.

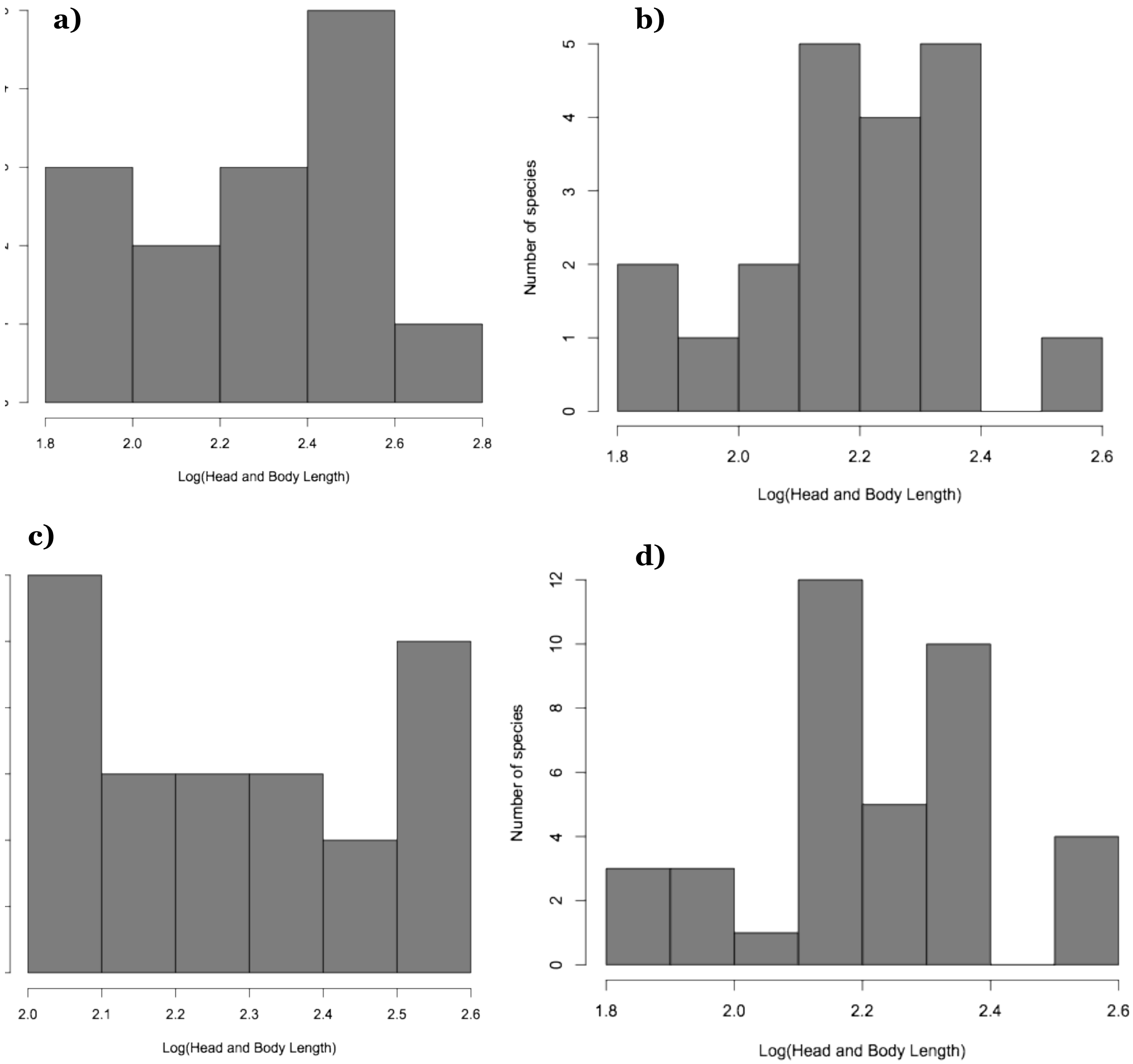


FIGURE 3.3: Randomly simulated frequency distributions (n=5000) of sizes generated from EcoSim. The mean of the observed distribution is marked with an arrow. a: nocturnal flying squirrels, b diurnal tree squirrels.

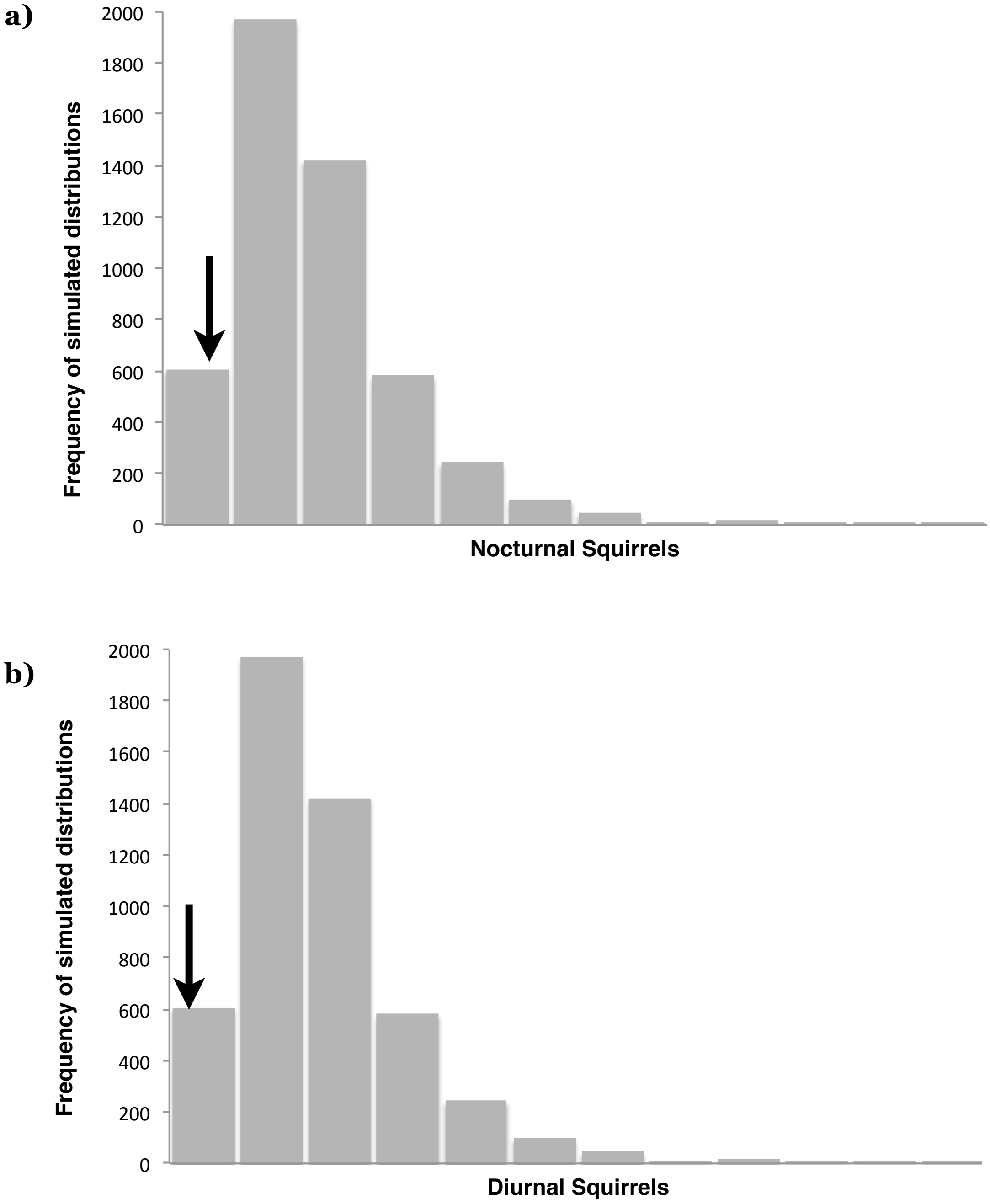
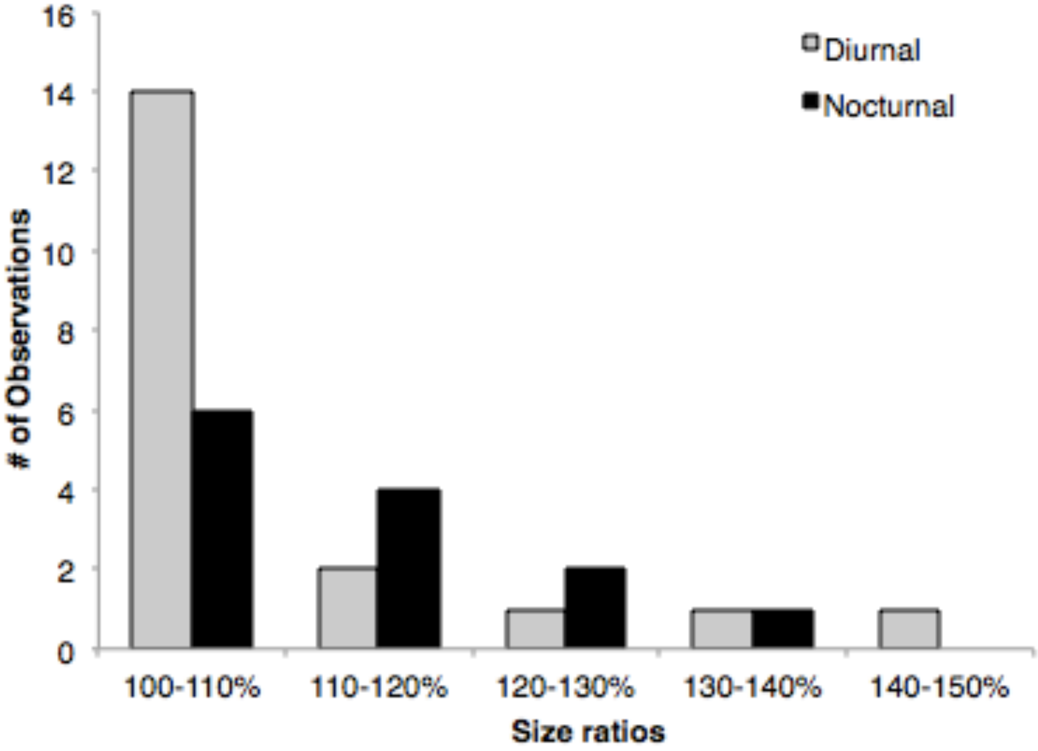


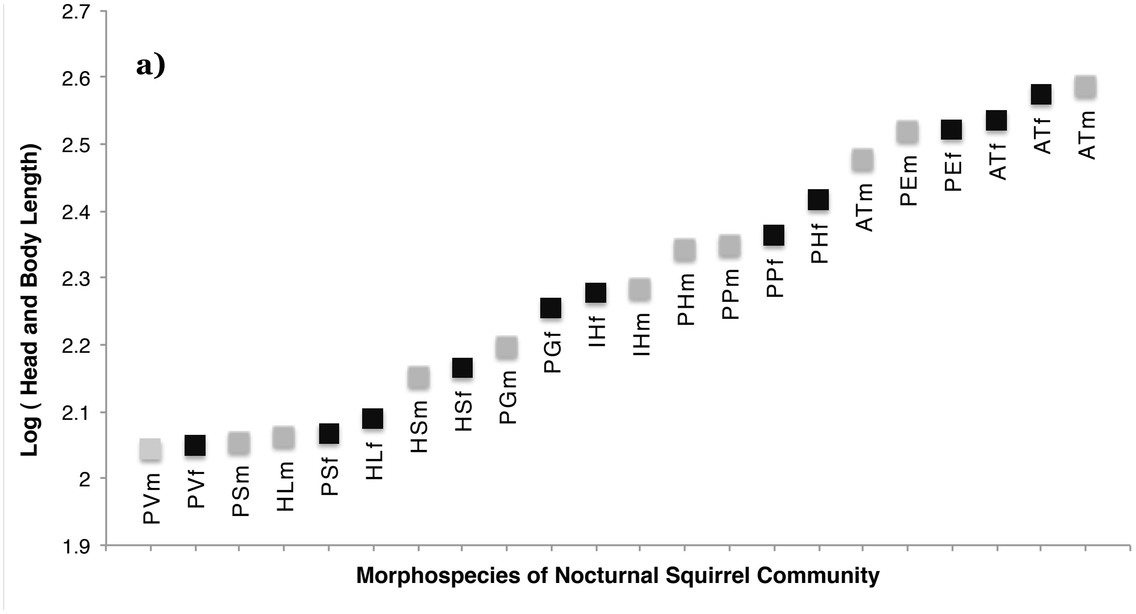
FIGURE 3.4: Number of size ratios observed between adjacent-sized squirrel species in diurnal and nocturnal assemblages.



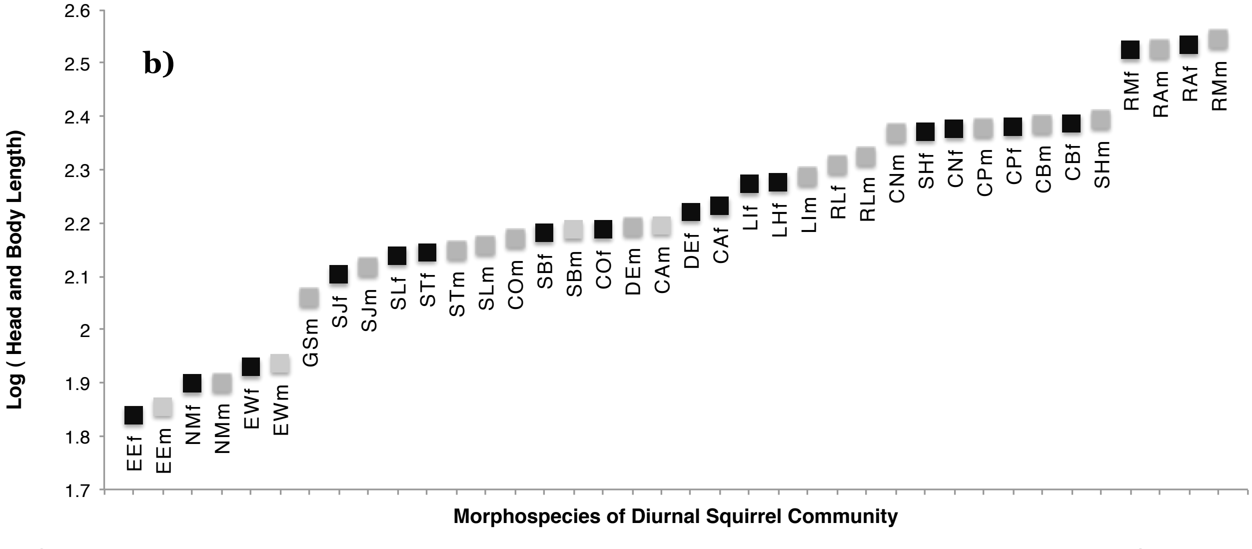
Partitioning of sexes as morphospecies

When sexes of species were treated as morphospecies and the analysis was conducted, we find that the sexes of species in both assemblages also separate along a non-overlapping size spectrum (Figure 3.5 a and b). Examining minimum segment length for the nocturnal flying squirrel morphospecies assemblage, the observed assemblage was not significantly different from the simulated assemblages (Standardised effect size= 0.30238, $p>0.05$, Table 3.3). A similar overall trend was seen for the diurnal tree squirrel morphospecies assemblage (Standardised effect size=-0.70302, $p>0.05$, Table 3.3).

FIGURE 3.5: Distribution of Head and body length of morphospecies of squirrels in Borneo. Males are shaded grey, and females are black squares. a: morphospecies of nocturnal flying squirrels, b: morphospecies of diurnal tree squirrels.



Species codes: PV: Petinomys vordermanni, PS: Petinomys setosus, HL: Hylopetes lepidus, PG: Petinomys genibarbis, HS: Hylopetes spadiceus, IH: Iomys horsfieldi, PP: Pteromyscus pulverulentus, PH: Petinomys hageni, PP: Petaurista petaurista, PE: Petaurista elegans, ATo: Aeromys thomasi, AT: Aeromys tephromelas



Species codes: EW: Exilisciurus whiteheadi, EE: Exilisciurus exilis, RH: Rheithrosciurus macrotis, GH: Glyphotes simus, LI: Lariscus insignis, SB: Sundasciurus brookei, CO: Callosciurus orestes, SH: Sundasciurus hippurus, SJ: Sundasciurus jentinki, ST: Sundasciurus tenuis, CA: Callosciurus adamsi, RL: Rhinosciurus laticaudatus, DE: Dremomys everetti, CN: Callosciurus notatus, LH: Lariscus hosei, NM: Nannosciurus melanotis, SL:Sundasciurus lowii, CB: Callosciurus baluensis, CP: Callosciurus prevostii, RA: Ratufa affinis

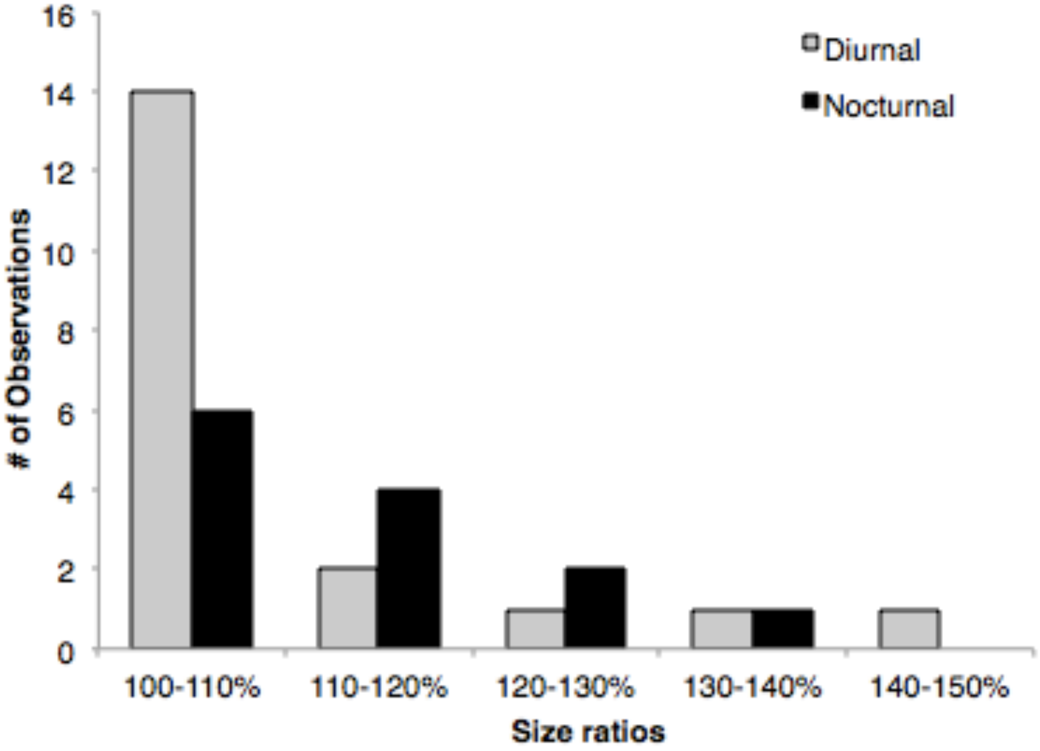
TABLE 3.3: Values of observed and simulated values of minimum-segment length and variance in segment length of squirrels arranged in order of ascending size of morphospecies. * indicates significance in the case when variance in segment length of observed assemblage > simulated assemblages.

	Minimum Segment Length		**Variance in segment length**	
	Observed	**Simulated**	**Observed**	**Simulated**
Flying squirrels	0.0032	0.0000	**0.0004***	0.0000
Tree squirrels	0.0002	0.0000	0.0008	0.0000

When variance in segment length was examined for the nocturnal flying squirrel morphospecies assemblage, the observed assemblage was significantly smaller than the simulated assemblages (Standardised effect size= -1.93096, $p<0.05$, Table 2.2). However, this result was not seen for the diurnal tree squirrel morphospecies assemblage (Standardised effect size=-0.29183, $p>0.05$, Table 3.3).

Size ratios between adjacent morphospecies in both the assemblages were different from the size ratios for species. The mean size ratio of nocturnal flying squirrel morphospecies was 1.06 (minimum 1.01 and maximum 1.15). The diurnal tree squirrels had a mean ratio of 1.04, with a minimum of 1.007 and a maximum of 1.35. When the two distributions were compared, they exhibited significant differences in the ratios (Wilcoxon test, W=168, $p < 0.05$, Figure 3.6).

FIGURE 3.6: Number of size ratios observed between adjacent-sized squirrel morphospecies in the diurnal and nocturnal assemblages.



DISCUSSION

In this study we hypothesized that the two temporally separated assemblages would show signs of character displacement, and we predicted that there would be a minimum size ratio separating species as well as morphospecies of squirrels. Additionally we predicted that they would be separated from each other at constant intervals. Our analysis of nocturnal and diurnal squirrel communities at the species level found that the two assemblages overlapped in body size distribution, and that, as predicted, the species within each of these assemblages were partitioned in order to reduce competition. Further, within the nocturnal assemblage, similar patterns of spacing were observed across morphospecies, implying that sexual size dimorphism possibly evolved to mitigate competition across both species and sexes. While the diurnal assemblage of squirrel species were separated from each other at constant intervals, sexes within these species did not exhibit signs of character displacement.

Temporal separation of squirrels and partitioning of species within each assemblage

The overlap of size distribution and the distribution of ratios across the two temporal communities suggests that these assemblages possibly occupy the same ecological niches during different diel cycle periods. Size ratios of spacing between size-adjacent species of diurnal and nocturnal squirrels were similar to those reported in other studies of mammals. The observed mean for both assemblages was lower than Hutchinson's (1959) ratio of 1.3; results similar to other studies on rodent assemblages (sciurid and non-sciurid rodent assemblages in Africa and South America: Parra et al. 1989). Millen-Parra and Loureau (1998) found that murid rodents in Japan had ratios of 1.05 to 1.43, similar to the range of ratios we found in this study. Heteromyid rodents in North America exhibited ratios of about 1.5, and seed-eating rodent guilds in both the New World (heteromyid rodents) and the Old World (gerbellid rodents) show non-random morphological pattern spacing (Brown and Lieberman 1973, Ben-Moshe et al. 2001). The largest ratios we found in the nocturnal assemblage were between the largest flying squirrels (genus *Aeromys*), and the smallest ratios were between the mid-sized flying squirrels (genera *Hylopetes* and *Petinomys*). Given the distribution of species, there were more mid-sized flying squirrels, and this possibly results in smaller size differences between species. With the diurnal tree squirrels, similar patterns were seen, with mid-sized tree squirrels showing the greatest overlap (genera *Callosciurus*, *Rhinosciurus*, *Dremomys*, *Nannosciurus* and *Lariscus*). The squirrels of these genera vary in their ecological habits, and might partition utilize different resources. *Callosciurus* and *Dremomys* are more arboreal while *Rhinosciurus*, *Nannosciurus* and *Lariscus* are more terrestrial, and utilizing different strata and consequently resources might allow for the co-existence of these different genera of diurnal squirrels.

Sexual size dimorphism and community assembly

Numerous studies have examined the partitioning of sexes as morphospecies within a community (for a review see Dayan and Simberloff 2005), and sexes are sometimes seen to display character displacement, minimising overlap with each other as well as other species (Dayan and Simberloff 1994b). In this study, the sexes within the nocturnal flying squirrel assemblage partitioned themselves out to minimize competition, while this trend was not as clear for diurnal squirrels. Flying squirrels are nocturnal gliding mammals, and are possibly more specialised to their environments than tree squirrels, given their unique mode of locomotion. Flying squirrels nest in tree hollows, and body size is known to be a determinant of the size and kind of cavities used both in flying squirrels (Nandini and Sinha 2006) as well as other species (Nilsson 1984). Two species of flying squirrels were seen to partition themselves vertically along the forest strata, and occupy different hollows at different heights on trees in rainforests (pers. obs. from Western Ghats, south India, Nandini and Sinha 2009). Morphospecies of tree squirrels don't display even patterns of spacing or character displacement. The dataset for tree squirrels was incomplete, with one sex of two species missing, and given limited museum collections and natural history data we could not obtain size data. These gaps in the dataset might have resulted in non-detection of size spacing across morphospecies of diurnal squirrels. Additionally, this pattern might be a result of differing patterns of sexual size dimorphism in diurnal squirrels. Squirrel species have differing patterns of sexual size dimorphism, with flying squirrels being female-biased in dimorphism and tree squirrels displaying both female-biased and male-biased size dimorphism. Female-biased dimorphism is supposed to have evolved to confer functional advantages to females and possibly aerodynamic advantages to males. Tree squirrels that are more arboreal display female-biased dimorphism, while more terrestrial squirrels are male-biased in dimorphism (see Chapter II). While species of tree squirrels showed signs of character displacement, sexes within these species are possibly evolving optimal sizes in response to selection pressures other than competition for resources.

This study suggests that interspecific competition in squirrel communities possibly resulted in character displacement, resulting in patterns of equal size ratios. Further, these seem to be operating in both the temporal and diurnal assemblages of squirrels, and the community compositions of both these communities mirror each other, suggesting that diurnal and nocturnal squirrels radiated to fill the same niche. While sexual size dimorphism patterns are clear in flying squirrels, they are not so clear in the diurnal assemblage, and further analyses with sympatric species of other families that occupy the same guild might provide more insights.

LITERATURE CITED

Adams, R.A. and K.M. Thibault. 2006. Temporal partitioning by bats at water holes. Journal of Zoology 270: 466 - 472.

Albrecht, M. and N.J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126: 134-141.

Atalato, R.V. and J. Moreno. 1987. Body size, interspecific interactions, and use of foraging sites in tits (Paridae). - Ecology 68: 2911773-1777.

Banks, E.A. 1931. A popular account of the mammals of Borneo. Journal of Malayan Branch of the Royal Asiatic Society 9: 1-139.

Barton, D.E. and F.N. David. 1956. Some notes on ordered random intervals. Journal of the Royal Statistical Society B 18:79-94.

Ben-Moshe, A., T. Dayan, and D. Simberloff. 2001. Convergence in morphological patterns and community organization between Old and New World rodent guilds. American Naturalist 158(5): 484-495.

Boecklen, W.J. and C. NeSmith. 1985. Hutchinsonian ratios and log-normal distributions. Evolution 39:695-698.

Brown, J.H. and G.A. Lieberman. 1973. Resource Utilization and Coexistence of Seed-Eating Desert Rodents in Sand Dune Habitats. Ecology 54(4): 788-797.

Brown, W. L. and E.O. Wilson. 1956. Character displacement. Systematic Zoology 5: 49-64.

Brown, J. H., B.J. Fox, and D.A. Kelt. 2000. Assembly rules: desert rodent communities are structured at scales from local to continental. American Naturalist 156 (3): 314-321.

Chasen, F.N. 1940. A handlist of Malaysian mammals. Bulletin of the Raffles Museum, Singapore, Straits Settlements, 15.

Cody, M.L. and J.M. Diamond. 1975. Ecology and the evolution of communities. Cambridge, Massachusetts, Harvard University Press.

Corbett, G.B. and J.E. Hill. 1992. The mammals of the Indomalay region: a systematic review. Natural History Museum Publications, London, UK.

Creighton, G.K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. Journal of Zoology 191(4): 435-443.

Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1989. Inter- and intraspecific character displacement in Mustelids. Ecology 70 (5): 1526-1539.

Dayan, T., D., Simberloff, E. Tchernov, and Y. Yom-Tov 1990. Feline Canines: community-wide character displacement among the small cats of Israel. American Naturalist 136: 39-60.

Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. Biological Journal of the Linnaean Society 45: 315-331.

Dayan, T. and D. Simberloff. 1994a. Morphological relationships among co-existing heteromyids: an incisive dental character. American Naturalist 143(3): 462-477.

Dayan, T. and D. Simberloff. 1994b. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. Ecology 75: 1063-1073.

Dayan, T. and D. Simberloff. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28 (3): 99–124.

Dayan, T. and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8: 875–894.

den Tex, R.-J., R.W. Thorington, J.E. Maldonado, and J.A. Leonard. 2010. Speciation dynamics in the SE Asian tropics: putting a time perspective on the phylogeny and biogeography of Sundaland tree squirrels, *Sundasciurus*. Molecular Phylogenetics and Evolution 55: 711-720.

Gertsch, W. and S.A. Reichert. 1976. The spatial and temporal partitioning of a desert spider community, with descriptions of new species. American Museum Novitates, 2604:1-25.

Glor, R.E. 2010. Phylogenetic insights on adaptive radiation. Annual Review of Ecology, Evolution, and Systematics 41:251-270.

Gotelli, N.J. and G.L. Entsminger. 2005. EcoSim: Null models software for ecology.

Greene, E. 1987. Sizing up size ratios. Trends in Ecology and Evolution 2:79-81.

Gutman, R. and T. Dayan. 2005. Temporal partitioning between spiny mouse species: An. experimental field study. Ecology 86(1):164-173.

Harrison, J. 1966. An introduction to mammals of Singapore and Malaya. Malayan Nature Society, Tien Wah Press, Singapore.

Hayssen, V. 2008. Patterns of body and tail length and body mass in Sciuridae. Journal of Mammalogy 89: 852-873.

Hill, J.E. 1960. The Robinson collection of Malaysian mammals. Bulletin of the Raffles Museum 29:1-112.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals ? American Naturalist 93: 145-159.

Irwin, J.O. 1955. A unified derivation of some well-known frequency distributions of interest in biometry and statistics. Journal of the Royal Statistical Society, A, 118:389–404.

Koprowski, J.L. and R. Nandini. 2008. Global hotspots, centers of diversity, and conservation of the tree and flying squirrels. Current Science 95: 851-856.

Kronfeld-Schor, N., E. Shargal, A. Haim, T. Dayan, N. Zisapel, and G. Heldmaier. 2001. Temporal partitioning among diurnally and nocturnally active desert spiny mice: energy and water turnover costs. Journal of Thermal Biology 26:139-142.

Kronfeld-Schor, N. and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology and Systematics, 34:153-181.

Macarthur, R.H. 1958. Population ecology of some warblers in northeastern coniferous forests. Ecology 39: 599-619.

Macarthur R.H. 1972. Geographical ecology. New York, Harper and Row.

MacKinnon K, G. Hatta, H. Halim, and A. Mangalik. 1998. The ecology of Kalimantan. Oxford University Press, London.

Medway, L. 1965. Mammals of Borneo: field keys and an annotated checklist. Malaysian. Branch, Royal Asiatic Soc., xiv + 193 pp.

Medway, L. 1969. The Wild Mammals of Malaya. London: Oxford University Press, Oxford, UK.

Mercer, J.M. and V.L. Roth. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568-1572.

Millien-Parra, V. and M. Loreau 2000. Community composition and size structure of murid rodents in relation to the biogeography of the Japanese archipelago. Ecography, 23: 413-423.

Nandini, R. and A. Sinha. 2009. Niche-partitioning and the impact of disturbance and fragmentation on two sympatric species of flying squirrels, the endemic Travancore flying squirrel and the Indian giant flying squirrel in the Western Ghats. Final Technical Report (2009) Submitted to the Ministry of Environment and Forests, Government of India.

Nilsson, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15: 167-175.

Parra, V., M. Loreau, and J.-J. Jaeger. 1999. Incisor size and community size in rodents: two tests of the role of competition. Acta Oecologica 20(2): 93-101.

Payne, J. and C.M. Francis. 1985. A field guide to the mammals of Borneo. Sabah Society (with WWF Malaysia), Kota Kinabalu.

Poole, R.W. and B.J. Rathcke. 1979. Regularity, randomness, and aggregation in flowering phenologies. Science 203(4379):470-1.

Roth, V.L. 1981. Constancy in the size ratios of sympatric species. American Naturalist 118:394-404.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist 156 (Supplement): S4–S16.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408–418.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Slater, G.J., S.A. Price, F. Santini, and M.E. Alfaro. 2010. Early adaptive diversification in body size without rapid cladogenesis in modern cetaceans. Proceedings of the Royal Society of London, B. published online 19thMay 2010 (doi 10.1098/rspb.2010.0408).

Simberloff, D., and W. Boecklen. 1981. Santa Rosalia reconsidered: size ratios and competition. Evolution 35: 1206-1228.

Strong, D.R., Jr., L.A. Szyska, and D.S. Simberloff. 1979. Tests of community-wide character displacement against null hypotheses. Evolution 33:897–913.

Thorington, R. and K. Ferrell 2006. Squirrels: the animal answer guide. Johns Hopkins University Press.

Weins, J.A. 1982. On size ratios and sequences in ecological communities: are there no rules ? Annales Zoologici Fennici 19: 297-308.

CHAPTER 4

FLYING SQUIRRELS FOLLOW RENSCH’S RULE: GLIDING AND FUNCTIONAL ADVANTAGES OF FEMALE-BIASED DIMORPHISM

INTRODUCTION

Body size is one of the most fundamental aspects of a species’ biology. So it is curious that the sexes of species exhibit variation in body size. For example, in many birds and mammals, males are larger than females (male-biased size dimorphism—MBSD), as Darwin (1871) noted. Such sexual size dimorphism (SSD) is often interpreted according to his theory of sexual selection (Trivers 1972). In fewer species, females are larger than males (reversed sexual size dimorphism or female-biased size dimorphism—FBSD), and the rarity of such cases makes them a curiosity for behavioral ecologists and evolutionary biologists. Within groups of related species, such as families, the relationship of sizes between the sexes is itself related to body size, and scales allometrically (Rensch 1960). The proportional body size differences between the sexes either increases or decreases with overall body size. The pattern of changing sexual-size ratios has come to be known as Rensch's rule, and seems to be pervasive across a multitude of taxa (from mosses to primates), following a predictable pattern (Rensch 1960). Rensch's rule predicts that when males are larger than females in a group of related species, MBSD increases with increasing body size across species, while in taxa where females are larger than males, FBSD decreases in larger species.

Many studies have investigated Rensch's rule across a variety of taxa, and while the rule is not universal, it seems to hold for most taxa (Fairbairn 1990 Abouheif and Fairbairn 1997). Rensch's rule is well supported for taxa that exhibit male-biased sexual size dimorphism (Abouheif and Fairbairn 1997), but patterns of allometry among taxa with female-biased size dimorphism are less clear, and there is evidence both for and against the rule (Tubaro and Bertelli 2003). While most groups that follow Rensch's rule exhibit one or the other form of dimorphism, in some groups of species both kinds of dimorphism exist, and Rensch's rule has been shown to 'cross the line' (Colwell 2000; Szekely et al. 2004).

Explanations for the evolutionary mechanisms responsible for the existence of the rule are unclear (Karubian and Swaddle 2001) and have ranged from genetic correlations between the sexes (Lande and Arnold 1983), sexual selection (Szekely et al. 2004), fecundity selection (Ralls 1976) and sexual differences in maturation times (Blanckenhorn et al. 2007). Examining mixed patterns of sexual dimorphism, Colwell (Colwell 2000) and Szekely et al. (Szekely et al. 2004) concluded that sexual selection acting on males was probably the most likely explanation for both male-biased and female-biased dimorphism. The strength of male-male competition for mates determines male body size, and while large males are a direct consequence of such contests, the presence of smaller males within the same taxa is explained by energetic constraints (Colwell 2000) or aerial agility contributing to displays (Szekely et al. 2004). Explanations for larger females include the need to carry offspring during pregnancy (Myers 1978) or behavioural (Jehl Jr and Murray Jr 1986; Mueller 1989) or reproductive (Schulte-Hostedde 2007) advantages to large size.

Flying squirrels are gliding rodents in the Family Sciuridae, and while the average dimorphism for rodents is significantly male-biased (1.09 male/female body size: size measured by head and body length; Lindenfors 2007), flying squirrels are one of the few exceptions that exhibit some species with reversed sexual size dimorphism (Lee et al. 1993b, Robins et al. 2000, Fokidis et al. 2007, Hayssen 2008), though other species seem to reveal the opposite pattern (Fox and Mulheisen 1999). In body size, they span over two orders of magnitude, from about 140 g (genus *Petaurillus*) to as much as 3 kg (genus *Petaurista*). Flying squirrels exhibit both a rare lifestyle (gliding) as well as a rare pattern of dimorphism. Besides providing a range of sexual size dimorphism and a good sample of species, flying squirrels might be expected to display Rensch's rule. Mating is likely socially polygynous or promiscuous in many of the species, as evidenced by observations of mating chases by males at the time that females are in estrus (Hanski and Selonen 2009, RN personal observations of *Petaurista philippensis* in South India). Thus, males should experience strong competition for mating opportunities, an aspect of sexual selection that is predicted to lead to male-biased sexual size dimorphism (Alexander and Borgia 1979).

Flying squirrels are gliding mammals, however, and thus females are subject to increased mass loads to the gliding membrane while they are pregnant and lactating (Myers 1978). Thus, increased size of females relative to males is predicted by this "big mother hypothesis". If the evolution of female-biased dimorphism has been favoured by functional advantages for females with respect to gliding, this should be evident in their morphological structure. Females should have larger gliding-enhancing structures than males to maintain the same wing-loading when pregnant. This should be more pronounced in gliders with reduced patagia rather than enhanced patagia, as larger airfoil relative to body size can accommodate more fluctuations in body mass. Gliders with reduced patagia will face more difficulties in gliding, and these females are expected to have more compensatory additions to the airfoil.

The purpose of our study was to examine the nature of sexual size dimorphism in species of flying squirrels, and test for evidence of Rensch's rule. Specifically, we wanted to know whether the degree of sexual dimorphism is associated with body size and how reversed sexual size dimorphism in flying squirrels can be explained as a function of their gliding lifestyle. We examine sexual size dimorphism in flying squirrels with respect to their gliding abilities and morphological structure. Finally, we asked whether the patterns of sexual size dimorphism in flying squirrels can illuminate any of the process-level explanations for Rensch's rule.

METHODS

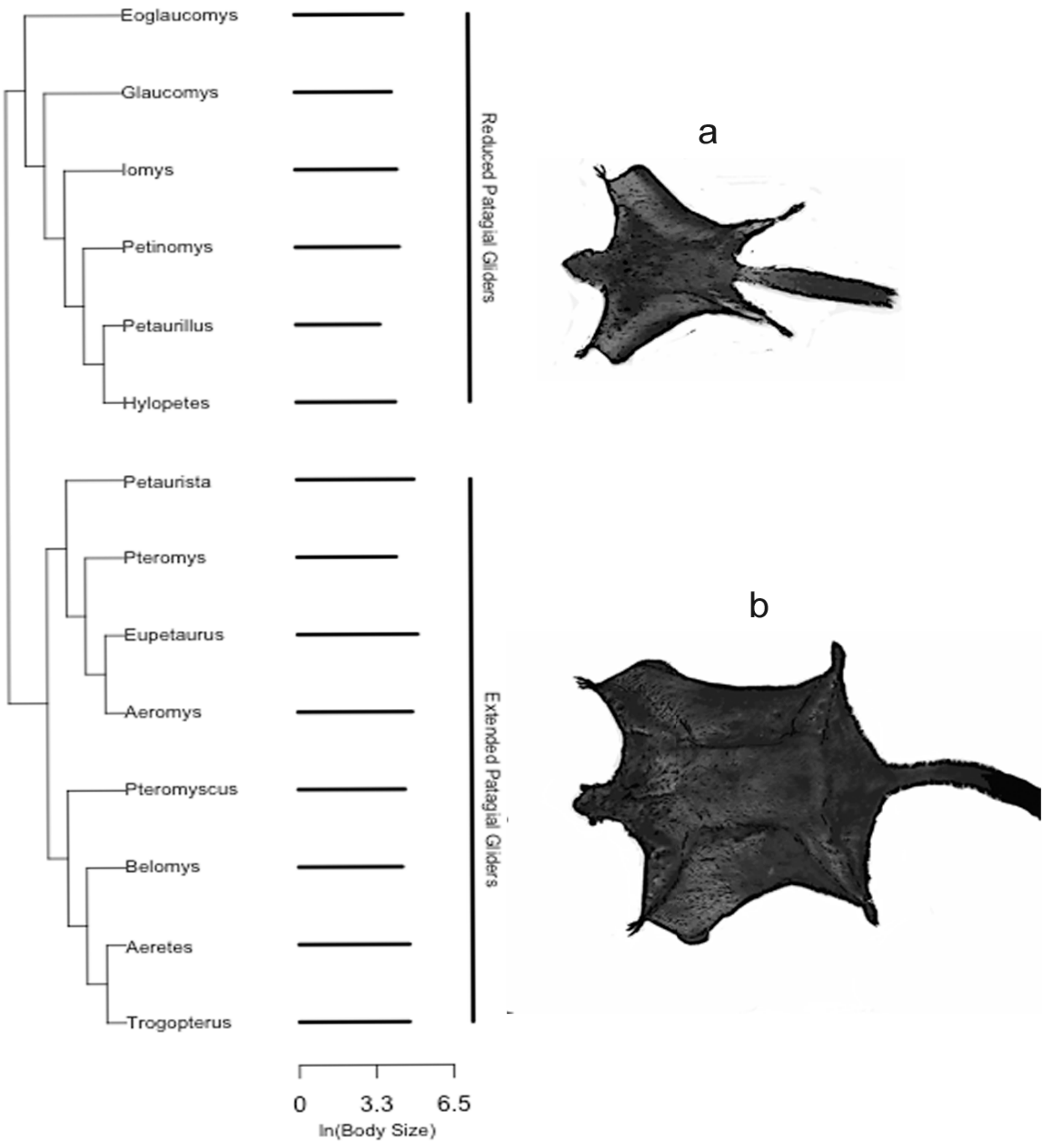
Flying squirrels

Flying squirrels (Family Sciuridae: Tribe Pteromyini) are nocturnal gliding rodents that are distributed mainly in the Old World with two species in North America. They occur mostly in tropical evergreen forests in south and southeast Asia, but also inhabit temperate forests outside of the tropics. They are incapable of powered flight, and their primary medium of long distance locomotion is gliding between trees. Flying squirrels glide primarily with the aid of patagia between their forelimbs and hindlimbs, but some species also have flaps of skin between the neck and forelimbs (plagiopatagia) and between the hindlimbs and tail (uropatagia) that provide extra gliding surfaces. This morphological distinction between gliders with larger and smaller patagia follows a phylogenetic pattern, with the two kinds of gliders forming distinct clades within the subfamily Pteromyinae (Figure 4.1). While each of the groups of gliders has species spanning a range of body sizes, the largest gliders tend to have more extensive patagia, while the smallest gliders tend to have less extensive patagia. In this study we refer to the groups of flying squirrels as the extended patagia group (EPG; genera–*Petaurista*, *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeromys*, *Eupetaurus*, *Aeretes* and *Pteromys*) and the reduced patagia group (RPG; genera–*Iomys, Glaucomys*, *Eoglaucomys*, *Hylopetes*, *Petaurillus*, and *Petinomys*).

Specimens and Measurements

Measurements of body size were collected from museum specimens in eight museums across North America, Europe and India. We followed the taxonomic classification of Thorington and Hoffmann (2005). Information on body size was recorded from the specimen tags of a total of 800 specimens of 27 of the 44 species of flying squirrels. We recorded head and body length, tail length, ear length, hind foot length and body mass. The sample sizes per species ranged from 1 to 40 individuals of each sex. Cranial measurements were also collected for all species, and we measured condylobasal length, greatest length of skull, zygomatic width, palatal length and the width and length of the lower jaw from approximately 1500 skulls. While body mass is usually used as an indication of body size, most specimen tags were missing this datum and we used head and body length as an index of size. When tags recorded total body length and tail length, we calculated head and body length as the difference between the two.

FIGURE 4.1. Phylogeny of flying squirrels used for the analysis. A composite phylogeny based largely on Mercer and Roth (2003) was used for the analysis. Phylogenetic data is available till the genus level, and species within genera were given equal branch lengths. Log body size (head and body length) for each genus is represented alongside each genus. This was calculated as the mean of both sexes for each species within that genus for which data was available. The vertical lines indicate the groupings of genera with different patagial body plans, and alongside are images of species from the group with spread patagium and accessory gliding structures. These photographs are of prepared specimens at the NHM, Smithsonian Institution.



Analysis

Body size is known to be strongly associated with phylogeny, and we conducted specific analyses that remove historical non-independence of body size among taxa. We used the phylogenies of Steppan et al. (2004) and Mercer and Roth (2003). Since there was no species-level relationship information for most genera of flying squirrels, species within genera were considered as polytomies. In the absence of a fully resolved tree, we set branch lengths equal to one for the purpose of this analysis. The phylogenetic independent contrasts method of Felsenstein (Felsenstein 1985) was used in comparative phylogenetic analysis using the ape package in R (Version 2.7.2, R development Core team, Paradis 2006).

Data were log transformed prior to analyses and sexual size dimorphism was calculated as contrasts in log (female body mass)/log (male body mass) (Smith 1999). If flying squirrels follow Rensch's rule we expected to see no consistent pattern of differences across species as the rule predicts diminishing dimorphism ratios with increasing body size. Wilcoxon paired tests were performed on log-transformed values to check for consistencies in the magnitude of difference in sizes of body measurements between males and females within species of flying squirrels.

Most studies that test Rensch's rule compare the log-size (either mass or body length) of adult females to adult males via regression analyses. A slope of 1.0 through the origin indicates that male and females sizes are similar among species, that is, that no sexual size dimorphism exists. A slope that is significantly less than 1.0 indicates that as body size increases, males become increasingly larger than females, and the reverse pattern as species body sizes decrease, the pattern of Rensch's rule. We tested Rensch's rule by fitting a major axis regression (model II regression) through the origin using phylogenetic independent contrasts as well as log-transformed values. For this analysis only species with at least six individuals of at least one sex were included in order to remove biases of extremely small samples.

Further, we analysed dimorphism in flying squirrels differentiated by their gliding patagia, to determine if gliders with more extensive patagia (EPG group) exhibited patterns of dimorphism different from gliders with reduced patagia (RPG group). We regressed female size on male size using a major axis regression for each of these groups to test for conformity to Rensch's rule within each group, and to determine the contribution of the two groups to the observed overall pattern of Rensch's rule observed. Separate independent contrasts for body size variables were calculated for each of these monophyletic groups of gliders (RPG and EPG).

Tail length, size of patagium and head size are all features that are known help to balance weight while gliding (Shine et al. 1998). Absolute area of the patagium is difficult to measure for all species given the paucity of well-prepared skins and the difficulty in capturing all species in the field. We estimated the degree of adaptation for gliding from tail length, in part due to its ready availability on specimen tags, and from condylobasal length and zygomatic arch breadth (which were measured on intact skulls). Tail length was used as a measure of features that counteract weight while gliding. In order to determine if females and males are different in how tail length scales to body length, we regressed tail length on body length (body length = head and body length–condylobasal length). We performed the same analysis within each subgroup of gliders, assuming that RPG should have more selection pressure to evolve balancing appendages than EPGs. Head size is speculated to be important while gliding/flying, and controls various aspects of flight (Fenton 1989). We used condylobasal length as well as zygomatic arch breadth as proxies for head size. Given that tail length, condylobasal length and zygomatic arch breadth were all found to be highly correlated, we used Principal Components Analysis to come up with a comprehensive measure of these three measures of size. PC1 scores were then used in regressions with body length for both log-transformed values and phylogenetically corrected data. All analyses were performed in R (Version 2.7.2, R development Core team) and package ggplot2 (Wickham 2009) was used to for plotting graphs.

RESULTS

Sexual size dimorphism

Flying squirrels were on average female dimorphic, with most species exhibiting female-biased dimorphism. The size dimorphism ratio (all ratios are expressed as female/male size) for head and body length averaged 1.03 (range 0.83-1.28, n=24 species). Flying squirrels "crossed the line" between male and female-biased body size. Tail length averaged 1.03 (range 0.85-1.31, n=24 species) and the dimorphism ratio for hind foot length averaged 1.04 (range 0.43-1.52, n=24 species) indicating marginally larger females, on average (Appendix 4.1). Wilcoxon paired tests for these three characteristics showed no significant differences, indicating that there were no consistent differences in magnitude of size differences across all species (Table 4.1).

TABLE 4.1: Wilcoxon paired tests for differences in means (log-transformed values) of male and female flying squirrel body sizes. Four measures of body size and size measures of crainal size were used.

Characteristic	***V***	***p***
Head and Body Length	210	0.090
Tail Length	203	0.135
Hind Foot Length	177	0.456
Ear Length	121	0.622
Greatest Length of Skull	226	0.208
Condylobasal Length	269	0.055*
Zygomatic Breadth	238	0.248
Palatal Length	308	0.0032
Mandibular Length	212	0.594
Mandibular Width	305	0.004*

An assessment of cranial characteristics revealed that males and females were nearly equal across species, with average condylobasal length and palatal length being 1.01, and average zygomatic arch width being 1.00 (n=27 species). The ratio of greatest length of skull of females to males, however, averaged 0.93 while condylobasal length averaged 1.01

(Appendix 2). Wilcoxon paired tests showed no significant differences across the sexes for most of the cranial characteristics, except for palatal length (Wilcoxon paired test, V=308, p=0.003) and mandibular width (Wilcoxon paired test, V=305, p=0.002; Table 4.1).

Renschs' rule

When log-transformed values of female head and body length were regressed against those for males, the slope was not significantly different from one (b=1.002, n=24, p>0.05). After correcting for phylogenetic relationships, however, the results indicated conformity with Rensch's rule (b=0.76, n=23, p<0.00; Table 4.2. Figure 4.2).

TABLE 4.2: Major axis regressions of log-transformed and independent contrasts of head and body lengths of female and male flying squirrels. P values presented are significance values for the slope tested against 1, not zero.

	Slope	***df***	***r2***	***p***
Log-transformed values				
All gliders	1.002	23	0.997	>0.05
RPG	1.006	13	0.999	>0.05
EPG	0.999	9	0.999	>0.05
Phylogenetic Independent Contrasts				
All gliders	0.767	22	0.647	< 0.05*
RPG	0.431	12	0.2061	>0.05
EPG	0.905	8	0.786	< 0.05*

We calculated PICs for each of the groups of gliders (EPG and RPG), and conducted major axes regressions for the two groups. While all gliders together had a slope of 0.76 when head and body length of females was regressed over males, each of the groups of gliders had very different slopes. The reduced patagia group had a slope of 0.435, significantly different from 1 (p>0.05), while the extended patagia group had a slope more close to one (b=0.905, p>0.05) (Table 4.2, Figure 4.3).

FIGURE 4.2. Sexual size dimorphism in flying squirrels and Rensch' rule. Log-transformed values of the Head and Body lengths of female and male flying squirrels, with extended patagial gliders (EPG) represented by the dark circles and reduced patagial gliders (RPG) represented by the light circles. The dotted line is the line of isometry. Most flying squirrels with the EPG body plan are mid-large sized species, while most flying squirrels with the RPG body plan are small-mid sized species.

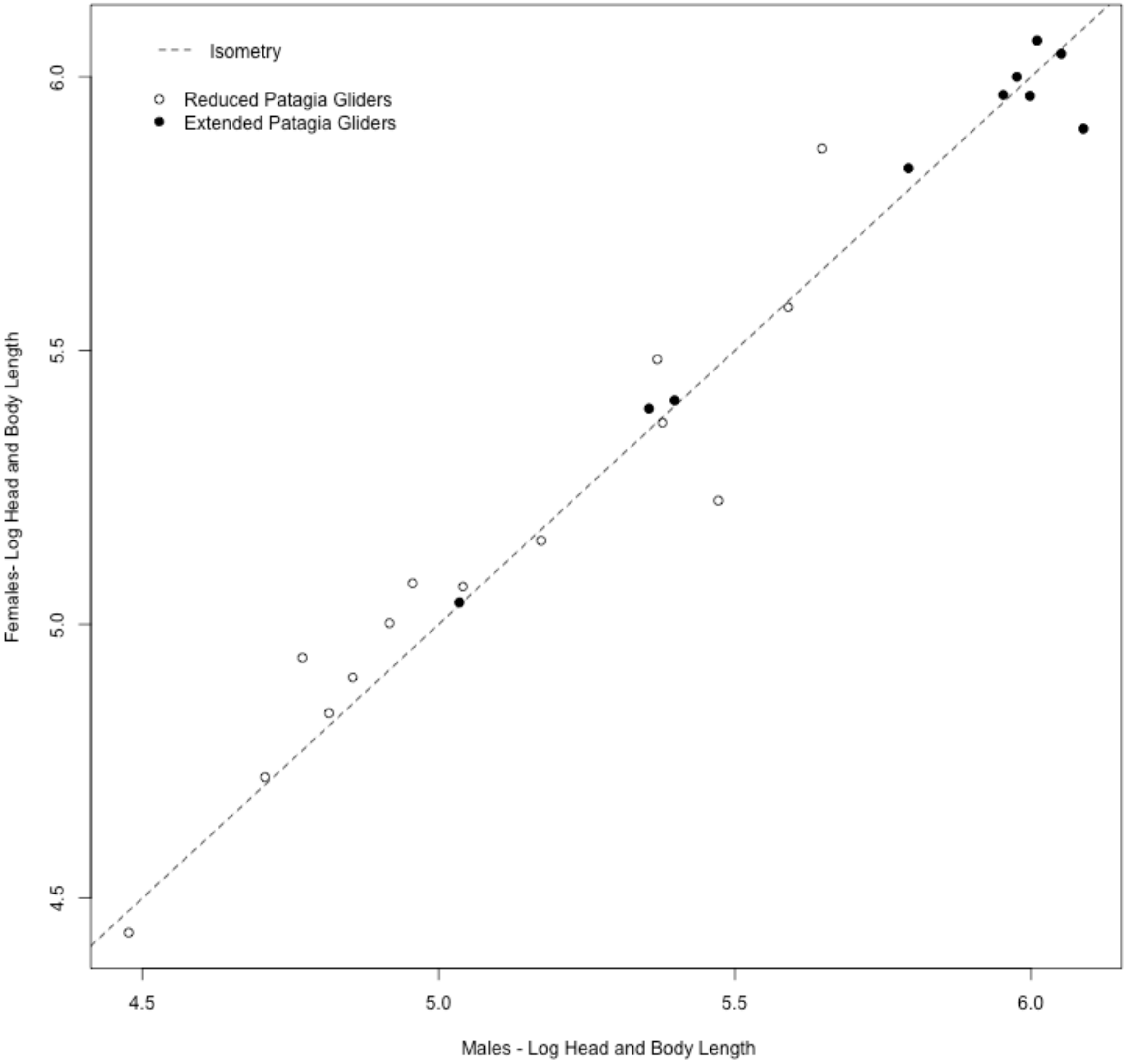
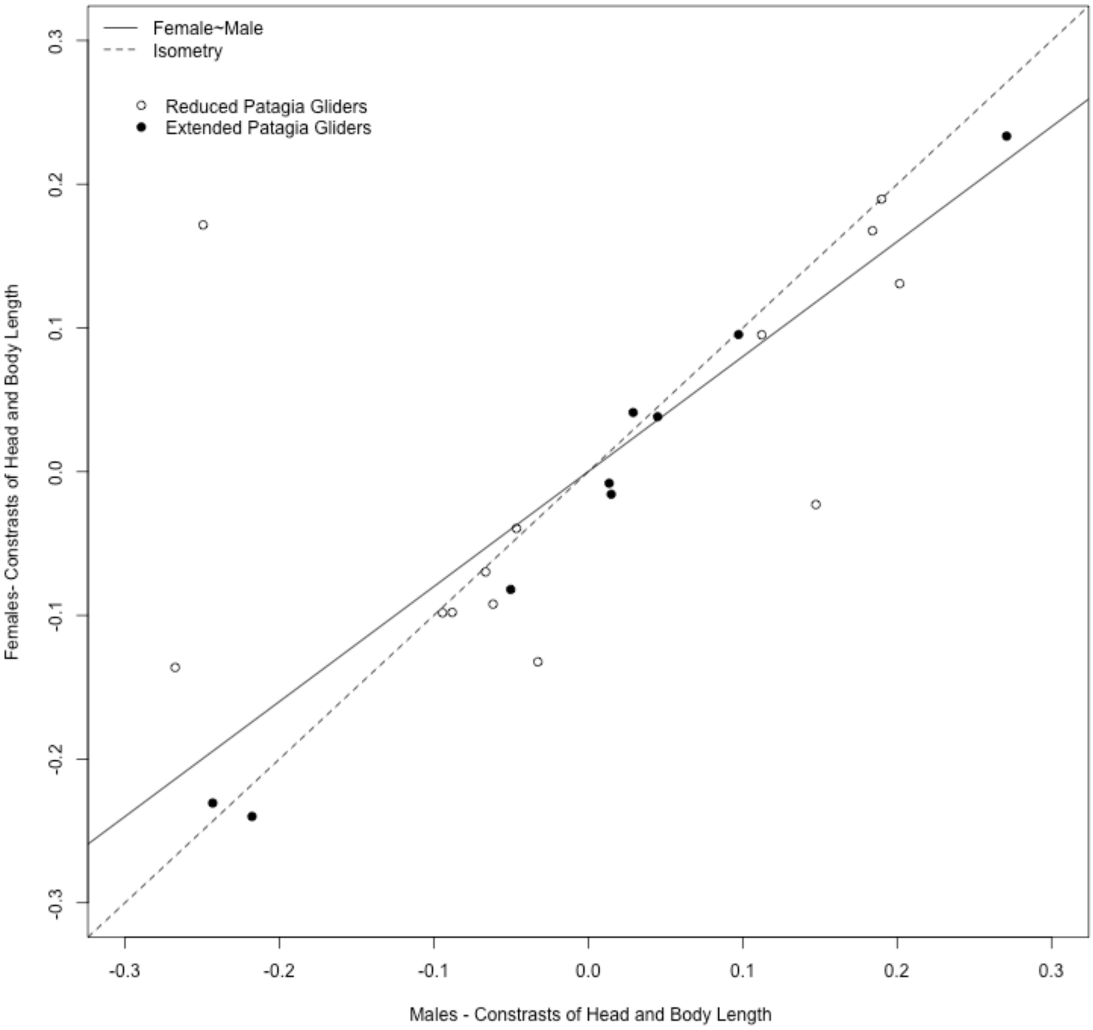


FIGURE 4.3. Rensch's rule in flying squirrels using a measure of body length. Plot of the contrasts of Female and Male Head and Body Length, with extended patagial gliders (EPG) represented by the dark circles and reduced patagial gliders (RPG) represented by the light circles. The dotted line is the line of isometry, and the solid line is the slope (0.80) calculated for the phylogenetic independent contrasts using a major axis regression.



Gliding and morphological adaptations

Female flying squirrels had proportionally longer tails with respect to their body size compared to males of the same size. While female and male tails did not scale differently with body length for the log-transformed data (F= 0.4962, df=44, 45, p> 0.05) females had a greater intercept than males (Table 4.3). When flying squirrels were divided into two groups–with reduced versus more extensive gliding membranes, RPG females had lower intercepts but higher slope relative to body size than RPG males. Females in the EPG group had greater intercepts but marginally smaller slopes than males (Table 4.3, Figure 4.4). When phylogenetic relationships were taken into account the slopes for females (b=0.658) was higher than for males (b=0.402)(F = 13.083, df=43, 44, p =0.00), though the intercept was greater for males than females (Table 4.4). Analysing the data group-wise (RPG and EPG) did not change the overall result, except that EPG females had tails that scaled with greater slopes than males (Table 4.4).

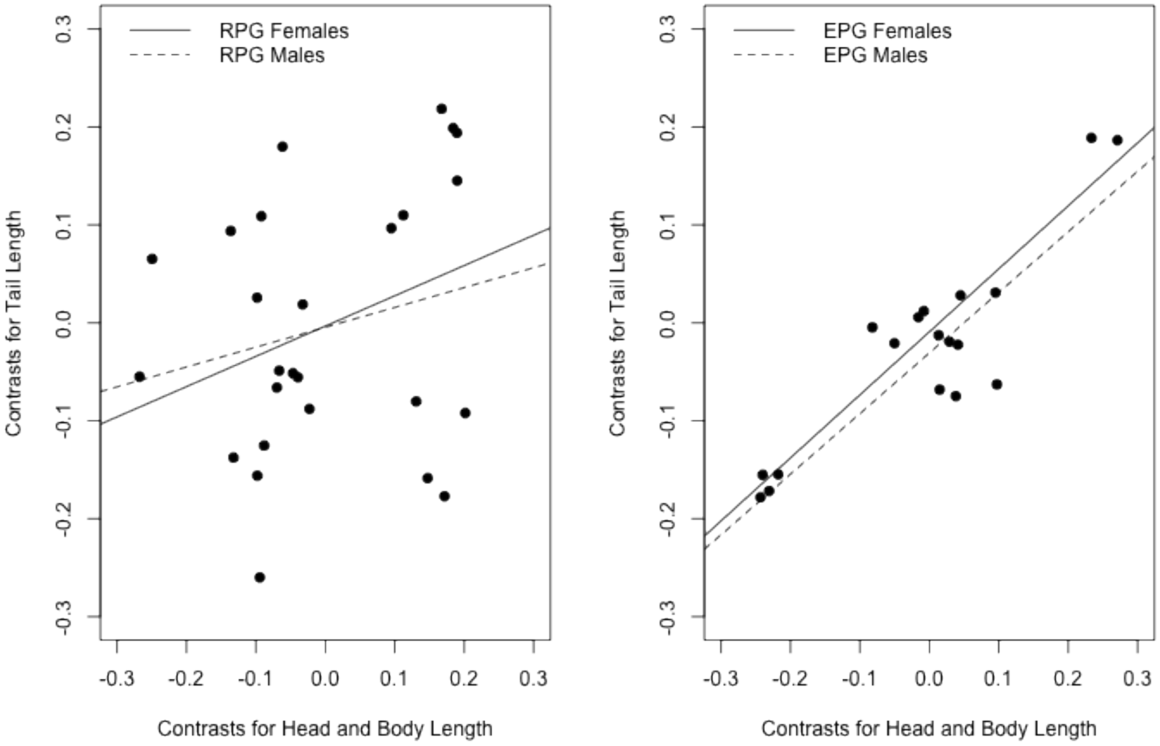
TABLE 4.3: Tail length regressed on body length. Values used for the models were log-transformed values.

	Intercept	***Slope***	***df***	***r2***	***p***
Females	-0.1891	1.0675	22	0.922	0.000*
Males	-0.1216	1.0603	22	0.964	0.000*
Reduced Patagial gliders					
Females	1.0832	0.8009	12	0.9448	0.000*
Males	0.364	0.9604	12	0.9102	0.000*
Extended Patagial gliders					
Females	-1.5423	1.317	8	0.884	0.000*
Males	-1.2098	1.253	8	0.988	0.000*

TABLE 4.4: Tail length regressed on body length. Values used for the models were phylogenetic independent contrasts.

	Intercept	***Slope***	***df***	***r2***	***p***
Females	-0.0439	0.5314	21	0.2179	0.024*
Males	-0.0794	0.6964	21	0.3098	0.005*
Reduced Patagial Gliders					
Females	0.0665	0.5510	11	0.449	0.04*
Males	0.0927	-0.0943	11	0.008	0.760
Extended Patagial gliders					
Females	-0.0981	1.1064	7	0.835	0.000*
Males	-0.0542	1.1279	7	0.820	0.000*

FIGURE 4.4. Tail length and Head and Body length in flying squirrels. Tail Length of females (solid lines) and males (dotted lines) were regressed separately against Head and Body Length for flying squirrels with the two different body plans–reduced patagia gliders (RPG), and extended patagia gliders (EPG). Phylogenetic independent contrasts of the morphometric measurements were used for the regression analyses.



DISCUSSION

Our study revealed that almost all flying squirrel species were slightly female-biased in dimorphism for most of the characteristics examined. We found evidence for Rensch's rule across all species of flying squirrels, but only when phylogeny was taken into account. We were able to explain this pattern of female-biased dimorphism across all species, and propose that smaller and larger gliders have different patterns of dimorphism corresponding to their gliding behaviour and morphology. Our evidence suggests that female flying squirrels are evolutionarily favoured if they possess morphological structures to help them cope with excess weight gain during pregnancy. Thus, female-biased dimorphism likely evolved to provide functional advantages to pregnant females. Female-biased dimorphism is common in invertebrates and cold-blooded vertebrates, but is rare among mammals. Though there are reports of FBSD from approximately 11 orders and 44 families of mammals (Ralls 1976). FBSD has been quantified only in a few studies. However, even within some of the better-studied groups of FBSD mammals, like bats (Myers 1978), lagomorphs (Davis and Roth 2008) and rodents like chipmunks and mice (Schulte-Hostedde 2007), this pattern of dimorphism is not uniformly common across genera or subfamilies. Sexual dimorphism is often the result of sex-specific pressures acting on both sexes simultaneously, and in most cases it is difficult to determine whether selection has favoured large female size, or whether it is an accidental outcome of the selection for smaller males, or if both sexes simultaneously experience differing selection pressures (Shine 1989).

Sexual dimorphism has largely been explained by sexual selection acting on males for both male-biased dimorphism (male-male combat; Alexander and Borgia 1979) and female-biased dimorphism (aerodynamic advantage; Jehl Jr and Murray Jr 1986). Birds that spend a large part of their lives in extended flight, like shorebirds, are female-biased in dimorphism, and males enjoy an “agility” advantage during display flights (Szekely et al. 2004, Sivinski and Dodson 1992). In species with extreme FBSD (eg: spiders, barnacles) where males are less than half the size of females, males are believed to be parasitic or “gigolo-like” in behaviour, thereby maximizing reproductive success with sedentary females at the cost of growth (Vollrath 1998). However, these reproductive advantages are not consistently seen across taxa, and in chipmunks, while there were no reproductive advantages to small male size, there was stabilizing survival selection with male body size (Schulte-Hostedde et al. 2002).

The “big mother” hypothesis is the most widely accepted reasoning is increased reproductive success of larger females (Ralls 1976). In cold-blooded vertebrates, female fecundity was seen to increase more rapidly with increasing body size than male fecundity with increasing male body size, suggesting that positive selection on large female size were responsible for patterns of FBSD (Shine 1979). Two studies of FBSD in squirrels showed some evidence for reproduction advantages of large female size. Yellow-pine chipmunks (*Tamias amoneus*) showed conflicting evidence of reproduction advantages across three years, and extreme climatic conditions was seen to influence female size as well as reproductive strategies (Schulte-Hostedde 2007). In southern flying squirrels (*Glaucomys volans*), large females had larger litters (Fokidis et al. 2007), suggesting that increased reproductive success of larger females might be responsible for the evolution of large size. Increased reproductive advantage to large female size, however, is not restricted to FBSD species, and has been observed in species with male-biased size dimorphism as well (Dobson and Michener 1995).

As part of the big-mother hypothesis, Ralls (1976) also suggested that there might be functional advantages to large female size. Animals that move in three-dimensional environments (air, water) have constraints placed on their growth and body proportions by their mode of locomotion. This study offers evidence in support of larger female size having evolved to provide gliding advantages to pregnant females, and we suggest that FBSD in flying squirrels might have arisen due to confer functional advantages and indirectly offset costs of reproduction.

Flight places strict constraints on size and proportions of different parts of the body, and increase in weight or change of shape affects flight performance directly. Increase in weight causes an increase in wing loading, which in turn affects speed, maneuverability, and energy expenditure during flight (Pennycuick 1989). While sexes or individuals of a species with different wing loading might have differing habits or exploit different niches, an increase in weight during an individuals lifetime will affect not only its flight performance but this will translate into other ecological aspects like foraging ecology, escape from predators, time spent in movement, distance covered, etc. (Pennycuick 1975; Hughes and Rayner 1991). In Juncos, a FBSD species, females were found to have greater wing loading than males and were probably less maneuverable than males (Chandler and Mulvihill 1992). Bats increased their weight by about 30 % when pregnant, resulting in a significant decrease in maneuverability, suggesting changes in foraging behaviour (Aldridge and Brigham 1988). Increase in mass due to fat storage and the subsequent negative effect on wing loading caused a reduction in ability of birds to escape predators in two species of sandpipers (Burns and Ydenberg 2002). Flying squirrels vary in how much mass they increase during pregnancy, but females carry between 5-15 % of their mass as in-utero fetuses during gestation.

For a gliding species, this can translate into significant loss of performance, and can result in shorter and steeper glides. Gliding is a simpler form of locomotion than powered flight, and wing loading is determined by the area of the lift-loading surface (or gross airfoil area) and mass of the animal (Alexander and Vogel 2004). The gross airfoil area of a glider can be calculated as the sum of the abdomen, limbs and patagia (Thorington and Heaney 1981). While fattening is linked to a significant aerodynamic cost, this can be offset by larger airfoil, larger balancing organs, and elongated limbs (Chandler and Mulvihill 1992; McGuire and Dudley 2005). Our study revealed that females of flying squirrels had longer tails relative to males of the same size, providing an additional lift surface. Longer tails also act like a rudder, helping to control direction as well as speed in other gliding vertebrates, and were seen to be important balancing organs in gravid female gliding agamids (*Draco*) (Shine et al. 1998).

The area and shape of airfoil of an animal affects it gliding capabilities, and while the area of the wing affects wing loading, the shape affects aspect ratios, and both of these are related to maneuverability. Aspect ratio is calculated as the length of the airfoil by its breadth, and gliders with lower aspect ratios are more maneuverable, have higher soaring capability, and are capable of low speed flight. Changes in wing shape could improve gliding performance even if the total area of the wing, and consequently wing loading, remains unchanged (McGuire 2003). Species with higher aspect ratios will be affected less by an increase in wing loading through weight gain than species with lower aspect ratios. Flying squirrels of the extended patagia (EPG) group, with more extensive patagia extending to the wrist and ankle, have higher aspect ratios than reduced patagia gliders (RPG). By the rationale outlined above, EPG gliders should be less affected by increased wing loading than reduced patagia gliders. Within species or groups, this translates to differing pressures on females when they are pregnant, and females of the RPG group were seen to be heavier than males relative to the extended patagia gliders. Compensatory morphological structures that contribute to the airfoil were also proportionately larger, and females of the reduced patagial group had longer tails compared to males than the extended patagia gliders. While the results of this study point conclusively to the evolution of larger female size to reduce gliding efficiency while pregnant, we cannot rule out that males might possibly obtain a maneuverability advantage due to their smaller size. Within species of flying squirrels, males are possibly more agile, and in *Glaucomys volans*, males are known to glide further than females for the same launch height (Vernes 2001). However, there is no evidence of gliding displays by males to attract females, and increased agility might not affect the ability to secure mates. There is no documentation of reproductive advantages with small male size in flying squirrels, there might be other advantages to small male size.

The two kinds of gliders (EPG and RPG) are phylogenetically separated, with the two patagial plans corresponding to two clades of flying squirrels. Additionally, the same two clades of flying squirrels are also separated according to body size, with small to mid-size species in the reduced patagia clade and mid-size to large species in the extended patagia clade. The patterns of allometric scaling of the sexes within the two groups together contribute to the pattern of Rensch's rule observed for flying squirrels. We find that the pattern of Rensch's rule observed is a direct result of differing adaptations by differently sized species to the pressures of increased weight gain and maintenance of optimal glide efficiency. The evolution of different airfoil designs with differing wing loading and aspect ratios probably required the evolution of differing strategies by females to compensate weight gain and maintain glide efficiency. Therefore, Rensch's rule and scaling of FBSD can be explained given the co-evolution of gliding structure and body size.

Most studies of Rensch's rule have found support for the rule with MBSD (Abouheif and Fairbairn 1997) but not FBSD (Tubaro and Bertelli 2003), though low sample sizes might be responsible for the lack of pattern. Given that Rensch's rule is a common repeatable pattern among MBSD species, Fairbairn and colleagues (Fairbairn and Preziosi 1994; Fairbairn et al. 2007) hypothesized that there must be an underlying explanation that applies across taxa. As of now there are many credible explanations supporting the evolution of MBSD across species and support for Rensch's rule, and almost all of these are related to sexual selection. Allometric scaling across MBSD species is easily explained with increasing size and greater sexual selection pressures are imaginable for larger species. Explanations for FBSD are less convincing and not consistent across taxa, and many studies that have examined scaling of FBSD have found contradictory results (Tubaro and Bertelli 2003). Considering that the rule can be satisfactorily explained for MBSD, but not for FBSD, Webb and Freckleton (Webb and Freckleton 2007) argue that Rensch's rule is not a general principle but rather a rule that can be explained by the incorporation of an additional factor related to the species in question. We agree with their explanation, and find that in the specific case of flying squirrels the evolution of larger female size is driven by functional advantages to offset costs of locomotion.

There is little ecological information on tropical flying squirrels, and our knowledge of species biology comes from few species. Smaller species of flying squirrels are known to have larger litters (*Glaucomys volans* has upto 4 or 5 individuals; Patterson and Patterson 2010) and giant flying squirrels (genus *Petaurista*) are known to have only one or occasionally two young (Lee et al. 1993a). Thus, across species, there is more scope for fecundity advantages in a species that has more than one or two young, and larger females in smaller species might derive more benefit from relatively large body size than in larger species with smaller litters. If this were the case it would imply that more than one factor results in the evolution of larger female body size, and quantifying the relative contribution of each of these would be an interesting exercise. Follow-up questions that arise from this research would be studying advantages of small male size in the context of gliding performance as well as reproductive success. A study of the gliding behaviour of free-ranging pregnant flying squirrels across different sized species and body plans would reveal the extent to which the gliding behaviour of pregnant females is altered.

LITERATURE CITED

Abouheif, E., and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule. American Naturalist 149:540-562.

Aldridge, H., and R. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5%" rule" of radio-telemetry. Journal of Mammalogy:379-382.

Alexander, D., and S. Vogel. 2004. Nature's flyers: birds, insects, and the biomechanics of flight. Johns Hopkins Univ Pr.

Alexander, R., and G. Borgia. 1979. On the origin and basis of the male-female phenomenon. Sexual selection and reproductive competition in insects:417-440.

Blanckenhorn, W. U., A. F. G. Dixon, D. J. Fairbairn, M. W. Foellmer, P. Gibert, K. van der Linde, R. Meier, S. Nylin, S. Pitnick, C. Schoff, M. Signorelli, T. Teder, and C. Wiklund. 2007. Proximate causes of Rensch's rule: Does sexual size dimorphism in arthropods result from sex differences in development time? American Naturalist 169:245-257.

Burns, J., and R. Ydenberg. 2002. The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). Behavioral Ecology and Sociobiology 52:128-136.

Chandler, C., and R. Mulvihill. 1992. Effects of age, sex, and fat level on wing loading in dark-eyed juncos. The Auk:235-241.

Colwell, R. K. 2000. Rensch's rule crosses the line: Convergent allometry of sexual size dimorphism in hummingbirds and flower mites. American Naturalist 156:495-510.

Davis, C. M., and V. L. Roth. 2008. The evolution of sexual size dimorphism in cottontail rabbits (<i>Sylvilagus</i>, Leporidae). Biological Journal of the Linnean Society 95:141-156.

Dobson, F., and G. Michener. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76:851-862.

Fairbairn, D. 1990. Factors influencing sexual size dimorphism in temperate waterstriders. American Naturalist 136:61-86.

Fairbairn, D., W. Blanckenhorn, T. SzÈkely, P. Lindenfors, J. Gittleman, K. Jones, T. Lislevand, J. Figuerola, R. Cox, and M. Butler. 2007. Sex, size and gender roles. Oxford University Press.

Fairbairn, D., and R. Preziosi. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, Aquarius remigis. American Naturalist: 101-118.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1.

Fenton, M.B. 1989. Head size and the foraging behaviour of animal-eating bats. Canadian Journal of Zoology 67: 2029-2035.

Fokidis, H. B., T. S. Risch, and T. C. Glenn. 2007. Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. Animal Behaviour 73:479-488.

Hanski, I., and V. Selonen. 2009. Female-biased natal dispersal in the Siberian flying squirrel. Behav. Ecol 20:60.

Hayssen, V. 2008. Patterns of Body and Tail Length and Body Mass in Sciuridae. Journal of Mammalogy 89.

Hughes, P., and J. Rayner. 1991. Addition of artificial loads to long-eared bats Plecotus auritus: handicapping flight performance. J. Exp. Biol 161:285.

Jehl Jr, J., and B. Murray Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Current Ornithology:1-86.

Karubian, J., and J. Swaddle. 2001. Selection on females can create ëlarger malesí. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:725.

Lande, R., and S. Arnold. 1983. The measurement of selection on correlated characters. Evolution:1210-1226.

Lee, P., Y. Lin, and D. Progulske. 1993a. Reproductive biology of the red-giant flying squirrel, Petaurista petaurista. Taiwan. Journal of Mammalogy 74:982-989.

Lee, P., D. Progulske, and Y. Lin. 1993b. Spotlight counts of giant flying squirrels (*Petarista petaurista* and *P. alborufus*) in Taiwan. Bulletin of the Institute of Zoology, Academia Sinica:54.

McGuire, J. 2003. Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. American Naturalist 161:337-349.

McGuire, J., and R. Dudley. 2005. The cost of living large: comparative gliding performance in flying lizards (*Agamidae: Draco*). American Naturalist 166:93-106.

Mercer, J., and V. Roth. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568.

Mueller, H. 1989. Aerial agility and the evolution of reversed sexual dimorphism (RSD) in shorebirds. The Auk 106:154-155.

Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. American Naturalist 112:701-711.

Paradis, E. 2006. Analysis of Phylogenetics and Evolution with R. Springer Verlag.

Patterson, J., and S. Patterson. 2010. Multiple Annual Litters in *Glaucomys sabrinus* (Northern Flying Squirrel). Northeast. Nat 17:167-169.

Pennycuick, C. 1975. Mechanics of flight. Avian biology 5:1-75.

Pennycuick, C. 1989. Bird flight performance: a practical calculation manual. Oxford University Press Oxford.

Ralls, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51:245-276.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 111:917.

Rensch, B. 1960. Evolution above the species level. Columbia University Press, New York.

Schulte-Hostedde, A. 2007. Sexual size dimorphism in rodents. Rodent Societies: An Ecological & Evolutionary Perspective:115ñ128.

Schulte-Hostedde, A., J. Millar, and H. Gibbs. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (Tamias amoenus): sex-specific patterns of annual reproductive success and survival. Evolution 56:2519-2529.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297-306.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64:419.

Shine, R., S. Keogh, P. Doughty, and H. Giragossyan. 1998. Costs of reproduction and the evolution of sexual dimorphism in a ëflying lizardíDraco melanopogon (Agamidae). J. Zool 246:203-213.

Smith, R. 1999. Statistics of sexual size dimorphism. J. Hum. Evol 36:423-459.

Steppan, S., B. Storz, and R. Hoffmann. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Molecular Phylogenetics and Evolution 30:703-719.

Szekely, T., R. P. Freckleton, and J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. Proceedings of the National Academy of Sciences of the United States of America 101:12224-12227.

Thorington Jr, R., and L. Heaney. 1981. Body proportions and gliding adaptations of flying squirrels (Petauristinae). Journal of Mammalogy 62:101-114.

Thorington Jr, R., and R. Hoffmann. 2005. Family Sciuridae. Mammal species of the world: a taxonomic and geographic reference (DE Wilson and DM Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland:754ñ818.

Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell, ed. Sexual Selection and the Descent of Man, 1871-1971, Aldine-Atherton, Chicago, pp. 136-179.

Tubaro, P. L., and S. Bertelli. 2003. Female-biased sexual size dimorphism in tinamous: A comparative test fails to support Rensch's rule. Biological Journal of the Linnean Society 80:519-527.

Vernes, K. 2001. Gliding performance of the northern flying squirrel (Glaucomys sabrinus) in mature mixed forest of eastern Canada. Journal of Mammalogy 82:1026-1033.

Vollrath, F. 1998. Dwarf males. Trends in Ecology & Evolution 13:159-163.

Webb, T., and R. Freckleton. 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch's rule. Plos One 2.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer New York

Appendix I

Literature sources for body size and ecological characteristics of squirrels.

- Ando, M., and S. Shiraishi. 1984. Relative growth and gliding adaptations in the Japanese giant flying squirrel, Petaurista leucogenys. Science Bulletin of the Faculty of Agriculture, Kyushu University 39:49–57.
- Alvarez-Castaneda, S.T., G. Arnaud, and E. Yensen. 1996. Spermophilus atrocapillus. Mammlian Species 521: 1-3.
- Banks, E.A. 1931. A popular account of the mammals of Borneo. Journal of Malayan Branch of the Royal Asiatic Society 9: 1-139.
- Bartels, M.A. and D.P. Thompson. 1993. *Spermophilus lateralis*. Mammalian Species 440:1-8.
- Bartig J.L., T.L. Best, and S.L. Burt. 1993. *Tamias bulleri*. Mammalian Species 438: 1-4.
- Best, T.L., Kitus, A.S, Caesar K, and C.L. Lewis. 1990. *Ammospermophilus harrisii*. Mammalian Species 366: 1-7.
- Best, T.L. and H.H. Thomas. 1991. *Spermophilus madrensis*. Mammalian Species 378:1-2.
- Best, T.L., J.L. Bartig , and S.L. Burt. 1992. *Tamias caniceps*. Mammalian Species 411: 1-5.
- Best, T.L. 1993. *Tamias palmeri*. Mammalian Species 443: 1-6.
- Best, T.L. 1993. *Tamias ruficaudus*. Mammalian Species 452: 1-7.
- Best, T.L. 1993. *Tamias sonomae*. Mammalian Species 444: 1-5.
- Best, T.L., S.L. Burt, and J.L. Bartig. 1993. *Tamias durangae*. Mammalian Species 437: 1-4.
- Best, T.L., and N.J. Granai. 1993. *Tamias merriami*. Mammalian Species 476: 1-9.

- Best, T.L., S.L. Burt, and J.L. Bartig. 1994. *Tamias quadrivittatus*. Mammalian Species 466: 1-7.
- Best, T.L., and N.J. Granai. 1994. *Tamias obscurus*. Mammalian Species 472: 1-6.
- Best, T.L., R.G. Clawson, and J.A. Clawson. 1994. *Tamias panamintinus*. Mammalian Species 468: 1-7.
- Best, T.L., R.G. Clawson, and J.A. Clawson. 1994. *Tamias speciosus*. Mammalian Species 478: 1-9.
- Best, T.L., K. Caesar, A.S. Titus, and C.L. Lewis. *Ammospermophilus insularis*. Mammalian Species 364: 11-4.
- Best, T.L. 1995. *Sciurus alleni*. Mammalian Species 501: 1-4.
- Best, T.L., and S. Reidel. 1995. *Sciurus arizonensis*. Mammalian Species 496: 1-5 .
- Best, T.L. 1995. *Sciurus collaei*. Mammalian Species 497: 1-4.
- Best, T.L. 1995. *Sciurus deppei*. Mammalian Species 505: 1-5.
- Best, T.L. 1995. *Sciurus nayaritensis*. Mammalian Species 492: 1-5.
- Best, T.L. 1995. *Sciurus occulatus*. Mammalian Species 498: 1-3
- Best, T.L. 1995. *Sciurus variegatoides*. Mammalian Species 500: 1-6.
- Best, T.L., R.L. Ruiz-Pinia, and L.S. Leon-Paniagua. 1995. *Sciurus yucatensis*. Mammalian Species 506: 1-4.
- Best, T.L. 1995. *Spermophilus adocetus*. Mammalian Species 504: 1-4.
- Best, T.L. 1995. *Spermophilus mohavensis*. Mammalian Species 509: 1-7.
- Best, T.L. 1995. *Sciurus annulatus*. Mammalian Species 508: 1-4.
- Best, T.L., and G. Ceballos. 1995. *Spermophilus perotensis*. Mammalian Species 507: 1-3.
- Burt, S.L., and T.L. Best. 1993. *Tamias rufus*. Mammalian Species 460: 1-6.
- Carr, K., and P. Myers. 2004. "*Sciurus variegatoides*" (On-line), Animal Diversity Web. Accessed November 03, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_variegatoides.html.
- Caraway, L.N., and B.J. Verts. 1994. *Sciurus griseus*. Mammalian Species 474: 1-7.
- Ceballos-G, G, and D.E. Wilson. 1985. *Cynomys mexicanus*. Mammalian Species 284:1-3.

- Chasen, F.N. 1940. A handlist of Malaysian mammals. Bulletin of the Raffles Museum, Singapore, Straits Settlements, 15.
- Clark, T.W., Hofmann, R.S., and C.F. Nadler. 1971. *Cynomys leucurus*. Mammalian Species 7:1-4.
- Clawson R.G., J.A. Clawson, and T.L. Best. 1994. *Tamias alpinus*. Mammalian Species 461: 1-6.
- Clawson R.G., J.A. Clawson, and T.L. Best. 1994. *Tamias qaudrimaculatus*. Mammalian Species 469: 1-6.
- Corbet, G.B., and J.E. Hill. 1992. The mammals of the Indomalayan region: a systematic review. Oxford University Press, London, United Kingdom.
- Crane, S. 2002. "*Sciurus griseus*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_griseus.html.
- Dolan, P.G., and D.C. Carter. 1977. *Glaucomys volans*. Mammalian Species 78: 1-6.
- Duckworth, J.W., B. Lee, and R.J. Tizard. 2008. *Callosciurus notatus*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 11 November 2008.
- Duckworth, J.W., E. Meijaard, B. Giman, and K.H. Han. 2008. *Ratufa affinis*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 05 November 2008.
- Duckworth, J.W., E. Meijaard, and K.H. Han. 2008. *Sundasciurus lowii*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 12 November 2008.
- Duckworth, J.W. and S. Molur. 2008. *Belomys pearsonii*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 12 November 2008.
- Edelman, A.J. 2003. *Marmota olympus*. Mammalian Species 736: 1-5.
- Eisenberg, J.F. 1989. Mammals of the Neotropics. Vol. 1. The northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, Illinois.

- Elliot, C.L., and J.T. Flinders. 1991. *Spermophilus columbianus*. Mammalian Species 372: 1-9.
- Emmons, L.H. 1979. Observations on Litter Size and Development of Some African Rainforest Squirrels, Biotropica 11: 207-213.
- Emmons, L.H. 1990. Neotropical rainforest mammals. University of Chicago Press, Chicago, Illinois.
- Ernest, K.A., and M.A. Mares. 1987. *Spermophilus tereticaudus*. Mammalian Species 274: 1-9.
- Eshelman, B.D., and C.S. Sonneman. 2000. *Spermophilus armatus*. Mammalian Species 637: 1-6.
- Fahey, B. 2001. *Sciurus niger* (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_niger.html
- Frase, B.A., and R.S. Hoffman. 1980. *Marmota flaviventris*. Mammalian Species 135: 1-8.
- Gannon, W.L., R.B. Forbes, and D.E. Kain. 1993. *Tamias ochrogenys*. Mammalian Species 445: 1-4.
- Gannon, W.L., and R.B. Forbes. 1995. *Tamias senex*. Mammalian Species 502: 1-6.
- Grubb, P. and N. Oguge. 2008. *Xerus rutilus*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 10 November 2008.
- Grubb, P. and J.K. Peterhans. 2008. *Heliosciurus mutabilis*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 10 November 2008.
- Harrison, J. 1966. An introduction to mammals of Singapore and Malaya. Malayan Nature Society, Tien Wah Press, Singapore.
- Hart, E.B. 1992. *Tamias dorsalis*. Mammalian Species 399: 1-6.
- Hayssen, V., A. Van Tienhoven, and A. Van Tienhoven. 1993. Asdell's patterns of mammalian reproduction. Cornell University Press, Ithaca, New York.
- Hayssen, V. 2008. Patterns of body and tail length and body mass in Sciuridae. Journal of Mammalogy 89: 852-873.

- Heaney, L.R. 1984. Climatic influences on life-history tactics and behaviour of north american squirrels. In Murie, J.O. and Michener, G.R (eds.) The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln and London.
- Herron, M.D., and J.W. Waterman. 2004. *Xerus erythropus*. Mammalian Species 748: 1-4.
- Hill, J.E. 1960. The Robinson collection of Malaysian mammals. Bulletin of the Raffles Museum 29:1-112.
- Hilton, C.D., and T.L. Best. 1993. *Tamias cinereicollis*. Mammalian Species 436: 1-5.
- Hoogland, J.L. 1996. *Cynomys ludovicianus*. Mammalian Species 535: 1-10.
- Hoogland, J.L. 2001. The black-tailed praire dog: social life of a burrowing mammals. Chicago University Press, Chicago
- Jenkins, S.H., and B.D. Eshelman. 1984. *Spermophilus beldingi*. Mammalian Species 221: 1-8.
- Jones, J.K, and H.H. Genoways. 1975. *Sciurus richmondii*. Mammalian Species 53: 1-2.
- Joshua, J., de A. Goonatilake, W.I.L.D.P.T.S. and Molur, S. 2008. *Ratufa macroura*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 05 November 2008.
- Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London and New York.
- Koprowski, J.L. 1994. *Sciurus niger*. Mammalian Species 479: 1-9
- Koprowski, J.L. 1994. *Sciurus carolinensis*. Mammalian Species 480: 1-9.
- Koprowski, J.L., Roth, L., Reid, F., Woodman, N., Timm, R. and Emmons, L. 2008. *Sciurus aureogaster*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 05 November 2008.
- Kwiecinski, G.C. 1998. *Marmota monax*. Mammalian Species 591: 1-8.
- Lawniczak, M. 2002. "*Sciurus carolinensis*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_carolinensis.html.

- Linzey, A.V., Hammerson, G. and Cannings, S. 2008. *Marmota broweri*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 12 November 2008.
- Lurz, P.W.W., J. Gurnell, and L. Magris. 2005. *Sciurus vulgaris*. Mammalian Species 769: 1-9.
- Means, C. 2003. "*Microsciurus flaviventer*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Microsciurus_flaviventer.html.
- Medway, L. 1965. Mammals of Borneo: field keys and an annotated checklist. Malaysian. Branch, Royal Asiatic Soc., xiv + 193 pp.
- Medway, L. 1969. The Wild Mammals of Malaya. London: Oxford University Press, Oxford, UK.
- Mejia, J. 1999. "*Sciurus aberti*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_aberti.html.
- Michener, G.R., and J.W. Koeppl. *Spermophilus richardsoni*. Mammalian Species 243: 1-8.
- Mowbray, W. and K. Francl. 2008. "*Sciurus oculatus*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_oculatus.html
- Munoz, P. 1999. "*Sciurus arizonensis*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_arizonensis.html.
- Nagorensen, D. W. 1987. *Marmota vancouverensis*. Mammalian Species 270:1–5.
- Nash, D.J., and R.N. Seaman. 1977. *Sciurus aberti*. Mammalian Species 80: 1-5.
- Nitikman, L.Z. 1995. *Sciurus granatensis*. Mammalian Species 246: 1-8.
- Nowak, R.M., and J.L. Paradiso. 1983. Walker's mammals of the world. 4th edition. Johns Hopkins University Press, Baltimore, Maryland.
- Oaks, E.C., P.J. Young, G.L. Kirkland, and D.F.Schmidt. 1987. *Spermophilus variegatus*. Mammalian Species 272: 1-8.
- O'Shea, T.J. 1991. *Xerus rutilus*. Mammalian Species 370: 1-5.

- Ostoff, A.C., and E.J. Fink. 1997. *Spermophilus franklinii*. Mammalian Species 724:1-5.
- Payne, J., and C.M. Francis. 1985. A field guide to the mammals of Borneo. Sabah Society (with WWF Malaysia), Kota Kinabalu.
- Pizzimenti, J.J., and G.D. Collier. 1975. *Cynomys parvidens*. Mammalian Species 52: 1-3.
- Pizzimenti, J.J., and R.S. Hoffman, R.S. 1973. *Cynomys gunnisoni*. Mammalian Species 25: 1-4.
- Pizzimenti, J.J., and R.S. Hoffman. 1973. *Cynomys parvidens*. Mammalian Species 52: 1-3.
- Rajamani, N., Molur, S. and Nameer, P.O. 2008. *Ratufa indica*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 05 November 2008.
- Rickhart, E.A. 1987. *Spermophilus townsendii*. Mammalian Species 268: 1-6.
- Rickhart, E.A., and E. Yensen. 1991. *Spermophilus washingtoni*. Mammalian Species 371: 1-5.
- Schlute-Hostedde, A. 2007. Sexual size dimorphism in rodents, in Wolff, J. O. and Sherman, P. W. (Eds.) Rodent Societies: An ecological and evolutionary perspective. The University of Chicago Press, Chicago. Pp 115-128.
- Shrestha, N., Sarkar, S.K., Lunde, D., Duckworth, J.W., Lee, B., Tizard, R.J. and Molur, S. 2008. *Callosciurus pygerythrus*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 11 November 2008.
- Silva, M., and J.A. Downing. 1995. CRC handbook of mammalian body masses. CRC Press, Boca Raton, Florida.
- Skurski, D.A., and J.W. Waterman. 2005. *Xerus inauris*. Mammalian Species 781: 1-4.
- Smith, A.T. and Johnston, C.H. 2008. *Petaurista xanthotis*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 12 November 2008.
- Steele, M.A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species 586: 1-9.
- Steele, M.A. 1999. *Tamiasciurus douglasii*. Mammalian Species 630: 1-8.

- Struebel, D.P., and J.P. Fitzgerald. 1978. *Spermophilus spilosoma*. Mammalian Species 103: 1-5.
- Sutton, D.A. 1992. *Tamias amoenus*. Mammalian Species 390: 1-8.
- Tamura, N., Hayashi, F., and K. Miyashita. 1988. Dominance hierarchy and mating behavior of the Formosan Squirrel, *Callosciurus erythraeus thaiwanensis*. Journal of Mammalogy 69(2): 320-331.
- Trombulak, S.C. 1998. *Spermophilus saturatus*. Mammalian Species 322: 1-4.
- Verts, B.J. and L.N. Carraway. 2001. *Tamias minimus*. Mammalian Species 653: 1-10.
- Waterman, J.W., and M.D. Herron. 2004. *Xerus princeps*. Mammalian Species 751: 1-3.
- Wells, N.M., and J. Gaicalone. 1985. *Syntheosciurus brochus*. Mammalian Species 249: 1-9.
- Wells-Gosling, N, and L.R. Heaney. *Glaucomys volans*. Mammalian Species 229: 1-8.
- Witt, E. 2000. "*Sciurus deppei*" (On-line), Animal Diversity Web. Accessed November 05, 2008 at http://animaldiversity.ummz.umich.edu/site/accounts/information/Sciurus_deppei.html.
- Yensen, E. and P. Sherman. 1997. *Spermophilus bruneus*. Mammalian Species 560:1-5.
- Young, C.J. and J.K. Jones. 1982. *Spermophilus mexicanus*. Mammalian Species 164:1-4.
- Zegers, D. 1984. *Spermophilus elegans*. Mammalian Species 214:1-7.
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Appendix II

Museum specimens of flying squirrels that were examined during this study. Tag details were noted where available and morphometric measurements were made on skulls when available. Musuem codes: AMNH-American Museum of Natural History, New York, USA; BNHS-Bombay Natural History Museum, Mumbai, India, Berlin-Berlim Museum of Natural History, Berlin, Germany; Frankfurt-Senckenberg Museum of Natural History, Frankfurt, Germany; NHM- Natural History Museum, London, UK; SI-National Musuem of Natural History, Smithsonian Institution, Washington D.C, USA; ZSI- Zoological Survey of India, Kolkata, India

Species	Sex	Museum	Collection Numbers
Aeretes melanopterus	f	AMNH	45328
	u	AMNH	56933
Aeromys tephromelas	f	NHM	40.68, 71.2736, 13.8.7.1, 61.1166
		SI	292649, 481190, 267398, 196743, 283511, 481192, 292650, 291285
	m	NHM	85.8.1.126, 51.265, 67.1617
		SI	481188, 481187
Aeromys thomasi	f	NHM	71.2737
	u	NHM	71.2738
Belomys pearsonii	f	AMNH	167890, 87419
		BNHS	6858, 6859
		NHM	8.4.1.41, 8.4.1.42, 15.5.5.44, 33.4.1.263
		SI	257845, 358355, 308160
	m	AMNH	167889, 114889, 87420, 174853
		ZSI	24267

	u	NHM	50.601
		SI	358356, 358354
Eoglaucomys fimbriatus	f	NHM	7.8.1.3, 85.8.1.129, 85.8.1.128, 5.11.19.4, 7.8.1.3, 83.1.13.4, 81.3.1.5, 79.11.20.3, 25.6.10.17, 28.9.9.1, 19.7.2.12, 79.7.2.12, 7.11.21.14
		SI	353235, 353237, 326365, 353238, 353230, 353233, 326363, 353239, 173361, 173364, 63468, 173368, 173366, 35494, 173373, 173363, 173365
		ZSI	21389, 20930, 20927
	m	NHM	83.1.13.3, 79.7.2.11, 23.11.4.13, 9.11.26.2, 7.11.21.13, 7.8.1.2, 65.1026, 85.8.1.130, 25.10.6.15, 23.9.1.36, 25.6.10.16, 9.11.26.1, 25.6.13.4
		SI	353232, 353234, 353236, 326364, 353231, 173370, 173372, 173362, 173367, 35946, 35490, 35492, 174082, 173371, 201086
		ZSI	20929, 20928
Glacuomys sabrinus	f	AMNH	147229, 120607, 127774, 75242, 147240, 74780, 147247, 147238, 138530, 147228, 146217, 147243, 120605, 128546, 122548, 258726, 138537, 127772, 258728, 39669, 98092, 62572, 39665, 140181, 129278, 138534, 147235, 39668, 127775, 258729, 147225, 147230, 120603, 147232, 138540, 39670, 138538, 184594, 122543, 120606, 163839, 129283, 98093, 138536, 97605, 129667, 138529, 129282, 128548, 147234, 258730, 39671, 98091, 147236, 120602, 122546, 124903, 64325, 97604, 120779, 122550, 138533, 146321
		Frankfurt	55484
		NHM	67.2135, 7.7.7.3994
	m	AMNH	122549, 120604, 122542, 146322, 258731, 184593, 138531, 146320, 98090, 147226, 95191, 122544, 95192, 147246, 147244, 163838, 120777, 129284, 146215, 147245, 147242, 147233, 146214, 120778, 127318, 138539, 147237, 129279, 124904, 129281, 120601, 129666, 124902, 122545, 120608, 146216, 137988, 129280, 147231, 100180, 127317, 127773, 62573, 147227, 184866, 122547, 147241, 138532, 124901, 64326, 39666, 146218, 39667
		NMH	67.2132, 67.2136, 67.2133, 67.2131, 1938.4.1.98, 1938.4.1.97
	u	AMNH	141771, 146828, 128547, 69378, 98100, 98089
		NHM	97.1.25.1

Glaucomys sp.	f	AMNH	143693
		NHM	7.7.7.3764, 7.7.7.3572, 7.7.7.3873
	m	NHM	20.7.8.2
	u	AMNH	41050, 146521
		NHM	7.1.1.52
Glaucomys volans	f	AMNH	240538, 188250, 23071, 143505, 7379, 242815, 9511, 1198, 97357, 219360, 208260, 240296, 215338, 149505, 219370, 258727, 242813, 242823, 242834, 240290, 240294, 23073, 240302, 166291, 219359, 240303, 13949, 131222, 130363, 242832, 240289, 242816, 242818, 240292, 188252, 38394, 212486, 1666, 130364, 148730, 242512, 13720, 258732, 31075, 9072, 165609, 165610, 242833, 242822, 954, 166288, 242812, 250156, 217924, 955, 240307, 13950, 240305, 11238, 144434, 93224, 164477, 13947, 31077, 242824, 254450, 1201, 13698, 242825, 219363, 219369, 1667, 240288, 31078, 217840, 129664, 217929, 163974, 242821, 13948, 250155, 242814
		Frankfurt	25909, 5414
		NHM	1939.2367
	m	AMNH	219362, 219519, 1200, 242820, 165612, 250154, 208249, 188249, 23072, 242810, 240301, 217928, 11237, 9510, 208251, 212510, 149504,166835, 13946, 240539, 219365, 240293, 73640, 242817, 242827, 17968, 149988, 250157, 164476, 212511, 242831, 208252, 135938, 166613, 129458, 219361, 242829, 166290, 217930, 38393, 23075, 240306, 242811, 149471, 219366, 123798, 166836, 31076, 219364, 131224, 15891, 215340, 90588, 240300, 240291, 131225, 3536, 240295, 16896, 219368, 143504, 1199, 267293, 149986, 163973, 173472, 165613, 29884, 131223, 212351, 208250, 258734, 242511, 242819, 240299, 269600, 129457, 219367, 258733, 952, 31074, 90890, 240297, 2304, 79918, 131221, 252709, 164478, 165611, 135740, 166286, 250158, 165614, 232259, 148732, 953, 188251, 129665, 131226, 254452, 238076
		Frankfurt	25870, 36441, 79508, 80376
		NHM	78.2894, 1938.4.1.99, 67.4.12.494, 40.83
	u	AMNH	189217, 166432, 173640, 122698, 165047, 180018, 2198, 135076
		Berlin	4529

		Frankfurt	1406, 25364, 35751, 752, 18186
		NHM	42.12.9.8, 562 a, 38.1.29.19
Hylopetes alboniger	f	AMNH	114886
		BNHS	7056, 7062, 7065, 7059, 7052, 7038, 7024, 7051, 7026, 7027
		NHM	45.8.24.2, 50.626, 20.6.6.10, 23.4.1.31, 74.606, 26.10.4.80, 76.1302, 47.269, 21.1.6.6, 16.3.25.60, 50.623, 47.271, 50.62, 85.8.1.133, 21.1.6.59, 27.12.1.102, 21.12.5.42, 26.10.4.82, 16.7.29.91, 47.27, 50.63, 50.627, 16.3.25.59, 21.1.6.61, 1939.2368
		SI	253609
		ZSI	23730, 23719
	m	AMNH	1.14884E+11
		BNHS	7028, 7029, 7030, 7031, 7035, 7037, 7045, 7053, 7055, 7057, 7058
		NHM	47.267, 47.268, 50.615, 50.616, 50.617, 50.618, 50.625, 50.629, 66.3413, 76.1304, 76.1305, 76.1306, 76.1307, 76.1308, 76.1362, 16.3.26.15, 21.1.6.56, 21.1.6.57, 21.1.6.58, 21.12.5.41, 23.4.1.30, 26.10.4.81, 32.11.1.60, 45.1.8.246, 79.11.12.382, 79.11.21.383
		SI	253611, 267206
	u	BNHS	7039, 7054, 7068
		NHM	50.628, 1939.2369, 23.4.1.94, 23.4.1.95, 23.4.1.96, 23.4.1.97, 45.1.8.247, 58.6.24.87, 75.8.24.2, 85.8.1.135, 86.7.2.4
		ZSI	24426
Hylopetes fimbriatus	f	BNHS	7077, 7081, 7105
	m	AMNH	54649, 54650
		BNHS	7076, 7078, 7079, 7082, 7084, 7085, 7087, 7088, 7094, 7098, 7099, 7100, 7101, 7104
		ZSI	15066
	u	BNHS	7086, 7102
Hylopetes lepidus	f	Frankfurt	90610, 90611, 90612, 90613, 90614
		NHM	51.4, 55.2435, 84.4.22.8

	m	Frankfurt	90615, 90616, 90617, 90618
		NHM	55.2433, 55.2434, 58.45, 71.2742, 84.4.22.9
	u	Frankfurt	90609
Hylopetes nigirpes	f	NHM	16.3.25.59, 26.10.4.82
		AMNH	203311, 203312, 203314, 242098
		Frankfurt	25982, 25984, 25985, 25986, 25987
	m	NHM	97.2.7.4
		AMNH	203309, 203310, 203313
		Frankfurt	25981
	u	NHM	16.5.5.1, 79.5.3.1, 79.5.3.3, 86.7.2.4
	u	AMNH	29719, 29720, 29721, 29722, 29723
		Frankfurt	26102
Hylopetes phayrei	f	AMNH	58138, 58158, 58159, 58160, 58161, 58164, 58166, 58168, 58175, 58176, 58179, 58182, 58185, 58186, 101431, 101437, 101439, 101440, 101441, 101710, 101833, 101834, 101835, 101838, 101839, 106737, 163553, 163557, 163558
		BNHS	7013, 7016, 7018, 7032, 7033, 7034
		NHM	14.7.19.100, 14.7.19.101, 14.7.19.102, 14.7.19.103, 14.7.19.99, 3.8.5.2, 3.8.5.3, 97.11.12.16, 98.2.8.16
		SI	253580, 260621, 294887, 294891, 294892, 294895, 294897, 297083, 297084, 297088, 308158, 355126, 355128, 355130, 355131, 355132
		ZSI	15040, 15043
	m	AMNH	58162, 58163, 58167, 58169, 58171, 58172, 58178, 58180, 58181, 58183, 58184, 58198, 101432, 101433, 101434, 101435, 101436, 101438, 101442, 101711, 101836, 101837, 101921, 103018, 106641, 106701, 106702, 163552, 163554, 163555, 163556, 163559, 163560, 163561, 163562, 163563, 163564
		BNHS	7015, 7017, 7020, 7021, 7036
		NHM	14.7.19.94, 14.7.19.95, 14.7.19.96, 14.7.19.97, 14.7.19.98, 97.11.12.15, SI

		SI	260622, 260623, 260624, 261082, 294888, 294889, 294890, 294893, 294894, 294896, 294898, 297085, 297087, 308159, 355127
		ZSI	15041, 15042
	u	AMNH	58199
		BNHS	7019
		SI	261081, 261083, 294889, 297086, 297090, 355129
Hylopetes sp.	f	AMNH	167891
		SI	297089
	m	AMNH	167893
	u	AMNH	167892
Hylopetes spadiceus	f	NHM	58.449, 71.1537, 485.15, 1939.237, 14.12.8.120, 99.12.9.37
	m	NHM	55.2431, 58.447, 58.448, 71.1538, 71.1539, 14.112.8.117, 14.112.8.118, 14.112.8.119, 14.7.19.104, 26.10.4.83, 27.12.1.103, 27.12.1.104, 5.3.1.9, 99.12.9.38
	u	NHM	39.4032, 41.569, 61.1142, 61.1143, 61.1144, 61.1145, 61.1146, 71.1536, 71.1537, 71.154, 34.12.11.1, 61.4.12.14, 78.6.17.20
Hylopetes thomasi	u	SI	317237
Iomys horsefieldi	f	AMNH	185170
		NHM	55.2429, 55.243, 63.1593, 67.1614, 71.1522
		SI	252321, 292653, 292654, 317240
	m	AMNH	185169, 103313
		NHM	55.2428, 63.1592, 67.1613, 71.152, 71.1521, 28.7.14.5, 28.7.14.6, 89.1.18.5
		SI	151792, 301024
	u	NHM	41.569, 88.8.12.1
		SI	317241
	u	AMNH	244886
Petaurillus emilae	f	NHM	0.7.29.26

Petaurillus hosei	f	NHM	63.1158
Petaurillus kinlochii	f	SI	488708, 488711
	m	SI	488709, 488710
Petaurista alborufus	f	AMNH	174854
		NHM	12.11.23.17, 16.3.26.13, 8.4.1.40
		ZSI	15059, 23785, 23787, 25526, NM 90
	m	AMNH	163577, 163578, 174855, 174856
		NHM	47.293, 47.294, 47.295, 47.296, 16.3.26.12, 47.295a, 47.295b
		ZSI	15058, 23784, NM 44, NM 45, NM 51, NM 59, NM 85
	u	AMNH	174858, 183145, 184534, 184916, 184917, 184918, 184919, 184920, 184921, 184933
Petaurista candidulus	m	NHM	15.5.5.40, 15.5.5.41
Petaurista elegans	f	AMNH	43183, 43186, 101778
		BNHS	6865
		NHM	61.1165, 71.2739, 76.131, 1934.6.14.3, 22.9.1.42, 22.9.1.44, 22.9.1.45
		ZSI	23250, 23251, 24270, 24271
	m	BNHS	6864
		NHM	75.277, 76.1311, 12.7.25.34, 12.7.25.35, 1937.6.14.2, 22.9.1.40, 22.9.1.41, 66.5.21.1
		ZSI	24268, 24269, 24272, 24273
Petaurista leucogenys	f	NHM	23.4.1.29, 5.6.30.22, 6.1.4.118, 6.1.4.119, 6.1.4.120, 80.3.3.1
	m	AMNH	85063
		NHM	23.4.1.27, 23.4.1.28, 5.3.3.16, 5.5.30.19, 5.5.30.21, 5.6.30.20, 96.12.22.1
	u	AMNH	148564, 163818
		NHM	45.4.18.1, 65.12.8.1, 65.12.8.2, 68.4.27.2

Petaurista leucogenys	f	Frankfurt	34598
	u	AMNH	184566
Petaurista magnificus	f	NHM	23.11.5.26, 26.10.8.59
		ZSI	7551
	m	BNHS	6883, 6884
		NHM	23.11.5.25
		ZSI	18616, 23259
	u	BNHS	6886
		Frankfurt	10745
		NHM	43.1.12.46, 45.1.8.9, 45.2.13.1, 557a, 557b, 557f, 557g
Petaurista melanotis	m	NHM	10.10.1.79
	u	NHM	60.5.4.68, 82.3.9.2, 82.7.24.4, 828 a
Petaurista nobilis	f	NHM	15.9.1.99
		ZSI	23254, 23255, 23258, 23260, 23262, 24274
	m	ZSI	23256, 23257, 23261, 23263, 23264, 23319, 24275, 24276
	u	NHM	43.1.12.42, 48.6.11.3, 58.6.24.82
Petaurista petaurista	f	AMNH	32643, 54814, 56936, 58201, 58210, 58213, 58214, 58217, 58219, 58220, 87416, 87418, 101700, 102032, 102165, 102166, 102169, 102170, 102451, 102915, 103415, 106633, 106634, 114894, 114896, 114901, 114902, 183143
		BNHS	6890, 6892, 6898, 6906, 6907, 6908, 6915, 6916, 6919, 6921, 6940, 6960, 6967, 6975, 6981, NHM, 40.683, 40.685, 40.686, 40.687, 55.1652, 61.1163, 61.1164, 65.1031, 76.1312, 77.464, 14.7.10.76, 34.7.18.114
		NHM	40.683, 40.685, 40.686, 40.687, 55.1652, 61.1163, 61.1164, 65.1031, 76.1312, 77.464, 14.7.10.76, 34.7.18.114, 5.11.19.2, 6.12.3.3, 6.12.3.6, 65.1030., 8.1.25.7, 85.8.1.123, 97.3.10.3, SI, 326355, 326357, 326359, 326360, 353203, 353204, 353207, 353211
		SI	326355, 326357, 326359, 326360, 353203, 353204, 353207, 353211, ZSI, 15048, 21293, 21296, 21297, m, AMNH, 32642, 56935, 58209, 58211, 58212, 58218, 58221, 87417, 101640, 101641, 101699, 102167, 102168

		ZSI	15048, 21293, 21296, 21297, m, AMNH, 32642, 56935, 58209, 58211, 58212, 58218, 58221, 87417, 101640, 101641, 101699, 102167, 102168, 106632, 112975, 114897, 114900, 163097, 174852, 183140, 240915, Berlin
	m	AMNH	32642, 56935, 58209, 58211, 58212, 58218, 58221, 87417, 101640, 101641, 101699, 102167, 102168, 106632, 112975, 114897, 114900, 163097, 174852, 183140, 240915, Berlin, 4533, BNHS, 6888, 6899, 6901, 6913
		Berlin	4533
		BNHS	6888, 6899, 6901, 6913, 6914, 6917, 6920, 6942, 6951, 6952, 6953, 6963, 6973, 6974, 6976, 6978, 6980, 6988, 6989, NHM, 40.681, 40.682, 40.684, 55.1648, 55.1649, 55.165, 55.1653, 55.1654
		NHM	40.681, 40.682, 40.684, 55.1648, 55.1649, 55.165, 55.1653, 55.1654, 55.1655, 55.1656, 55.1957, 57.473, 65.1027, 1939.2375, 14.7.10.75, 21.12.5.44, 23.11.4.12, 23.9.1.33, 23.9.1.34, 23.9.1.35, 25.6.10.14, 32.11.1.69, 6.12.3.4, 6.3.20.5, 6.3.220.6, 7.6.18.14, 7.6.18.5, 8.1.25.6
		SI	326354, 326356, 326358, 326361, 353201, 353202, 353205, 353206, 353208, 353209, 353210
		ZSI	11414, 15045, 15046, 15047, 15052, 15053, 15054, 15055, 21294, 21295
	u	AMNH	183141, 183142, 183144, 184922, 184923, 184924, 184925, 184926, 184927, 184928, 184929, 184935, 184936, 184937, 184938, 184939, 184940, 184942, 184943, 184954
		BNHS	6887, 6889, 6891, 6902, 6903, 6911, 6912, 6954, 6959, 6961, 6969, 6970, 6977
		Frankfurt	731, 10744, 39244
		NHM	71.274, 71.2741, 74.96, 1162, 1939.2374, 1162.c, 19.11.12.18, 1938.7.19.12, 20.6.27.5, 22.8.1.2, 26.10.8.56, 26.10.8.57, 26.10.8.58, 26.10.8.60, 26.8.13.1, 44.9.30.18, 58.5.4.308, 58.5.4.309, 58.5.4.401, 6.12.3.5, 6.6.16.1, 65.5.20.2, 7.6.18.16, 8.1.25.6, 80.12.28.2, 84.5.19.4, 84.7.30.1, 9.1.5.741, 9.1.5.742, 91.107.64, 95.7.3.2, sk.106.a
Petaurista philippensis	f	Berlin	3938, 91291
		NHM	71.783, 13.8.22.36, 13.8.22.37, 13.8.22.39, 15.4.3.69, 16.3.1.61, 23.1.6.51, 23.1.6.52, 25.1.1.43, 31.9.11.14, 31.9.11.4, 31.9.11.5, 33.4.1.257, 7.1.5.4, 7.1.5.5

		ZSI	15068, 15069, 15071, 20073
	m	AMNH	164069
		NHM	0.10.7.6, 12.11.28.77, 12.11.28.78, 12.11.28.79, 12.3.8.6, 13.11.3.5, 13.8.22.33, 13.8.22.34, 13.8.22.35, 13.8.22.38, 15.4.3.68, 19.6.2.26, 25.1.1.41, 25.10.1.12, 27.11.18.15, 30.5.24.126, 30.5.24.127, 30.6.8.1, 31.9.11.2, 31.9.11.3, 33.4.1.261, 7.1.5.2, 7.1.5.3, 91.10.7.66, 96.11.7.4, 98.10.5.42
		ZSI	15067, 15070
	u	NHM	1408 a, 77.3.14.11, 77.3.14.9, 79.11.21.38, 85.8.1.125, 9.10.11.13, 94.11.22.2, 94.7.1.14
		NHM	33.4.1.262
Petaurista primrosei (= philippensis)	f	NHM	23.1.6.54
Petaurista punctatus	f	NHM	50.611
Petaurista sp.	f	AMNH	229, 164071, 167903
		NHM	1939.2373, 21.8.2.17, 45.8.12.8, 8.7.6.26, 91.10.17.61
	m	Berlin	4532
		NHM	1939.2372, 21.8.2.15, 34.8.3.6, 95.7.3.1, 99.6.91.1
	u	AMNH	54625, 54626
		Frankfurt	75375
		NHM	39.381, 39.383, 39.862, 39.864, 39.865, 39.866, 114.e, 43.1.12.48, 45.10.2.8, 60.2.11.14, 82.2.6.4, 99.6.19.2
Petinomys crinitis	m	AMNH	207540, 207541
Petinomys crinitus	f	Frankfurt	1405, 32527, 32529, 32532
Petinomys genibarbaris	f	Frankfurt	82086
		NHM	65.346, 78.4.26.1
	m	NHM	64.784, 93.4.1.42
	u	NHM	60.5.4.82, 82.11.9.2, 82.7.11.3
Petinomys	f	AMNH	103150, 103151

lugens	m	AMNH	103149, 103318
Petinomys sagitta	f	NHM	49.636, 49.637, 9.1.5.744, 9.1.5.745
	m	Frankfurt	90608
		NHM	49.635, 23.1.2.31, 9.1.5.746, 9.1.5.747
		ZSI	15031
	u	NHM	12.4.12.3
Petinomys setosus	u	Frankfurt	16244, 16245, 16323
Petinomys vordermanni	f	NHM	17.1.26.1
		SI	124986, 481147, 481149, 481150, 481151, 481152, 481155, 481156, 481157, 481158, 481163, 481167
		SI	481148, 481153, 481154, 481159, 481160, 481161, 481162, 481164, 481165, 481166, 481168, 481169, 481172, 481173, 481174, 481175, 481176
Petinomys fuscocapillus	f	NHM	15.2.1.62
		SI	loan from ceylon
	m	NHM	87.3.2.1
Petinomys hageni	f	NHM	90.1.20.3
	u	NHM	78.2945
Petinomys setosus	f	NHM	58.452, 71.1528, 74.1524, 74.1525, 28.7.14.4, 89.1.18.6
	m	NHM	58.451, 74.1523, 74.1526, 74.1527, 23.1.2.32, 84.4.22.10, 93.4.1.43
Petinomys vordermanni	m	NHM	63.1594, 71.1529, 71.153, 71.1531, 71.1532
Pteromys caniceps (=Petaurista elegans)	u	NHM	53.8.16.9
Pteromys momonga	f	NHM	6.1.4.124, 6.1.4.125, 6.1.4.126, 6.1.4.127
	m	NHM	6.1.4.121, 6.1.4.123
	u	NHM	22.8.24.6, 5.1.4.51, 75.11.10.1
Pteromys	f	AMNH	85466

volans		NHM	14.11.1.16, 20.7.74.21
		SI	270545, 172619, 172620, 172621, 172623
	m	NHM	57.16, 1.6.9.1, 14.11.1.15, 1938.8.8.1, 20.7.4.20
		SI	254934
	u	AMNH	19526, 19534
		SI	155557, 172624, 172625, 172626, 174993
		NHM	1937.6.12.1, 1937.6.12.2, 43.8.18.1, 44.10.29.1, 44.18.29.1, 53.12.6.29, 7.1.1.53, 7.1.1.54
Pteromys momonga	m	Berlin	88688
Pteromys sp.	m	Berlin	91374
		Berlin	90917
Pteromys volans	f	Berlin	28253, 88305, 88308
	m	Berlin	88304, 88306, 88689
	u	Berlin	1459, 32532, 40573, 88307, 88309, 88310, 88686, 88695, 88715, 94111
Pteromyscus pulverulentus	f	NHM	71.1533, 71.1535
		SI	481177, 481178, 481179, 481180, 481181, 481182, 481185, 481186, 488684, 488685, 488686, 488688, 488689, 488690, 488692, 488693, 488694, 488696, 488698, 488703, 488704, 488707, 489502, 489503, 489505, 489507, 489511, 489513, 489515, 489518, 489519, 489520, 489523, 489526
	m	NHM	49.638, 71.1534
		SI	481183, 481184, 488687, 488691, 488695, 488697, 488699, 488701, 488702, 488705, 489504, 489506, 489508, 489509, 489510, 489512, 489514, 489516, 489517, 489521, 489522, 489524, 489525, 489527
	u	NHM	25.7.14.2, 28.7.14.2
Trogopterus xanthipes	f	AMNH	111355
		NHM	48.309, 22.9.1.46
		SI	241271, 258520

u	NHM	1996.535, 4.5.25.1, 8.8.11.61, 8.8.11.62, 9.7.21.5, 91.10.7.62

Appendix III

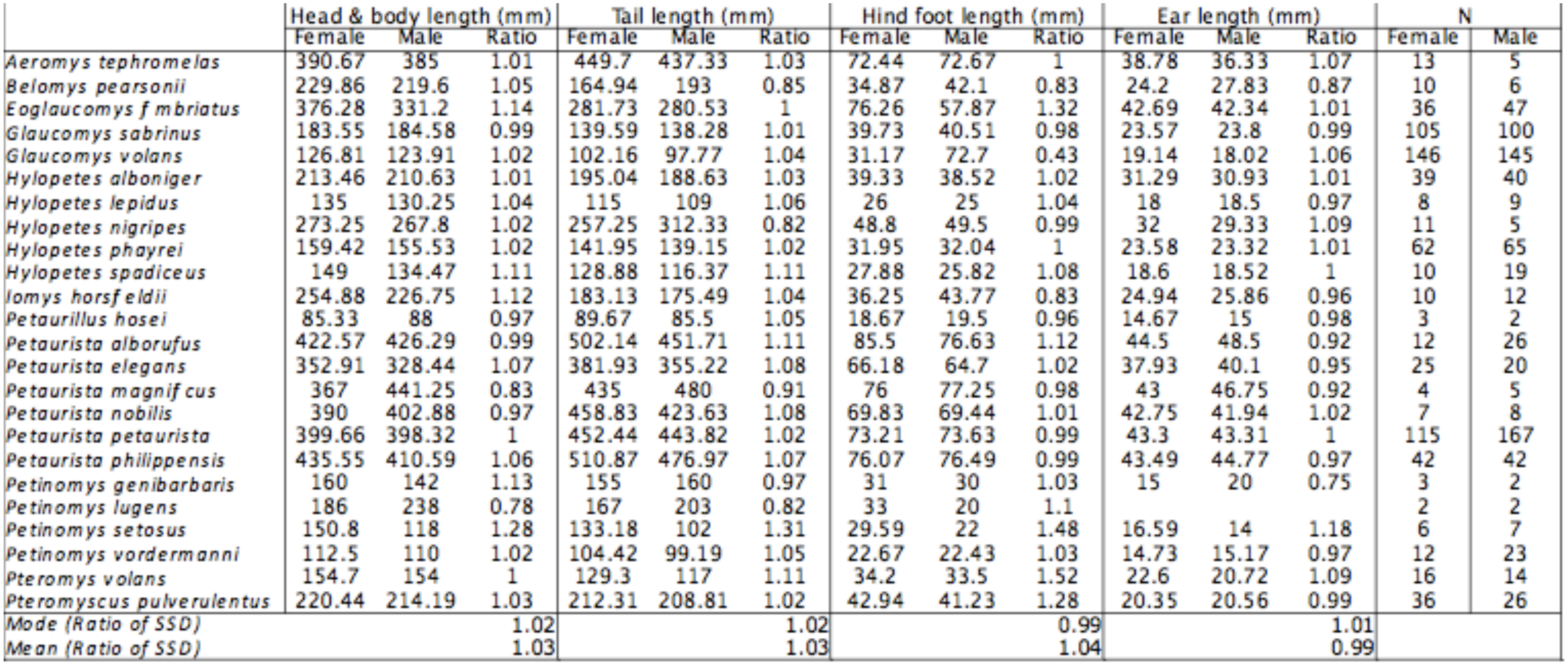
GenBank accession numbers of sequences used for reconstruction of the phylogenetic tree. Sequences are of squirrels (Family Sciuridae), and three outgroup species (marked with ***): + Family Aplodontiidae, ++ Family Dipodidae and +++ Family Gliridae.

Species	**Accession #**	**Species**	**Accession #**
Aeretes melanopterus	AY227593.1	*Petaurillus kinlochii*	AY227602.1
Aeromys tephromelas	AY227594.1	*Petaurista alborufus*	AY227601.1
Ammospermophilus harrisii	AY227583.1	*Petinomys setosus*	AY227604.1
Atlantoxerus getulus	AY227623.1	*Prosciurillus murinus*	AY227574.1
Belomys pearsonii	AY227595.1	*Protoxerus stangeri*	AY227592.1
Callosciurus notatus	AY227566.1	*Pteromys volans*	AY227605.1
Cynomys leucurus	AY227584.1	*Pteromyscus pulverulentus*	AY227603.1
Dremomys rufigenis	AY227567.1	*Ratufa bicolor*	AY227608.1
Eoglaucomys fimbriatus	AY227597.1	*Rheithrosciurus macrotis*	AY227611.1
Epixerus wilsoni	AY227589.1	*Rhinosciurus laticaudatus*	AY227575.1
Eupetaurus cinereus	AY227596.1	*Rubrisciurus rubriventer*	AY227576.1
Exilisciurus exilis	AY227569.1	*Sciurillus pusillus*	AY227617.1
Funambulus palmarum	AY227579.1	*Sciurotamias davidianus*	AY227621.1
Funisciurus pyrropus	AY227581.1	*Sciurus vulgaris*	AY227620.1
Glaucomys volans	AY227598.1	*Spermophilopsis leptodactylus*	AY227624.1
Glyphotes simus	AY227630.1	*Spermophilus lateralis*	AY227586.1
Heliosciurus ruwenzorii	AY227590.1	*Spermophilus tridecemlineatus*	AF297278.1
Hylopetes phayrei	AY227599.1	*Sundasciurus brookei*	AY227577.1
Hyosciurus heinrichi	AY227570.1	*Syntheosciurus brochus*	AY227628.1

Iomys horsfieldi	AY227600.1	*Tamias striatus*	AY227588.1
Lariscus insignis	AY227571.1	*Tamiasciurus hudsonicus*	AY227622.1
Marmota monax	AY227585.1	*Tamiops swinhoei*	AY227578.1
Menetes berdmorei	AY227572.1	*Trogopterus xanthipes*	AY227606.1
Microsciurus flaviventer	AY227610.1	*Xerus rutilus*	AY227625.1
Myosciurus pumilio	AY227591.1	*Allactaga sibirica****+	AY326076.1
Nannosciurus melanotis	AY227573.1	*Aplodontia rufa****++	AF297284.1
Paraxerus alexandri	AY227582.1	*Glirulus japonicus****+++	AB253965.1

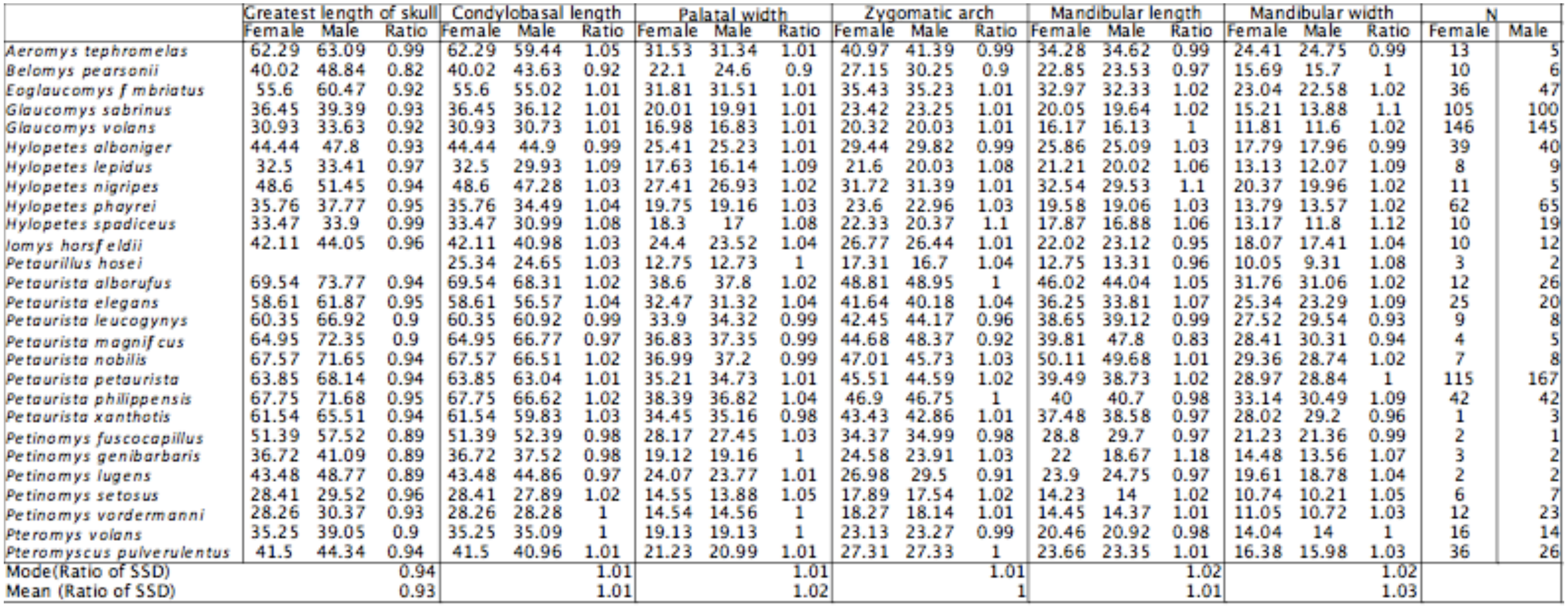
Appendix IV

APPENDIX 4.1: Sexual size dimorphism (female/male) and average morphometric measurements of 24 species of



	Head & body length (mm)			Tail length (mm)			Hind foot length (mm)			Ear length (mm)			N	
	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male
Aeromys tephromelas	390.67	385	1.01	449.7	437.33	1.03	72.44	72.67	1	38.78	36.33	1.07	13	5
Belomys pearsonii	229.86	219.6	1.05	164.94	193	0.85	34.87	42.1	0.83	24.2	27.83	0.87	10	6
Eoglaucomys fimbriatus	376.28	331.2	1.14	281.73	280.53	1	76.26	57.87	1.32	42.69	42.34	1.01	36	47
Glaucomys sabrinus	183.55	184.58	0.99	139.59	138.28	1.01	39.73	40.51	0.98	23.57	23.8	0.99	105	100
Glaucomys volans	126.81	123.91	1.02	102.16	97.77	1.04	31.17	72.7	0.43	19.14	18.02	1.06	146	145
Hylopetes alboniger	213.46	210.63	1.01	195.04	188.63	1.03	39.33	38.52	1.02	31.29	30.93	1.01	39	40
Hylopetes lepidus	135	130.25	1.04	115	109	1.06	26	25	1.04	18	18.5	0.97	8	9
Hylopetes nigripes	273.25	267.8	1.02	257.25	312.33	0.82	48.8	49.5	0.99	32	29.33	1.09	11	5
Hylopetes phayrei	159.42	155.53	1.02	141.95	139.15	1.02	31.95	32.04	1	23.58	23.32	1.01	62	65
Hylopetes spadiceus	149	134.47	1.11	128.88	116.37	1.11	27.88	25.82	1.08	18.6	18.52	1	10	19
Iomys horsfeldii	254.88	226.75	1.12	183.13	175.49	1.04	36.25	43.77	0.83	24.94	25.86	0.96	10	12
Petaurillus hosei	85.33	88	0.97	89.67	85.5	1.05	18.67	19.5	0.96	14.67	15	0.98	3	2
Petaurista alborufus	422.57	426.29	0.99	502.14	451.71	1.11	85.5	76.63	1.12	44.5	48.5	0.92	12	26
Petaurista elegans	352.91	328.44	1.07	381.93	355.22	1.08	66.18	64.7	1.02	37.93	40.1	0.95	25	20
Petaurista magnificus	367	441.25	0.83	435	480	0.91	76	77.25	0.98	43	46.75	0.92	4	5
Petaurista nobilis	390	402.88	0.97	458.83	423.63	1.08	69.83	69.44	1.01	42.75	41.94	1.02	7	8
Petaurista petaurista	399.66	398.32	1	452.44	443.82	1.02	73.21	73.63	0.99	43.3	43.31	1	115	167
Petaurista philippensis	435.55	410.59	1.06	510.87	476.97	1.07	76.07	76.49	0.99	43.49	44.77	0.97	42	42
Petinomys genibarbaris	160	142	1.13	155	160	0.97	31	30	1.03	15	20	0.75	3	2
Petinomys lugens	186	238	0.78	167	203	0.82	33	20	1.1				2	2
Petinomys setosus	150.8	118	1.28	133.18	102	1.31	29.59	22	1.48	16.59	14	1.18	6	7
Petinomys vordermanni	112.5	110	1.02	104.42	99.19	1.05	22.67	22.43	1.03	14.73	15.17	0.97	12	23
Pteromys volans	154.7	154	1	129.3	117	1.11	34.2	33.5	1.52	22.6	20.72	1.09	16	14
Pteromyscus pulverulentus	220.44	214.19	1.03	212.31	208.81	1.02	42.94	41.23	1.28	20.35	20.56	0.99	36	26
Mode (Ratio of SSD)			1.02			1.02			0.99			1.01		
Mean (Ratio of SSD)			1.03			1.03			1.04			0.99		

APPENDIX 4.2: Sexual size dimorphism (female/male) and average cranial measurements of 27 species of male and female flying squirrels.



	Greatest length of skull			Condylobasal length			Palatal width			Zygomatic arch			Mandibular length			Mandibular width			N	
	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male	Ratio	Female	Male
Aeromys tephromelas	62.29	63.09	0.99	62.29	59.44	1.05	31.53	31.34	1.01	40.97	41.39	0.99	34.28	34.62	0.99	24.41	24.75	0.99	13	5
Belomys pearsonii	40.02	48.84	0.82	40.02	43.63	0.92	22.1	24.6	0.9	27.15	30.25	0.9	22.85	23.53	0.97	15.69	15.7	1	10	6
Eoglaucomys fimbriatus	55.6	60.47	0.92	55.6	55.02	1.01	31.81	31.51	1.01	35.43	35.23	1.01	32.97	32.33	1.02	23.04	22.58	1.02	36	47
Glaucomys sabrinus	36.45	39.39	0.93	36.45	36.12	1.01	20.01	19.91	1.01	23.42	23.25	1.01	20.05	19.64	1.02	15.21	13.88	1.1	105	100
Glaucomys volans	30.93	33.63	0.92	30.93	30.73	1.01	16.98	16.83	1.01	20.32	20.03	1.01	16.17	16.13	1	11.81	11.6	1.02	146	145
Hylopetes alboniger	44.44	47.8	0.93	44.44	44.9	0.99	25.41	25.23	1.01	29.44	29.82	0.99	25.86	25.09	1.03	17.79	17.96	0.99	39	40
Hylopetes lepidus	32.5	33.41	0.97	32.5	29.93	1.09	17.63	16.14	1.09	21.6	20.03	1.08	21.21	20.02	1.06	13.13	12.07	1.09	8	9
Hylopetes nigripes	48.6	51.45	0.94	48.6	47.28	1.03	27.41	26.93	1.02	31.72	31.39	1.01	32.54	29.53	1.1	20.37	19.96	1.02	11	5
Hylopetes phayrei	35.76	37.77	0.95	35.76	34.49	1.04	19.75	19.16	1.03	23.6	22.96	1.03	19.58	19.06	1.03	13.79	13.57	1.02	62	65
Hylopetes spadiceus	33.47	33.9	0.99	33.47	30.99	1.08	18.3	17	1.08	22.33	20.37	1.1	17.87	16.88	1.06	13.17	11.8	1.12	10	19
Iomys horsfieldii	42.11	44.05	0.96	42.11	40.98	1.03	24.4	23.52	1.04	26.77	26.44	1.01	22.02	23.12	0.95	18.07	17.41	1.04	10	12
Petaurillus hosei				25.34	24.65	1.03	12.75	12.73	1	17.31	16.7	1.04	12.75	13.31	0.96	10.05	9.31	1.08	3	2
Petaurista alborufus	69.54	73.77	0.94	69.54	68.31	1.02	38.6	37.8	1.02	48.81	48.95	1	46.02	44.04	1.05	31.76	31.06	1.02	12	26
Petaurista elegans	58.61	61.87	0.95	58.61	56.57	1.04	32.47	31.32	1.04	41.64	40.18	1.04	36.25	33.81	1.07	25.34	23.29	1.09	25	20
Petaurista leucogynys	60.35	66.92	0.9	60.35	60.92	0.99	33.9	34.32	0.99	42.45	44.17	0.96	38.65	39.12	0.99	27.52	29.54	0.93	9	8
Petaurista magnificus	64.95	72.35	0.9	64.95	66.77	0.97	36.83	37.35	0.99	44.68	48.37	0.92	39.81	47.8	0.83	28.41	30.31	0.94	4	5
Petaurista nobilis	67.57	71.65	0.94	67.57	66.51	1.02	36.99	37.2	0.99	47.01	45.73	1.03	50.11	49.68	1.01	29.36	28.74	1.02	7	8
Petaurista petaurista	63.85	68.14	0.94	63.85	63.04	1.01	35.21	34.73	1.01	45.51	44.59	1.02	39.49	38.73	1.02	28.97	28.84	1	115	167
Petaurista philippensis	67.75	71.68	0.95	67.75	66.62	1.02	38.39	36.82	1.04	46.9	46.75	1	40	40.7	0.98	33.14	30.49	1.09	42	42
Petaurista xanthotis	61.54	65.51	0.94	61.54	59.83	1.03	34.45	35.16	0.98	43.43	42.86	1.01	37.48	38.58	0.97	28.02	29.2	0.96	1	3
Petinomys fuscocapillus	51.39	57.52	0.89	51.39	52.39	0.98	28.17	27.45	1.03	34.37	34.99	0.98	28.8	29.7	0.97	21.23	21.36	0.99	2	1
Petinomys genibarbaris	36.72	41.09	0.89	36.72	37.52	0.98	19.12	19.16	1	24.58	23.91	1.03	22	18.67	1.18	14.48	13.56	1.07	3	2
Petinomys lugens	43.48	48.77	0.89	43.48	44.86	0.97	24.07	23.77	1.01	26.98	29.5	0.91	23.9	24.75	0.97	19.61	18.78	1.04	2	2
Petinomys setosus	28.41	29.52	0.96	28.41	27.89	1.02	14.55	13.88	1.05	17.89	17.54	1.02	14.23	14	1.02	10.74	10.21	1.05	6	7
Petinomys vordermanni	28.26	30.37	0.93	28.26	28.28	1	14.54	14.56	1	18.27	18.14	1.01	14.45	14.37	1.01	11.05	10.72	1.03	12	23
Pteromys volans	35.25	39.05	0.9	35.25	35.09	1	19.13	19.13	1	23.13	23.27	0.99	20.46	20.92	0.98	14.04	14	1	16	14
Pteromyscus pulverulentus	41.5	44.34	0.94	41.5	40.96	1.01	21.23	20.99	1.01	27.31	27.33	1	23.66	23.35	1.01	16.38	15.98	1.03	36	26
Mode(Ratio of SSD)			0.94			1.01			1.01			1.01			1.02			1.02		
Mean (Ratio of SSD)			0.93			1.01			1.02			1			1.01			1.03		