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Roosting Ecology of the Grey-headed Flying Fox: Spatial Dispersion in a Summer Camp

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To the Graduate Council:

I am submitting herewith a thesis written by Jennifer L. Holmes entitled "Roosting Ecology of the Grey-headed Flying Fox: Spatial Dispersion in a Summer Camp." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Gary F. McCracken, Major Professor

We have read this thesis and recommend its acceptance:

Gordon M. Burghardt, Dewey Bunting

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Major Professor

Thomas G. Hallam_____
Department Head

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and recommend its acceptance:

Gordon M. Burghardt______

Dewey Bunting___________

Accepted for the Council:

Dr. Anne Mayhew______
Vice Provost and
Dean of Graduate Studies

(Original signatures are on file in the Graduate Student Services Office.)

Roosting Ecology of the Grey-headed Flying Fox, *Pteropus poliocephalus*: Spatial Distribution in a Summer Camp

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jennifer L. Holmes
May 2002

Dedication

This thesis is dedicated to

the fascinating, intelligent, and beautiful flying foxes
that share the Earth with us,
and to all the people who endeavor
to save and protect them

and

to my mother,
Joyce Holmes,
who always encouraged me
to be inquisitive, adventurous,
and true to myself.

Acknowledgements

The time spent earning this degree has been one of the most fun and rewarding experiences of my life. I am grateful to my friends and family for supporting yet another of my crazy ventures.

I have benefited greatly from my relationships with the faculty and graduate students in the Department of Ecology and Evolutionary Biology. I am particularly grateful to my advisor, Gary McCracken, for his encouragement, patience, and guidance. I am also indebted to my other committee members, Gordon Burghardt and Dewey Bunting, for their helpful suggestions and input. I would also like to thank my labmates and friends, Florencia Fernandez-Campon, Amy Russell, Leslie Saidak, Sunitha Vege, and Betsy Von Holle for their support, input, and most of all, friendship.

I owe a special debt of gratitude to Kerryn Parry-Jones, without whom this thesis could not have been completed. Her incredible generosity, support, and guidance while I was doing my fieldwork enabled me to pursue a long held dream.

Thank you also to Peggy Eby for her help and advice with this project.

I would like to thank the Department of Ecology and Evolutionary Biology for their generous financial support, as well as the University of Tennessee McClure Fund for International Studies.

Finally, I would like to thank the Sydney Royal Botanic Gardens for allowing me to conduct my study on their grounds, particularly David Bidwell, who provided me important and extremely useful information and data on the bats and the Gardens.

Abstract

A colony of Grey-headed flying foxes (*Pteropus poliocephalus*) in the Royal Botanic Gardens in Sydney, Australia was studied over a ten-week period before, during and after the mating season to assess spatial distribution of individuals, specifically investigating age and sex segregation. Ground censusing techniques were used to determine weekly estimates of the numbers of bats in the colony and numbers of bats within each tree. Surveys were used to document sexes and ages of bats occupying each tree. Unlike Nelson's (1965) findings, the social structure of the colony was based not on mating strategies of individual bats but on age and sex. Adult and subadult bats clearly segregated within the colony with adult bats roosting in significantly taller trees than non-adult (subadult and juvenile) bats. Among both adults and subadults, bats also segregated by sex, except during the mating season.

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I. Introduction

Aggregation of animals may lead to competition for resources (reviewed by Wilson 1975). Thus competition can be a strong factor driving the evolution of social systems and behaviors that ultimately create and maintain organization and structure within groups (Pusey and Packer 1997).

Of the social animals, bats (Order Chiroptera) are of particular interest. Although bats make up more than one fifth of all mammal species, their social structures have been relatively little studied (McCracken and Wilkinson 2000). While some species of bats appear to be solitary, many species live in large communal groups and are quite gregarious (Nowak 1994; Altringham 1996). Increasing focus on these animals has revealed a wide variety of highly complex social behaviors. In the case of the Grey-headed flying fox, *Pteropus poliocephalus*, which can congregate in colonies of over 50,000 individuals, the competitive resource driving social organization may be roosting sites.

The Grey-headed flying fox, *Pteropus poliocephalus* (Suborder Megachiroptera, Family Pteropodidae), is endemic to Australia, occupying the eastern coast from Rockhampton, Queensland to Bass Strait, Victoria (Fig 1). This species roosts communally in trees within camps that vary in size from a few hundred to many thousand individuals (Parry-Jones, pers.comm.). Historically, *P. poliocephalus* camps were much larger. Ratcliffe (1931) reported colony size estimates of over a million bats. Nelson's 1965 studies estimated over 200,000 bats in many colony sites, and

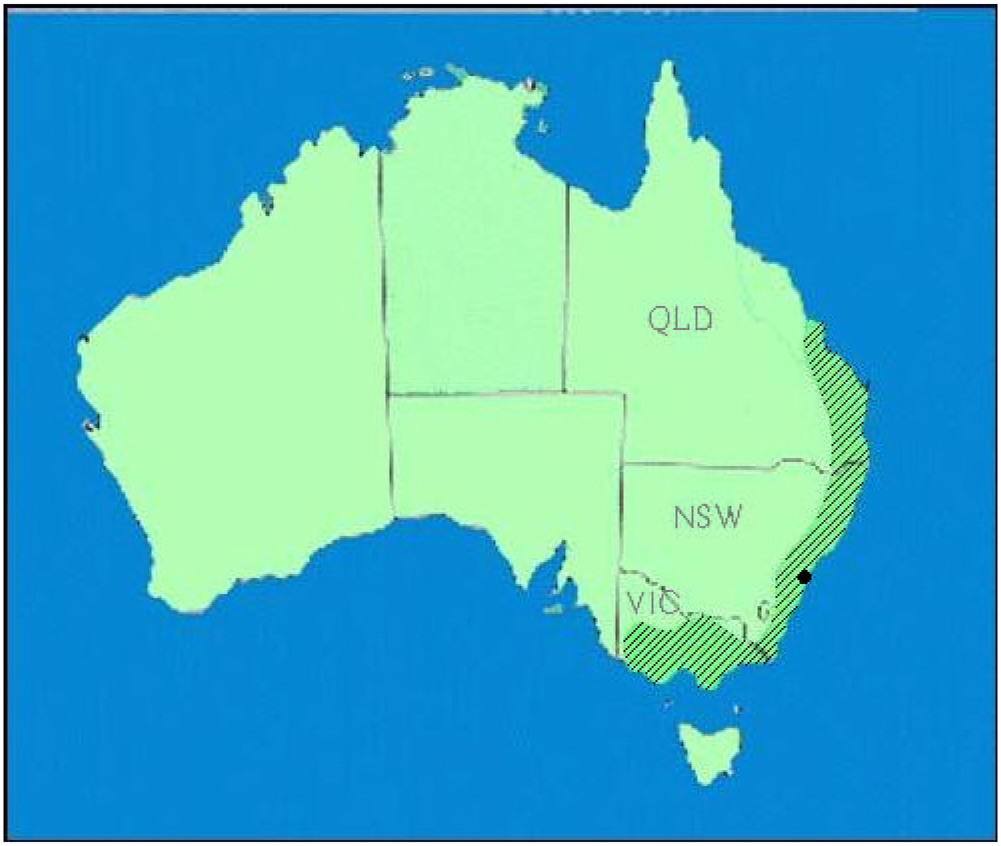


Figure 1. *Range of the Grey-headed flying fox (from Churchill 1998). Study site indicated by · .*

even the in the early 1990s, researchers continued to find such large camps (Eby 1991). Recent (2001) count estimates, however, found only a few colonies over 50,000 individuals. An average colony size is now considered to be around 20,000 individuals (K. Parry-Jones, pers.comm.). Like other chiropterans, these flying foxes roost by day and fly out to feed at night. As obligate nectarivores and frugivores, *P. poliocephalus* feed predominantly on the blossoms of Myrtaceae (particularly *Eucalyptus*) and Proteaceae trees from which they take pollen and nectar. The bats also feed on fruits of native and introduced tree species (Parry-Jones and Augee 1992). Food sources are temporally and spatially patchy, requiring mobility to take advantage of local abundance. Radio tracking studies have revealed that these bats commonly fly 25 km from the colony site to reach food (Spencer et al 1991), but will travel up to 50 km to a particular food source (Eby, unpub. data).

Grey-headed flying foxes readily move from one major day roost to another (Eby 1991; Spencer et al 1991; Parry-Jones and Augee 1992), sometimes migrating hundreds of kilometers within a few days (Eby 1991). These longer migrations generally coincide with temperature and food availability (Parry-Jones 1985; Eby 1991; Parry-Jones and Augee 1992), not unlike bird migrations. However, because flowering of trees throughout Australia is less regular than the seasonal flowering of trees in temperate regions, these migrations are not nearly as predictable as bird migrations in Europe and North America. Nonetheless, there do appear to be some broad patterns. The availability of food resources appears to be the primary motivation for migration. Patchiness of food supplies is also believed to be a driving force behind the evolution of these large colonies. These bats generally move north in the autumn to escape lower temperatures and decreasing food supplies on the southeastern coast. In spring, the bats move south again to take advantage of blossoming trees. Traditional camps are used irregularly depending on the local food supplies. Although some camps are occupied year round, genetic studies (Webb and Tidemann 1996) reflect the high mobility of this bat, showing that the population is apparently panmictic throughout its range.

Early researchers referred to the seasonal camps as summer and winter camps (Nelson 1965). Summer camps are commonly referred to as maternity colonies (Eby

1991) since females give birth and raise their young at these sites. Females give birth to a single young each year. Mating generally occurs between mid-March and early April and, after a six-month gestation period, pups are born in September and October.

P. poliocephalus colonies appear to be casual groups, with individuals and groups of bats frequently moving from one camp to another. Previous research has shown that some bats move in subgroups made up of a few individuals, arriving and leaving colonies together (Nelson 1965), but very little is known about the composition of these subgroups.

While many species of bats roost in tight clusters (Kunz 1982), Grey-headed flying foxes tend to maintain individual distances from conspecifics and will readily defend their roosting territory. The minimal individual spacing is approximately one half meter (Puddicombe 1981), except for subgroups such as harem groups or mother-pup pairs in which bats will roost less than half a meter apart. Females in a harem as well as mothers and their dependent or semi-independent young often roost on a branch side by side with bodies touching (see Fig 2).

In the earliest research on the social organization of flying foxes within a colony, Nelson (1965) observed that locations of individual bats within summer camps are based primarily on mating strategy. According to his study, polygamous groups of bats can be found in the center of the colony, while monogamous bats are found on the outer edges. Bachelor males and independent juveniles congregate on the outskirts of the colony. However, current researchers report that they have never seen this spatial structure as described by Nelson (Parry-Jones, pers. comm.; Peggy Eby, pers.comm.).

Figure 2. *Roosting* ***P. poliocephalus*** *demonstrating individual spacing.*

Nelson (1965) also noted that the dispersion of bats within a *P. poliocephalus* colony appeared to be most dense at the center of the colony with 400 or more bats per tree and progressively less dense toward the periphery of the colony. This pattern indicates that the optimal roosting sites may be at the center of the colony. As congregating in large numbers may increase protection from predators (Hoogland 1981; van Schaik et al 1983), presumably, the closer a bat is to the center of the colony, the safer it will be.

Competition for resources has been found to play a role in both intraspecific and interspecific segregation of individuals (Martin and Thibault 1996; Lockhart et al 1990; Schoener 1968) and competition for roosting territories may be a factor underlying social organization within *P. poliocephalus* colonies. Among species in which intraspecific segregation occurs, from brown trout to bighorn sheep, it frequently occurs in the form of age or sex segregation (Bleich et al 1997; Morgantini and Hudson 1981; Stewart and Delong 1995; Haraldstad and Jonsson 1983). Age segregation often occurs because adults control access to the better resources (Allen and Aspey 1986; Bennett 1986; Catterall et al 1989), indicating an age-based dominance hierarchy (Sherry and Holmes 1989; Sandell and Smith 1991). Observations of captive Grey-headed flying foxes indicate that older males dominate younger bats, and older males may force younger males to roost in lower positions in trees (Parry-Jones, pers. comm.). This behavior suggests that adults may have dominance over subadults and control the best roosting habitat. Therefore, roosting position may indicate social rank or dominance.

Nelson (1965) also noted that in summer camps the sexes are segregated from September to early December. The extent of the segregation varies from tree to tree, with some trees having only one sex and others having both sexes in fairly equal numbers.

Little research has been done since Nelson (1965) on the social organization of Australian megachiropteran colonies, and basic knowledge of the social organization within a particular group is necessary before more in-depth studies can be conducted. Hewitt and Butlin (1997) argue that “differences in age, caste, morph and sex structure of populations and species can have important effects on the genetic variation present and significant consequences for the evolution of behavior.” As unpublished observations have not seen the patterns reported by Nelson, there is a need for new studies that expand knowledge in this area.

In-depth study of the structure within *P. poliocephalus* roosting assemblages will not only give us further insight into factors underlying social systems, but will also provide much-needed information about an organism that plays an important role in ecosystem dynamics. Grey-headed flying foxes are vital to the survival of many native Australian plant species due to their role in seed dispersal and pollination (Eby 1991; Parry-Jones and Augee 1991). *P. poliocephalus* has been classified as a vulnerable species in Queensland and New South Wales due to increasing loss of habitat and drastic decreases in population size since the early 20th century (Richards and Hall 1994). The need for conservation efforts and management plans for this species has been recognized; however, much about the ecology and behavior of fruit bats is still unknown. Information gathered through behavioral studies is necessary to lay the groundwork for research on population genetic structure, evolution of social behavior, and conservation.

The main objective of this study was to investigate patterns of spatial dispersion in a summer colony of *P. poliocephalus* by looking at usage patterns of trees. This thesis addresses spatial dispersion of bats within a colony, specifically looking at age- and sex-related roosting patterns. I investigated (1) segregation of Grey-headed flying foxes by age and sex within roosts, (2) the possibility of social dominance hierarchies within colonies of *P. poliocephalus* and (3) whether roosting territory was the limiting resource fostering segregation. I pursued these objectives by describing the usage patterns of bats in trees of varying heights, diameter at breast height (DBH), and canopy breadth. I hypothesized that *P. poliocephalus* segregates by age and by gender, that adult bats are dominant over non-adult bats, and that adult bats roost in taller trees that non-adults.

II. Methods

Study site and dates. The study colony, defined as a group of bats roosting in an assemblage of trees, is located in the Royal Botanic Gardens in Sydney, New South Wales, Australia (Fig 3). The site is different than typical colony sites of these bats in that many of the trees in which the bats roost are non-native (see Appendix A). The trees are planted in beds separated by paved pathways, facilitating ease of access to the trees for research on the resident bats. The area of the Gardens in which the bats roost is fairly level and has a small stream flowing through the center of the colony. The ground cover beneath most trees occupied by bats was straw, wood chips, leaf litter, small bushes, and/or flowering plants. Some trees had larger bushes growing adjacent to them. A few of the trees occupied by bats were located on manicured lawns (Fig 4). This colony was chosen for the study because it presented near optimal conditions for research on the social organization of these bats. Although not quantitatively assessed, the varying heights of trees in the Gardens appears to be more pronounced than in camps located in non-urban settings, such as rainforests and sclerophyl forests. The relatively small size of the colony (approximately 5500 individuals at the onset of the study) facilitated daily counts and surveys of each tree that would be impossible for a single investigator in larger colonies.

The study was conducted for ten consecutive weeks between February 5 and April 13, 2001. At the onset of the study, the colony size was estimated at 5500 bats. The study site was divided into five sections containing approximately 1100 bats each.

Figure 3. *Location of study site in Sydney indicated by ★.*

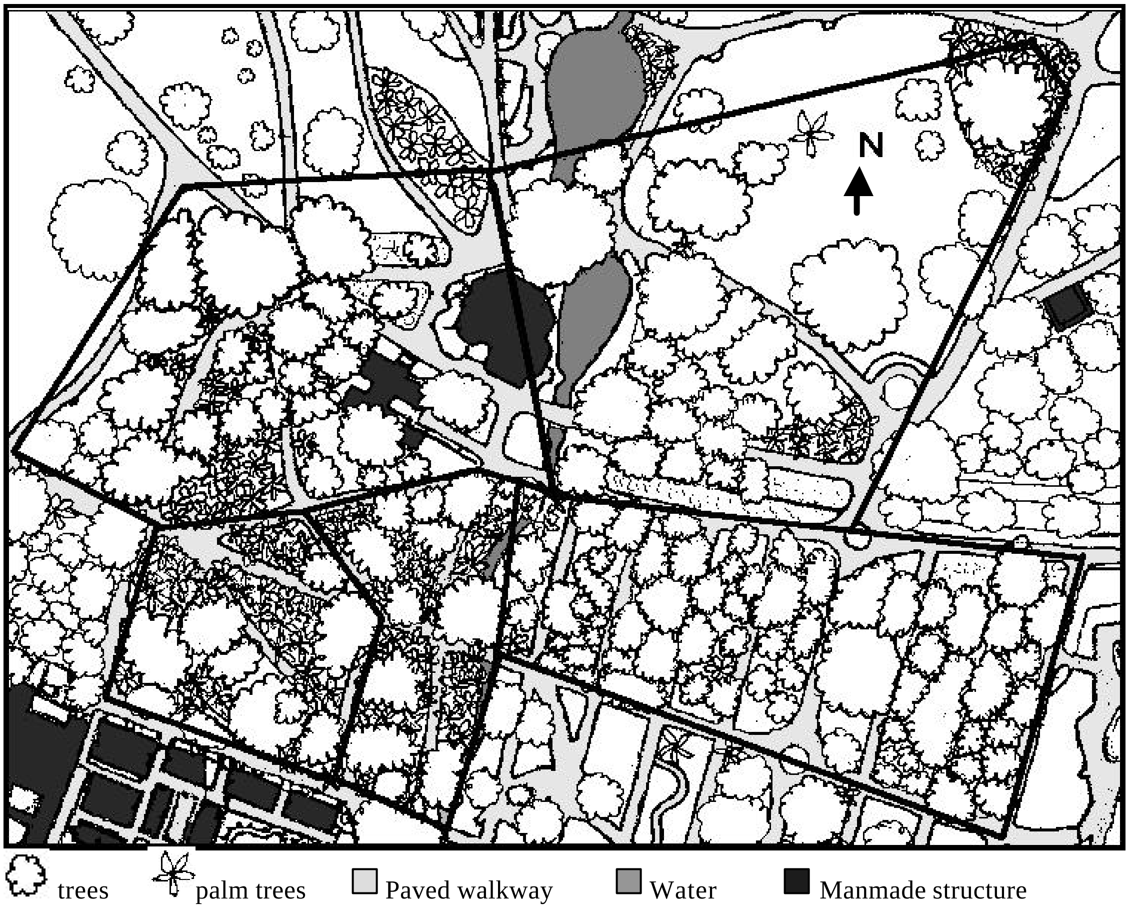


Figure 4. *Map of colony site within Sydney Royal Botanic Gardens showing colony area divided into five study sections.*

Because I was conducting the study without field assistants, time constraints mandated that each section of the colony could be surveyed only once per week.

Counts. The first step in analyzing dispersion of bats within the colony was to determine numbers of bats in each tree relative to the location of the tree. A map of the Botanical Gardens colony was created, including the location of each of the 87 trees occupied by bats. Numbers of bats in each tree were determined by counts from the ground. Between February 5 and March 25, each count was done twice. Between March 26 and April 13, each count was done three times. The average count for each tree was calculated. Resulting counts are *close estimates* of the actual number of bats. Experienced bat biologists have determined that counts conducted from the ground often result in under-estimations of the actual numbers of bats as compared to fly-out counts (Parry-Jones, pers. comm.). However, for purposes of this study, exact numbers of bats are not necessary since the objective is not a complete census but rather to determine usage patterns within and among different trees within the colony.

Surveys. Ages and sexes of bats occupying each tree were determined using survey techniques. I recorded the age and sex as possible for bats on different parts of each tree to examine the spatial distribution of bats by age and sex throughout the tree. Dispersion by age and sex was examined only for those surveys where a minimum of 10% of the bats counted were identified to age and sex. For trees containing less than 100 bats, more than 10% of the bats present were identified to age and sex, and if a tree was occupied by only 5 or 10 bats, an attempt was made to ascertain age and sex of all or most of the bats. In all cases, the largest possible numbers of bats were identified to age and sex. Trees with fewer than 10 bats were excluded from statistical tests.

Sex identification. Adult and subadult male bats of the genus *Pteropus* have relatively large genitals, making them easily distinguishable from females (Fig 5). Although males tend to be larger than females, the overlap in weight and forearm length makes these two measures inadequate for differentiating between the sexes, particularly when observing them from a distance in the field. Due to lack of physical maturation of genitals, juvenile males are difficult to distinguish from juvenile females unless the bats are in the hand. Therefore, sex of juveniles was not recorded.

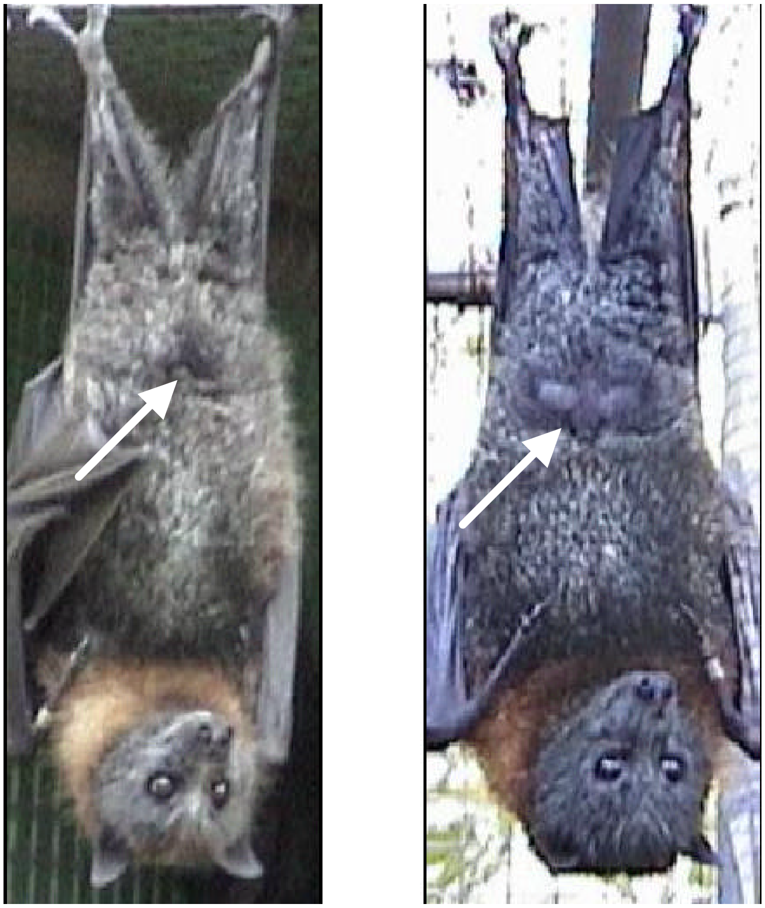


Figure 5. *Adult female and male Pteropus poliocephalus.*

Age identification. Previous researchers have divided *P. poliocephalus* into three age categories (Nelson 1965): Adult (24+ months); subadult (12 to 24 months); juvenile (less than 12 months). Age was determined by observing several morphological characteristics:

(1) differences in body size and muscle development

Adult bats are generally larger than subadults; subadult bats are generally larger than juveniles. Adults have more muscle development, particularly in the shoulders.

Age	Weight	Forearm length
Adult	600-1000g	150-180mm
Subadult	500-700g	120-160mm
Juvenile	50-600g	60-130mm

(2) proportional size of eyes and ears to overall size of head (Fig 6)

In juveniles, the eyes and ears are larger in comparison to head size. Juvenile bats also have narrower faces and the length of the ears is greater than the width of the cheeks from the eye to the side of the head. In subadults, the length of the ears is similar to the width of the cheek from the eye to side of head. In adults, the head and the face are broader; the length of the ears is generally less than the width of the cheek from the eye to the side of the head.

(3) proportion of size of head to size of body (Fig 7)

In juveniles, the head is large relative to the size of the body and the head appears to be slightly wider than the width of the shoulders. In subadults, the width of the shoulders and width of the head are fairly comparable. The shoulders of adult bats tend to be wider in proportion to the width of the head.

(4) length of legs relative to torso (Fig 7)

In juveniles and subadults, the legs make up approximately one third of the body length. In adults, the legs make up approximately one fourth of the body length.

(5) size of feet relative to body (Fig 8)

The feet of juveniles are nearly adult size; therefore, the feet of juveniles are much larger relative to length of legs and overall body size as compared to the feet of subadults and adults.

(6) development of genitals

The testacles are not well-developed in juveniles. Only subadult and adult males have well-developed testacles.

Juvenile

Subadult

Adult

Figure 6. *Age identification of Grey-headed flying foxes based on facial features.*

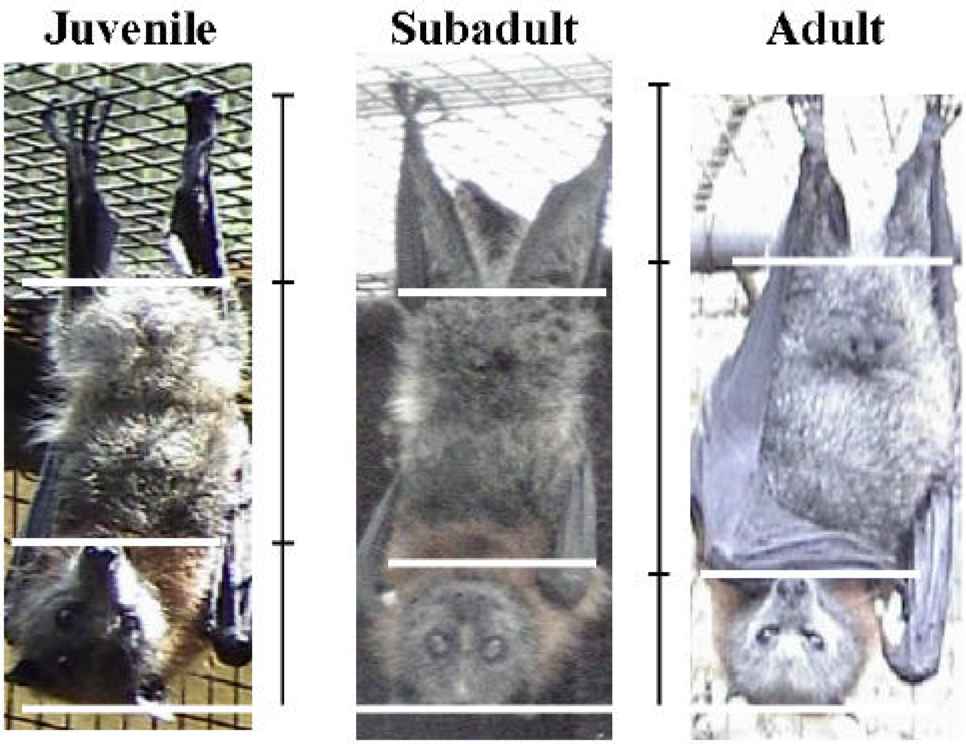


__Figure 7.__ Age identification of Grey-headed flying foxes based on proportional features.

__Figure 8.__ Age identification of Grey-headed flying foxes based on proportional size of feet.

Bats were categorized as: adult male (AM); adult female without pup (AFN); adult female with pup (AFB); subadult male (SM); subadult female without pup (SFN); subadult female with pup (SFB); juvenile without parent (J).

Tree characteristics. Height of trees was estimated using a clinometer. Bole diameter was measured using a tape measure at breast height. Tree canopies were assumed to be parabola-shaped and volume (Fig 9) was estimated using the following formula (Mawson et al 1976):

Tree volume = $2\pi R^2 HC/3$

where R is crown radius and HC is crown height. HC was calculated by estimating tree height and then subtracting 5.8 meters. No bats were ever seen to roost less than 5.8m from ground level regardless of the height of the tree or the how close the foliage came to the ground. Therefore, the volume estimated for each tree was potential roosting space for bats in the colony.

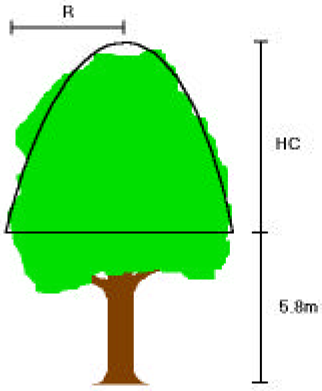


Figure 9. *Estimating tree volume taking into account lowest roosting height of bats. R = crown radius; HC = crown height; 5.8m = lowest roosting height of bats in Gardens colony. See formula above.*

Statistics. Spatial distribution was investigated by calculating the density of bats within each tree relative to the location of the tree within the colony. Density was calculated by dividing the number of bats roosting in a tree by the volume of the tree canopy. In 67 out of 78 occupied trees, 90% or more of the bats were either adults or non-adults (Fig 10). Therefore, trees that were occupied by more than 90% non-adults were classified as “non-adult” trees. All other trees were classified as “adult” trees (Table 1). The Wilcoxon Rank Sums test was used to compare the occupational densities of trees occupied by adults versus trees occupied by non-adults. A t-test was used to compare the heights of trees occupied by adults versus the heights of trees occupied by non-adults. Regression tests were run on data sets for each of the ten weeks of the study, and then compiled into one data set, to investigate the relationship between the number of adults in a tree and the height, DBH, canopy breadth, and volume of the tree, as well as interactions between those variables. Variables were inserted and deleted to determine the best model for predicting the number of adults. Sex segregation was examined using a chi square test. In order to investigate male dominance, a regression test was used to investigate the relationship between percentage of roosting males and heights of trees. All tests were run with an alpha level of 0.05. SAS software was used for all statistical analyses (Schlotzhauer and Littell 1997).

Table 1. *Numbers of adult and non-adult trees.*

Week	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	**Mar 12**	**Mar 19**	**Mar 26**	**Apr 2**	**Apr 9**
Adult trees	39	41	35	29	32	29	32	34	28	10
Non-adult trees	40	39	33	31	34	31	26	27	26	27
Total trees	79	80	68	60	66	60	58	61	54	37

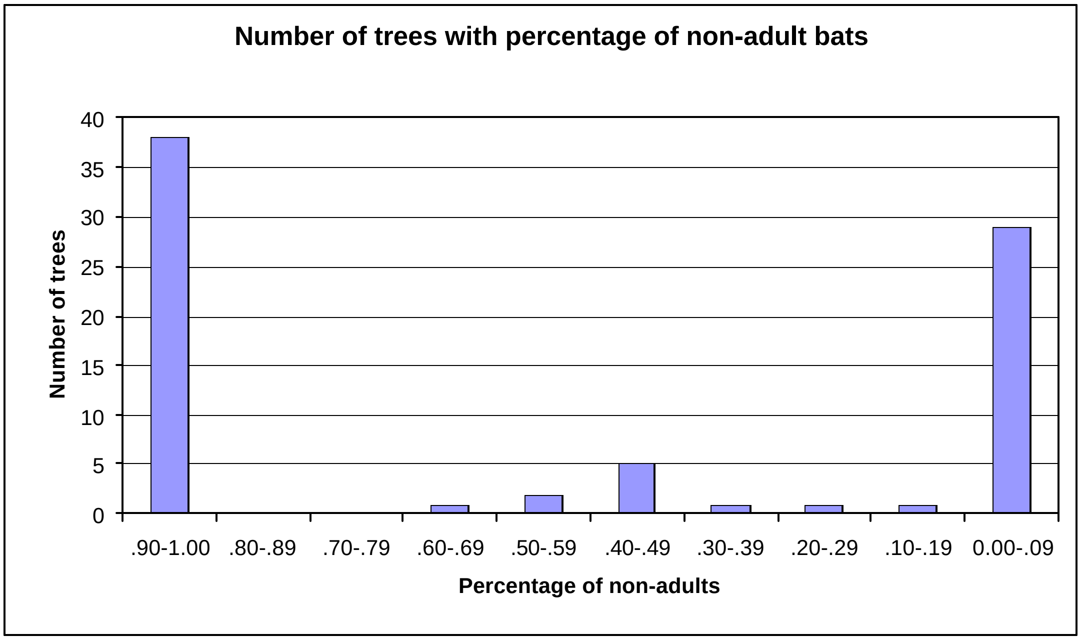


Figure 10. *Number of trees with percentage of non-adult bats.*

III. Results

Spatial distribution. The number of bats in the colony fluctuated throughout the study (Fig 11). Regardless of the number of bats in the colony, at no time during the study did the spatial distribution of bats resemble that described by Nelson (1965). Densities of bats within the trees varied widely from 0.001 bats/m^3 to 2.68 bats/m^3. The most densely occupied trees were scattered throughout the colony rather than being centralized within the colony as described by Nelson (Fig 12). Even when considering the number of bats per tree (not controlling for the size of the tree), the most highly occupied trees do not follow Nelson's pattern (Fig 13).

Eight of the top ten most densely occupied trees in the colony were occupied by non-adult bats. Overall, the most densely occupied trees were those used by non-adults (Table 2, Fig.14). This pattern of occupation was maintained throughout the 10-week study except February 26 – March 4 (p=0.246) when the mean roosting density of non-adults decreased and densities of adults and non-adults did not differ. Differences in mean roosting densities of adults and non-adults also was not statistically significant (p=0.064) during March 19–25.

Segregation. The number of bats in each age/sex category fluctuated each week throughout the study (Table 3). Despite these variations, age- and sex-specific patterns of occupation within the colony were observed.

Age segregation. The roosting locations of adult versus non-adult bats differed and reflected age segregation (Fig 15, Table A2). Adults roosted in trees that were significantly taller than the trees occupied by non-adults (Fig 16). This pattern

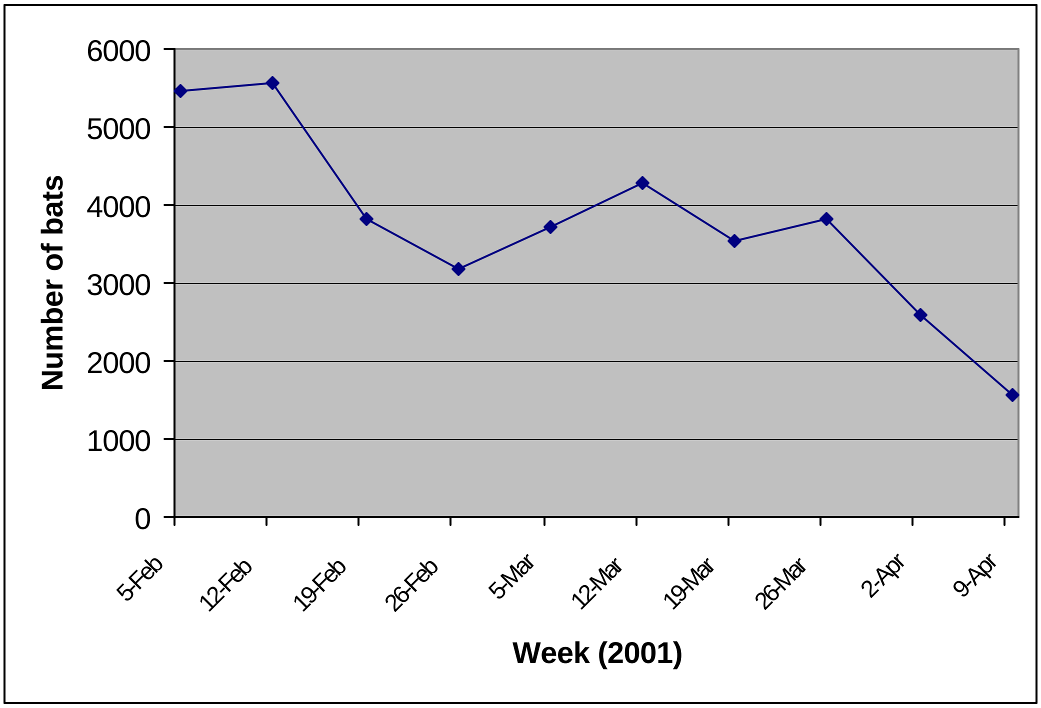
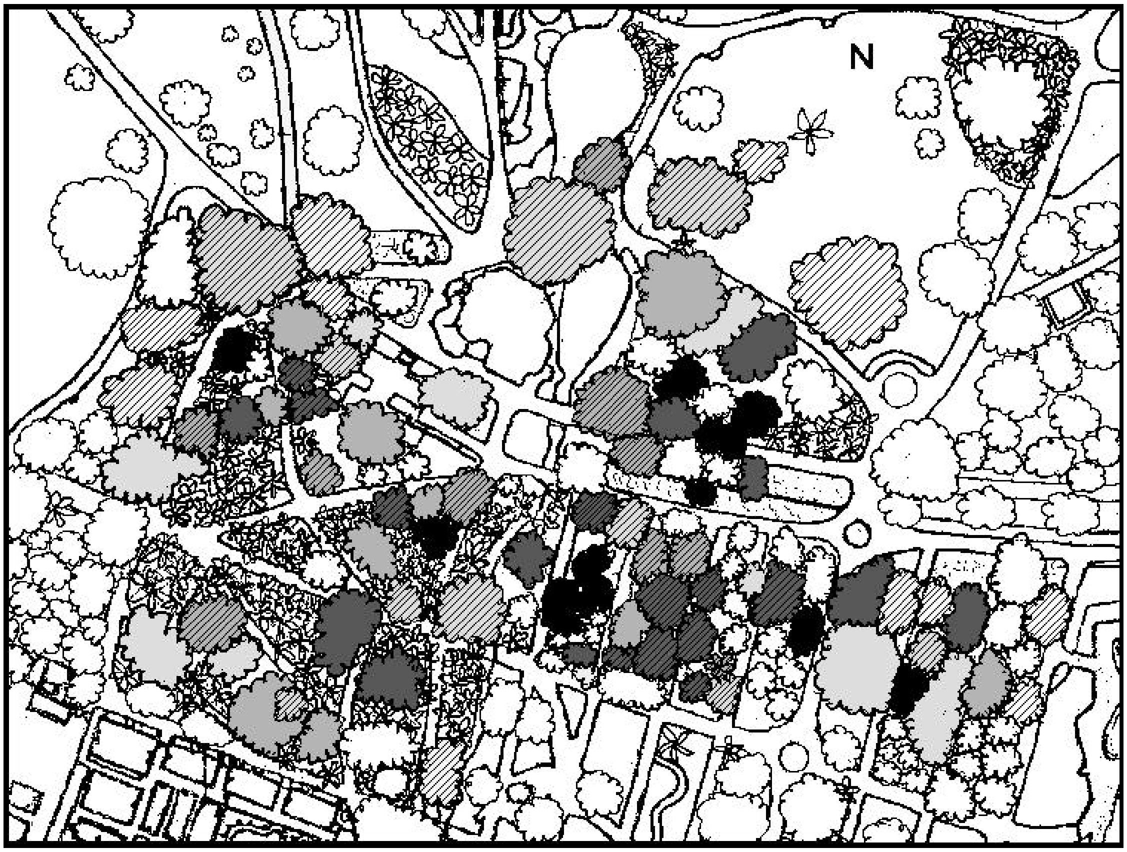


Figure 11. *Weekly fluctuations in total numbers of bats.*



Densities (bats/m^3)

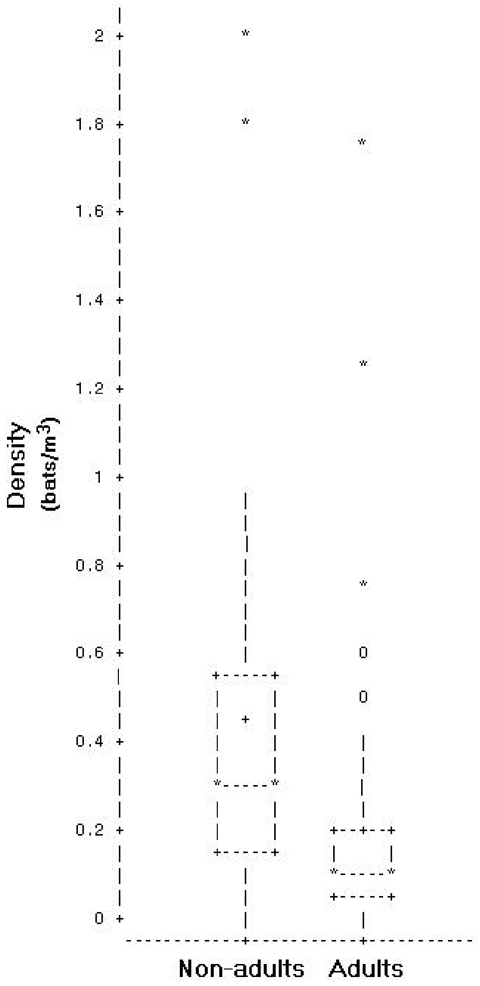
■ 1.028 – 2.680
▨ 0.581 – 0.777
■ 0.380 – 0.540
▨ 0.229 – 0.377
■ 0.187 – 0.228
▨ 0.103 – 0.181
□ 0.048 – 0.100
▨ 0.001 – 0.047

Figure 12. *Density of occupied trees Feb 12-19 when colony was at its largest. Darker shading indicates higher density.*

Figure 13. *Number of bats per tree during Week 2 of study (12-19 Feb) when colony was at its largest. Each dot represents ten bats.*

Table 2. *Age and roosting density. Results of comparison between roosting densities of adult bats vs. non-adult (subadult and juvenile) bats using the Wilcoxon Rank Sums test.* m_{adult} *= mean roosting density of adults.* $m_{non\text{-}ad}$ *= mean roosting density of non-adults. Dates in italics indicate the peak mating period.*

Week	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	***Mar 12***	***Mar 19***	***Mar 26***	**Apr 2**	**Apr 9**
$m_{\mathbf{adult}}$	0.194	0.220	0.178	0.212	0.166	0.218	0.214	0.196	0.140	0.156
$m_{\mathbf{non\text{-}ad}}$	0.470	0.424	0.374	0.218	0.376	0.460	0.374	0.412	0.410	0.240
p-value	0.0010	0.0005	0.0028	0.246	0.011	0.004	0.064	0.013	0.0007	0.0100


Roosting densities Feb 12-19 (p=0.0005)

+ = mean roosting density (Non-adults: µ=.22, SD=0.336, SE=.052; adults: µ=.426, SD=.425, SE=.068)
0 = outliers between 1.5 and 3 interquartile ranges from the end of the box
***** = outliers beyond 3 interquartile ranges from the end of the box

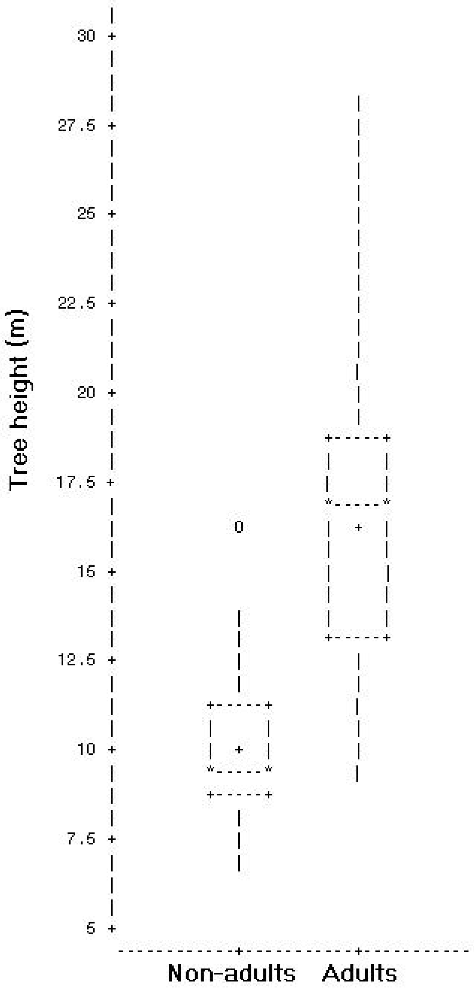
Figure 14. *Mean and standard deviation of roosting densities of adult vs. non-adult bats during the two weeks when the colony population was at its highest (Feb 12 - 18). P-value indicates results of Wilcoxon Rank Sums test comparing roosting density of adults vs. non-adults.*

Table 3. *Numbers of bats. Date indicates first day that each 5-day survey was conducted. AD = adults, M=all males, F=all females, AM=adult males, AF= adult females, AFN=adult females without pups, AFB=adult females with pups, SA=subadults, SM=subadult males, SF=subadult females, J= juveniles without parent.*

wk	date	#bats	AD	M	F	AM	AF	AFN	AFB	SA	SM	SF	J
1	**5 Feb**	5469	3258	1777	2029	1294	1501	219	1283	1738	483	527	473
2	**12 Feb**	5570	3194	1860	2108	1154	1176	257	919	2203	706	932	273
3	**19 Feb**	3832	2133	1175	2149	736	1363	320	1043	1322	440	786	359
4	**26 Feb**	3171	1928	931	1672	666	1180	181	999	835	265	492	409
5	**5 Mar**	3728	2153	1169	1875	789	1355	318	1037	996	380	520	579
6	**12 Mar**	4271	2207	1314	1837	875	1292	487	805	1011	440	545	1053
7	**19 Mar**	3530	1907	1230	1502	896	1003	467	536	887	334	499	726
8	**26 Mar**	3831	2071	1489	1322	1083	949	575	374	806	407	373	954
9	**2 Apr**	2600	1157	1227	693	740	366	311	55	848	487	327	577
10	**9 Apr**	1575	305	498	296	191	113	103	10	494	308	183	773

Figure 15. *Age segregation. Distribution of adults and non-adults in the colony.*

Tree heights and age groups Feb 12-19 (p<0.0001)



+ = mean tree height (Non-adults: µ=10.6, SD=2.65, SE=0.43; adults: µ=16.0, SD=4.43, SE=0.70)
0 = outliers between 1.5 and 3 interquartile ranges from the end of the box

Figure 16. *Mean and standard deviation of tree heights and age groups. Mean height of trees occupied by non-adults vs. mean height of trees occupied by adults.*

held for the duration of the study (Table 4, Table A3). Taller trees also had more adults roosting in them than shorter trees. From Feb 5-11 and Feb 19-Apr 8, the best model for predicting the number of adult bats in a tree included only the height-DBH interaction term ($p<0.0001$, $r^2=0.42$). During one week when the colony size was greatest from Feb 12-18, canopy and volume were also significant factors ($p<0.0001$, $r^2=0.49$). In the final week of the study from Apr 9-13, after 85% of adults had left the colony, none of the variables was significant ($p=0.064$). However, when the data from all weeks were combined, the height-DBH interaction proved to be a highly significant factor in predicting number of adult bats in a tree ($p<0.0001$, $r^2=0.30$) (Fig 17). Other variables did not significantly improve the model. Density of roosting adults did not increase with tree height.

Table 4. *Age segregation and tree height. P_{Ttest} = p-values from T-test comparing heights of trees occupied by adults vs. heights of trees occupied by non-adults. P_{Corr} = p-values from tests measuring correlation between tree height and number of adults. R = the correlation between tree height and number of adult bats. For more information, see Table A3.*

Week	Feb 5	Feb 12	Feb 19	Feb 26	Mar 5	Mar 12	Mar 19	Mar 26	Apr 2	Apr 9
P_{Ttest}	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
P_{Corr}	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.0010	0.618
R	0.700	0.713	0.629	0.646	0.632	0.673	0.612	0.517	0.435	0.085

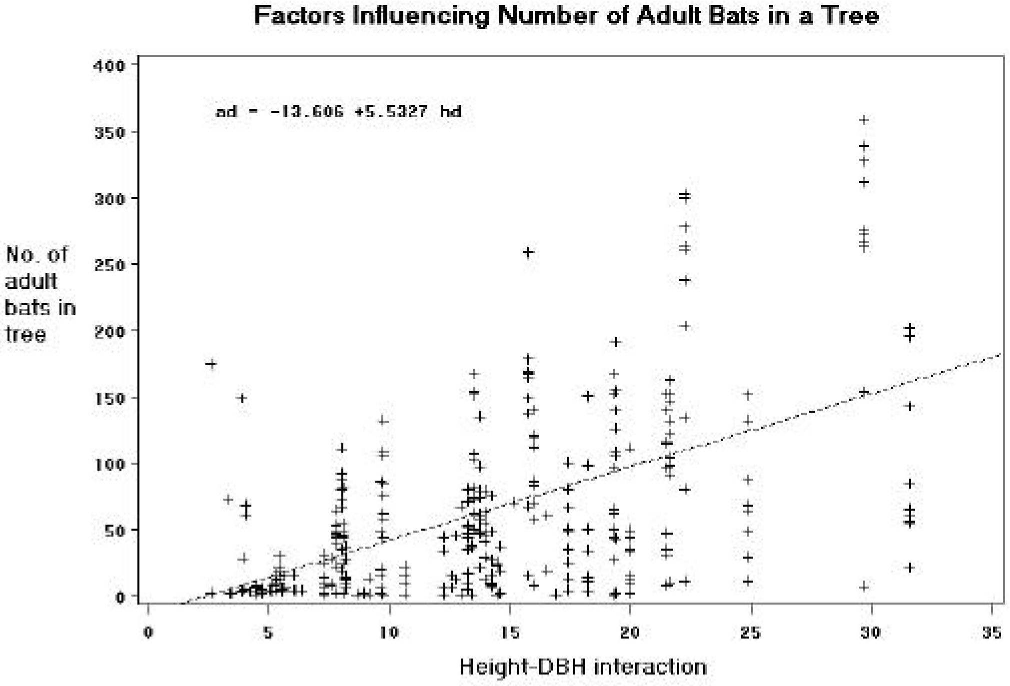


Figure 17. *Tree height-DBH vs. number of adult bats for all weeks of the study: p<0.0001, r=0.30, n=308. In equation above: ad=adults; hd=height-DBH interaction term*

Sex segregation. Bats also segregated by sex, except during the peak mating period (Table 5). Significant segregation by sex was observed from February 5 through March 4. Bats were not significantly segregated by sex between March 5 and April 1. Sex segregation was significant again from April 2–8, and then was not significant April 9–13. No relationship was found between heights of trees and percentage of roosting males, indicating that males do not roost in taller trees than females.

Survey data showed that the changes in sex distribution during the peak mating period occurred as a result of movement of males and females. Out of 44 trees, half showed movements of bats into and out of trees that changed the balance of males and females within each tree. In twelve trees, the numbers of females decreased and the numbers of males increased in trees that had been predominantly occupied by females. In five cases, the number of females within a tree did not change while the number of males increased. In two cases the number of females decreased while numbers of males remained constant. And in two cases, where the trees had been predominantly occupied by males, the number of males decreased. In only one case, a tree on the outer edge of the colony that had been mainly occupied by males, the number of females increased and the number of males decreased.

Sex ratios. The ratio of males to females fluctuated throughout the study (Tables 6 and 7). For the first seven weeks, females outnumbered males, peaking between February 19 and March 4, when there were almost twice as many females as males. By April 2, the colony was occupied by nearly twice as many males as females.

Table 5. *Sex segregation among adults. P-values and degrees of freedom (d.f.) generated by Chi-square contingency tables to investigate distribution of males and females throughout the colony. Dates in italics indicate mating period.*

Week	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	***Mar 12***	***Mar 19***	***Mar 26***	**Apr 2**	**Apr 9**
p-value	0.0017	<.0001	<.0001	<.0001	0.0004	0.167	0.795	0.886	0.016	0.829
c^2	3.19	15.30	63.90	24.18	3.57	0.16	1.81	0.002	5.78	0.25
d.f.	27	22	24	21	25	21	24	23	19	5

Table 6. *Ratio of adult and subadult males (M) to adult and subadult females (F) throughout the colony. Dates in italics indicate the peak mating period.*

Week	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	***Mar 12***	***Mar 19***	***Mar 26***	**Apr 2**	**Apr 9**
M:F	1:1.2	1:1.1	1:1.8	1:1.8	1:1.	1:1.4	1:1.2	1.1:1	1.8:	1.7:1

Table 7. *Ratio of adult males (M) to adult females (F) throughout the colony. Dates in italics indicate the peak mating period.*

Week	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	***Mar 12***	***Mar 19***	***Mar 26***	**Apr 2**	**Apr 9**
M:F	1:1.2	1:1	1:1.9	1:1.8	1:1.	1:1.5	1:1.1	1.1:1	2:1	1.7:1

IV. Discussion

Despite highly variable movement patterns of *P. poliocephalus* among colony sites (Parry-Jones 1987), there are consistent patterns of organization by age and sex within the Sydney Royal Botanic Gardens colony. As predicted, bats do segregate by age and gender, with adults occupying significantly taller trees than non-adults, indicating social dominance of older bats. The influence of age and gender as factors underlying social structure in this *P. poliocephalus* colony will be addressed in the following discussion.

Spatial distribution of roosting bats. The spatial distribution of bats within the Gardens colony did not follow the pattern described by Nelson (1965). Contrary to Nelson, spatial distribution and occupational density of Grey-headed flying foxes within individual trees appears to be influenced by the age of the bats rather than the relative location of the tree.

Roosting densities of subadults were greater than those of adults except for two weeks (26 Feb – 4 Mar and 19 – 25 Mar) (Table 2), both at a time when the colony population decreased. During these dates, the roosting density of non-adults decreased and roosting density of adults had slightly increased; however, during this period, the numbers of both non-adults and adults decreased. The lower roosting density of non-adults was most likely a direct result of the 37% decrease in number of non-adults and a smaller 10% decrease in adult numbers.

Age segregation and roosting patterns. Usage patterns of trees within the Gardens colony show that adults and non-adults not only segregate in different trees, but adult bats also roost in significantly taller trees than non-adult bats. Numerous studies have shown that age is a significant factor underlying social rank in many species (primates: Sade 1967; Hrdy and Hrdy 1976; ungulates: Wells and von Foldschmidt-Rothschild 1979; birds: Ketterson 1979; Rohwer et al. 1981; Rutberg 1983; Hogstad 1989). This pattern is found in many species of bats as well, with older males often outranking younger males (McCracken and Bradbury 1981; Wilkinson 1985; Brooke 1997). Use of space also may be determined by social rank, whereby animals of higher rank have access to more-preferred sites (Robitaille and Prescott 1993). In the fishing bat, *Noctilio leporinus*, older dominant males roost in a position above other bats in the night roosts and aggressively defend these roosting territories from other males (Brooke 1994). Within colonies of a tree-dwelling tropical fruit bat, *Pteropus giganteus*, dominant males roost at the tops of the trees while non-dominant males roost in lower branches (Neuweiler 1969).

Sex segregation. Although males and females were found roosting together throughout the study, segregation by sex was significant except during the peak mating period (March 12 – April 1). Bats exhibit a wide variety of social behaviors, particularly where mating is involved (McCracken and Wilkinson 2000). In some bat species that form summer breeding colonies, sexes segregate during late pregnancy and lactation (Bhat and Sreenivasan 1981; Karim and Banerjee 1989; Romano et al 1999) and then roost in mixed sex groups for mating (Karim and Banarjee 1989; Goymann et al 2000). McGuckin and Blackshaw (1991) showed that male *P. poliocephalus* achieve highest plasma testosterone concentrations in mid-March, with concentrations peaking on March 19. An earlier study (McGuckin and Blackshaw 1985) suggests that daylength plays in important role in regulating male hormones. This pattern in circulating hormones suggests that when males are experiencing their highest testosterone levels, they move into the trees that are predominantly occupied by females. While female hormonal levels may also be subject to daylength, Martin *et al* (1987) hypothesize that female *P. poliocephalus* may be receptive year-round, and their capitulation to coition determined primarily by male behavior. The increase in male testosterone levels also coincides with the timing of juvenile independence.

These sex segregation findings differ from Nelson (1965), who reported that the sexs are segregated from early September, when bats begin to arrive at the summer camp, until early December, when males begin courting females, indicating that the sexes were not segregated throughout lactation. Ratcliffe (1931), however, observed that females segregated in the camps during the later stages of pregnancy and throughout lactation. Nelson also reported that sexs segregated during the winter months. In a study of the Gordon Colony in the Ku-rin-gai Reserve 13.5km north of Sydney, bats that resided in the colony year-round maintained mixed-sex groups throughout the winter (Puddicombe 1981). Grey-headed flying foxes may follow the three-phase "temperate cycle" as described by Bradbury (1977) for many temperate and tropical bat species. The three phases consist of mixed sex associations in winter, sexually segregated groups at parturition and during lactation, and then mixed sex groups during the breeding season.

Sex ratios. During most weeks of the study, females in the colony outnumbered males both among adults and subadults. Unbalanced sex ratios have been found in many temperate and tropical species of bats, despite 1:1 sex ratios among juveniles (Bradbury 1977; Krishna and Dominic 1982). Different rates of maturation, mortality and longevity as well as differential use of the environment may all contribute to biased sex ratios in bats. *P. poliocephalus* females reach sexual maturity at the age of 18 months during the second breeding season after birth while males do not reach sexual maturity until the third breeding season after birth at age 30 months (Martin et al 1987), which may account at least in part for the fact that adult females appear to outnumber adult males. Mortality rates and longevity are not well-documented in this species.

During the peak mating period, the number of males in the colony increased while the number of females decreased. A recent study by Parry-Jones and Augee (2001) shows that next to food resources, the next most important factor influencing colony size is availability of potential mates. During the peak mating season, males showed a slight increase in numbers, while females showed a decrease. Males and females may have been moving into and out of the Gardens colony, respectively, in search of mating opportunities. At the onset of the peak mating period (March 12), the ratio of males to females was 1:1.5. During the final week of the peak mating period (March 26 – April 1), the ratio was 1.1 to 1.

Comparison with previous research. I can only speculate as to why the organization of bats in the Royal Botanic Gardens in Sydney differs from that observed by Nelson (1965). Nelson's studies were conducted near Brisbane, much further north (973km). Colonies in the north may have different social organization than colonies in the more southerly areas of the bats' range. The fact that these bats readily move long distances both north and south, however, does not support inherent behavioral differences among bats in different areas. In addition, biologists currently studying this species near the Brisbane area have not seen the same organization as described by Nelson (Peggy Eby, pers. comm.), suggesting either that what Nelson saw was unique to those colonies or that the social organization of the bats has changed since his studies were conducted in 1965 (the colonies studies by Nelson no longer exist due to human development). If the latter is true, then further studies of social organization may enlighten us as to the cause(s) of such change. It may be that drastic changes in the bat's habitat by human development have impacted roosting behavior of these bats.

The observations made of the spatial distribution and organization of this colony may be an artifact of its urban location. However, as Grey-headed flying foxes continue to lose habitat due to development, increasingly greater numbers of them will seek refuge in urban areas. Recent surveys estimate that between 34.2% and 54.6% of Grey-headed flying fox colonies in New South Wales occupy urban locations (a colony is considered urban if it is within 500m of development). An interesting follow-up to this study would be to compare social organization in an urban colony versus social organization in a "wild" colony.

That the above findings vary dramatically in some cases from previous research on the social organization of *P. poliocephalus* is evidence of need for further research on this species. Hopefully this study can serve as a springboard for future research on social behavior, population genetic structure, and conservation of the Grey-headed flying fox.

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Appendix

Table A1. *Tree species occupied by bats in the Sydney Royal Botanic Gardens.*

Tree No.	**SPECIES**	**Height(m)**	**DBH(m)**	**Canopy(m)**	**Volume (m^3)**
23a-1	*Keteleeria fortunei*	19.0	0.83	13.2	1209.1
23b-1	*Keteleeria fortunei*	20.4	0.60	13.0	1291.3
25-1	*Stenopcarpus sinuatus*	16.6	0.88	10.5	620.8
25-2	*Pseudobombax grandiflora*	16.8	0.79	7.6	331.6
25-3	*Tristaniopsis laurina*	17.0	0.81	17.2	1736.0
25-4	*Serianthes sachetae*	20.0	1.00	10.6	835.0
25-5	*Harpullia pendula*	20.0	0.41	10.0	744.6
25-6	*Flindersia xanthoxyla*	20.8	0.77	11.8	1087.5
26-1	*Waterhousea floribunda*	16.0	1.39	15.2	1231.7
28a-1	*Agathis moorei*	28.0	1.06	9.3	996.2
28a-2	*Agathis robusta*	27.0	1.17	12.2	1643.2
28a-3	*Agathis ovata*	13.0	0.60	11.6	507.0
28a-4	*Agathis macrophylla*	19.5	0.99	13.4	1285.5
28a-6	*Agathis laurifolia*	16.8	0.48	3.3	61.9
28a-8	*Podocarpa totara*	9.0	0.39	4.8	38.6
28b-1	*Cryptocarya obovata*	19.0	0.96	14.8	1505.0
29-1	*Poutaria wakere*	8.4	0.32	9.9	133.9
29-2	*Melicope octandra*	10.4	0.61	10.2	251.0
29-3	*Brachychiton discolor*	10.4	0.88	9.1	198.5
29-4	*Nothofagus moorei*	9.6	0.59	8.8	153.7
29-5	*Alloxylon flammeum*	9.0	0.47	4.7	36.5
29-6	*Poutaria lucuma*	9.2	0.48	8.7	134.1
30-1	*Diospiros fasiculosa*	11.4	0.46	8.7	219.8
30-2	*Macadamia tetraphylla*	8.4	0.50	5.5	41.2
30-3	*Alphotonia excelsa*	9.6	0.61	11.6	268.1
30-4	*Vitex lucens*	7.8	0.32	7.1	53.1
30-5	*Citharexylum montividense*	6.8	0.51	12.9	87.2
30-6	*Arytera divaricata*	9.7	0.27	8.5	146.4
31-1	*Backhousea citriodora*	9.6	0.46	10.1	201.3
31-2	*Jubea chilliensis*	13.0	1.01	5.2	102.3
31-3	*Fraxinus ornus*	7.6	0.68	8.9	74.3
31-4/6	*Arytera distylis/Juglans hindsii*	9.5	0.53	10.1	198.7
31-5	*Davidsonia pruriens*	7.6	0.35	4.6	19.5
32-1	*Metasequoia glyptostroboides*	10.0	0.61	4.8	50.9
32-2	*Beilschmiedia elliptica*	8.8	0.60	11.6	211.3
33b-1	*Picconia excelsa*	9.1	0.83	11.8	241.7
33b-2	*Hernandia cordigera*	9.1	1.17	13.6	318.0
33b-3	*Planchonella australis*	13.2	0.42	7.2	201.9
34-1	*Phytolacca dioica*	18.8	0.88	16.1	1759.1
34-2	*Phoebe nanmu*	9.6	0.41	6.8	92.2
34-3	*Backhousea sciadophora*	11.2	0.36	6.8	129.1
34-4	*Maclura pomifera*	10.2	0.59	8.8	177.9
35-1	*Quercus macrocarpa*	14.0	0.62	7.4	236.3
35-2	*Heritiera trifoliolata*	21.0	1.06	10.7	910.7
35-3	*Heritiera actinophylla*	16.8	0.76	11.8	796.1

Table A1. *Continued.*

Tree No.	**SPECIES**	**Height(m)**	**DBH(m)**	**Canopy(m)**	**Volume (m^3)**
35-4	*Dysoxylum mollisimum*	15.0	0.84	14.6	1031.9
35-5	*Pleiogynium timoriense*	15.0	0.73	10.3	844.6
41-1	*Waterhousea floribunda*	12.5	1.72	15.5	1135.8
41-2	*Chorisia speciosa*	11.0	1.23	20.4	146.8
41-3	*Planchonella australis*	8.6	0.41	10.0	475.5
41-4	*Bauhinia X blakeana*	9.5	0.47	15.7	609.1
41-6	*Cinnamomum camphora*	12.5	0.78	13.2	20.6
41-7	*Pachira aquatica*	7.0	0.23	5.7	76.5
41-8	*Flindersia schottiana*	8.4	0.70	7.5	202.3
41-9	*Ginkgo biloba cv. Fastigiata*	12.6	0.74	7.5	30.9
41-10	*Markhamia obtusifolia*	7.6	0.23	5.7	168.8
42-1	*Liriodendron tulipifera*	9.0	0.44	10.0	225.6
43-1	*Backhousea citriodora*	10.0	0.53	10.1	65.6
43-2	*Funtumia africana*	9.5	0.32	5.8	198.9
43-5	*Ficus laurifolia*	11.0	0.35	8.6	2355.6
50-1	*Syzygium francissii*	16.5	1.31	20.5	307.8
50-3	*Tristaniopsis laurina*	13.5	0.54	8.7	1510.2
53-1	*Elaeocarpus kirtonii*	13.0	0.82	20.0	1217.1
56-2	*Cedrella mexinana*	13.8	0.65	17.1	819.9
57-1	*Phoebe nanmu*	15.0	0.65	13.1	71.4
57-2	*Sloanea australis*	9.6	0.49	6.0	68.1
57-3	*Davidsonia pruriens*	9.6	0.35	5.9	43.7
57-4	*Schefflera elegantissima*	10.0	0.26	4.5	122.0
57-5	*Hovenea dulcis*	10.4	0.32	7.1	1662.3
58-1	*Podocarpus elatus*	20.4	0.95	14.8	707.7
58-2	*Podocarpus elatus*	18.4	0.76	10.4	60.2
58-3	*Aleurites moluccana*	9.6	0.39	5.5	544.5
58-4	*Aleurites moluccana*	13.6	0.55	11.6	282.9
59-2	*Araucaria rulei*	20.0	0.67	6.2	272.1
59-3	*Araucaria birimulata*	16.0	0.34	7.1	192.2
59-4	*Endiandra discolor*	16.0	0.50	6.0	446.9
59-5	*Melaleuca styphelioides*	16.0	0.95	9.2	1318.1
60-1	*Casuarina cunninghamiana*	17.6	0.81	14.6	1012.2
60-2	*Casuarina cunninghamiana*	16.8	0.86	13.3	1883.0
60-3	*Bischofia javanica*	19.0	1.31	16.5	1748.2
60-4	*Cryptocarya obovata*	13.0	0.94	21.5	730.1
94-1	*Afrocarpus falcatus*	11.0	1.18	16.4	1380.4
L24-1	*Ficus virens*	13.0	1.34	19.1	1053.7
L24-2	*Harpephylum caffrum*	11.2	1.51	19.3	927.0
L24-3	*Melaleuca quinquinervia*	12.5	1.06	16.3	277.5
L5-1	*Melaleuca styphelioides*	10.6	0.91	10.5	1031.9

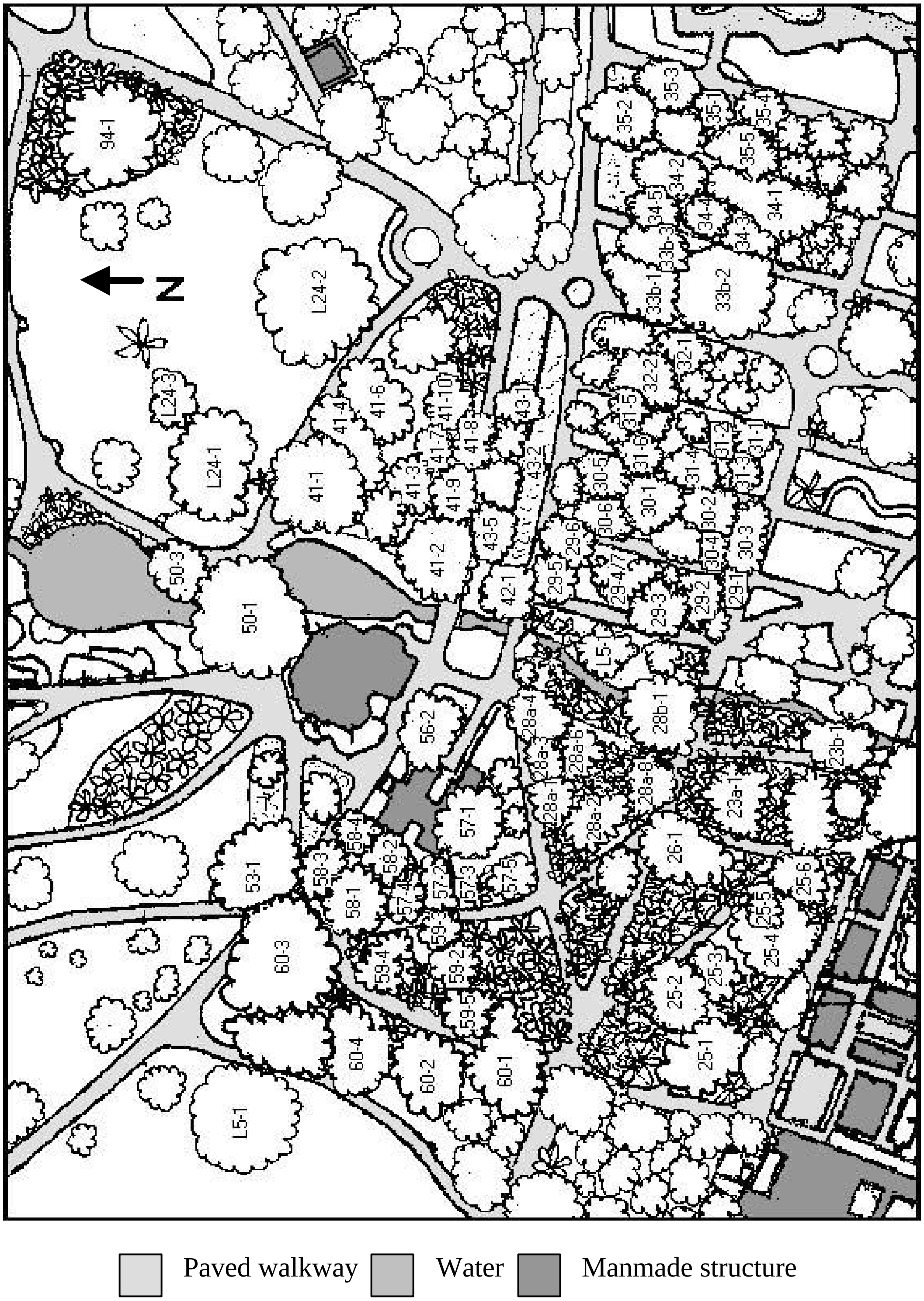

Figure A1. *Map of garden indicating location of each tree.*

Table A2. *Age segregation by tree between adults and non-adults for all weeks of the study. # = total number of bats in the tree. Trees with fewer than 10 bats were not included in statistical analyses.*

	Week																			
	Feb 5		Feb 12		Feb 19		Feb 26		Mar 5		Mar 12		Mar 19		Mar 26		Apr 2		Apr 9	
Tree	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**
23a-1	171	169:2	259	259:0	181	179:2	221	168:53	200	165:34	203	167:36	174	149:25	196	138:58	81	67:14	25	15:10
23b-1	44	44:0	34	34:0	6	6:0	0		0		0		0		1	1:0	0		0	
25-1	37	37:0	19	19:0	2	2:0	0		0		0		0		0		0		0	
25-2	80	80:0	71	71:0	55	52:3	54	47:7	65	53:11	67	52:15	53	44:9	40	35:5	21	17:4	0	
25-3	146	135:11	97	97:0	81	74:7	69	47:22	91	49:42	96	61:35	79	57:22	90	79:11	39	21:19	0	
25-4	115	111:4	104	35:69	59	44:15	29	13:16	49	49:0	44	33:11	20	15:5	9	9:0	2	2:0	0	
25-5	37	37:0	43	28:15	15	10:5	17	13:4	23	13:10	18	12:6	17	14:3	6	6:0	0		0	
25-6	143	141:2	140	120:19	121	112:9	94	86:8	130	121:9	109	83:26	103	70:33	71	57:13	8	8:0	0	
26-1	318	134:184	303	303:0	300	300:0	301	278:23	271	261:10	248	204:44	334	264:70	254	238:16	107	80:27	18	11:7
28a-1	330	328:2	359	359:0	328	312:16	339	339:0	303	275:28	331	263:67	297	267:30	332	273:58	186	154:32	39	7:32
28a-2	198	196:2	202	202:0	152	143:9	65	65:0	61	56:4	92	84:8	80	55:25	66	61:5	42	21:20	0	
28a-3	48	47:1	55	53:2	53	45:8	62	48:14	50	39:11	64	64:0	54	48:6	56	44:12	28	22:6	25	2:23
28a-4	153	153:0	168	168:0	119	96:23	90	65:24	67	44:22	70	65:5	78	62:16	133	50:83	78	27:51	77	1:76
28a-6	81	81:0	81	81:0	50	48:2	59	46:13	54	45:9	62	54:8	50	44:6	59	46:12	28	24:4	31	2:29
28a-8	0		10	10:0	8	8:0	0		20	20:0	14	14:0	8	7:1	10	10:0	3	3:0	0	
28b-1	151	151:0	98	98:0	0		0		11	11:0	0		3	3:0	35	34:1	14	14:0	50	50:0
29-2	33	0:33	74	0:74	67	0:67	47	0:47	39	0:39	57	0:57	33	4:29	41	0:41	19	0:1	20	0:20
29-3	208	0:208	139	0:139	93	13:80	57	0:57	35	0:35	122	0:122	72	13:59	90	1:88	60	0:60	7	0:7
29-4/7	113	0:113	100	0:100	80	15:65	69	6:63	42	0:42	102	0:102	94	0:94	83	0:83	89	0:89	84	0:84
29-5	74	0:74	3	0:3	59	0:59	25	3:22	45	0:45	47	0:47	50	0:50	65	0:65	63	0:63	28	0:28
29-6	8	0:8	58	0:58	10	0:10	7	0:7	3	0:3	9	0:9	10	0:10	6	0:6	6	0:6	1	0:1
30-1	78	0:78	76	0:76	92	0:92	74	4:70	103	0:103	99	0:99	97	10:86	91	0:91	60	0:60	21	0:21
30-2	0	0:0	71	0:71	15	0:15	40	0:40	50	0:50	45	0:45	25	0:25	38	2:35	19	0:19	5	0:5
30-3	43	0:43	29	0:29	33	0:33	14	0:14	21	0:21	32	0:32	19	0:19	25	0:25	13	0:13	2	0:2
30-4	20	0:20	21	0:21	19	0:19	8	0:8	10	0:10	16	0:16	23	0:23	16	0:16	11	0:11	1	0:1

Table A2. *Continued.*

	Feb 5		Feb 12		Feb 19		Feb 26		Mar 5		Mar 12		Mar 19		Mar 26		Apr 2		Apr 9	
Tree	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**
30-5	5	0:5	15	0:15	8	0:8	12	2:10	4	0:4	7	0:7	8	0:8	8	0:8	3	0:3	0	
30-6	28	0:28	22	0:22	24	0:24	10	0:10	15	0:15	42	0:42	16	0:16	17	0:17	14	0:14	0	
31-1	10	1:9	18	0:18	12	0:12	0		2	0:2	0		0		0		0		0	
31-2	19	0:19	20	0:20	4	0:4	0		4	0:4	0		0		2	0:2	0		0	
31-3	30	0:30	33	8:24	12	0:12	5	0:5	18	0:18	26	3:23	10	0:10	8	0:8	14	0:14	3	0:3
31-4/6	73	0:73	65	0:65	59	4:55	24	0:24	44	0:44	92	0:92	40	0:40	44	0:44	31	0:31	11	0:11
32-1	88	0:88	76	0:76	52	0:52	3	0:3	55	0:55	41	0:41	21	0:21	28	4:25	49	0:49	0	
32-2	110	0:110	85	0:85	74	0:74	41	0:41	100	0:100	98	0:98	73	0:73	50	0:50	35	0:35	31	0:31
33b-1	71	28:42	70	0:70	28	9:19	0		13	8:5	16	0:16	0		0		0		0	
41-1	121	0:121	89	0:89	82	35:47	75	47:28	139	116:23	157	140:17	102	96:6	205	153:51	135	115:20	23	8:16
41-2	99	81:18	147	73:73	117	50:67	147	107:40	162	74:88	159	103:56	151	62:89	212	154:58	198	152:46	224	168:56
41-3	75	0:75	98	0:98	69	0:69	76	0:76	85	0:85	103	0:103	68	0:68	82	0:82	53	0:53	29	0:29
41-4	33	0:33	15	0:15	15	7:0	7	0:7	0		25	8:18	21	6:15	17	7:10	10	8:2	0	
41-6	120	0:120	170	0:170	179	0:179	31	0:31	80	0:80	118	0:118	42	0:42	54	0:54	137	0:137	259	0:259
41-7	6	0:6	11	0:11	6	0:6	5	0:5	9	0:9	1	0:1	8	0:8	10	0:10	7	0:7	0	
41-8	98	0:98	103	0:103	44	0:44	14	0:14	67	0:67	81	0:81	61	0:61	72	0:72	75	0:75	39	0:39
41-9	59	0:59	48	0:48	58	0:58	76	0:76	76	0:76	43	0:43	89	0:89	92	0:92	86	0:86	47	0:47
42-1	10	0:10	0		0		0	0:0	8	0:8	32	0:32	2	0:2	18	5:13	11	0:11	20	0:20
43-1	35	0:35	52	0:51	22	0:22	47	0:47	41	0:41	62	0:62	45	0:45	71	13:58	62	16:47	33	0:33
43-2	30	0:30	38	0:38	29	0:29	26	0:26	29	0:29	36	0:36	20	0:20	28	0:28	22	0:22	6	0:6
43-5	8	0:8	27	0:27	35	0:35	30	0:30	27	4:22	30	3:27	48	0:48	33	0:33	30	0:30	51	4:46
50-1	190	153:37	149	149:0	138	122:16	161	132:29	170	163:7	224	147:77	155	91:63	139	104:35	120	98:21	15	0:59
50-3	59	0:60	60	1:15	16	2:14	7	25:0	25	9:34	43	0:11	11	14:21	35	7:66	74	10:5	67	0:67
53-1	28	22:6	31	31:0	1	1:0	1	1:0	10	10:0	0		0		0		0		0	
56-2	18	2:16	40	0:40	0		2	0:2	0		0		0		10	2:8	0		0	
57-1	108	108:0	101	0:101	58	44:15	80	62:17	100	75:25	123	105:18	106	84:22	149	132:17	86	58:28	1	1:0
57-2	33	0:33	28	0:28	29	0:29	22	0:22	29	0:29	27	2:24	35	5:30	15	4:10	12	2:10	0	
57-4	25	0:25	18	0:18	14	0:14	11	0:11	18	0:18	18	0:18	15	2:13	0		Tree cut down			

Table A2. *Continued.*

	Feb 5		Feb 12		Feb 19		Feb 26		Mar 5		Mar 12		Mar 19		Mar 26		Apr 2		Apr 9	
Tree	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**	**#**	**ad : non**
57-5	29	0:29	24	0:24	28	0:28	29	0:29	48	0:48	35	0:35	34	0:34	24	0:24	12	0:12	0	
58-1	140	140:0	175	175:0	140	108:32	160	126:33	148	126:22	211	192:19	184	155:29	141	105:35	59	43:16	2	2:0
58-2	46	46:0	72	72:0	49	29:20	46	46:0	72	63:9	86	79:7	68	55:13	58	41:17	14	12:2	0	
58-4	0		5	0:5	38	0:38	25	0:25	39	0:39	30	15:15	50	5:45	38	0:38	0		9	0:9
59-2	47	38:9	73	36:36	8	0:8	0		18	0:18	6	0:6	1	0:1	45	1:44	0		0	
59-3	33	0:33	31	0:31	24	0:24	27	22:5	30	30:0	16	10:6	19	12:7	19	16:3	18	18:0	0	
59-4	105	92:12	111	111:0	109	88:21	91	72:20	100	88:12	111	80:31	79	66:13	53	35:18	26	19:7	0	
59-5	20	0:20	70	70:0	0		0		0		0		0		0		0		0	
60-1	48	48:0	75	75:0	27	27:0	10	10:0	9	9:0	7	7:0	16	16:0	8	8:0	0		0	
60-2	23	23:0	25	25:0	1	1:0	0		0		0		0		0		0		0	
60-3	132	132:0	152	152:0	48	29:18	51	48:2	100	87:13	89	64:25	83	68:15	0		11	11:0	0	
L24-1	109	100:9	97	49:49	80	80:0	59	13:46	56	50:6	69	66:3	39	35:4	49	49:0	25	25:0	4	4:0
L5-1	60	0:60	70	0:70	48	15:33	3	2:1	11	0:11	36	0:36	6	6:0	56	48:8	149	86:63	264	20:244

Table A3. *Mean (μ), standard deviation (SD), and standard error (SE) of heights of trees occupied by adults versus heights of trees occupied by non-adults.*

	Feb 5		Feb 12		Feb 19		Feb 26		Mar 5		Mar 12		Mar 19		Mar 26		Apr 2		Apr 9	
	Adult	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**	**Adult**	**Non**
m	14.4	9.3	16.0	10.6	16.3	10.3	16.4	9.7	16.0	10.1	16.1	9.8	15.8	9.8	15.6	9.7	16.2	9.3	16.1	9.8
SD	3.37	2.19	4.43	2.65	4.46	2.72	4.70	1.69	4.71	2.41	4.83	2.33	4.78	2.69	4.87	1.87	4.80	1.51	4.67	1.85
SE	0.70	0.35	0.70	0.43	0.90	0.47	0.87	0.30	0.82	0.41	0.88	0.43	0.83	0.54	0.80	0.38	0.91	0.30	1.20	0.39

Table A4. *Ratios of male and female adult bats in each tree for all weeks of the study. All ratios are males:females. Number in parentheses indicates number of adult bats in the tree. Sample sizes of less than 10 were not included in statistical calculations (indicated by "n/a").*

	Week									
Tree	**Feb 5**	**Feb 12**	**Feb 19**	**Feb 26**	**Mar 5**	**Mar 12**	**Mar 19**	**Mar 26**	**Apr 2**	**Apr 9**
23a-1	1.5:1 (169)	n/a	1.6:1 (179)	1.2:1 (168)	1:3 (165)	1:1.3 (167)	1.1:1 (149)	3.2:1 (138)	2.9:1 (67)	4:1 (15)
25-2	n/a	n/a	1:3.5 (52)	1:2 (47)	1:2.5 (53)	1:1 (52)	1:1.5 (44)	1:1.3 (35)	all M (17)	no bats
25-3	1:2 (135)	n/a	1:23 (74)	1:5 (47)	1:3 (49)	1:2.5 (61)	1:2.2 (57)	2.4:1 (79)	2:1 (21)	no bats
25-4	n/a	n/a	1:2 (44)	3:1 (13)	1:2 (49)	1:2 (33)	1:1 (15)	n/a	n/a	no bats
25-5	1.3:1 (37)	all M (28)	all F (10)	1.3:1 (13)	1:3 (13)	1:3.5 (13)	1:1.5 (14)	n/a	no bats	no bats
25-6	1.5:1 (141)	1.1:1 (120)	1.1:1 (112)	1:1.1 (86)	1.2:1 (121)	1:1.2 (83)	1:1.1 (70)	2.1:1 (57)	n/a	no bats
26-1	1:1 (318)	1:4.6 (303)	1:6.3 (300)	1:5.7 (278)	1:2 (261)	1:2.1 (204)	1:1.5 (264)	1:1.7 (238)	2:1 (80)	4:1 (11)
28a-1	1:3.9 (328)	1:1 (359)	1:2.2 (312)	1:1.3 (339)	1:2.1 (275)	1:1.4 (263)	1.7:1 (267)	1:1.2 (273)	3:1 (154)	1.3:1 (50)
28a-2	1:8.5 (196)	1:1.7 (202)	1:1.7 (143)	n/a	1:1.3 (56)	1:1.1 (84)	1:1.2 (55)	1.6:1 (61)	20:1 (21)	1.3:1 (168)
28a-3	1:7.5 (46)	1:25 (53)	1:2.6 (45)	1.3:1 (48)	1:1.5 (39)	1:2.5 (64)	1:1.9 (48)	2.2:1 (44)	1.7:1 (22)	1:2 (10)
28a-4	1:1.2 (152)	2:1 (168)	1:2.5 (96)	1:1.7 (65)	1:2.3 (44)	1:1.2 (65)	1:1 (62)	2:1 (50)	1.8:1 (27)	all M (20)
28a-6	1.1:1 (81)	n/a	1:3.2 (48)	1:1.8 (46)	1:4 (45)	1:2.1 (54)	1:1.1 (44)	1.1:1 (46)	1:1 (24)	n/a
41-1	n/a	n/a	1:5 (35)	1.5:1 (47)	1.5:1 (47)	1:2.4 (140)	1:1.1 (96)	1:1.5 (153)	1.9:1 (115)	n/a
41-2	1:1.5 (81)	1:1.5 (73)	1:2 (50)	1:1 (107)	1:1.2 (74)	1:1.2 (103)	1:1 (62)	1:1 (154)	1.3:1 (152)	1.3:1 (168)
50-1	1:2.1 (153)	1:1.6 (149)	1:2.3 (122)	1:1.3 (132)	1:3.4 (163)	1:1.7 (147)	1:1.4 (91)	1:2 (104)	1.2:1 (98)	1:2.3 (10)
57-1	1:3.6 (108)	n/a	1:2 (44)	all F (62)	1:2 (75)	1:1.4 (105)	1:1.1 (84)	1.3:1 (132)	2.2:1 (58)	no bats
58-1	1:1.2 (140)	1:1.1 (175)	1:1.8 (108)	all F (126)	1:3.3 (126)	1:2.1 (192)	1:1.3 (155)	1:1.1 (105)	1.6:1 (43)	n/a
58-2	all F (46)	n/a	2:1 (29)	1:1.7 (46)	1:2.8 (63)	1:1.9 (79)	1:3.3 (55)	1:1 (41)	5:1 (12)	no bats
59-3	no adults	no adults	no adults	1:3.4 (22)	all F (30)	2:1 (10)	1:4.1 (12)	7:1 (16)	17:1 (18)	no bats
59-4	1.1:1 (92)	1:20 (111)	1:1.9 (88)	1:4.5 (72)	1:2.2 (88)	1:2.3 (80)	1.2:1 (66)	1:1 (35)	18:1 (19)	no bats
60-1	1:1 (48)	all M (75)	all M (27)	n/a	n/a	n/a	all M (16)	n/a	no bats	no bats
60-3	7.3:1 (132)	n/a	1.7:1 (29)	2.9:1 (51)	3.5:1 (87)	1:1.2 (64)	1:1 (68)	2:1 (38)	n/a	no bats
L24-1	1:2.8 (100)	5:1 (49)	1.6:1 (80)	all F (13)	1.7:1 (50)	6:1 (66)	1.5:1 (35)	2:1 (49)	2.5:1 (25)	n/a

Vita

Jennifer Lee Holmes was born in Royal Oak, Michigan on April 11, 1971. Her family moved to Henderson, North Carolina in 1979, where she attended public schools and graduated from Vance Senior High School in June, 1989. She received a Bachelor of Science in Biology in 1993 from Guilford College in Greensboro, NC. She then went on to the Maxwell School of Citizenship and Public Affairs at Syracuse University. From 1996-1997, during a leave of absence from Syracuse University, she taught Math and Science for the Durham Public School System. She returned to Syracuse University and received her Master of Public Administration in 1997. She then spent two years working as a Project Manager in the Information Technology Department for Carrier Transicold Division of Carrier Corporation in Syracuse, NY. In autumn 1999, she entered the graduate program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville and officially received her Master's degree in May 2002.