Arboreality has allowed for the evolution of increased longevity in mammals

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The evolutionary theory of aging predicts that species will experience delayed senescence and increased longevity when rates of extrinsic mortality are reduced. It has long been recognized that birds and bats are characterized by lower rates of extrinsic mortality and greater longevities than nonvolant endotherms, presumably because flight reduces exposure to terrestrial predators, disease, and environmental hazards. Like flight, arboreality may act to reduce extrinsic mortality, delay senescence, and increase longevity and has been suggested as an explanation for the long lifespans of primates. However, this hypothesis has yet to be tested in mammals in general. We analyze a large dataset of mammalian longevity records to test whether arboreal mammals are characterized by greater longevities than terrestrial mammals. Here, we show that arboreal mammals are longer lived than terrestrial mammals at common body sizes, independent of phylogeny. Subclade analyses demonstrate that this trend holds true in nearly every mammalian subgroup, with two notable exceptions—metatherians (marsupials) and euarchontans (primates and their close relatives). These subgroups are unique in that each has experienced a long and persistent arboreal evolutionary history, with subsequent transitions to terrestriality occurring multiple times within each group. In all other clades examined, terrestriality appears to be the primitive condition, and species that become arboreal tend to experience increased longevity, often independently in multiple lineages within each clade. Adoption of an arboreal lifestyle may have allowed for increased longevity in these lineages and in primates in general. Overall, these results confirm the fundamental predictions of the evolutionary theory of aging.

senescence | extrinsic mortality | terrestriality | marsupials | primates

Senescence, or aging, is an intrinsic biological phenomenon that limits an organism's maximum potential lifespan, even in the absence of extrinsic sources of mortality such as predation, disease, and environmental hazards. Its evolution is of particular interest in life-history studies (1, 2), in part because it is not immediately clear why senescence persists in the presence of natural selection, which might be expected to eliminate it. The evolutionary theory of aging, in its several, nonmutually exclusive forms (3–8), proposes that senescence is the result of late-acting, deleterious mutations that accumulate because of the diminishing effectiveness of selection with increasing age. Extrinsic mortality is one major factor that contributes to the accumulation of deleterious mutations by limiting exposure of these late-acting mutations to selection; thus, the evolutionary theory of aging predicts that extrinsic mortality will be a principal determinate of the rate of senescence in age-structured populations (9). This theory predicts that populations experiencing high extrinsic mortality rates will accumulate more deleterious mutations, evolve earlier senescence and reproduction, low somatic maintenance, and shorter maximal lifespans. Conversely, populations subject to low extrinsic mortality rates will eliminate late-acting deleterious mutations more effectively and evolve delayed senescence, late fecundity, durable somas, and greater longevities. These relationships have been demonstrated in laboratory (10–12), wild (13–15), and simulation (16) studies.

In the wild, flying birds and bats experience lower rates of extrinsic mortality (17) and greater longevity (18–23) than their nonvolant relatives, presumably because of decreased predation. Although other factors such as hibernation and reproductive rate have been shown to play a role in bat longevity (22), these factors are accordant with evolutionary theory of aging, and it is clear that the exceptional longevity of Chiroptera as a whole is the result of flight. In addition to flying birds and mammals, gliding mammals are longer-lived than nonvolant, nongliding mammals (21, 23). As with flight and gliding behavior, arboreality may act to lower extrinsic mortality rates and increase longevity by providing a relatively protected environment with reduced exposure to predation, disease, and environmental hazards. Indeed, Darwin himself (ref. 24, p. 169) identified an association between arboreality and extrinsic mortality, recognizing the "power of quickly climbing trees, so as to escape from enemies." Furthermore, several researchers have suggested that primates are long-lived among mammals at least in part because they are largely arboreal (25, 26). If so, then we might expect arboreal mammals in general to possess greater longevities than their terrestrial counterparts. Using analysis of covariance (ANCOVA) and an analysis of phylogenetically independent contrasts (PIC), we test this hypothesis by comparing longevity records for arboreal and terrestrial mammals in a molecular phylogenetic context (Fig. 1 and Fig. S1).

Results and Discussion

Overall, in agreement with previous studies (27, 28), body mass accounts for 60% of the variance in maximal lifespan in nonvolant, nonaquatic mammals. Longevity, like many life-history traits, is negatively allometric, so that lifespan increases at between one-fourth and one-third the rate of body mass (Fig. 2). An initial analysis on the entire dataset indicates that the slope for semi-arboreal species is significantly different from the arboreal and terrestrial slopes. A separate analysis of Eutheria alone results in common slopes for all three groups (see below; Table 1), suggesting that the departure of the semiarboreal slope results from the influence of marsupials. Because of this result, semiarboreal species were removed for analysis on the overall dataset, and an ANCOVA was conducted on the remaining habitat groups (arboreal and terrestrial). This analysis demonstrates that, at common body sizes, arboreal mammals are characterized by greater longevities than terrestrial mammals ($P < 0.001$) (Table 1 and Fig. 2). Results of the PIC analysis on the mammalian dataset also are significant ($P < 0.001$), indicating the effect of habitat type on longevity remains even when the effects of phylogeny are removed.

Results of subsequent ANCOVA are listed in Table 1. In 8 of the 10 subclades included in the analysis, arboreal mammals are characterized by greater longevities than terrestrial mammals (Table 1). Semiarboreal eutherian mammals are either intermediately long-lived or are not significantly different from one or the other habitat type (Table 1 and Fig. 3). Results for two subclades, Metatheria (marsupials) and Euarchonta (primates and their close relatives),
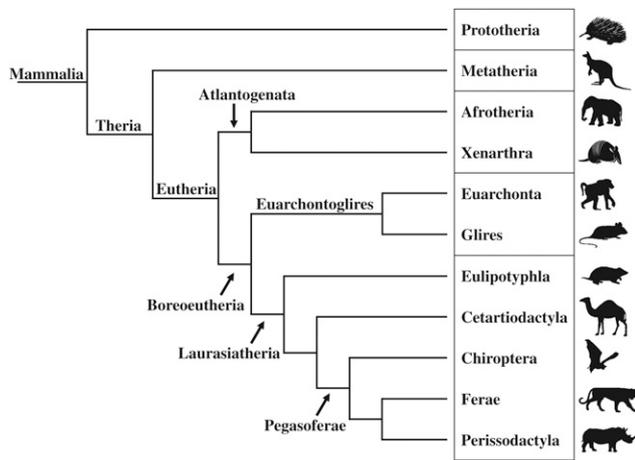
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Fig. 1. Molecular phylogeny of Mammalia. Prototheria: monotremes. Metatheria: marsupials. Afrotheria: aardvark, tenrecs, elephant shrews, hyraxes, manatees, dugongs, elephants. Xenarthra: sloths, anteaters, armadillos. Euarchonta: tree shrews, colugos, primates. Glires: rodents, rabbits. Eulipotyphla: moles, hedgehogs, shrews. Cetartiodactyla: bovids, cervids, suiforms, camelids, hippopotamids, cetaceans. Chiroptera: bats. Ferae: *Pholidota* (manids) and Carnivora (canids, ursids, musteloids, pinnipeds, felids, viverrids, herpestids, hyaenids). Perissodactyla: horses, tapirs, rhinos.

Fig. 2. Maximal lifespan plotted against body mass for 776 mammals in log space. The solid line is the least squares regression for terrestrial mammals; the dashed line is the least squares regression for arboreal mammals. The slopes for these regression lines are common, and the intercepts are significantly different ($P < 0.001$). OLS regression for arboreal mammals: $y = 0.245x + 1.64$, $r^2 = 0.499$, $P < 0.001$. OLS regression for terrestrial mammals: $y = 0.222x + 1.39$, $r^2 = 0.756$, $P < 0.001$.

differ from the overall results. Within Metatheria, although arboreal and terrestrial marsupials are not significantly different from each other, both are significantly longer-lived than semiarboreal taxa (Table 1). Our results therefore confirm a previous finding that arboreality is not associated with increased longevity in marsupials (29). In Euarchonta, our analyses did not reveal significant differences between any of the habitat types (Table 1). However, taken together, the overall results demonstrate that there is a general, significant relationship between habitat type and longevity in mammals. That is, arboreal mammals have evolved greater longevities than terrestrial mammals, and semiarboreal mammals tend to fall intermediately between these two groups. Even in the most specific clade we analyzed, the superfamily Sciuroidea, arboreal squirrels are longer-lived than terrestrial squirrels at common body sizes ($P < 0.001$; Fig. 3).

Previous authors have suggested that primates are particularly long-lived among mammals, in part because they are largely arboreal (25, 26). However, among both euarchontans and marsupials, arboreal species do not possess greater longevities than terrestrial species. Arboreality is the primitive condition for
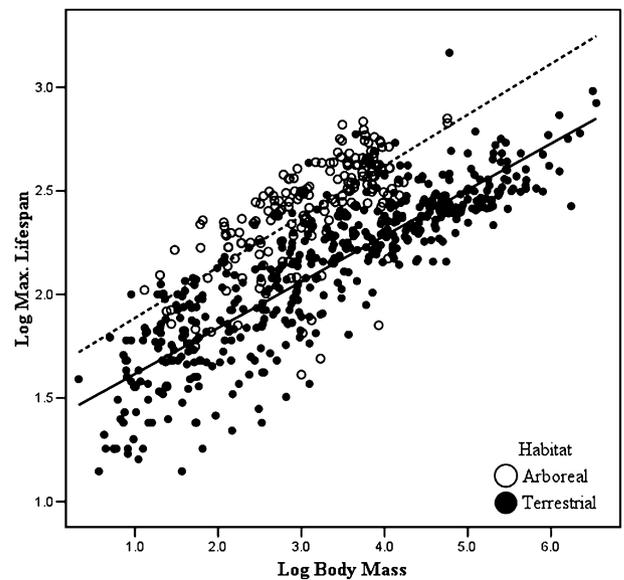
primates, initially evolved in an ancestral euarchontan (30–35). Marsupials also probably are primitively arboreal (34, 36–38), with subsequent and repeated events of terrestriality (38). In contrast, many other eutherian orders and placental mammals in general are likely characterized by terrestrial evolutionary histories, with subsequent events of arboreality derived multiple times in these lineages (34, 39). (See ref. 34 and sources therein for a recent and thorough review of this topic.) The nature of these dichotomies may play out in the evolution of longevity. We propose that the lack of significant differences between arboreal and terrestrial euarchontans, and possibly marsupials, may be the result in part of the long history and persistence of arboreality in their evolutionary histories (30–38). Unlike euarchontans, however, marsupials are not characterized by increased longevity in general (Fig. 4). Compared with marsupials, the extremely high degree of arboreality throughout the evolution of Euarchonta,

Table 1. Clades, sample sizes, and significance

Clade	Sample size total A:S:T	Significance (*P* value)*		
		Arboreal vs. terrestrial	Arboreal vs. semiarboreal	Terrestrial vs. semiarboreal
Mammalia	776 (189:118:469)	**<0.001**	N/A	N/A
Metatheria	081 (022:011:048)	NS	**0.003**	*0.015*
Eutheria	693 (167:107:419)	**<0.001**	**<0.001**	**<0.001**
Atlantogenata	030 (003:006:021)	**0.030**	NS	NS
Boreoeutheria	663 (164:101:398)	**<0.001**	**<0.001**	**<0.001**
Laurasiatheria	281 (015:035:231)	**<0.001**	**0.050**	**<0.001**
Ferae	122 (015:035:072)	**<0.001**	NS	**0.002**
Euarchontoglires	382 (149:066:167)	**<0.001**	N/A	N/A
Euarchonta	154 (119:031:004)	NS	NS	NS
Glires	228 (030:035:163)	**<0.001**	**0.012**	**0.050**
Sciuroidea	051 (019:014:018)	**<0.001**	**0.032**	NS

*Bold *P* values indicate that the intercept for the more arboreal taxon is significantly greater than the intercept for the more terrestrial taxon at the α = 0.05 level. Italicized *P* values indicate that the intercept for the more terrestrial taxon is significantly greater than the intercept for the more arboreal taxon. A:S:T, arboreal: semiarboreal:terrestrial, N/A, assumptions of ANCOVA are not met (i.e., slopes were not found to be common); NS, nonsignificant *P* value (> 0.05).
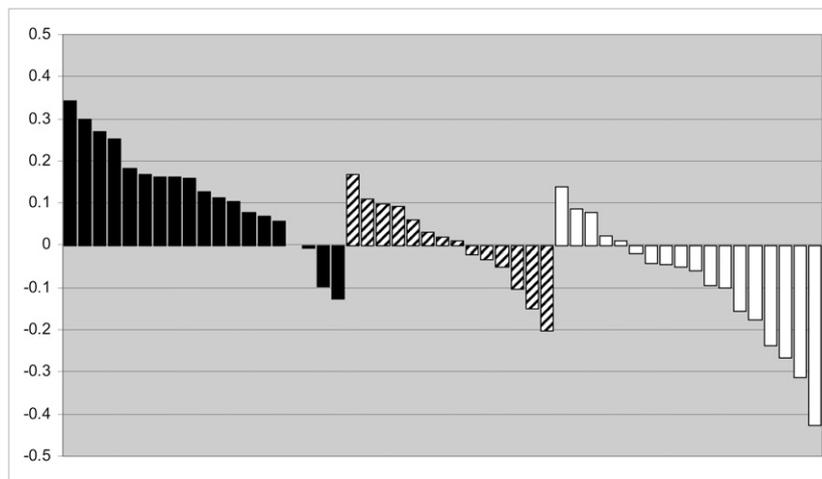
Fig. 3. Residuals extracted from least squares regression on Sciuroidea. The black bars are residuals for arboreal squirrels ($n = 19$), the hatched bars are semiarboreal squirrels ($n = 14$), and the white bars are terrestrial squirrels ($n = 18$). Although the arboreal and terrestrial ($P < 0.001$) and arboreal and semiarboreal ($P = 0.032$) intercepts are significantly different from each other, the semiarboreal and terrestrial intercepts are not ($P > 0.05$). OLS regression: $y = 0.1531x + 1.736$, $r^2 = 0.241$, $P < 0.001$.

and specifically within primates, may explain this discrepancy. A highly arboreal evolutionary history may have allowed increased longevity in all primates.

In addition to a long arboreal evolutionary history, it has been suggested that terrestrial primates may not experience increased extrinsic mortality because they have evolved physiological, social, and behavioral defenses against predation (40, 41). First, ground-dwelling primates have increased body size upon transitioning to a terrestrial lifestyle. Unlike other groups of mammals (e.g., carnivores; ref. 42), body mass is significantly correlated with habitat type in primates (43). It is likely that the larger body size of terrestrial primates decreases their susceptibility to predation, thus lowering the risk of spending time on the ground (1, 40, 41, 43, 44). Predation

on small-bodied, arboreal primates by birds of prey and arboreal carnivores and leopard predation on primates both on the ground and in the trees may render arboreal and terrestrial primates equally susceptible to predation (40, 41). Second, primates are highly social, and the advantages of group living provide social defenses such as large group size, vigilance, and alarm calls (40). Terrestrial primates live in larger social groups than arboreal primates (40, 41, 43, 44), thus supporting this hypothesis. Humans, the most terrestrial of all primates, have reduced extrinsic mortality and increased longevity resulting from the obvious advantages provided by sociality and culture.

Similar arguments may be made for some marsupial species. Terrestrial marsupials that occupy open habitats are generally large and capable of fast speed (e.g., macropodids). In addition, they live in large social groups and demonstrate vigilance behavior, contrasting with the lack sociality of marsupials in general (45–47). These factors might contribute to decreased predation risks associated with terrestriality and explain the lack of significant difference in longevity between arboreal and terrestrial marsupial species. However, as noted previously, marsupials are not long-lived in general, regardless of habitat type. This observation suggests that other confounding factors, such as development, brain size, or various aspects of physiology may significantly influence longevity in these species. We therefore are more cautious in our interpretation of marsupial longevity.

Many evolutionary transitions to arboreality among mammals have resulted in increased longevity, demonstrated by longer-lived arboreal taxa in the majority of mammalian clades. As with flight and gliding behavior, arboreality appears to have reduced extrinsic mortality and allowed increased longevity in many groups of placental mammals. Future studies should test this hypothesis by comparing mortality rates among closely related species that occupy different habitats. The highly arboreal evolutionary history of Euarchonta, and especially primates, may have allowed increased longevity in the group as a whole. This hypothesis will require further testing, as will other mechanisms that might influence extrinsic mortality, and therefore longevity, including body size, sociality, behavioral and morphological defenses, and adaptation to other habitat types (e.g., fossoriality). In summary, results of this study support the hypothesis that primates and other arboreal mammals are characterized by greater longevities than terrestrial mammals and confirm the fundamental predictions of the evolutionary theory of aging.
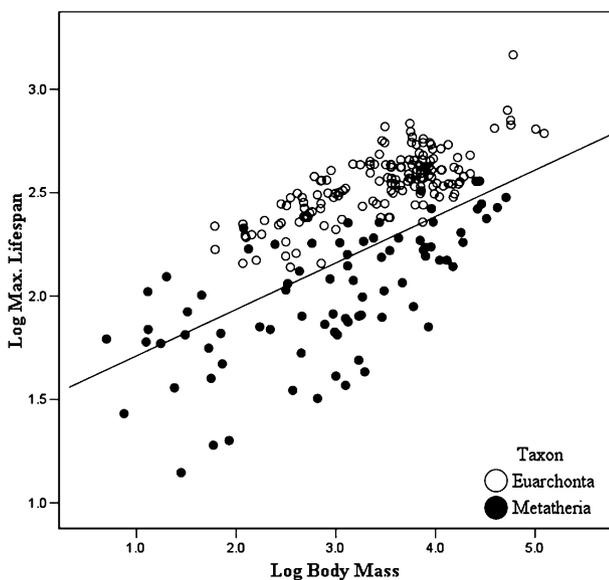

Fig. 4. Maximal lifespan plotted against body mass for Metatheria and Euarchonta in log space. In both groups, arboreal and terrestrial intercepts are not significantly different from each other ($P > 0.05$). The solid line is the least squares regression for Mammalia, demonstrating the proximity of marsupials ($n = 81$) and euarchontans ($n = 154$) to this line. OLS regression for Mammalia: $y = 0.225x + 1.49$, $r^2 = 0.594$, $P < 0.001$.

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Materials and Methods

Analyses were conducted on published data on 776 species, representing 24 orders from all major divisions of Mammalia (Fig. 1). The dataset for longevity was compiled from published maximal lifespan records (48, 49). Both captive and wild records are included; in fact, captive records are preferred, because maximum potential lifespan is of interest. Average adult body masses and habitat categories (arboreal, semiarboreal, or terrestrial) were obtained from various sources (48, 50–53). Although brain mass was once argued to be a better predictor of longevity than body mass in mammals (27), it has been demonstrated that other body organ masses are equally or more highly correlated with longevity, suggesting that organ mass may be a better proxy for body size than body mass (25, 28, 54). However, data for body mass are more widely available than data for various organ masses; therefore, we use body mass as a covariate in our study. Where quantitative data are available, the following criteria are used to determine habitat type: 75–100% time spent in trees is considered arboreal, 25–75% time spent in trees is considered semiarboreal, and 0–25% time spent in trees is considered terrestrial. However, for most species examined, this type of information is not available (although many cases are obvious, such as many "ungulates," which are strictly terrestrial). For these species, categories are determined based on qualitative descriptions. Those species described as "arboreal/primarily arboreal" and "terrestrial/primarily terrestrial" are classified arboreal and terrestrial, respectively; those described as "semiarboreal," "semiterrestrial," "occasionally arboreal," or "arboreal and terrestrial" are classified semiarboreal.

We constructed a mammalian supertree based on recently published molecular phylogenies (Fig. 1 and Fig. S1). To control for the effects of shared phylogenetic history, two methods were employed. First, several taxonomic groups were analyzed independently using ANCOVA to determine whether overall results were significantly influenced by one or a few subgroups. Taxonomic groups were chosen so that they contained sufficient numbers of arboreal and terrestrial species to conduct an ANCOVA. In some cases (e.g., Xenarthra), assumptions of ANCOVA are not met (slopes are not different from zero), so there is no linear relationship between body mass and longevity, presumably because of inadequate sample size for one or more habitat categories. Minimally, this analysis required at least three taxa in each category, although in most cases the number was much higher (Table 1). Furthermore, taxonomic groups were chosen to minimize redundancy. For example, the group primates is not analyzed separately from Euarchonta because only three nonprimate euarchontans are included in this dataset, and their inclusion (or exclusion) does not affect the results. Likewise, Carnivora and Rodentia are not analyzed separately but rather are subsumed within the larger clades Ferae (Carnivora + *Pholidota*) and Glires (Rodentia + Lagomorpha). In our dataset, 10 subclades are nonredundant and meet minimal sample size requirements (Table 1). Second, PIC (55, 56) were calculated and analyzed on the entire dataset using the AOT function in Phylocom (57) to determine the significance of habitat category on longevity and body mass after the influence of phylogeny is removed (29).

Ordinary least squares (OLS) regression lines were fitted to the total dataset and to the 10 relevant subgroups. ANCOVA tests were conducted on the total dataset and on the subclades to determine whether intercepts for habitat type are significantly different from each other using Bonferroni posthoc tests. Because phylogenetic relationships can obscure the independence of data points (55, 56), the potential effects of phylogeny were tested using the AOT function in Phylocom (57) to calculate and analyze PIC. The AOT function is used to create PIC between continuous and categorical traits. Because it is designed to work with a binary categorical variable, only arboreal and terrestrial taxa are used in this portion of the analysis. Following Fisher and colleagues (29), we first calculated a set of PIC using only the two continuous variables (body mass and longevity). Using these contrasts, we calculate the slope of the linear regression, m, with the intercept forced through the origin. The equation for the regression line is then $y = mx$. Next, a second set of PIC are calculated by contrasting body mass and longevity against habitat type, creating body mass contrasts relative to habitat (M_R) and longevity contrasts relative to habitat (L_R). The original regression line obtained using only continuous variables ($y = mx$) then is applied to the second set of contrasts to calculate residuals. This calculation is accomplished by subtracting the longevity contrasts relative to habitat (L_R) from the product of the original slope (m) and the body mass contrasts relative to habitat (M_R). That is, residuals are calculated as $mM_R − L_R$. These residuals then are subjected to a one-way t test to determine if they are significantly different from zero. A significant result ($P < 0.05$) indicates that habitat type has a significant effect on longevity relative to body mass. Because two aspects of our phylogeny are controversial, namely Atlantogenata (58, 59) and Pegasoferae (60), we analyze independent contrasts using modified phylogenies that do not recognize sister relationships between Afrotheria and Xenarthra or Perrisodactyla and Ferae, in addition to the main phylogeny presented in this analysis (Fig. 1 and Fig. S1).

1. Harvey PH, Martin RD, Clutton-Brock TH (1987) *Primate Societies*, eds Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (Univ of Chicago Press, Chicago), pp 181–196.
2. Leigh SR, Blomquist GE (2007) *Primates in Perspective*, eds Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (Oxford Univ Press, New York), pp 396–407.
3. Medawar PB (1952) *An Unsolved Problem in Biology* (H.K. Lewis, London).
4. Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411.
5. Hamilton WD (1966) The molding of senescence by natural selection. *Evolution* 12:12–45.
6. Charlesworth B (1994) *Evolution in Age-Structured Populations* (Cambridge University Press, Cambridge), 2nd Ed.
7. Kirkwood TBL (1977) Evolution of ageing. *Nature* 270:301–304.
8. Partridge L, Barton NH (1993) Optimality, mutation and the evolution of ageing. *Nature* 362:305–311.
9. Kirkwood TBL, Austad SN (2000) Why do we age? *Nature* 408:233–238.
10. Rose M, Charlesworth B (1981) Genetics of life history in *Drosophila melanogaster*. II. Exploratory selection experiments. *Genetics* 97:187–196.
11. Luckinbill LS, Arking R, Clare MJ, Cirocco WC, Buck SA (1984) Selection for delayed senescence in *Drosophila melanogaster*. *Evolution* 38:996–1003.
12. Stearns SC, Ackermann M, Doebeli M, Kaiser M (2000) Experimental evolution of aging, growth, and reproduction in fruitflies. *Proc Natl Acad Sci USA* 97:3309–3313.
13. Harvey PH, Zammuto RM (1985) Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature* 315:319–320.
14. Promislow DEL, Harvey PH (1990) Living fast and dying young: A comparative analysis of life-history variation among mammals. *J Zool (Lond)* 220:417–437.
15. Austad SN (1993) Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *J Zool (Lond)* 229:695–708.
16. Ricklefs RE (1998) Evolutionary theories of aging: Confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am Nat* 152:24–44.
17. Pomeroy D (1990) Why fly? The possible benefits for lower mortality. *Biol J Linn Soc Lond* 40:53–65.
18. Bouliere F (1958) The comparative biology of aging. *J Gerontol* 13:16–24.
19. Comfort A (1979) *The Biology of Senescence* (Churchill Livingstone, Edinburgh), 3rd Ed.
20. Jurgens KD, Prothero J (1987) Scaling of maximal lifespan in bats. *Comp Biochem Physiol* A 88:361–367.
21. Austad SN, Fischer KE (1991) Mammalian aging, metabolism, and ecology: Evidence from the bats and marsupials. *J Gerontol* 46:B47–B53.
22. Wilkinson GS, South JM (2002) Life history: Ecology and longevity in bats. *Aging Cell* 1:124–131.
23. Holmes DJ, Austad SN (1994) Fly now, die later: Life-history correlates of gliding and flying in mammals. *J Mammal* 75:224–226.
24. Darwin C (1871) *The Descent of Man and Selection in Relation to Sex* (Murray, London).
25. Austad SN, Fischer KE (1992) Primate longevity: Its place in the mammalian scheme. *Am J Primatol* 28:251–261.
26. Kaplan HS, Robson AJ (2002) The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proc Natl Acad Sci USA* 99:10221–10226.
27. Sacher GA (1959) *Ciba Foundation Colloquia on Ageing, Vol. 5: The Lifespan of Animals*, eds. Wolstenholme GEW, O'Connor M (Churchill, London), pp 115–133.
28. Prothero J, Jurgens KD (1986) *Evolution of Longevity in Animals: A Comparative Approach*, eds Woodhead AD, Thompson KH (Plenum, New York), pp 49–74.
29. Fisher DO, Owens IPF, Johnson CN (2001) The ecological basis of life history variation in marsupials. *Ecology* 82:3531–3540.
30. Jones FW (1916) *Arboreal Man* (Edward Arnold, London).
31. Szalay FS, Drawhorn G (1980) *Comparative Biology and Evolutionary Relationships of Tree Shrews*, ed Luckett WP (Plenum Press, New York), pp 133–169.
32. Dagosto M (1988) The implications of postcranial anatomy for the origin of euprimates. *J Hum Evol* 17:35–56.
33. Sussman RW (1991) Primate origins and the evolution of angiosperms. *Am J Primatol* 23:209–223.
34. Szalay FS (2007) *Primate Origins: Adaptations and Evolution*, eds Ravosa MJ, Dagosto M (Springer, New York), pp 457–487.
35. Kirk EC, Lemelin P, Hamrick MW, Boyer DM, Bloch JI (2008) Intrinsic hand proportions of euarchontans and other mammals: Implications for the locomotor behavior of plesiadapiforms. *J Hum Evol* 55:278–299.

36. Bensley BA (1901) On the question of an arboreal ancestry of the Marsupalia, and the interrelationships of the mammalian subclasses. *Am Nat* 35:117–138.

37. Luo ZX, Ji Q, Wible JR, Yan CX (2003) An early Cretaceous tribosphenic mammal and metatherian evolution. *Science* 302:1934–1940.

38. Weisbecker V, Archer M (2008) Parallel evolution of hand anatomy in kangaroos and vombatiform marsupials: Functional and evolutionary implications. *Palaeontology* 51: 321–338.

39. Haines RW (1958) Arboreal or terrestrial ancestry of placental mammals. *Q Rev Biol* 33:1–23.

40. Cheney DL, Wrangham RW (1987) *Primate Societies*, eds Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (Univ of Chicago Press, Chicago), pp 227–239.

41. Isbell LA (1994) Predation on primates: Ecological patterns and evolutionary consequences. *Evol Anthropol* 3:61–71.

42. Gittleman JL (1985) Carnivore body size: Ecological and taxonomic correlates. *Oecologia* 67:540–554.

43. Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *J Zool* 183:1–39.

44. Janson CH, Goldsmith ML (1995) Predicting group size in primates: Foraging costs and predation risks. *Behav Ecol* 6:326–336.

45. Kaufmann JH (1974) The ecology and evolution of social organization in the kangaroo family (Macropodidae). *Am Zool* 14:51–62.

46. Jarman PJ, Wright SM (1993) Macropod studies at Wallaby Creek. IX. Exposure and responses of Eastern Grey kangaroos to dingoes. *Wildl Res* 20:833–843.

47. Croft DB, Eisenberg JF (2006) *Marsupials*, eds Armati PJ, Dickman CR, Hume ID (Cambridge Univ Press, Cambridge, UK), pp 229–298.

48. Ernest SKM (2003) Life history characteristics of placental nonvolant mammals. *Ecology* 84:3402.

49. Weigl R (2005) *Longevity of Mammals in Captivity; From the Living Collections of the World* (Kleine Senckenberg-Reihe, Stuttgart).

50. Hutchins M, et al. (2003) *Grzimek's Animal Life Encyclopedia* (Gale, Detroit), 2nd Ed.

51. Nowak RM (1999) *Walker's Mammals of the World* (Johns Hopkins Univ Press, Baltimore), 6th Ed.

52. Smith RJ, Jungers WL (1997) Body mass in comparative primatology. *J Hum Evol* 32: 523–559.

53. Rowe N (1996) The Pictorial Guide to the Living Primates (Pogonias Press, Charlestown, RI).

54. Economos AC (1980) Brain-lifespan conjecture: A reevaluation of the evidence. *Gerontology* 26:82–89.

55. Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15.

56. Garland TG, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 41:18–32.

57. Ackerly DD (2006) Analysis of Traits (AOT): A module of Phylocom, Version 3.1. Available at: http://www.phylodiversity.net/phylocom. Accessed March 15, 2009.

58. Murphey WJ, Pringle TH, Crider TA, Springer MS, Miller W (2007) Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Res* 17:413–421.

59. Nikolaev S, et al. (2007) Early history of mammals is elucidated with the ENCODE multiple species sequencing data. *PLOS Genet* 3:3–8.

60. Nishihara H, Hasegawa M, Okada N (2006) Pegasoferae, an unexpected mammalian clade revealed by tracking ancient retroposon insertions. *Proc Natl Acad Sci USA* 103: 9929–9934.

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