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I, Sara E Hyams, hereby submit this original work as part of the requirements for the degree of:

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Arboreal Habitat Structure Affects Locomotor Speed and Path Choice of White-footed Mice (Peromyscus leucopus)

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Arboreal Habitat Structure Affects Locomotor Speed and Path Choice of White-footed Mice (*Peromyscus leucopus*)

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by

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Abstract

Arboreal habitats pose several challenges for locomotion resulting from narrow cylindrical surfaces, steep inclines, and branches that obstruct straight paths. I determined whether different diameters, inclines, or complexity of branches affected speed of movement and path choice for a semi-arboreal rodent (*Peromyscus leucopus*). We videotaped laboratory trials of locomotor performance of mice running on cylinders with diameters of 10, 16, 28, 54, and 116 mm, oriented at inclines of 0° and 45° (uphill and downhill), and a subset of diameters horizontally oriented that had secondary branches (pegs) every 10 or 20 cm. For similar branch diameters the speeds of mice were usually faster when running horizontally rather than on inclines, and pegs decreased running speed compared to unobstructed surfaces. When pegs were present, the frequency and duration of pauses increased, speed decreased with decreased distance between pegs, and larger diameters enhanced speeds by reducing the need of mice to use a convoluted trajectory to avoid the pegs. The difficulties of maintaining balance and avoiding toppling seem likely to have caused much of the decrease in speed and increased amounts of pausing. Thus, branch diameter, incline, and the presence of and spacing of secondary branches often had widespread and significant interactive effects on locomotor performance, and additional experiments revealed some of these factors significantly influenced the routes chosen by mice.
Acknowledgements

I thank Guy N. Cameron for his guidance as my mentor and advisor, B. Jayne for his contribution to this work, helpful comments, suggestions, and direction, K. Petren for advice, G. Klein and J. Loomis for guidance, S. Jacob for assistance with fieldwork and experiments, and The Ohio Division of Natural Resources for permission to conduct research on their wildlife preserve. This work was funded by the Wieman-Wendell-Benedict Fund of the University of Cincinnati, Department of Biological Sciences.
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Introduction

Despite their considerable anatomical and phylogenetic diversity, the large number of animal species that are found in arboreal habitats face similar challenges for locomotion, not often found in terrestrial ground habitats, including narrow cylindrical surfaces, inclines, and branches that obstruct movement (Cartmill, 1985; Lammers and Biknevicius, 2004; Astley and Jayne, 2009). When animals move along narrow cylindrical surfaces, toppling sideways and slipping can occur, and steep inclines increase the risk of slipping. Secondary branches, protruding from primary branches, may create obstacles that animals must negotiate. Such characteristics of the habitat present unique physical constraints on efficient movement of arboreal animals, often leading to species-specific responses (Losos and Sinervo, 1989; Mattingly and Jayne, 2004; Delciellos and Vieira, 2006).

Arboreal habitat structure, characterized by branches of different diameters, inclinations, and complexity, affects speed of movement and frequency and duration of pausing of animals, responses that vary among different species of animals (Mattingly and Jayne, 2004; Gallardo-Santis et al., 2005; Delciellos and Vieira, 2006). Effects of branch diameter on speed and choice of pathways have been studied extensively for Anolis lizards. Maximal running speed declined on thinner branches for Anolis lizards (Losos and Sinervo, 1989); however, when turn angle was introduced Anolis lizards would pause and negotiate the turn to continue on a larger diameter cylinder than continuing on a straight path using a smaller diameter cylinder (Higham et al., 2001; Mattingly and Jayne, 2005). In contrast, perches with smaller diameters were more beneficial for uphill locomotion for rat snakes, as they were unable to climb perches with diameters >57 mm (Astley and Jayne 2007, 2009). Rat snakes can crawl faster and traverse previously impassible perches when secondary branches are present, and when given a choice

Arboreal activity is closely related to the morphology, behavior, and ecology of a species (Packer and Layne, 1991; Gallardo-Santis et al., 2005). Many arboreal animals have specialized structures or change their behavior to adhere to or grip surfaces, which decrease their risk of slipping or toppling. *Anolis* lizards with short limbs make use of narrow branches and have slower running speeds than ecomorphs with longer limbs due to shorter stride lengths (Spezzano and Jayne, 2004). Primates and opossums adjust their limb placement and walking patterns to maneuver within arboreal environments, and also changed speed and paused on varying substrates during their locomotor behavior (Preuschoft, 2002; Lemelin et al., 2003; Lammers and Biknevicius, 2004; Lammers et al., 2006; Stevens, 2008). Small quadrupedal mammals, such as mice, keep their toes spread apart and rely on claws and friction-enhancing specializations such as elevated pads (plantar tubercles) on the bottom of their feet to grip climbing surfaces and also changed gaits based on substrates and speed preferences (Horner, 1954; Layne, 1970; Cartmill 1985). Studies regarding gait sequencing have also focused on kinematics and kinetics, in which animals traversed treadmills or cylinders at a constant speed and forces and torque were described during locomotion (oppossums: Schmitt and Lemelin, 2002; Lemelin et al. 2003; Lammers and Biknevicius, 2004; Lammers, 2007; primates: Franz et al. 2005; Stevens, 2008; rats: Pereira et al. 2006; Garnier et al. 2008).

The cylindrical nature of arboreal perches creates footholds that limit the lateral placement of feet and branches with smaller diameters have large curvatures relative to branches of larger diameters which begin to resemble more terrestrial, or flat, substrates (Cartmill, 1974). Larger diameter perches are a concern for all arboreal animals; however semi-arboreal rodents,
such as white-footed mice (*Peromyscus leucopus*) lack conspicuously prehensile feet making it
difficult for them to wrap their feet around a branch of larger diameter for a secure, opposing,
grip. Therefore, not only is foot placement important in maintaining balance and grip, but speed
and pausing is the best predictor of successful escape from predators (M’Closkey and Lajoie,
1975; Ilany and Eilam, 2008).

While many studies have verified that small rodents such as *Peromyscus leucopus* use
arboreal habitats, none have determined how they traverse vertical habitat structures (Meserve
1977, 1981; Wolff and Hurburtt, 1982; Barry et al. 1984; Christopher and Barrett, 2006; Klein et
al. in press). The purpose of this study was to examine how structural variation similar to that
commonly found in arboreal habitats affected locomotor speed and pathway choice by *P.
leucopus*. The specific predictions I tested were: (1) running speed would be adversely affected
by decreased diameters, increased incline, and the presence of secondary branches, and (2) mice
would prefer to run on branches that maximize running speed or are visually more conspicuous.

**Methods**

**Study species**

*Peromyscus leucopus* is a common small mammal occurring in eastern deciduous forests
(Whitaker & Hamilton 1998). *P. leucopus* is nocturnal and semi-arboreal, and regularly uses
trees, shrubs, and downed logs when selecting microhabitats as foraging sites, nest sites, day
refuges, or travel paths (Kaufman et al., 1983; Barnum et al. 1992; McCay, 2000). In addition,
*P. leucopus* may occupy arboreal nests placed 5-10 m above the ground in trees (Wolff and
Hurlbutt, 1982; Barry et al., 1984). Preferred habitats have complex vertical structure and white-
footed mice are capable of traversing varying substrates, which allows them to take advantage of
different types of cover in forest habitat to find food and mates, and to escape predators (Kaufman et al., 1983; Barnum et al., 1992).

**Trapping Protocol**

I collected animals with Sherman live traps (7.62 x 8.89 x 22.86 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) from June-August 2008 (n = 45), March-May 2009 (n = 20), and September 2009 (n = 17). Traps were baited with rolled oats and sunflower seeds, set 1 h prior to sunset and retrieved 1 h after sunrise. For each animal captured, I recorded sex, age class (determined by secondary sexual characteristics), body mass, body length, tail length, length of hind foot, and number of bot fly infestations. The lengths of tail and hind foot were used to verify species identity since it can be difficult to distinguish *P. leucopus* from *P. maniculatus* (Sternburg and Feldhamer 1997; but see Bruseo et al. 1999). Trapping protocol and methods of animal care conformed to guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Cincinnati Institutional Animal Care and Use Committee (IACUC 07-12-12-01).

All field observations and capture of *P. leucopus* occurred in the East Fork Wildlife Area, Williamsburg, Ohio, USA (39°1’N, 84°4’W), an eastern deciduous forest, interspersed with fields sowed in soybeans or sunflowers.

**Field Observations**

During June-July 2008, I released animals (n = 23) directly onto trees or shrubs at their site of capture and used a Sony Digital 8 DCR-TRV140 camcorder to videotape their escape through the vegetation. I used these video recordings to identify the branches used in escape pathways. The diameters of these branches ranged from 6 to 260 mm (n = 26; mean ± SE = 41 ± 7 mm), the unobstructed distance between branch nodes ranged from 4 to 47 mm (n = 59; mean
± SE = 14 ± 1 mm), and the inclines of the pathways varied from straight up (90°) to down a 70° slope (n = 18; mean absolute value ± SE = 29° ± 6°). I used these field observations to guide my selection of diameters for the artificial branches used in the laboratory experiments.

**Laboratory Tests of Performance**

After *P. leucopus* trapping in August 2008 and March-May 2009, I transported animals to the laboratory to determine locomotor performance. I completed all tests within one week of capture and then released the mice at their original capture site. The artificial branches for the performance tests were constructed from 120-cm long cylinders wrapped with cork tape (Selev Cork Ribbon®, WesternBikeworks, Portland, OR, USA). Each cylinder had reference marks placed every 20 cm. All cylinders were placed approximately 1 m above ground to simulate an arboreal situation.

For each performance trial, mice were released through a Sherman live trap on one side of the branch. All trials were videotaped with a camera that was perpendicular to the long axis of the branch and opposite its midpoint. For all performance experiments, three consecutive trials were conducted in rapid succession for each mouse for each experiment. The order of presentation of branches of different diameters, inclines, and combinations of spacing of secondary branches was random among different trials.

For each of 22 mice during August 2008 (Experiment 1), I determined maximal running speeds for 15 combinations of five branch diameters (10, 16, 28, 54, and 116 mm) and three inclines (horizontal, +45°, and -45° slopes). During March-May 2009, 20 different individuals were used to determine effects of branch diameter and presence of and spacing of secondary branches for all branch diameters that were oriented horizontally. To simulate the greater complexity created by secondary branches, I added cylindrical wooden pegs (0.6 x 10 cm) every
10 or 20 cm along the top center of the running surface. All five branch diameters were used for
the 10-cm peg spacing (Experiment 2), but only the three smallest branch diameters were used
for the 20-cm peg spacing (Experiment 3) because a difference in running speed was detected
among those diameters in Experiment 1 (Appendix 2).

I analyzed running speed within the center 80 cm of each branch to reduce the potential
effects associated with mice leaving the starting area or approaching the end of the racetrack
(e.g., first and last 20 cm). I used Adobe Premiere Pro® (Adobe Systems Inc., v. 7, San Jose,
CA, USA) and iMovie® (Apple Inc., v. 8.0.5, Cupertino, CA, USA) to make digital video files,
which were subsequently analyzed with MaxTraq® (Innovision Systems Inc., v. 2.13,
Columbiaville, MI, USA) using a de-interlacing option that generated 60 images per second. I
quantified the elapsed times and positions of each mouse along the long axis of the branch at the
point nearest the beginning and end of the middle 80 cm, as well as at each point where the
mouse paused and then resumed running. Running speed $s_r$ was determined by $s_r = \frac{d}{t_r}$ and
travel speed $s_t$ was determined by $s_t = \frac{d}{t_{tot}}$, where $d$ is the total distance traveled (0.8 m), $t_r$ is
the time spent running, and $t_{tot}$ is the total time including the duration of all the pauses in
seconds.

**Laboratory Tests of Path Choice**

For all choice tests, I used a Y-shaped branch network that was positioned in a horizontal
plane. All three portions of the Y-shaped branch network were 120-cm long cylinders, covered
with cork tape (Fig. 1). The stem of each Y-shaped branch network, upon which each individual
was released, always had a diameter of 28 mm and lacked pegs, and the arms of the Y-shaped
branch network veered 45º to the left and 45º to the right of the stem. Sherman live traps were
placed at the end of each of these branches to recapture animals.
I constructed branch networks to assess whether the diameter of primary branches (#1-2), presence of pegs (#3-4), or spacing of pegs affected path choices by mice (#5-7; Fig. 1). Other branch networks were constructed based on performance data (Exp. 1-3) to discover whether interactive effects of branch diameter and presence of pegs on one or both arms (#8-9) or branch diameter and spacing of pegs (#10-11) affected path choice by mice (Fig. 1). Choice tests were conducted in September 2009 using two batches of mice (n = 6; n = 11), in which the presentation of branch networks had different randomized orders. I conducted six trials for each mouse on each branch network and, after conducting the first three trials, I reversed the position of the left/right option to account for any turn bias. All tests within a batch of mice occurred within four days, and approximately 15 minutes rest was allowed between each trial.

Data Analysis

The data for males and females were not analyzed separately because their body masses did not differ significantly (mean ± SE, females: 21.3 ± 0.52 g, n = 41; males: 20.4 ± 0.41 g, n = 41).

For all analyses of variance (ANOVA) the independent categorical variables of diameter, incline, presence of pegs, and spacing of pegs were fixed and crossed factors. For the data obtained from Experiment 1, I used a three-way ANOVA with independent variables of branch diameter (n = 5) and incline (n = 3), and individual animal (n = 22) was a random effect. For horizontal surfaces with or without pegs (Experiment 2), I used a three-way ANOVA with independent variables of branch diameter (n = 5), absence or presence of pegs spaced at 10-cm intervals (n = 2), and individuals were random and nested within the peg factor. To determine the effects of peg spacing for the three branches with smallest diameters (Experiment 3), I used a three-way ANOVA with independent variables of branch diameter (n = 3) and peg spacing (n =
2), and individual animal (n = 20) was a random effect. I used post-hoc Tukey-HSD tests to determine whether particular pairs of values of mean performance differed significantly. I used JMP v. 7 (SAS Institute, Inc., Cary, NC, USA) to perform all of these analyses separately with the trial that had the fastest running speed or travel speed for each individual.

For each individual within each test of path choice, I calculated the proportion of six trials that a particular branch was chosen. Subsequently, for each choice test I calculated the overall mean (n = 17 individuals) proportion (Pref1) of trials that a particular branch was chosen, and I used a two-tailed t-test to determine if this proportion differed significantly from the expectation for randomly selecting between the alternative branches (0.5).

For all statistical tests, the criterion for significance was $p \leq 0.05$.

Results

Laboratory Tests of Performance

Running speed - Diameter, incline, and their two-way interaction term all significantly affected running and travel speeds (Experiment 1; Fig. 2a-b; Table 1). Running speeds on branches with the smallest diameter (10 mm) were similar for all inclines, whereas running horizontally was faster than running either uphill or downhill for all remaining diameters (Fig. 2a; Appendices 1 & 2). For all horizontal surfaces, running speed increased with increased diameter among the branches with the three smallest diameters (10-28 mm), but little change occurred with further increases in branch diameter. The fastest (1.44 m/s) and slowest (0.87 m/s) mean running speeds on branches without pegs were for running horizontally on the branch 28-mm diameter branch and downhill on the 116-mm diameter branch, respectively (Fig. 2a; Appendices 1 & 2).
The significant negative effect of pegs on running speed was much larger than that of decreased diameter for horizontal branches lacking pegs (Experiment 2; Fig 2a; Table 1). The presence of pegs at 10-cm intervals also had significant interactive effects with diameter on running speed (Experiment 2; Fig. 2a; Table 1). Consequently, speed increased over the entire range of diameters for branches with pegs, whereas mice running on the three largest diameters of branches lacking pegs attained very similar speeds (Fig. 2a, Appendix 3). On branches with pegs at 10-cm intervals, the fastest (0.94 m/s) mean running speed occurred on the 116-mm diameter branch whereas the slowest (0.38 m/s) mean running speed occurred on the 10-mm diameter branch (Fig. 2a; Appendices 3 & 4).

For horizontal branches, the three smallest diameters with pegs spaced at 10- or 20-cm intervals, mice ran significantly faster on surfaces with a greater distance between pegs (Experiment 3; Fig. 2a; Table 1). Similar to horizontal branches lacking pegs, mice ran faster with increased diameter on branches with diameters of 10-28 mm for both peg treatments. On branches with smaller diameters (10-28 mm) and with pegs, mice usually wove between the pegs, whereas they often ran directly along the sides of pegs on branches with larger diameters.

Pause data - More animals paused and the number of pauses per individual were greater on inclined than on horizontal branches, and pausing was more frequent for downhill running compared to uphill running (Table 2a). In addition, pegs caused a greater number of individuals to pause more frequently among all diameters (Table 2a). Mice also had a propensity to pause near pegs, regardless of branch diameter, oftentimes with at least one hind foot resting on a peg. Furthermore, inclines and pegs caused pauses of greater duration, although pause duration was inconsistent among all diameters (Table 2b).
Travel speed – Although pausing resulted in travel speeds that were 0-10% slower than running speed, the effects of diameter and presence of pegs were similar to those for running speed (Fig. 2a vs 2b).

Laboratory Tests of Path Choice

For equal branch diameters (either 28 mm or 10 mm) the mice had a significant preference for branches with secondary branches compared to those with none (Fig. 1; Table 3: choice tests #3-4). When both choices had secondary branches (20-cm intervals) the mice preferred the 28-mm diameter compared to the 10-mm diameter (Fig. 1; Table 3; choice test #9). For the eight remaining tests no significant preferences were observed (Table 3).

Discussion

Both running and travel speed by *P. leucopus* on branches at a horizontal orientation without pegs peaked on branches 28 mm in diameter, yet were similar among all other branch diameters, except on the 10-mm diameter branch where speed was slower (Fig 2a). This effect was maximum on branches 28 mm in diameter for 45° inclines. Branches with a diameter of 28 mm had a circumference of approximately 88 mm, whereas the mean lateral distance between adjacent forefeet and adjacent hindfeet of white-footed mice running on a horizontal flat surface was 31 mm (SE = 1.6 mm; n = 15). Thus, mice were not able to use an opposing grip while climbing branches with diameters ≥ 28 mm, leading to decreased running and travel speed and increased pausing on inclines for branches with diameters > 28 mm (Fig 2a, Table 2). This finding was further supported by video observations of white-footed mice traversing sloped branches with large diameters, where slipping forward for downhill movement became apparent. However, on branches with smaller diameters, mice grasped the sides of branches, which
resulted in similar performance on the 10-mm diameter cylinder for all inclines (Fig. 2a).

Reduced running and travel speeds and increased pausing were mechanisms that enhanced the ability of animals to maintain balance and avoid toppling on branches of different diameters and different inclines (Lammers and Biknevičius, 2004; Lammers 2007). Thus, foot placement on sloped branches with differing circumferences may have significantly affected speed of movement.

In contrast to *P. leucopus*, *Anolis* lizards ran faster as diameters of branches increased when incline was held constant at 45° (Losos and Sinervo, 1989). However, speed of corn snakes (*Elaphe guttata*) followed a pattern similar to that of *P. leucopus*, where speed decreased as slope increased and remained relatively constant on the horizontal (Astley and Jayne, 2007). These results suggest that different body plans impact an animal’s ability to maneuver along arboreal substrates.

Different morphological adaptations are apparent for species that inhabit different environments. For example, many arboreal reptiles and amphibians (e.g. *Bolitoglossa*, tree frogs, anoles, and geckos) have specialized feet that rely on adhesion or suction that allow these animals to adhere to substrates that are not horizontal (Albrech, 1981; Hanna and Barnes, 1991; Autumn and Peattie, 2002). *Peromyscus* spp., on the other hand, rely on toe-spreading and claws to increase surface area for gripping and use plantar tubercles to enhance gripping of the climbing surface (Horner, 1954; Layne, 1970; Cartmill, 1985). Horner (1954) discovered common patterns in climbing behavior regarding gaits (running and walking) and tail usage for 10 species of *Peromyscus* in an extensive laboratory study. As mice progressed forward slowly they moved their feet individually in a similar sequence (either fore foot, contralateral hind foot, ipsilateral fore foot, contralateral hind foot) that allowed three feet to remain in contact
simultaneously with the substrate to provide balance and stability (Horner, 1954). However, as running speed increased, there were short intervals when only two feet were simultaneously in contact with the substrate (Horner 1954). Thus, alterations in footfall patterns, in addition to gripping adaptations, low body mass, and long tails, make *P. leucopus* extraordinarily good climbers (Horner 1954; Layne, 1970; Wright and Pagels, 2002).

These adaptations for climbing enable *P. leucopus* to navigate narrow branches by altering speed to negotiate arboreal obstacles. When pegs increased arboreal complexity in my experiments, the free running surface area became obstructed. This reduction in surface area for running forced mice to weave between pegs on branches with small diameters (10-28 mm), while mice were able to run along the sides of pegs on branches with larger diameters (54-116 mm). In contrast to branches without pegs, mice increased running and travel speed as diameter of branches increased and pegs were added (Fig 2a-b). In addition to the interaction between pegs and diameter of branches on running speed, pegs positioned closer together also negatively affected running speed by creating more obstacles that had to be negotiated. Accordingly, running speed was slower on the three branches with the smallest diameters (10-28 mm) and with pegs spaced 10-cm apart compared to those branches with pegs spaced 20-cm apart (Fig. 2).

Pauses associated with presence of pegs on branches decreased total travel speed (Fig. 2b; Table 2). The number of times that individual mice paused increased at least 2.5 fold for branches of a certain diameter when pegs were placed at 10-cm intervals compared to branches without pegs (Table 2). During pauses along cylinders containing pegs, white-footed mice often would stop with at least one hind foot on a peg, possibly to aid in maintaining balance, as there was no apparent increase in speed associated with using pegs to push off during travel. In contrast to this pausing posture by white-footed mice, corn snakes (*Elaphe guttata*) use
secondary branches to aid in forward propulsion, thereby enhancing their forward locomotor speed (Astley and Jayne, 2009). In addition to affecting travel speed, pausing in natural settings allows mice to be more vigilant and observe their surroundings (Vasquez et al. 2002). Pausing also makes animals less likely to be seen by predators as most visual predators more easily spot moving prey than those that are sedentary (Vasquez et al. 2002); however, animals that stop in open surroundings while trying to evade predators are caught more frequently than animals that seek shelter (Ilany and Eilam, 2008). Increases in the number of pauses and in the duration of pauses associated with pegs may make white-footed mice less visible to predation, albeit secondary branches also may make escape more difficult by hampering or obstructing movement when detection by a predator occurs.

Path choice also may aid in success of foraging and avoidance of predators for animals moving in arboreal habitats and is affected by diameter of branches and presence of secondary branches (McMillan and Kaufman, 1995). White-footed mice prefer habitats with more cover and a more rapid running speed is advantageous for avoidance of predators along unobstructed pathways (Howland, 1974; M’Closkey, 1975; Barry and Franq, 1980; Kaufman et al., 1983; Graves et al., 1988; Barnum et al., 1992; Planz and Kirkland, 1992; Cummings and Vessey, 1994; Harney and Dueser, 1987). However, white-footed mice showed no preference for branches with different diameters or spacing of pegs except when peg spacing was the same, and preferred a branch containing pegs only when it was paired with a branch of equal diameter without pegs. These results suggest that white-footed mice did not prefer travel routes based on how fast they could run, but rather preferred paths on branches that contained more obstructions, possibly because these branches offered more protection. Hence, preference of branches with
obstructions could reflect a tactic to avoid predators, albeit snakes can move faster when
secondary branches are present than when they are not (Astley and Jayne, 2009).

Movement in arboreal habitats is of ecological relevance because the way that animals
use above-ground space may profoundly affect their survival. *P. leucopus* tend to escape along
the same travel routes that permit silent passage and may select branches in the above-ground
habitat that provide such safe travel routes irrespective of the speed with which they can traverse
those branches (Fitzgerald and Wolff, 1988; Graves et al., 1988; Planz and Kirkland, 1992).

Performance, or speed of movement, has predictive qualities in determining how likely it is for
an animal to survive when it encounters a predator (Howland, 1974; Weihs and Webb, 1984).

Even though speed is the best predictor of escape, escape also can be enhanced by sporatic
movements, hiding, or blending in with surroundings (Ilany and Eilam, 2008; Furuichi, 2002;
Howland, 1974; Djawdan, 1993). Determining running speed and preferred pathways among
branches in an arboreal habitat that vary in diameter, incline, and in the presence of and spacing
of secondary branches provides insight into how small mammals maneuver in above-ground
habitats.

Costs and benefits associated with inclines vary with animal size, the amount of energy
expended to maneuver in a complex habitat, the relative availability of food or shelter, and the
relative availability of protection from predators (Full and Tullis, 1990). Since small animals (≤
30 g) such as *P. leucopus* experience similar energy costs when running on a horizontal or a
sloped surface, the benefits of foraging in arboreal structures often outweigh the costs associated
with traversing them (Taylor et al., 1972; Full and Tullis, 1990). For other arboreal animals, the
benefits of foraging may be a function of individual size since costs of arboreal movement may
dependent on body size. For example, inclines caused a significant decrease in maximal velocity
for large (>40 g) individuals of an arboreal lizard (*Stellio*), but had virtually no effect on maximal velocity of small individuals (<40 g; Huey and Hertz, 1982).

Quantifying kinematics of locomotion for white-footed mice could provide further insight into how locomotion of gaits, relating to forces and torque, differ on various arboreal structures. Such information also may help in assessing whether differences in patterns of gait sequence are beneficial for negotiating narrow supports as suggested for primates and opossums (Schmitt and Lemelin, 2002; Lemelin et al. 2003; Lammers and Biknevicius, 2004; Stevens, 2008). Future implications of this work would be to elucidate the biomechanical energetics and mechanisms that white-footed mice use when traversing arboreal components of their habitat and may provide valuable insight into the types of structures that are most beneficial for optimal movement and survival.
Table 1. Effects of diameter, pegs, and peg spacing on performance.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Running Speed</th>
<th>Travel Speed</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>F</td>
<td>d.f.</td>
</tr>
<tr>
<td>Experiment 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter (D)</td>
<td>15.51</td>
<td>4,84</td>
</tr>
<tr>
<td>Incline (I)</td>
<td>13.1</td>
<td>2,42</td>
</tr>
<tr>
<td>D x I</td>
<td>7.3</td>
<td>8,168</td>
</tr>
<tr>
<td>Experiment 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter (D)</td>
<td>29.14</td>
<td>4,160</td>
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<tr>
<td>Pegs Present (P)</td>
<td>162.53</td>
<td>1,40</td>
</tr>
<tr>
<td>D x P</td>
<td>13.96</td>
<td>4,160</td>
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<tr>
<td>Experiment 3</td>
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<td></td>
</tr>
<tr>
<td>Diameter (D)</td>
<td>63.14</td>
<td>2,38</td>
</tr>
<tr>
<td>Peg Spacing (S)</td>
<td>95.91</td>
<td>1,19</td>
</tr>
<tr>
<td>D x S</td>
<td>1.25</td>
<td>2,38</td>
</tr>
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</table>
Table 2. Descriptive statistics for (a) number of individuals who paused (e.g., stopped traveling along branch) during tests of performance with total number of pauses summed over all individuals who paused in parentheses; and (b) mean pause duration of total individuals who paused in seconds ± SE. (Incline: n = 22; Peg Intervals: n = 20)

<table>
<thead>
<tr>
<th>Diameter (mm)</th>
<th>Incline</th>
<th>Peg Intervals</th>
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<tbody>
<tr>
<td>(a)</td>
<td>0°</td>
<td>+45°</td>
</tr>
<tr>
<td>10</td>
<td>1 (1)</td>
<td>3 (3)</td>
</tr>
<tr>
<td>16</td>
<td>0</td>
<td>2 (2)</td>
</tr>
<tr>
<td>28</td>
<td>1 (1)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>54</td>
<td>0</td>
<td>1 (1)</td>
</tr>
<tr>
<td>116</td>
<td>2 (2)</td>
<td>0</td>
</tr>
</tbody>
</table>

| (b)          |         |               |               |       |       |
| 10           | 0.38    | 1.32 ± 0.43   | 1.67 ± 0.22   | 1.04 ± 0.26 | 1.30 ± 0.17 |
| 16           | 0       | 1.36 ± 0.56   | 0.89 ± 0.24   | 0.84 ± 0.21 | 1.01 ± 0.17 |
| 28           | 1.35    | 0.68          | 1.21 ± 0.06   | 1.40 ± 0.22 | 0.93 ± 0.11 |
| 54           | 0       | 0.82 ± 0      | 2.33 ± 0.13   | 0.51 ± 0.27 | -       |
| 116          | 1.06 ± 0.12 | 0        | 1.15 ± 0.34   | 0.66 ± 0.12 | -       |
Table 3. Effects of branch structure on path choice. P10 and P20 indicate the presence of pegs along the top center of the branch spaced at 10- or 20-cm intervals, respectively. Pref1 is the mean (n = 17 individuals) proportion of trials when individuals selected Branch1. Underlined descriptions of branches indicate the predicted preference based upon results of running speed, whereas * indicates a significant observed preference; t = t-test value; p = probability level.

<table>
<thead>
<tr>
<th>Descriptor</th>
<th>Choice Test #</th>
<th>Branch 1 Diameter (mm)</th>
<th>Branch 2 Diameter (mm)</th>
<th>Pref1 ± SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter Effect (D)</td>
<td>1</td>
<td>28</td>
<td>10</td>
<td>0.57 ± 0.068</td>
<td>1.00</td>
<td>0.3322</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>116</td>
<td>28</td>
<td>0.51 ± 0.065</td>
<td>-0.15</td>
<td>0.8842</td>
</tr>
<tr>
<td>Peg Presence Effect (P)</td>
<td>3</td>
<td>28 (P20)</td>
<td>28</td>
<td>0.63 ± 0.046</td>
<td>-2.75</td>
<td>0.0143*</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>10 (P20)</td>
<td>10</td>
<td>0.64 ± 0.051</td>
<td>-2.64</td>
<td>0.0178*</td>
</tr>
<tr>
<td>Peg Spacing Effect (S)</td>
<td>5</td>
<td>28 (P20)</td>
<td>28 (P10)</td>
<td>0.56 ± 0.046</td>
<td>1.31</td>
<td>0.2102</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>10 (P20)</td>
<td>10 (P10)</td>
<td>0.50 ± 0.044</td>
<td>0.00</td>
<td>1.0000</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>116 (P20)</td>
<td>116 (P10)</td>
<td>0.50 ± 0.058</td>
<td>0.00</td>
<td>1.0000</td>
</tr>
<tr>
<td>D x P Effect</td>
<td>8</td>
<td>28 (P20)</td>
<td>10</td>
<td>0.60 ± 0.058</td>
<td>-1.71</td>
<td>0.1062</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>28 (P20)</td>
<td>10 (P20)</td>
<td>0.70 ± 0.051</td>
<td>3.92</td>
<td>0.0012*</td>
</tr>
<tr>
<td>D x S Effect</td>
<td>10</td>
<td>28 (P10)</td>
<td>10 (P20)</td>
<td>0.56 ± 0.058</td>
<td>1.03</td>
<td>0.3179</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>28 (P20)</td>
<td>54 (P10)</td>
<td>0.58 ± 0.058</td>
<td>1.33</td>
<td>0.2033</td>
</tr>
</tbody>
</table>
Figure 1.

top value = branch diameter  
bottom value = avg. fastest running speed  
* = predicted choice based on performance data  
NP; P10; P20 = No pegs; Pegs at 10 cm and 20 cm intervals, respectively  
No Pref. = no predicted preference
Figure 2.
Literature Cited


Graves S, Maldonado J, Wolff JO. 1988. Use of ground and arboreal microhabitats by

Peromyscus leucopus and Peromyscus maniculatus. Canadian Journal of Zoology 66:

277-278.


Horner, BE. 1954. Arboreal adaptations of Peromyscus, with a special reference to use of the tail. Contributions from the Laboratory of Vertebrate Biology of the University of Michigan 61: 1-84.


Klein GP, Christopher CC, Cameron GN, Barrett GW. In press. Effect of bot fly parasitism on vertical habitat use by *Peromyscus leucopus*. *Northeastern Naturalist*.


Appendices

Appendix 1. Running speed (mean ± SE; m/s) on branches of varying diameter within each incline. Diameters with similar superscripts are not significantly different. F ratios result from two-way ANOVAs, where incline was held constant, diameter was a fixed effect, and individual was a random effect.

<table>
<thead>
<tr>
<th>Branch diameter (mm)</th>
<th>0º</th>
<th>+45º</th>
<th>-45º</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>1.18 ± 0.06&lt;sup&gt;B&lt;/sup&gt;</td>
<td>1.23 ± 0.05&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>1.09 ± 0.06&lt;sup&gt;AB&lt;/sup&gt;</td>
</tr>
<tr>
<td>16</td>
<td>1.31 ± 0.05&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>1.32 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.04 ± 0.05&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
<td>28</td>
<td>1.44 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.30 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.16 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
<td>54</td>
<td>1.31 ± 0.06&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>1.07 ± 0.07&lt;sup&gt;BC&lt;/sup&gt;</td>
<td>1.16 ± 0.08&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
<td>116</td>
<td>1.36 ± 0.07&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.00 ± 0.08&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.89 ± 0.07&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>F</td>
<td>4.76</td>
<td>10.88</td>
<td>18.40</td>
</tr>
<tr>
<td>p(4,84)</td>
<td>0.0018</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Appendix 2. Running speed (mean ± SE; m/s) at different inclines for each branch diameter. Inclines with similar superscripts are not significantly different. F ratios result from two-way ANOVAs, where diameter was held constant, incline was a fixed effect, and individual was a random effect.

<table>
<thead>
<tr>
<th>Branch diameter (mm)</th>
<th>0º</th>
<th>+45º</th>
<th>-45º</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>1.18 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.31 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.44 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
<td>16</td>
<td>1.23 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.32 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.30 ± 0.05&lt;sup&gt;AB&lt;/sup&gt;</td>
</tr>
<tr>
<td>28</td>
<td>1.09 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.04 ± 0.05&lt;sup&gt;B&lt;/sup&gt;</td>
<td>1.16 ± 0.06&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
<td>54</td>
<td>1.36 ± 0.07&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.00 ± 0.08&lt;sup&gt;C&lt;/sup&gt;</td>
<td>0.87 ± 0.07&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
<td>F</td>
<td>2.26</td>
<td>16.37</td>
<td>10.49</td>
</tr>
<tr>
<td>p(2,42)</td>
<td>0.1171</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

27
Appendix 3. Running speed (mean ± SE; m/s) on branches of varying diameter with and without secondary branches spaced at 10-cm intervals. Diameters with similar superscripts are not significantly different. F ratios result from two-way ANOVAs, where presence of secondary branches was held constant, diameter was fixed, and individual was a random effect.

<table>
<thead>
<tr>
<th>Branch diameter (mm)</th>
<th>No Secondary Branches</th>
<th>Secondary Branches Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>1.18 ± 0.06&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.38 ± 0.02&lt;sup&gt;D&lt;/sup&gt;</td>
</tr>
<tr>
<td>16</td>
<td>1.31 ± 0.05&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>0.46 ± 0.03&lt;sup&gt;D&lt;/sup&gt;</td>
</tr>
<tr>
<td>28</td>
<td>1.44 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.60 ± 0.04&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>54</td>
<td>1.31 ± 0.06&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>0.75 ± 0.04&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
<td>116</td>
<td>1.36 ± 0.07&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.94 ± 0.05&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
<td>F</td>
<td>4.76</td>
<td>62.43</td>
</tr>
<tr>
<td>d.f.</td>
<td>(4, 84)</td>
<td>(4, 76)</td>
</tr>
<tr>
<td>p</td>
<td>0.0018</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Appendix 4. Running speed (mean ± SE; m/s) with or without secondary branches spaced at 10-cm intervals for each branch diameter. Similar superscripts within categories of secondary branches indicate no significant difference. F ratios result from two-way ANOVAs, where diameter was held constant, presence of secondary branches was fixed, and individual was a random effect.

<table>
<thead>
<tr>
<th>Secondary Branches</th>
<th>Branch diameter (mm)</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Not Present</td>
<td></td>
<td>10</td>
<td>16</td>
<td>28</td>
<td>54</td>
<td>116</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.18 ± 0.06&lt;sup&gt;A&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present (10-cm spacing)</td>
<td>0.38 ± 0.02&lt;sup&gt;B&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>142.10</td>
<td>191.83</td>
<td>136.46</td>
<td>58.90</td>
<td>23.96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p(1,40)</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix 5. Running speed (mean ± SE; m/s) among branches with smallest diameters within each category of spacing of secondary branches. Diameters with similar superscripts are not significantly different. F ratios result from two-way ANOVAs where spacing was held constant, diameter was a fixed effect, and individual was a random effect.

<table>
<thead>
<tr>
<th>Branch diameter (mm)</th>
<th>Spacing of Secondary Branches</th>
<th>10 cm</th>
<th>20 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.38 ± 0.02&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.56 ± 0.02&lt;sup&gt;A&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>0.46 ± 0.03&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.70 ± 0.03&lt;sup&gt;B&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>0.60 ± 0.04&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.80 ± 0.03&lt;sup&gt;A&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>25.01</td>
<td>29.45</td>
<td></td>
</tr>
<tr>
<td>p(2,38)</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Appendix 6. Differences in running speed (mean ± SE; m/s) on branches of different diameters and with different spacing between secondary branches. Similar superscripts within each category of secondary spacing indicate no significant difference. F ratios result from two-way ANOVAs where diameter was held constant, spacing of secondary branches was a fixed effect, and individual was a random effect.

<table>
<thead>
<tr>
<th>Spacing of Secondary Branches</th>
<th>Branch diameter (mm)</th>
<th>10</th>
<th>16</th>
<th>28</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 cm</td>
<td>0.38 ± 0.02&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.46 ± 0.03&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.60 ± 0.04&lt;sup&gt;B&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>20 cm</td>
<td>0.56 ± 0.02&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.70 ± 0.03&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.80 ± 0.03&lt;sup&gt;A&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>42.69</td>
<td>34.86</td>
<td>31.95</td>
<td></td>
</tr>
<tr>
<td>p(1,19)</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
<td></td>
</tr>
</tbody>
</table>