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COMMENTARY

Fallback Foods, Preferred Foods, Adaptive Zones, and Primate Origins

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Appreciation has grown for the impact of tropical forest seasonality and fallback foods on primate diets, behaviors, and morphology. As critically important resources in times of shortage, seasonal fallback foods may have an outsized role in selecting for form and function while the diversity of preferred plant foods has played an equally prominent role in shaping primate evolution. Here, hypotheses of primate origins are examined in the context of food choice models developed by Marshall and Wrangham [2007] and related to the broader concepts of adaptive zones and radiations. The integrated evolution of primate diet and positional behavior is consistent with a growing reliance on angiosperm products—not prey—as preferred and seasonal fallback foods, temporally and phylogenetically coordinated with evolutionary phases of the angiosperm adaptive radiation. Selection for an incisor oriented but non-specialized heterodont dentition, in contrast with most other orders, attests to the universal role of a highly varied vegetation diet as the primates' primary food resource, with diverse physical properties, phenology and high seasonality. A preference by plesiadapiforms for eating small protein- and lipid-rich seeds may have predisposed the primates and advanced angiosperms to diversify their evolving ecological interdependence, which established the primate adaptive zone and became realized more fully with the rise of the modern euprimate and angiosperm phenotypes. The "narrow niche" hypothesis, a recent challenge to the angiosperm co-evolution hypothesis, is evaluated further. Finally, I note support for visual predation as a core adaptive breakthrough for primates or euprimates remains elusive and problematic, especially considering the theoretical framework provided by the Marshall–Wrangham model, updated evidence of primate feeding habits and the counterpoint lessons of the most successful primate predators, the tarsiiforms. Am. J. Primatol. 9999:1–8, 2013.

Key words: seasonal fallback foods; primate origins; adaptive zones; angiosperms; visual predation

INTRODUCTION

Recent compendia [Constantino and Wright, 2009; Cuozzo et al., 2012] have added to our understanding of primate diets and dentition, with important implications for defining the primate adaptive zone and reconstructing primate origins. Like other orders of mammals [Osborn, 1902; Simpson, 1953; Van Valen, 1971], the primate adaptive radiation occupies an exclusive ecological domain made possible by distinctive key characteristics—Osborn stressed morphological combinations underlying locomotion and diet—that evolved in response to environmental parameters, location of food, and mode of food acquisition. While participants in the ongoing debate on primate origins [e.g., Bloch et al., 2007; Cartmill, 1992; Sargis et al., 2007; Silcox et al., 2007a,b; Soligo and Martin, 2006] are keenly intent to explain anatomical features in the context of the arboreal milieu in which primates first evolved, new studies present a fresh set of principles with which to test, elaborate and/or refocus competing adaptive hypotheses. Here, I concentrate primarily on the implications for the fruit eating hypothesis [Szalay, 1968] and the visual predation hypothesis [Cartmill, 1974]. The primate/angiosperm co-evolution hypothesis [Sussman, 1991], recently reviewed in this journal [Sussman et al., 2012], is not treated separately since co-evolution was by definition a prevalent, driving factor in primate evolution,

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although a critique by Orkin and Pontzer [2011] warrants attention. Nor is it necessary to distinguish derivatives such as the grasp-leaping hypothesis [Szalay and Dagosto, 1980] or the nocturnal visual predation hypothesis [Ravosa et al., 2000], which have more to do with euprimates than with primates *sensu lato*. Accordingly, to avoid confusion over terms and taxonomic concepts, particularly how authors variously compose the Order Primates, the taxonomy employed here is made clear: plesiadapiforms are stem primates [e.g., Bloch et al., 2007]; euprimates consist of strepsirhines, including fossil adapiforms, and haplorhines, including anthropoids and tarsiiforms.

Food, feeding and adaptation

It is now evident from in-depth, long-term field studies across all radiations that primate feeding strategies are strongly influenced by *shortages*. Rarely eaten foods appear to often be a more salient and widespread source of selection for feeding adaptations than commonly eaten foods or overall consumption [see Constantino and Wright, 2009; Cuozzo et al., 2012; van Schaik and Pfannes, 2005]. The selective role of uncommon foods was introduced in morphology as the critical-function hypothesis [Rosenberger, 1992; Rosenberger and Kinzey, 1976]: in the interaction between organism and environment, behaviors that involve more challenging biomechanical requirements govern the evolution of form. Field workers developed an ecological compliment to the critical-function hypothesis, the fallback foods hypothesis [e.g., Lambert, 2007; Lambert et al., 2004], and Marshall and Wrangham [2007] extended this synthetic model by redefining primate dietary categories operationally, thus providing a framework for integrating adaptive characteristics across anatomical systems. While these associations are often acknowledged, they are rarely correlated robustly or have their connectivity grounded in theory. In the Marshall–Wrangham paradigm, preferred foods (PFs) are chosen more often than would be expected given their temporal-spatial abundance in a habitat, and they provide a plentiful source of easily consumed calories. Thus, collecting PFs drives selection of sensory, cognitive and positional/locomotor adaptations. Fallback foods are non-preferred but highly important *seasonally*, when PFs are scarce. To emphasize their seasonal nature, and the point that this is not a rare phenomenon but a regular and consistent part of evolutionary adaptation, I refer to them as seasonal fallback foods (SFBFs). SFBFs are typically abundant but may be hard to process, requiring specializations to access, ingest, masticate or digest. Recent empirical studies that attempt to take into account the three-dimensional structure of molars, thus capturing more functional information than earlier efforts based on linear features [e.g., Kay, 1975 *et seq*.], tend to illustrate a stronger linkage between adaptive morphology and SFBFs than with more conventional dietary classifications (frugivore, insectivore, folivore) of species [Boyer, 2008]. Having said that, it is nevertheless important to recognize examples where species and even higher taxonomic groups, such as platyrrhine pitheciins, have adapted by making challenging foods their standard, non-seasonal PFs. In fact, successfully shifting feeding adaptations employed at times of scarcity toward seasonally abundant foods has been suggested as a key to the origins of this group [Rosenberger, 1992].

Food scarcity is a fact of primate life, as even tropical forests are cyclically influenced by climate and weather [van Schaik and Pfannes, 2005], bringing the evolutionary roles of PFs and SFBFs sharply into focus. The pressure of food shortages exists in spite of the great biodiversity of the tropics and the enormous numbers of plant species primates consume. Faced with seasonally depleted PFs, primates do not migrate, hibernate, or cache food to tide them over like many other mammals. They switch to SFBFs. New leaves, mature leaves and vegetable matter rank highest as SFBFs, followed by fruits and animals [Hemingway and Bynum, 2005], but the rarity and taxonomic distribution of primates feeding on animals as SFBFs indicates this coping strategy is not an easily utilized option. Two of the five taxa that regularly do are persistently predaceous, specialized clades, cebines and callitrichines, while there are no morphological suggestions that animalivory has imposed significant selective pressure on the others, the several pitheciins, lemurids and cercopithecines. Obligate animalivory, either as a PF or SFBF, should thus be regarded as a highly specialized primate diet, present in tarsiers, some platyrrhines, and lorisiforms [see Campbell et al., 2011] that exhibit complexes of unique predatory adaptations.

The Primate Adaptive Zone

Discussion of adaptive zones and reconstructed origins must assume continuity between modern and past conditions and focus on synergistic attributes of ecology and morphology. The concept of an ordinal adaptive zone is also restrictively multiplicative: once the niche is attained in the group's ancestry by virtue of key adaptations, essentially *all* descendant members of that radiation are expected to exhibit the lifestyle made possible by those traits, with few exceptions but potentially many variations. Thus, basically all carnivorans slice flesh to eat, some in aquatic environments but most on land; all rodents tooth-gouge to feed, some as arboreal gliders but most as ground dwellers; all artiodactyls grind leaves or grass, some amphibiously but most in relatively open country.

For primates, several parameters and synergistic attributes frame the analysis. (1) Primates are an arboreal tropical radiation and experience seasonal food scarcity. (2) Fruits constitute the basic PF diet and vegetation remains favored as SFBFs during periods of scarcity. (3) Primate dentitions are characteristically eutherian-primitive, retaining a heterodont pattern without dramatic modifications for harvesting or processing a narrow food class. (4) Primates are athletic, generalized locomotors with prehensile cheiridia and deploy an enormous behavioral repertoire to meet ever-changing substrate conditions. (5) Primate vision emphasizes a centralized binocular gaze and good close-range depth perception as opposed to a large field of view and monocular peripheral vision.

One can now reformulate Van Valen's [1971] primate adaptive zone: a tropical, arboreal, seasonally challenging domain where a wide variety of fruits are PFs and a narrower spectrum of fruits, plus leaves and other vegetation are principal SFBFs. This constrains predictions regarding ancestral primate anatomy and guards against reductionism or over-generalization. While a single molar tooth may be a proper object of consideration in investigating primate origins, it typically can only address part of a primate's dietary profile [Rosenberger, 2010a]. Other factors may be required to elucidate SFBFs, or to identify the most challenging items fed upon or encountered in accessing foods, and knowledge of many facets is required to establish overall niche. For instance, while both *Aloutta* and *Brachyteles* each have well documented "folivorous" molars, they differ profoundly in cranial, skeletal and gut anatomy, relative brain size, sociality, and use of space. Beyond dental adaptations, only *Alouatta* conforms bodily and behaviorally to the folivory model [Rosenberger et al., 2011].

DISCUSSION

Fruit As the Original Primate Diet

The Marshall–Wrangham [2007] model predicts that ancestral euprimates should have a generalized feeding system able to effectively harvest and masticate fruits with a wide variety of physical properties as PFs, a locomotor system to facilitate discovery of these fruits, a sensory system able to detect PFs reliably, and coordinated subsystems to facilitate access, ingestion, mastication and digestion of seasonally useful fruit, leaves and other vegetation as SFBFs. These predictions are borne out by the modern primate dentition. While diversified, it normally lacks constraining specializations – no razor sharp or milling teeth; no cheek tooth gaps filled by storage pouches; only rare occurrences of spiky premolar and molar crowns. Functionally versatile cheek teeth reflect the broad range of physical properties a primate encounters consuming a wide variety of vegetation. They evidence a basal, frugivorous PF diet with the potential for evolving morphological compromises extending the dentition to permit efficient consumption of arthropods or leaves as well, which only require modest shape changes to augment puncturing, cutting or shearing potential [e.g., Kay and Hiiemae, 1974; Rosenberger and Kinzey, 1976]. Rather than emphasizing the comparatively primitive and retentive nature of the primate dentition in a non-ecological context [e.g., Clark, 1959], it is more instructive to regard its inherent biomechanical flexibility as an asset under selection, balancing the varied physical properties of primate foods.

As the digestive system's point of contact between the organism and the environment, incisors (like cheiridia) are exquisitely sensitive to selection. This makes it noteworthy that non-tarsiiform euprimate dentitions commonly present cropping incisors for harvesting fruit and foliage. While especially evident among the spatulate-incisored anthropoids, lemuriform strepsirhines also have wide upper incisors, though comparatively reduced in height and thickness, a configuration more than serviceable for harvesting vegetation, for example, stripping leaves without employing a hard bite against the often delicate toothcomb. In conjunction with the relatively low metabolism of extant species [Snodgrass et al., 2007], this suggests leaves were important to basal strepsirhines. Among them, the primitive notharctid adapiforms have upper incisors closely resembling those of lemuriforms [e.g., Rosenberger et al., 1985], spatulate lower incisors and bunodont, moderately crested molar teeth [Gilbert, 2005], a combination suitable for fruits as PFs and other vegetation as SFBFs. The dentally derived adapids have more advanced cropping incisors, more crested cheek teeth and, in cases where it is well documented, a less agile postcranium [Dagosto, 1983; Gebo, 1988], possibly suggesting a shift to a predominantly semi-folivorous PF/SFBF diet analogous to the above mentioned large platyrrhines [Rosenberger et al., 2011].

One outstanding nonhuman exception to these generalizations about diet, dentition and adaptive zone —a lesson in and of itself—involves tarsiers, which eat absolutely no plant material [Gursky, 2007]. In a way tarsiers present a functionally homodont dentition: to the greatest possible extent, incisors, canine, premolars and molar cusps are configured as a series of piercing cones and cutting blades, with acutely cusped and crested molar crowns presenting enhanced puncturing and shearing functions. They also have radically specialized visual, cranial and postcranial adaptations designed to support the tarsier's method of prey capture [e.g., Rosenberger, 2011]. In contrast, despite their equally small body size, the molars of most Eocene tarsiiform genera, and especially the basal anaptomorphines, do not exhibit high levels of shearing [Strait, 2001] while their crania and postcrania present galago-like advances toward a tarsier-like pattern in terms of orbital enlargement and leaping adaptations [e.g., Rosenberger and Preuschoft, 2012]. This indicates a continued reliance on fruit coupled with a new capacity to exploit prey in a nocturnal milieu by evolving novel—not primitive—features in combination. The marked departure from a "standard" euprimate morphology across these systems, which as a package is clearly antecedent to the *Tarsius* pattern, is an indication of the group's shift to incorporate prey as part of their PF menu, and the intense selective challenges associated with such a change. Thus any super predatory members that may potentially be found as fossils belonging to the exclusive tarsier lineage are likely to be adaptive outliers as well, with limited relevance to reconstructing the ancestral tarsiiform or euprimate feeding and foraging strategies.

The first appearances of euprimates in the early Eocene [Gingerich, 1986; Ni et al., 2004; Smith et al., 2006] co-occur with a burst of Tertiary angiosperm biodiversity and innovation [e.g., Sussman et al., 2012], including an increase in seed size and predominance of closed-canopy forests [e.g., Eriksson, 2008; Tiffney, 2004], thus forging the critical link between diet and locomotion anticipated by Osborn [1902]. Consistent with this ecological reconstruction is evidence that euprimates present a transformed locomotor system capable of powerful hindlimb grasping and leaping [e.g., Dagosto, 1988]. Thus, at a moderate body size, adapiforms would have been able to forage widely through a continuous canopy via intersecting terminal branches, to locate an increasingly large number of larger fruit species serving as PFs, using enhanced sensory and cognitive means to detect them—relatively larger eyes and brains than the more primitive plesiadapiforms [Silcox et al., 2009]. Smaller forms would have also exploited angiosperms in the understory where early phase flowering plants were successful [Field et al., 2004]. As noted, neither the majority of adapiforms, nor all the tarsiiforms, evidence widespread, advanced morphological indications of insectivory, although it is not possible to exclude a sizeable soft-bodied insect fraction on the basis of molar form. This is particularly true of the taxonomically diverse tarsiiforms. They radiated within a small body mass class and, as good leapers, probably were ecologically segregated by specializing in the use of the understory stratum. They also present some unexpected cross-system morphological combinations. For example, as noted by Rosenberger and Preuschoft [2012], the European sister-taxa *Necrolemur* and *Microchoerus* combine complex, low-relief, non-shearing molar crowns with enlarged orbits, elongate feet and, as documented at least in the former, a fused tibio-fibula.

Plesiadapiforms were preadaptively disposed to the ancestral euprimate vegetation diet but they did not pass a particular adaptive threshold. While the majority of the dental inferences discussed apply to them as well, various elements of the feeding-locomotor system remain more primitive. Their bunodont, nondescript cheek teeth suggest a reliance on vegetation. But at a small body size [mostly <50–300 g: Fleagle, 1999; see also Silcox et al., 2007a,b], meaning also a proportionately short jaw length and limited gape, plesiadapiforms would have been restricted to a range of small, berry-sized fruits, probably with a narrower spectrum of physical properties than modern primates encounter. This is consistent with the characteristics of primitive angiosperms, which had not yet evolved the modern features highly attractive to mammalian and avian seed dispersers. The conical central incisors of plesiadapiforms that distinguish them from modern euprimates probably relate to harvesting the early proto-fruits. While frequently high-crowned, proclivus and pointed in advanced lineages, the simpler, primitive forms are aptly designed for axial loading, used as a probe and/or pincer suitable for prying loose small pre-Eocene fruits and seeds [<10 mm: Tiffney, 2004] in beak-like fashion [Rosenberger, 2010b].

Seeds, in addition to fruit pulp and aril, play an enormous role in the food webs of vertebrates and invertebrates [Sallabanks and Courtney, 1992]. Although specialized seed harvesting has been inferred for some highly modified plesiadapiforms as well, such as the plagiaulacoid-toothed carpolestids [Biknevicius, 1986], it is likely that wind dispersed seeds played a broadly important role in plesiadapiform feeding [Rosenberger et al., 2011], perhaps more so than we have thought, for large-seed, fleshy fruits were not as common during the late Cretaceous and early parts of the Paleocene. Seed-eating may have predisposed stem primates to the ecological interdependence attained during the Eocene among euprimates and modern angiosperms. By then, larger, fleshy fruit had evolved to attract pulp-eating frugivorous animals [see Sussman et al., 2012] with a desirable, energy-rich alternative or compliment to seeds [Rosenberger et al., 2011], thus selectively promoting primates to evolve a new role as seed-disperser instead of seed-predator. This transition is also marked by a shift in locomotor competence, for the non-acrobatic arborealism of known plesiadapiforms [Bloch and Boyer, 2007; Sargis et al., 2007] suggests wide-ranging foraging to dispersed fruit patches was not central to their PF pattern. Small eyes and lack of expansive, sensitive fingertips indicate a less advanced form of food detection and manipulation, foraging travel and arboreal maneuverability, in which pedal prehension may have been more advantageous for stable feeding postures and quadrupedal walking than gap-crossing, acrobatic locomotion [e.g., Bloch and Boyer, 2002].

Since this line of reasoning coincides with the angiosperm co-evolution hypothesis [Sussman, 1991], it seems fitting to comment on a recent challenge, the "narrow niche" hypothesis of Orkin and Pontzer [2011]. They pose the same question as Cartmill [1974] in his critique of the classic arboreal hypothesis of primate evolution: If foraging in terminal branches introduced selective pressures that drove the evolution of euprimate features, why are squirrels not more like them? This appeal to an *extrinsic extra-ordinal analogy* as the primary explanatory model is a common method in origination studies—the presence of forward facing eyes in primates and cats means that primates are visual predators—and quite different from the perspective I share with Sussman et al. [2012], which seeks to integrate functional morphology with ecological rules generalized *intrinsically* from studies spanning the primate order and the notion of mammalian adaptive zones [Van Valen, 1971].

Orkin and Pontzer [2011] conclude from their study of squirrel arboreal locomotion that an additional term must be included in the angiosperm hypothesis to make end branches the springboard that selectively induced the primates' derived locomotor characteristics. They argue it is not the attainment of arboreal behaviors but the loss of others that effectively "narrowed" the euprimate niche from its broader, pre-euprimate dimensions. I see several difficulties with their argument: (1) It turns on a difference in semantics and emphasis. By insisting there is more heuristic value in specifying a "loss" of locomotor competence as opposed to the widely acknowledged generalized "shift" in primate positional behaviors, Orkin and Pontzer dwell on the *historical process* by which euprimate attributes arose, whereas Sussman et al. [2012] seek to explain the *ecological context* of a new realized niche. (2) By failing to consider the entirety of fossil evidence in this evolutionary sequence, Orkin and Pontzer miss the ecological attributes that their "loss" model stipulates. Plesiadapiforms, in their scansorial arborealism, are arguably analogous to squirrels in locomotor competence, so a reduction in claw-based locomotion without pedal grasping [Sargis et al., 2007] is inherently part of the transition from that morphological *gestalt* toward the euprimate condition. This is precisely what many believe happened as primates became adept at living among angiosperm terminals, including Szalay [1968], Cartmill [1974], and Sussman and Raven [1978]. (3) Orkin and Pontzer apparently maintain that all small mammals living in the terminals should inexorably evolve euprimate-like traits. This has never been an axiom of the angiosperm co-evolutionary model, though it follows the thrust of Cartmill's reasoning [1974]. In any event, such strict adherence to the presumption of mirror image convergence among orders is never warranted. It is evident that arboreality comes in many forms, stemming from many alternative basal conditions involving different phyletic origins, evolutionary histories and constraints, and it evolves with a variety of ecological compromises regarding the degree and manner by which taxa are adapted to the physicality of arboreal life. At a basic level, squirrels are a flawed convergence model and should not be expected to evolve many euprimate resemblances because they are bound to an arbo-terrestrial existence, foraging and sheltering in the trees but caching food on the ground, which selects for scansorialism. Their eyes, orbits and skulls cannot be primate-like because their heads house a massively specialized, somewhat peculiar masticatory apparatus that constrains its architecture. (4) The Orkin-Pontzer model also suffers limitations in that it tries to explain only one dimension of the primate adaptive zone. At a minimum, a truly robust origination model needs to account for and integrate adaptation to habitat, food, use of space, and time of activity (which I admittedly do not address here either). It requires a framework that conforms to ecological principles derived from knowledge of primate patterns and universals, as in the Marshall–Wrangham paradigm [2007].

Prey As The Original Primate Diet?

Emmons [2000], Muchlinski [2012], and Sussman et al. [2012] point out that among small non-chiropteran mammals the predation niche is very rare and scattered taxonomically, save mostly for the few specialized primates mentioned above. This raises questions about its relevance to primate and euprimate [and anthropoid; see Ross, 2000] origins and its viability as an adaptive zone concept. The hypothesis that insect, arthropod or vertebrate prey was the formative dietary component of euprimates or plesiadapiforms is also difficult to reconcile with the Marshall–Wrangham [2007] model. Among extant primates, animals very rarely serve as PFs or SFBFs, so the universality criterion, or even a lesser commonality standard, is not met: predation does not comply with the very notion of a primate adaptive zone shaping primate biodiversity. If predation was the ecological breakthrough that ushered in the primate ordinal niche, one would expect the majority of living primates to be obligate—not variously facultative—predators, with animalivorous adaptations evident across bodily systems. Neither fieldwork, dental or postcranial morphology supports this. For example, while persistent stalking is typical of lorises, it is accompanied by a host of cranial and postcranial autapomorphies that make it possible. Tarsiers employ the opposite strategy as sit-and-wait ambush predators and they, too, are radically specialized. Incidental gleaning of overt prey and unburying concealed prey does occur across the order but without coordinated support from clear-cut, cross-system, universal adaptive complexes. To wit, the two-handed prehension patterns of strepsirhines, tarsiers and marmosets, while quite advanced relative to the "unemancipated" limbs of other mammals, seem primitively awkward in the process of snapping up prey.

Paleontologically, the case for the small-eyed, large-snouted plesiadapiforms being visual predators is confoundingly prohibitive, even for species whose molars appear to be shaped for insectivory [see Silcox et al., 2007a,b]. For omnivorous-frugivorous animals, seeds—an archetypical terminal branch food eaten by an enormous array of small mammals, both arboreal and terrestrial—may have provided a reliable source of proteins and lipids within the vegetation spectrum, less haphazardly and more cheaply than insects. While some families within the diverse plesiadapiform radiation were probably more insectivorous [Kay and Cartmill, 1977] and other advanced forms more folivorous [Boyer et al., 2010], the majority of examples drawn from every lineage surrounding the origins of euprimates (plesiadapoids, adapiforms, and tarsiiforms) suggest that vegetation was the predominant source of PFs and SFBFs, as with living primates.

Advocates of the visual predation hypothesis rely on non-dental features said to reflect prey detection via stereoscopy: the postorbital bar and convergent eyes of euprimates [e.g., Cartmill, 1992, 2012; Noble et al., 2000; Ravosa et al., 2000]. However, no explicit connection *between the bar and predation* is likely to ever be made and the actual perceptual benefits of stereoscopy are difficult to determine. Nakayama [2005] maintains stereopsis provides "unambiguous information about depth" [p. 6] that triggers awareness of object boundaries, an effect that would benefit canopy locomotion and foraging, among other faculties. Still, if correct, interpreting this aptitude as a predatory adaptation suffers from over-specification by presuming a one-to-one correspondence between a single physiological function and one of many potential biological roles. Multiple and diverse selective benefits may have advantaged early euprimates with comparatively close-set and forward-facing eyes.

For instance, experimental evidence [Patla et al., 2002] has shown that the absence of stereoscopic vision impedes "adaptive" locomotion, especially in an object-filled environment. Modern primates, if anything, are adaptive locomotors. Also, the integration of tactile and visual sensory systems is often overlooked in discussions of optical advances across the primate-euprimate divide [see Yau et al., 2009]. The extent of their interconnectedness is easily demonstrated by our own capacity to recognize shapes via tactile input under blind conditions. The close-quarters visual acuity and comprehension emphasized in the "X-ray vision" explanation of orbital convergence and frontation [Changizi and Shimojo, 2008] would greatly benefit such a system and contribute to the evolution of highly dynamic locomotion. This capacity presupposes the ability to interpolate and integrate the spread fingers of the hand, branch dimensions, contour, texture, and complex surroundings as the vestibular system learns and calibrates itself via visual-tactile feedback. Similarly, experimental studies have suggested various explanations for the postorbital bar, regarding it, on the one hand, as a cranial strut that *facilitates* mastication [Ravosa et al., 2000] and, on the other, as an attachment site for eye-stabilizing ligaments that *counteracts* the effects of mastication [Heesy, 2005]. To extend Rosenberger and Preuschoft's [2012] modeling study of the tarsier partial postorbital septum, the bar may also serve as a stabilizer of the eye under challenging locomotor conditions, such as the high g-force accelerations and decelerations of leaping. All these possibilities suggest that absent a more comprehensive, system-integrating analysis, it is not possible to determine that stereoscopy was selected solely, or even preferentially, for roles underlying visual predation as opposed to other behaviors. *Inferring the specifics of food type from the cranium requires the support of dental evidence, especially when it hypothesizes an exception to the ordinal ecological rule*.

CONCLUSION

Morphological continuity and adaptive overlap between crown and stem taxa, and the near universality of vegetation as today's core PFs and SFBFs, suggests it was also the basal diet of the first recognizable primates as they entered the primate adaptive zone. A more precise inference may be difficult to square with the power of resolution of gross morphological methods except by exclusion, that is, by eliminating leaf and insect eating among the most relevant fossils. A thorough re-evaluation of Paleocene-Eocene primate diets using modern methodologies [see Boyer, 2008], an updated paleontological model of primate food choice based on new evidence from the living forms, and an approach that emphasizes evolutionary transitions and preadaptation rather than a static morphology would be most informative [see Silcox et al., 2007a,b]. Today, the rarity of insects as PFs or SFBFs makes it unlikely that an annual or seasonal diet reliant on prey was the predominant driver of selection for augmented vision as a euprimate or primate universal. The evident coordination of keen eyesight, slicing cheek teeth and fleet quadrupedalism (among many other attributes) lends a robust measure of credibility to the inference that orbital orientation was a central element in achieving the carnivoran predatory adaptive zone. But it logically faults the visual predation hypothesis of primate origins, where no comparable cross-system interconnectedness has been demonstrated among any of the early forms. By analogy, the multimodal prey detection method of mouse lemurs, integrating hearing, vision and olfaction [Piep et al., 2008], argues against the primacy of any one channel being the ancestral key to primate animalivory. The highly derived and integrated visual and auditory systems of tarsiers [Rosenberger, 2010b], where olfactory competence has probably been degraded, also exemplifies the outsized multimodal sensory needs of primates that turn to predation, and the extraordinary degree, essentially paralleled in lorises, to which the eyes, heads and bodies of these exceptional primates require modifications from primitive conditions in connection with visual predation. Narrowly invoking a prey-based diet to explain the adaptive significance of a different set of cranial features and a different set of eyeball parameters in ancestral euprimates, where functional significance remains vague, is not a parsimonious solution. For Occam's razor has been crisply sharpened by the framework of the Marshall–Wrangham [2007] model, abetted by numerous studies on living primates and other arboreal mammals [e.g., Emmons, 2000; Sussman et al., 2012]. A new fusion of theory and empiricism provides a stronger argument concerning the significance of PFs, SFBFs and tropical ecology for the evolution of primate diets, the vegetation-based origins of the order and the primate adaptive zone.

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