The Narrow Niche Hypothesis: Gray Squirrels Shed New Light on Primate Origins

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ABSTRACT   Current hypotheses for primate origins propose that nails and primate-like grasping hands and feet were important early adaptations for feeding in fine branches. Comparative research in this area has focused on instances of convergence in extant animals, showing that species with primate-like morphology feed predominantly from terminal branches. Little has been done to test whether animals without primate-like morphology engage in similar behavior. We tested the fine-branch niche hypothesis for primate origins by observing branch use in Eastern gray squirrels, *Sciurus carolinensis*, a species lacking primate grasping adaptations that has been understudied in the context of primate origins. We hypothesized that because gray squirrels lack primate-like grasping adaptations, they would avoid feeding and foraging in terminal branches. Instantaneous focal animal sampling was used to examine the locomotor and postural behaviors used while feeding and foraging. Our results demonstrate habitual and effective usage of terminal branches by gray squirrels while feeding and foraging, primarily on tree seeds (e.g., oak, maple, and elm). Discriminant function analysis indicates that gray squirrels feed and forage like primates, unlike some other tree squirrel species. Given the absence of primate-like features in gray squirrels, we suggest that although selection for fine-branch foraging may be a necessary condition for primate origins, it is not sufficient. We propose an alternative model of primate origins. The Narrow Niche hypothesis suggests that the primate morphological suite evolved not only from selection pressure for fine branch use, but also from a lack of engagement in other activities. Am J Phys Anthropol 000:000–000, 2011.   © 2011 Wiley-Liss, Inc.

The selection pressures involved in the evolution of the modern primates (i.e., primates of modern aspect) remain the subject of intense debate. The ever improving fossil record for early primates has shown that the distinctive morphological traits shared by euprimates, including nails, grasping hands and feet, and orbital convergence, appear early, although not simultaneously, in primate evolution (Gebo, 2004). The appearance of these primate synapomorphies early in the primate lineage has often been linked to primates' arboreal lifestyle (Jones, 1916; Cartmill, 1974b; Sussman and Raven, 1978). Other primate specializations, such as compliant, diagonal-sequence walking gaits (Schmitt, 2003) have also been proposed as adaptations for arboreal locomotion. In this article, we examine the locomotor ecology of an arboreal specialist that lacks these primate specializations, the Eastern Gray squirrel *Sciurus carolinensis*, to examine whether species that lack these primate specializations are precluded from habitually and effectively using arboreal habitats in a primate-like way.

Current hypotheses for primate origins propose that primate specializations including nails and grasping hands and feet were important early adaptations for feeding in fine branches. Cartmill (1974b) proposed the Nocturnal Visual Predation hypothesis, suggesting that early primates required both binocular vision (and hence orbital convergence) and grasping hands and feet to cautiously and quietly approach insects on fine branches at night. These adaptations would have facilitated their ability to visually focus on and stalk insect prey without disturbing unstable supports. Sussman and colleagues (1991, 1978) proposed an alternative model for primate origins, the Angiosperm Coevolution hypothesis, suggesting that grasping abilities were adaptations to maneuvering in a fine branch niche and exploiting newly available angiosperm foods including fruits, flowers, insects, and nectars. While the Nocturnal Visual Predation and Angiosperm Coevolution hypotheses focus on different foraging and locomotor behaviors, they share a common focus on the use of fine, terminal branches as an important selection pressure driving the evolution of grasping hands, nails, and orbital convergence. Alternatively, Szalay and colleagues (Szalay and Delson, 1979; Szalay and Dagosto, 1980) argue that the origin of primates does not require a fine branch model. Instead, they propose a Grasp-Leaping hypothesis, contending that the primate morphotype can be explained most parsimoniously by having a habitually leaping ancestor, rather than one reliant on slow, cautious locomotion (Dagosto, 2007).

Terminal-branch hypotheses for primate origins suggest a functional link between morphology and ecology, in which proposed primate adaptations are critical for habitual feeding and foraging in fine branches. Comparative studies of other arboreal species have been used to support the hypothesis that terminal branch use was an important selection pressure for the evolution of primate grasping adaptations. Several terminal branch specialists, including some marsupial species (Rasmussen and Sussman, 2007), tree shrews (Sargis, 2001), and

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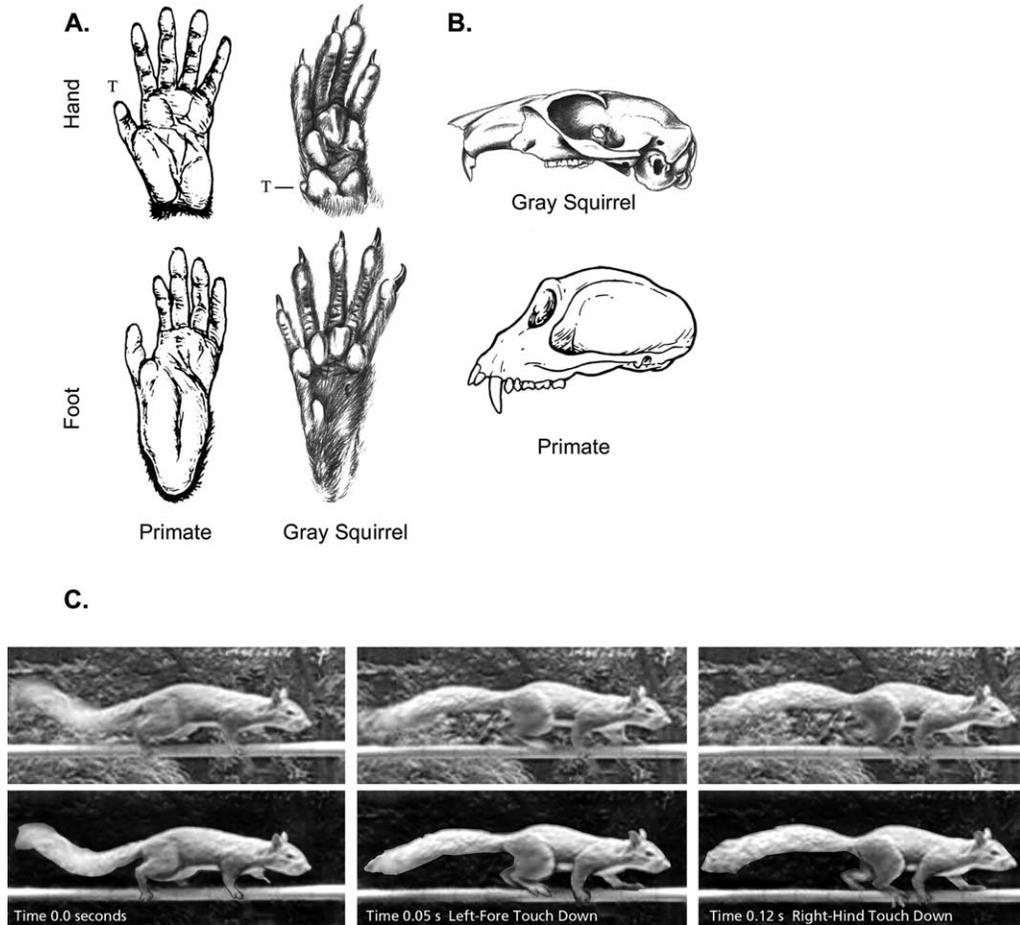
Fig. 1. Comparison of squirrel and primate anatomy. (**A**) The hands and feet of primates have opposable first digits and nails, while those of squirrels retain the primitive condition, lacking opposable digits and having claws. The opposable thumb of baboons and vestigial "thumb" of gray squirrels are indicated with a T. (**B**) As demonstrated in this lateral view of the skull, squirrels retain the primitive condition of laterally facing orbits, while primate orbits face forward, providing stereoscopic vision. (**C**) A gray squirrel walking on the wooden rod of a bird-feeder using a lateral sequence gait. In the first frame, the left hind paw has just touched down. The left forepaw then touches down in the second frame, followed by the right hind paw touching down in the third frame. In contrast, primates typically use a diagonal sequence gait, in which touch down of the left hind paw is followed by touch down of the right forepaw, and then the right hind paw. Bottom row is modified to highlight foot position. Figures A and B adapted from Fleagle (1988) and Schwartz and Schwartz (1986).

chameleons (Cartmill, 1974b) have been shown to possess hand and foot morphology functionally similar to primates, suggesting evolutionary convergence for grasping performance. Field studies of Didelphids have demonstrated that that these marsupials display similar branch use patterns to primates (Rasmussen, 1990).

Tree squirrels provide an alternative yet underutilized point of comparison for terminal branch models of primate origins. Because squirrels lack the derived grasping hands and feet, orbital convergence, and footfall pattern (Fig. 1) of primates, terminal branch models of primate origins would predict that squirrels forage less effectively in the terminal branch environment. There is, however, conflicting evidence on this point. In his refutation of Smith's (1912) Arboreal Theory of primate origins, Cartmill (1974a, 1974b) suggested that gray squirrels are adept terminal branch foragers despite their lack of primate-like features. However, he noted that while lorises are capable of approaching insects on slender supports with silent deliberation, gray squirrels move about this environment noisily, and often

relocate their food items to larger supports for consumption. Although Cartmill's (1974a, 1974b) evidence was largely anecdotal, a more rigorous study of the feeding ecology of the red-tailed squirrel, *Sciurus granatensis*, Garber and Sussman (1984) demonstrated that these tree squirrels avoid terminal branches. Similar patterns have since been shown in other rainforest squirrels (Youlatos, 1999). However, these results might be confounded by the preference of those particular species for foods such as hard-shelled palm nuts, which require intensive processing (Garber and Sussman, 1984), or arthropods, that are often found in lianas and the bark of large branches (Emmons, 1980). Tree squirrels are diverse in their foraging habits and feed on a variety of arboreal foods including berries, drupes, and seeds, often in competition with but not excluded by primates (Gautier-Hion et al., 1980, 1985). Thus, a better model of the proposed link between terminal branch foraging and primate adaptations would be in squirrels that prefer terminal branch foods. If such squirrels exhibit primate-like branch use without primate-like features,

this would indicate that habitual exploitation of a terminal branch niche does not by itself explain the evolution of primate morphological specializations.

To investigate this issue, we examined the branch use pattern of gray squirrels (*S. carolinensis*), which commonly feed on terminal branches (Schwartz and Schwartz, 1986) and compared their branch usage behavior to a sample of wild primates obtained from previously published accounts. We tested the prediction that gray squirrels, unlike primates, will avoid terminal branches during feeding and foraging due to their lack of primate-like specializations. That is, while gray squirrels may harvest foods such as acorns from terminal branches, we predicted they, unlike arboreal primates, would need to process and consume them on more stable supports, resulting in branch use patterns similar to other squirrels (Garber and Sussman, 1984; Youlatos, 1999). Conversely, if the morphology of gray squirrels does not hinder their ability to feed and forage in terminal branches, we expect their branch use pattern to resemble that of arboreal primates.

METHODS

A population of gray squirrels (*S. carolinensis*) was studied in both suburban and forested areas in St. Louis, Missouri, using 30-s instantaneous focal animal sampling (Altmann, 1974). Focal animals were selected at random and followed until they were out of view for two or more samples. Individuals were not marked. Five hundred ninety-six data points (283 while feeding and foraging) were collected during April 2007, September 2007, and October 2008. For the purposes of this study, we operationally define "foraging" as actively pursuing or harvesting food items and "feeding" as masticating or processing food items for immediate consumption. The following positional behaviors were recorded: quadrupedal progression; sit/squat; prehensile climb; grasp (suspensory or standing); leap; vertical cling; vertical range; and other/unknown (Garber and Sussman, 1984). All the aforementioned data were collected simultaneously.

Branch size categories were modeled after Stafford et al. (2003) and Garber and Sussman (1984). Five categories of branch size data were recorded relative to the size of a gray squirrel:

1. *Terminal*: capable of being grasped with a closed hand;
2. *Small*: capable of being grasped with an open hand;
3. *Medium*: about the diameter of a squirrel's torso;
4. *Large*: can be encircled halfway with forelimbs;
5. *Very large*: cannot be encircled halfway with forelimbs.

The additional category "6—*Ground*" was added to this framework. Although the maximum diameter of branch Type 1 varies from 2 cm (Youlatos, 1999) to 1.5 cm (Garber and Sussman, 1984), it refers to terminal branches for both of the aforementioned studies. The support size and positional behavior of gray squirrels during feeding and foraging were compared with corresponding data from red-tailed squirrels and Panamanian tamarins taken from Garber and Sussman (1984), two species of Amazonian tree squirrels from Youlatos (1999), five species of arboreal old world monkeys taken from McGraw (1998), and two New World monkeys from Fleagle and Mittermeier (1981).

TABLE 1. Observations of gray squirrels by branch size

Branch size	All seasons		Feeding and foraging		Total (%)
	Feeding (%)	Foraging (%)	Spring (%)	Fall (%)	
Terminal	54	48	46	62	53
Small	26	21	24	26	25
Medium	9	8	9	8	9
Large	4	0	4	0	3
Very large	0	3	1	0	1
Terrestrial	6	20	15	4	10
Total observations	193	75	158	110	268

Spring and fall observations include both feeding and foraging.

For each substrate category, the proportions of feeding and foraging samples between gray squirrels and Panamanian tamarins (the only species for which equally delineated data were available) were compared with Fisher's exact test of two proportions using Minitab v14. To assess branch use in a broad comparative sample, we condensed the five arboreal categories to three, following Fleagle and Mittermeier (1981): Terminal branches, secondary branches (small and medium combined); and bough (large and very large combined). These condensed data were analyzed to determine the group membership of gray squirrels using discriminant function analysis generated with SPSS v16, using percentage of feeding and foraging in each of three branch types. Differences were considered significant at $P < 0.05$.

RESULTS

Gray squirrels both fed and foraged predominantly while supporting themselves on terminal branches. Of 268 feeding and foraging observations, 141 (52.6%), were in terminal branches (i.e., Type 1: branches approximately 1.5 cm diameter and smaller), 67 (25.0%) observations were in small branches (Type 2: ~1.5–3 cm), 24 (9.0%) in medium branches (Type 3: ~3–8 cm), 7 (2.6%) in large branches (Type 4: ~8–16 cm), 2 (0.8%) in very large branches (Type 5: >~8 cm), and 27 (10.1%) were terrestrial (Table 1). These percentages were similar for both foraging (i.e., pursuing food) and feeding (i.e., processing and consuming food) (Table 1). Patterns of branch use in gray squirrels were similar across seasons, and hence across plant species harvested (almost exclusively oak, maple, and elm seeds and buds; Table 1). The predominant foods for each season were terminal branch foods, consistent with previous data on gray squirrel diet in other forests (Korschgen, 1981). When in terminal branches, gray squirrels used a range of gaits including slow walking and fast bounding, and they often supported themselves on multiple terminal branches (Fig. 2).

Gray squirrel branch use preferences were nearly identical to those reported for Panamanian tamarins (Garber and Sussman, 1984). In fact, the only significant differences in feeding and foraging substrate use were on the largest branches (very large category) and the ground: Panamanian tamarins fed and foraged significantly more often on very large branches, while gray squirrels spent significantly more time on the ground ($P < 0.001$ Fisher's exact test of two proportions; all other substrate comparisons $P > 0.05$) (Fig. 3). When we condensed our data from five branch-size categories to three to compare branch use among a broader sample of
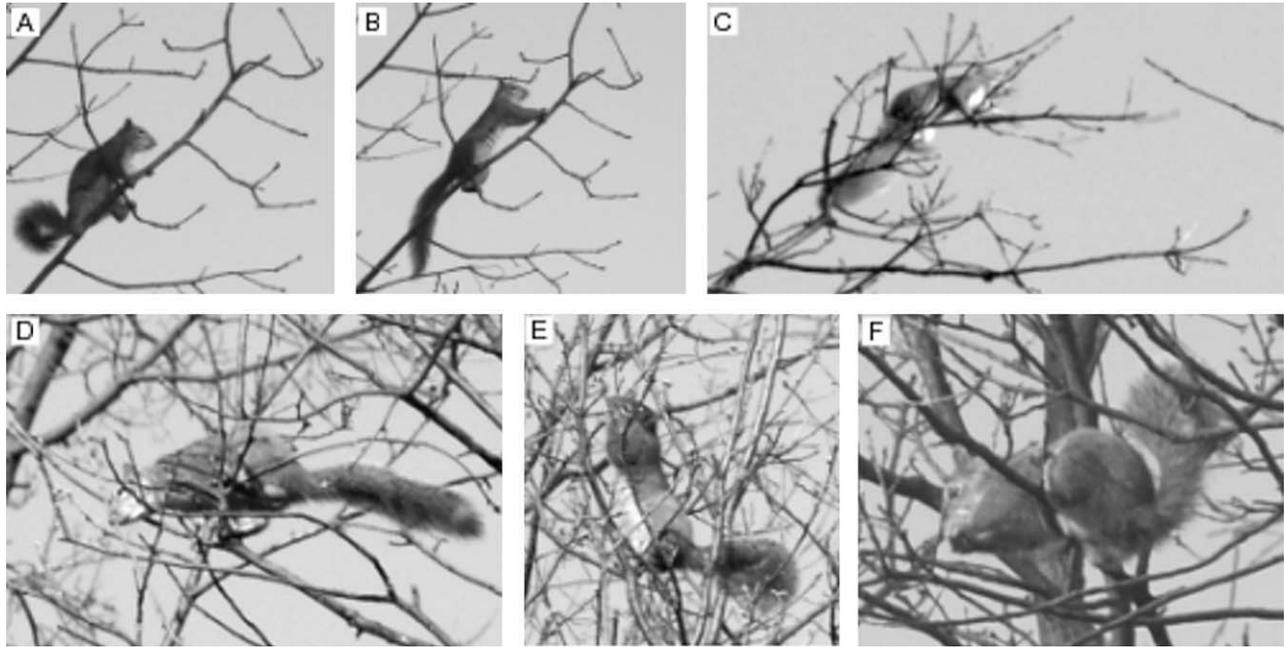
Fig. 2. Branch use by gray squirrels. (**A, C**) Use of multiple terminal branches for support during cautious walking. (**B**) Foraging. (**D**) Squatting. (**E, F**) Feeding and foraging in complex terminal branch environment.
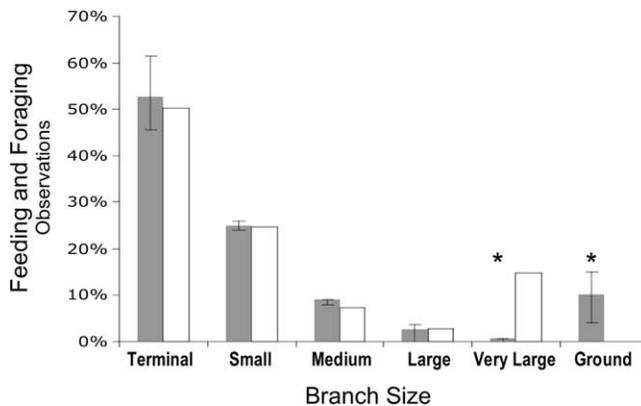

Fig. 3. Gray squirrel (gray bars) and Panamanian tamarin (white bars) feeding and foraging by branch size. Error bars represent seasonal variation. *Indicates significant difference between species ($P < 0.001$ Fisher's exact test).

Fig. 4. Percentage of arboreal feeding and foraging observations in terminal branches (smallest diameter), secondary branches, and boughs (largest diameter) for gray squirrels (G), arboreal primates (P), and tree squirrels (S). Data are scaled to exclude terrestrial and other types of locomotion (13% or less of total in all cases).

primates and other tree squirrels (Fig. 4), the feeding and foraging habits of gray squirrels were clearly in the primate range of variation. Percents of time spent in terminal branches, secondary branches, and large branches (boughs) were entered into a discriminant function analysis (SPSSv16) with group membership (primate or squirrel) assigned to comparative taxa; gray squirrel group membership was not assigned. Because of the small number of variables and large differences in branch use patterns between squirrels and primates, 100% of the variance in group membership was accounted for by the first canonical function. The value of the first canonical function for gray squirrels (1.52) was in the range of values for primates (mean: 0.94; range: -0.39 to 3.32) and distinct from the range of values for other squirrel species (mean: -2.49; range: -2.96 to -2.05). Post hoc group assignment placed gray

squirrels in the primate group with a probability of 0.999 (Table 2).

DISCUSSION

Our results demonstrate primate-like usage of terminal branches by gray squirrels while feeding and foraging. Unlike the feeding pattern observed in other tree
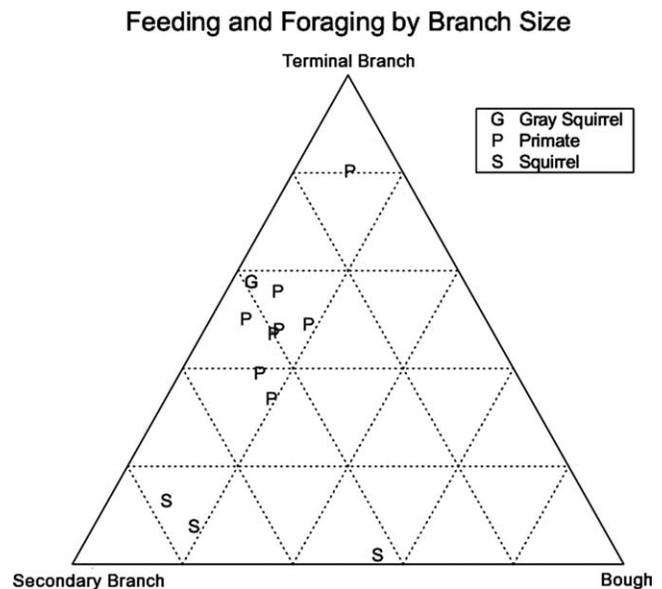
TABLE 2. Percentage of arboreal feeding and foraging observations in terminal branches (smallest diameter), secondary branches, and boughs (largest diameter) for gray squirrels, arboreal primates, and tree squirrels used in this study

Species	Terminal	Branch	Bough	Canonical function 1	Group
Saimiri sciureus	0.82	0.09	0.09	3.32	1
Sciurus carolinensis	0.59	0.38	0.03	1.52	1
Cercopithecus diana	0.57	0.34	0.09	1.37	1
Colobus verus	0.51	0.43	0.06	0.91	1
Saguinus oedipus	0.50	0.32	0.18	0.83	1
Cebus apella	0.49	0.38	0.13	0.74	1
Cercopithecus campbelli	0.48	0.12	0.40	0.67	1
Colobus polykomos	0.40	0.46	0.14	0.03	1
Colobus badius	0.35	0.19	0.46	−0.39	1
Sciurus granatensis	0.13	0.76	0.10	−2.05	2
Sciurus igniventris	0.08	0.74	0.18	−2.47	2
Microsciurus flaviventer	0.02	0.44	0.54	−2.96	2

Data from Fleagle (1981), Garber and Sussman (1984), McGraw (1998), Youlatos (1999), and this study are scaled to exclude terrestrial and other types of locomotion (13% or less of total in all cases). The first canonical function accounted for 100% of the variance in group membership.
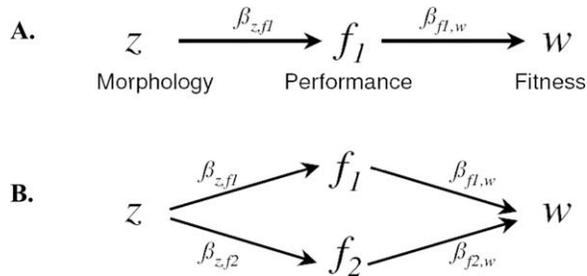

Fig. 5. Modeling selection on locomotor morphology. (**A**) Following Arnold (1983), the selection gradient $\beta_{z,w}$ acting on a given aspect of morphology, z, can be calculated as the product of the performance gradient β_{zf1} between the morphology and some aspect of performance, f_1, and the fitness gradient $\beta_{f1,w}$ between performance f_1 and fitness, w, so that $\beta_{z,w} = \beta_{zf1}\beta_{f1,w}$. (**B**) Multiple aspects of performance (f_1, f_2, ..., f_i) may be considered this way by summing the products of the performance and fitness gradients for each aspect of performance, so that $\beta_{z,w} = \beta_{zf1}\beta_{f1,w} + \beta_{z,f2}\beta_{f2,w} + \ldots \beta_{z,fi}\beta_{fi,w}$.

squirrels (Garber and Sussman, 1984; Youlatos, 1999), the habitual use of terminal branches by gray squirrels suggests that the primate morphological package of opposable first digits, convergent orbits, and a diagonal sequence-walking gait is not necessary for a small arboreal mammal to feed effectively in a terminal branch niche; the primitive state for these characters, evident in gray squirrels, is sufficient. These results challenge the Angiosperm Coevolution model, which suggests that primate morphology evolved directly in response to the demands of terminal branch feeding, primarily on stationary foods. However, because gray squirrels were not observed feeding on insects or grasp-leaping, our results cannot directly address the validity of the Nocturnal Visual Predation or Grasp-Leaping models.

Standard models of morphological evolution (Arnold, 1983; Futuyma, 1998) require that a trait must provide a performance (and ultimately reproductive) advantage to be favored by natural selection. Following Arnold (1983), the selection gradient, $\beta_{z,w}$, acting on a given aspect of morphology, z, can be calculated by multiplying the performance gradient, β_{zf1}, between the morphology and an ecologically relevant aspect of performance, f_1, by the fitness gradient $\beta_{zf1,w}$, between the performance variable and fitness, such that $\beta_{z,w} = \beta_{zf1}\beta_{zf1,w}$ where w is fitness (Fig. 5A). A performance gradient can be calculated as the partial regression between the morphology in question and the relevant measure of performance holding other aspects of morphology constant; a fitness gradient can be calculated as the partial regression of the performance variable and reproductive fitness (Arnold, 1983). Where two or more performance variables are being considered, the products of the performance and fitness gradients for each performance variable are summed to calculate the net selection gradient (Fig. 5B). For example, one might calculate the selection gradient on limb length in a terrestrial mammal by calculating the independent effects of limb length on both running speed and walking economy and multiplying these performance gradients by the fitness gradients for economy and speed.

While it is often difficult to calculate partial regression coefficients between morphology and performance, or performance and fitness (but see Altmann, 1991), Arnold's (1983) model nonetheless provides a useful framework for evaluating primate origins models in light of our data. The Angiosperm Coevolution model proposes that fine branch foraging became an ecologically important aspect of performance with the spread of angiosperm plants, creating a strong fitness gradient for early primates which specialized on these newly available foods (Fig. 6A) and hence a strong selection gradient favoring euprimate morphology. While convergence on primate-like morphology in other terminal-branch feeding taxa has been used to support the Angiosperm Coevolution model (Rasmussen and Sussman, 2007), the absence of primate-like features in gray squirrels (Ravosa and Dagosto, 2007) challenges this view. Gray squirrels use terminal branches extensively for feeding and foraging just as most arboreal primates do (Fig. 4), indicating that fine branch foraging is an ecologically important aspect of their locomotor performance. The lack of grasping hands and feet and orbital convergence in gray squirrels suggests that either the importance of these morphological features for fine branch foraging has been overestimated, or that other aspects of performance must be considered in models of primate origins. That is, the branch use patterns observed in gray squirrels indicate that adding terminal branch feeding to a species' locomotor repertoire is not sufficient to produce primate-like morphology.
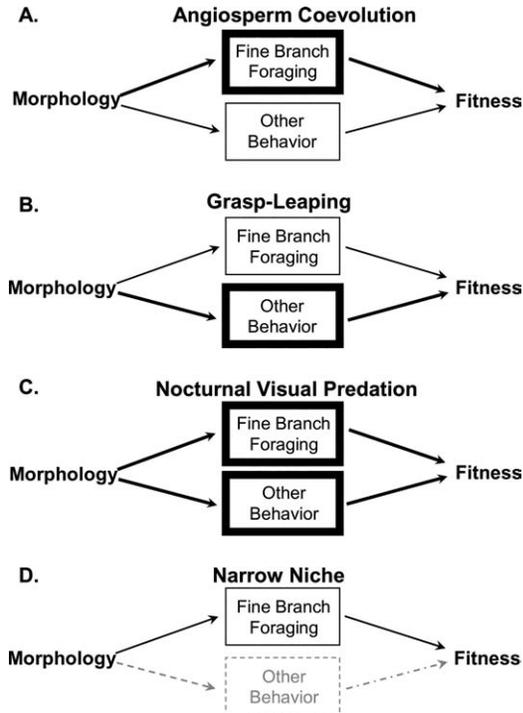
Fig. 6. Models for the selection pressures shaping early primates using the framework from Arnold (1983). Bold pathways indicate stronger performance or fitness gradients. (**A**) In the Angiosperm Coevolution model for primate origins, fine branch foraging led to a new, strong selection pressure on locomotor morphology, leading to the evolution of the primate morphological suite. The selection gradient for other aspects of locomotor ecology is relatively weak. (**B**) For the Grasp-Leaping model and similar hypotheses, novel behaviors led to new, strong selection pressures on early primate morphology. The selection gradient for terminal branch use is relatively weak. (**C**) For the Nocturnal Visual Predation model, fine branch foraging and novel behaviors combined to create strong selection pressures on locomotor and visual morphology, leading to the primate morphological suite. (**D**) The Narrow Niche model proposes that, as other behaviors were lost from the locomotor repertoire, the selection gradient for fine branch foraging became relatively stronger.

Hypotheses for primate and gray squirrel morphology

There are three general explanations for the absence of primate-like morphology in Eastern gray squirrels. First, terminal branch use may be neither necessary nor sufficient in selecting for primate-like morphology; selection on some other aspect of performance is needed. Second, the use of terminal branches may be necessary, but not sufficient, for selecting primate-like morphology; some other, complementary change in locomotor or behavioral ecology is needed. And finally, historical or genetic constraints on squirrel anatomy may limit evolutionary change in their morphology, resulting in suboptimal anatomical design.

Of these three general explanations, the hypothesis that squirrel morphology is constrained and therefore suboptimal for their ecology is the least compelling. While it is conceivable that the Sciuridae are not as morphologically labile as primates (an idea dating back to Jones, 1916) and cannot modify their basic body plan without a dramatic fitness cost, we find this idea

unlikely given the amount of time available for evolution in sciurids and the morphological changes of other species within the clade. The Sciuridae fossil record extends to the late Eocene (Korth, 1994), and while the genus *Sciurus* has remained virtually unchanged since the early Miocene (Emry and Thorington, 1984), other members of the family, such as the flying squirrels, have diverged anatomically (Thorington and Heaney, 1981). Testing the hypothesis that gray squirrels are morphologically constrained will require further understanding of sciurid development.

The hypothesis that terminal branch use is neither necessary nor sufficient to produce primate-like morphology cannot be addressed satisfactorily with our data, but deserves consideration. Under this scenario, the adoption of a new locomotor strategy, such as Grasp-Leaping (Szalay and Dagosto, 1980; Szalay and Delson, 1979), produces selection pressures leading to primate-like morphology, and the selection gradient between terminal branch use and fitness is relatively negligible (Fig. 6B). Our data from gray squirrels do not challenge this model, as the squirrels in our sample did not engage in frequent grasp-leaping and also lack primate-like morphology. However, a better test of this hypothesis would be a morphological analysis of nonprimate species that habitually engage in grasp-leaping. Similarly, other primate origin models that do not stress fine branch use ought to find convergent morphological evolution among species with similar locomotor patterns.

Hypotheses proposing that terminal branch use was a necessary, but not sufficient, pressure in the evolution of primate morphology suggest that some other change in the locomotor repertoire acted in concert with fine branch foraging. Changes to the locomotor repertoire might have involved the addition of novel behaviors. For example, the Nocturnal Visual Predation model proposes that the adoption of nocturnal insect hunting created selection pressures for both visual predation and careful fine branch locomotion (Cartmill, 1974b) and that these combined pressures produced the necessary and sufficient selection gradients favoring primate-like morphology (Fig. 6C). As with the Grasp-Leaping model, our data cannot directly address the importance of insect predation on small mammal morphology because the squirrels in our sample do not hunt insects. However, the Nocturnal Visual Predation model could be tested using nonprimate species that do hunt insects in fine branch contexts. For example, laboratory studies might examine stability or success rates in tree squirrels like *Heliosciurus rufobrachium* and *Aethosciurus poensis* that regularly capture insects (flying *Lepidoptera*) in their outstretched forepaws (Emmons, 1980). While these squirrels are diurnal and typically catch insects from larger supports, these conditions could be manipulated in a laboratory setting to determine if grasping and orbital convergence are necessary for the adoption of nocturnal insect hunting in fine branches.

Alternatively, sufficient changes to the locomotor repertoire of early primates might have involved the loss of behaviors and the narrowing of the locomotor niche. In this scenario, it is both terminal branch feeding and the relaxation of selection pressures outside the terminal branch niche, rather than the adoption of some novel behavior or increased selection for terminal branch use alone, that led to the evolution of the derived features common to primates. In this Narrow Niche model, terminal branch feeding is a relatively weak selective

pressure, and is not sufficient to produce primate synapomorphies without the concurrent relaxation of the selective gradient for other locomotor demands. Gray squirrels habitually and effectively feed in terminal branches, yet they retain a number of primitive features in their locomotor anatomy. This is likely because they maintain a broad locomotor repertoire that includes fine branch locomotion as well as frequent climbing of large trunks, where claws may be advantageous for maintaining purchase, and terrestrial locomotion and digging, which may favor their more generalized hand and foot morphology. Terrestrial locomotion may also increase predator exposure, favoring divergent orbits with a broader field of view. Early primates might have abandoned frequent terrestrial travel and/or use of large vertical trunks, essentially eliminating the selection pressures for these activities (Fig. 6D). While this scenario shares some elements with other models for primate origins—namely, that fine branch foraging is an important selection pressure for primates—the Narrow Niche hypothesis differs from other models in the implied ecological context for primate evolution. Rather than implicating some novel behavior or foraging strategy, the Narrow Niche hypothesis suggests that the arboreal behavior of early primates could have remained unchanged while terrestrial behaviors were lost. The loss of terrestrial behaviors might have been caused by any number of factors unrelated to arboreal foraging. For example, increased predation risk associated with terrestrial travel, or changes in the canopy structure that made terrestrial travel unnecessary for traveling between trees, could have promoted the abandonment of terrestrial behaviors even while the diet and arboreal locomotor behavior of early primates remained unchanged.

Although all adaptive models for primate origins invoke specialization, in the sense that the derived morphology is specialized to fit a novel ecological niche, the Narrow Niche model differs from previous explanations of primate origins that focus on arboreal specialization. Arboreal specialization hypotheses of primate origins remain indebted to Smith's (1912) and Jones' (1916) teleological suggestion that primates evolved from primitive, generalized stock that adapted to life in the trees. These early models did not address the selection pressures maintaining generalized morphology in primate forbears and instead considered arboreal locomotion as a novel ecological addition for early primates. Similarly, modern terminal branch explanations for primate origins typically neglect the pressures acting on the morphology of primate ancestors and instead focus on the adoption of new behaviors. By focusing on the loss of prior selective gradients, niche narrowing incorporates the selective environment of ancestral primates into the evolution of primates of modern aspect.

The Narrow Niche hypothesis is consistent with previous work on nonprimate arboreal species whose morphology is convergent with primates. For example, data from Rasmussen (1990) indicate that one of the largest difference in substrate use between the morphologically primitive *Didelphis* and the derived, primate-like *Caluromys* is that *Didelphis* is both arboreal and terrestrial while *Caluromys* is a dedicated arborealist. Similarly, Rose (1991) has suggested that chimpanzee and human locomotor anatomy differ primarily because the locomotor demands on chimpanzees include both arboreal climbing and terrestrial walking, whereas humans are dedicated terrestrial bipeds. In fact, the Narrow Niche model may be applicable across a wide range of ecological contexts. For example, sea lion and dolphin body plans may differ because, while they are both agile aquatic hunters, sea lions retain adaptations for locomoting on land whereas dolphins, with their narrower niche, do not (Nowak, 1999). To test the Narrow Niche hypothesis for primate origins, locomotor behaviors of arboreal primates could be examined to determine whether species with broader ecological niches have correspondingly variant morphologies. For example, tamarins have secondarily derived claws (Hamrick, 1998), which may be an evolutionary response to the expansion of their formerly narrowed niche to include locomotion on large-diameter trunks (Garber and Sussman, 1984). Similarly, the Narrow Niche model would predict that the cursorial adaptations of baboons and other terrestrial primates (Fleagle, 1999) reflect the importance of terrestrial locomotion but do not necessarily hinder branch use in the canopy.

Limitations of primate origin models and the utility of squirrels

Results from this study, as well as data from previous work on arboreal mammals, lead us to favor a Narrow Niche hypothesis for primate origins. The Narrow Niche hypothesis is consistent with previous work on sciurids and primate-like marsupials and is parsimonious in not requiring a novel locomotor behavior or dietary specialization. However, it should be noted that all primate origin models, including the Narrow Niche hypothesis, likely oversimplify the evolution of primates by focusing on a small number of selection pressures and treating the origin of primates as a single, discrete event. Primates exhibit a mosaic pattern of morphological features that did not evolve concurrently (Dagosto, 2007; Sargis et al., 2007). And there were likely multiple forces driving the evolution of primate morphology (e.g., the evolution of grasping might not be related to orbital convergence). Some aspects of primate morphology might even be exaptations or spandrels, evolved for different functions than those for which they are used today, or emerging as selectively neutral byproducts of other evolutionary changes (Gould and Vrba, 1982; Raichlen et al., 2009). While broad evolutionary models may provide a useful framework for understanding primate origins, future work might focus on the evolution of individual traits rather than treating the primate morphological suite as a singular entity. Experimental work examining specific aspects of primate morphology independently, combined with an improved fossil record of the timing and ecological context of primate trait acquisition, will provide a deeper understanding of their origins.

CONCLUSIONS

This study highlights the potential utility of the sciurid radiation for testing hypotheses of primate origins. Our results indicate that pedal grasping, orbital convergence, and diagonal sequence gait are unnecessary for a small arboreal mammal to feed on stationary angiosperm products in terminal branches. We propose that the selective consequences of terminal branch feeding during primate evolution have been overstated. It is likely that only with the relaxation of former selection pressures (i.e., niche narrowing) or when combined with

other pressures that terminal branch feeding could affect the evolution of primate morphology. The breadth of tree squirrel foraging ecology and the evolutionary success of these small-bodied arborealists, despite their lack of primate locomotor adaptations, make them an important point of comparison for modern primates.

ACKNOWLEDGMENTS

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