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Ecological implications of the relative rarity of fossil hominins at Laetoli

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ABSTRACT

Hominins are a very rare component of the large-mammal fauna at Laetoli. Although no equivalent data are available for Hadar, the much higher count and relative abundance of hominins suggests that they may have been more common at the latter site. The apparent relative rarity of hominins at Laetoli may have significant implications for understanding the ecology of *Australopithecus afarensis*. However, it is essential to first assess the extent to which taphonomic variables might have been a contributing factor. Using data from fossil ruminants, we show that the survivability of skeletal elements at Laetoli relates to the extent to which they can resist carnivore scavenging and their likelihood of being entirely buried by volcanic ashes and tuffaceous sediments. The rarity of hominins at Laetoli is probably due in part to the influence of these two taphonomic factors. However, these factors cannot account entirely for the difference in hominin relative abundance between these two sites, and ecological differences were probably a contributing factor. The highest population densities of chimpanzees today occur in forest and closed woodland, with reduced densities in open woodland. If similar levels of population-density variation characterized *A. afarensis*, the differences between Hadar and Laetoli may relate to the quality/optimality of the habitats. Hadar was, in general, much more densely wooded and mesic than Laetoli, with permanent and substantial bodies of water. In contrast, Laetoli was predominantly a woodland-shrubland-grassland mosaic supported only by ephemeral streams and ponds. The apparent greater relative abundance of hominins at Hadar compared with Laetoli suggests that, like chimpanzees, *A. afarensis* may have been more successful in more densely wooded habitats. Compared with Hadar, Laetoli probably represented a less optimal habitat for the foraging and dietary behavior of *A. afarensis*, and this is reflected in their inferred lower abundance, density, and biomass.

Introduction

The mid-Pliocene site of Laetoli in northern Tanzania has yielded the second largest sample of *Australopithecus afarensis* after Hadar in Ethiopia. However, compared with the 149 specimens of *A. afarensis* recovered from Hadar (counting the 201 associated specimens from A.L. 333 as 13 specimens based on the estimated minimum number of individuals; Johanson et al., 1982; Johanson, 2004; Kimbel et al., 2004), Laetoli has yielded only 31 specimens (White, 1979, 1980, 1981; Leakey, 1987; Kyauka and Ndessokia, 1990; Harrison, unpubl. data). The greater temporal span of the Hadar Formation (2.94–3.42 Ma) compared with that of the Upper Laetolil Beds (3.46–3.76) may contribute to the greater number of hominins recovered, but their proportions relative to other large mammals gives some indication of the degree of their rarity at Laetolii. Based on the Laetoli collections for which data on faunal counts are available, hominins constitute only 0.2% ($n = 27$) of the large mammals recorded ($n = 12{,}932$) in the Mary Leakey (1974–1981) and Terry Harrison (1998–2005) collections combined. Apparently, hominins represent a very rare taxon at Laetoli, being most comparable in their frequency of occurrence to aardvarks and large felids. Comparable data from Hadar are not available, but it is reasonable to assume from the much higher number of fossil hominins recovered from Hadar that they represented a more common component of the large-mammal community than they did at Laetoli (i.e., the large-mammal assemblage from Hadar would have to comprise over 62,000 specimens for the hominins to be as rare as those from Laetoli, whereas only 7571 non-hominin vertebrates are currently listed in the Hadar Catalog; Reed, 2008).

If this assumption is valid, then it may have important implications for understanding the ecology of *A. afarensis*. If it were determined, for example, that *A. afarensis* at Laetoli had a low biomass, comparable to that of aardvarks or large felids, then it would suggest a relatively high degree of ecological or dietary

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specialization. Similarly, if it could be shown definitively that *A. afarensis* was much less common at Laetoli compared with Hadar, a comparative study of the two sites might reveal critical factors of the environment and/or ecology that could contribute to this difference. With a wider range of such comparisons, it might be possible to use these data to deduce which variables best correlate with relative abundances, and thereby determine what constitutes optimal versus suboptimal habitats for *A. afarensis*. However, factors other than ecological differences might explain the relative rarity, at least in part, of hominins at Laetoli. One important factor that needs to be considered is the potential impact of taphonomy on the relative abundance of hominin remains. Were hominins as rare an element of the fauna during the Pliocene as the abundance of their recovered remains would imply? Could it be that there was a taphonomic bias at Laetoli that produced differential preservation of the various large-mammal remains disproportionate to their frequency of occurrence in the original fauna? This paper aims to explore these questions by examining several aspects of the taphonomy and ecology that may have had an impact on hominin abundance at Laetoli.

The sedimentary setting and the preservation of bones at Laetoli indicate that the remains of animals were scattered on a series of land surfaces that were subsequently buried by subaerially deposited tuffs and tuffaceous sediments (Hay, 1987; Su, 2005; Harrison, unpubl. data). Evidence of disarticulation, rodent gnawing, insect damage, and weathering indicate that bones were exposed on the surface for variable periods of time after decomposition of the carcass and prior to being buried (Su, 2005). The diversity of the carnivore guild,[1] the common occurrence of bite marks on large-mammal bones (6.1% of the assemblage; Su, 2005), and the occurrence of carnivore coprolites at Laetoli all attest to the importance of carnivore activity at the site. Given these conditions, it is very likely that carnivores had a significant impact on the taphonomy at Laetoli through the differential destruction of carcasses and individual bones prior to fossilization. Moreover, one of the unusual characteristics of the hominin assemblage at Laetoli is that the collection is predominantly composed of craniodental remains. Of the total sample of 31 hominins from Laetoli, postcrania are represented by the partial skeleton of an immature individual (LH 21) and an undescribed patella (constituting only 6.5% of the hominin collection). A similar pattern is exhibited by fossil cercopithecids from Laetoli, with craniodental specimens dominating the collection (86.0% of the total remains). This pattern is not due to collection bias, however, because the Harrison team (and to a large extent, the Leakey team) made every effort to recover all identifiable fossils, including very small remains such as isolated teeth and cheiridial elements of micromammals. We can be certain, therefore, that hominin postcrania are underrepresented in the Laetoli collections relative to craniodental remains because they were not preserved proportionally in the fossil record.

Such a marked discrepancy in the representation of craniodental and postcranial remains is typically associated with the activities of scavenging carnivores, where carcass parts with high nutrition and low density (i.e., limb bones) are consumed first (Blumenschine, 1986; Lyman, 1994). In this case, the rarity of hominins at Laetoli might be due, at least in part, to the influence of carnivore scavenging. To test this hypothesis, we extend the comparison to bovids and giraffids, the two most abundant large-mammal taxa at Laetoli (constituting over 80% of all large mammals), to see if the relationship between craniodental and postcranial elements is consistent for other potential prey species. In addition to their abundance in the fossil record, ruminants exhibit diversity in body size that encompasses the estimated body mass of *A. afarensis* (29–45 kg, McHenry, 1992). The Laetoli ruminants range in size from *Madoqua avifluminis*, an extinct species of dik-dik, estimated at ~4 kg, to the giant giraffid *Sivatherium maurusium*, with an estimated body mass exceeding 2000 kg (based on comparisons with postcranial elements of extant ruminants). This size range allows differences in preservation due to body size to be taken into consideration. In carnivore-ravaged assemblages, the overall size of prey animals is likely to be a major factor in the preservation of their bones because those of large species tend to be more resistant to destruction than those of small species (Behrensmeyer et al., 1979; Behrensmeyer and Dechant-Boaz, 1980; Damuth, 1982).

Using these data, it is possible to examine two key questions: (1) Is the disproportionate representation of craniodental specimens in hominins (and cercopithecids) observed in other large-mammal taxa at Laetoli? (2) If so, is the size class of mammals to which hominins belong differentially affected compared to other size classes of mammals? If the answer to either of these questions is "yes," then the observed phenomena are not unique to hominins, and it may be possible to propose more general explanations to account for them. This is an important starting point for answering the question of whether or not the apparent rarity of hominins at Laetoli reflects their original representation in the mammalian community or whether it is simply a consequence of taphonomic or preservational factors. Subsequent interpretations about the paleobiology and paleoecology of hominins at Laetoli are contingent upon resolving this critical question.

Material and methods

The material used in this analysis comprises the fossil ruminants (i.e., bovids and giraffids) from the Upper Laetolil Beds collected by Terry Harrison and his team at Laetoli from 1998 to 2001. This sample provides a good skeletal and taxonomic representation of the much larger collections made by Mary Leakey (1974–1981) and Terry Harrison (1998–2005). The specimens were all surface finds, and the collecting technique involved the recovery of all anatomically identifiable specimens (i.e., isolated and associated teeth, mandibular and maxillary fragments with or without teeth, other substantial cranial fragments with recognizable anatomical structures, including horn cores and ossicones, and all postcranial elements preserving at least one articular surface) so that any possible collecting bias between craniodental and postcranial remains is minimized. A slight bias may be introduced by the fact that teeth, regardless of their preservation, are more likely to be considered anatomically identifiable by collectors than are cranial or postcranial remains in a similar state of preservation. However, such a bias is unlikely to have a significant impact on the results, and it would presumably apply uniformly across different weight classes.

The sample includes 2373 craniodental and postcranial specimens. Isolated cranial fragments, incisors, vertebrae, ribs, sternal fragments, external and medial cuneiforms, and sesamoid bones were excluded from the analysis due to the difficulty in identifying them taxonomically and/or in obtaining meaningful counts. Horn cores and ossicones, which commonly break into numerous identifiable pieces, were also excluded to avoid introducing a bias through overrepresentation of these elements. Specimens were recorded as number of identified specimens (NISP). All skeletal elements (i.e., isolated teeth, maxillae, mandibles, and postcrania) were assumed to be paired, and no effort was made to side the individual bones. Individual elements in associated specimens, such as partial skeletons and jaw fragments with multiple teeth, were counted separately (i.e., each individual bone and tooth was counted as a separate specimen).

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[1] Twenty-eight species are currently recorded (L. Werdelin and R. Dehghani, pers. comm.), which is identical in count to the entire modern-day Serengeti carnivore fauna, but with a greater proportion of large hyaenids and felids.

Because all of the taxa included in the analysis have identical craniodental and postcranial counts, there was no need to correct for differences in element count between different anatomical regions (such as teeth, phalanges, and metapodials). In a complete ruminant skeleton (taking into account typical breakage patterns at Laetoli, in which limb bones and metapodials are most commonly collected as proximal and distal ends, excluding the elements listed above, and assuming that the cheek teeth have been detached from hemimandibles and maxillae), craniodental remains represent 28.6% of the total skeletal elements (28 craniodental versus 70 appendicular postcranial elements). Using this as a constant, we calculated a craniodental-postcranial index (CD-PC index), which is the percentage of craniodental specimens in the fossil sample divided by 28.6. Any deviation from the expected proportion of craniodental and postcranial remains in a fully represented ruminant skeleton (i.e., a CD-PC index of 1.00) observed in the fossil record provides a guide to the intensity of taphonomic bias in the Laetoli ruminant samples.

Laetoli bovids and giraffids were categorized into six weight classes (WC) (Table 1; Su, 2005). The method used to allocate individual specimens to weight classes differed for craniodental and postcranial remains, which needs to be taken into account when assessing the results. Regression analyses of maxillary and mandibular M3 mean length in relation to average body weight in modern-day African bovids and giraffids allowed an estimation of the average body weight for fossil taxa (Table 2). The fossil taxa were then assigned to their appropriate weight class based on this estimation, and all craniodental specimens attributed to that species were included in that weight class (Table 1). This produced a more accurate allocation of specimens to an appropriate weight class than would be achieved by estimating body weight based on the dimensions of individual craniodental specimens (which have been shown to be less reliable than postcrania for estimating body weight; see Delson et al., 2000). However, because unassociated postcranial remains cannot be attributed to a specific taxon, the same method cannot be applied to them. In this case, regression analyses of the individual postcrania of modern-day African ruminants were carried out, and an estimated body weight was obtained for each fossil postcranial element (Table 2). This results in the craniodental remains of each species being assigned unambiguously to a single point within each weight class, whereas their postcranial remains are distributed around a mean, possibly resulting in postcranial remains of a single species extending across two or more weight categories. However, given that the weight-class categories are very coarse, this potential problem should not present a significant source of error, except in those cases where relatively abundant species lie close to the boundary between two size categories.

Table 1
Weight-class distribution of Laetoli fossil ruminants and percentage of specimens in each weight class

Weight class	Weight range (kg)	Laetoli ruminant taxa	% of specimens
I	<25	*Madoqua avifluminis* *Raphicerus* sp.	33.4
II	25–50	*Gazella janenschi* Cephalophini sp. indet.	10.0
III	50–100	*Tragelaphus* sp. aff. *Pelea* sp. indet. *Brabovus nanincisus*	12.0
IV	100–250	*Parmularius pandatus* Hippotragini sp. indet. Alcelaphini sp. indet.	27.7
V	250–500	*Giraffa stillei*	8.2
VI	>500	*Simatherium kohllarseni* *Giraffa jumae* *Sivatherium maurusium*	8.8

Closer examination of the raw data revealed that the only case where the latter issue had a significant impact on the results is for the allocation of *Gazella janenschi*, a relatively common species (but still less than 10% of the entire ruminant fauna). The molar regression provides an estimated average body weight for the species of 33.4 kg, which places it in WC II. However, a number of postcrania assigned to the upper end of the size range (15–25 kg) of WC I are clearly too large to be attributed to *Madoqua* or *Raphicerus*, and evidently belong to *Gazella*. It seems, therefore, that the postcranial remains of *Gazella janenschi* are distributed between WC I and WC II, while all of the craniodental remains are placed in WC II. Such a distribution is not unexpected given that *Gazella janenschi*, like modern *Gazella* species, shows a significant degree of sexual dimorphism. Fortunately, it was possible to assess the impact of this "misallocation" because it is a simple matter to identify neotragine versus non-neotragine postcrania allocated to WC I. Of the 506 postcrania in WC I, 67 are non-neotragine (13.2%), and these presumably represent small individuals of *Gazella*. In this case, WC I is artificially skewed towards an overrepresentation of postcranial remains compared to craniodental elements, thereby producing a lowered CD-PC index. However, after removing the postcranial remains of *Gazella* from WC I and recomputing the CD-PC index, the value increased from 1.54 to only 1.67, a relatively minor adjustment given the overall magnitude of differences observed in this index across the weight classes.

For comparison, similar data were collected on fossil ruminants from the overlying Ndolanya Beds (dated to 2.6–2.7 Ma) and on modern skeletal remains from the Laetoli area. The Ndolanya sample ($n = 921$) comprises material collected by Harrison (1998–2001) using the same collection criteria and methods as for the Upper Laetolil Beds. In 2000, the authors laid out a transect along the northern side of the Gadjingero River Valley, about 7 km north of Laetoli, in order to systematically record the density and distribution of vertebrate skeletal remains exposed on the modern-day land surface. The transect ran parallel to the river, through an area of grassland, about 300 m from the edge of the riverine woodland. For each skeletal element and bone fragments over 30 mm long, the following information was recorded (where possible): taxonomic identification, anatomical part, adult versus nonadult, size class, degree of disarticulation, weathering stage, breakage and other damage, and maximum length and breadth of fragment. The total number of individual bones or partial carcasses recorded was 649, and the majority of these were identified as belonging to wildebeest, zebra, and Thomson's and Grant's gazelles.

Results

The CD-PC index for the Laetoli ruminants is 2.18 (Table 3), which demonstrates that craniodental remains are significantly overrepresented compared with postcranial elements. This implies that the apparent rarity of postcrania in hominins is not unique to this taxon, but is a phenomenon related to broader taphonomic factors that affected Laetoli large mammals in general.

Compared to the preferential preservation of craniodental remains of ruminants in the Laetolil Beds, a different pattern is seen in the overlying Upper Ndolanya Beds. The CD-PC index for Ndolanya ruminants is 0.98, indicating that the craniodental and postcranial elements are represented proportionately in the collections. This is probably a result of sedimentary and taphonomic variables that favored more rapid burial and preservation of larger and more robust skeletal elements in the Upper Ndolanya Beds. This comparison demonstrates that skeletal representation of

Table 2
Regression equations used to estimate body weights of bovid and giraffid specimens (from Su et al., 2003)

Element	Measurement	Regression equation	r^2
Maxillary M3	Mesiodistal length	$y = 2.7598x - 1.5154$	0.888
Mandibular M3	Mesiodistal length	$y = 2.9623x - 2.1071$	0.913
Scapula	Maximum breadth of glenoid fossa	$y = 2.5620x - 1.8949$	0.970
Humerus	Maximum breadth of humeral head	$y = 2.5729x - 2.2163$	0.968
	Maximum breadth of distal end	$y = 2.4185x - 1.9558$	0.963
Radius	Maximum breadth of proximal end	$y = 2.3505x - 1.8358$	0.962
	Maximum breadth of distal end	$y = 2.3604x - 1.7109$	0.969
Ulna	Height of olecranon process	$y = 2.4192x - 2.254$	0.938
Femur	Maximum depth of femoral head (dorsoventral breadth)	$y = 2.7934x - 2.1316$	0.974
	Maximum breadth of distal end	$y = 2.7905x - 2.8623$	0.972
Tibia	Maximum breadth of proximal end	$y = 2.4336x - 2.3681$	0.933
	Maximum breadth of distal end	$y = 2.6566x - 2.2305$	0.959
Fibula	Greatest depth (dorsoventral breadth)	$y = 2.7073x - 1.6446$	0.961
Metacarpal	Maximum breadth of proximal end	$y = 2.4823x - 1.8142$	0.962
	Maximum breadth of distal end	$y = 2.2151x - 0.6672$	0.912
Metatarsal	Maximum breadth of proximal end	$y = 2.7586x - 2.1387$	0.961
	Maximum breadth of distal end	$y = 2.5819x - 1.0497$	0.954
Scaphoid	Maximum breadth	$y = 2.4756x - 1.4743$	0.930
Semilunar	Maximum breadth	$y = 2.5137x - 1.5159$	0.954
Unciform	Maximum proximodistal height	$y = 2.4536x - 1.2839$	0.961
Magnum	Maximum mediolateral diameter	$y = 2.4507x - 1.5603$	0.940
Cuneiform	Maximum length	$y = 2.4788x - 1.4696$	0.958
Naviculocuboid	Anteroposterior length of midline	$y = 2.6076x - 2.0617$	0.961
Astragalus	Maximum length of lateral half	$y = 2.9440x - 2.5951$	0.966
Calcaneus	Proximodistal length of tuber calcis	$y = 2.8113x - 3.5071$	0.837
	Total proximodistal length	$y = 2.7732x - 2.9631$	0.851
Proximal phalanx	Height of proximal articular surface	$y = 2.9161x - 1.9447$	0.942
	Total length on peripheral side	$y = 2.9578x - 3.2122$	0.810
Middle phalanx	Height of proximal articular surface	$y = 2.6229x - 1.4924$	0.931
	Total length on peripheral side	$y = 3.5262x - 3.3904$	0.872
Terminal phalanx	Height of proximal articular surface	$y = 2.8209x - 1.9157$	0.947
	Maximum diagonal length of the sole	$y = 2.5720x - 2.1882$	0.992

All regressions were statistically significant ($p < 0.01$). Standard measurements of elements follow those of von den Driesch (1976).

large mammals at Laetoli can be profoundly influenced by taphonomic and sedimentary circumstances, and that the distinctive pattern seen in the Upper Laetolil Beds is likely governed by such factors.

When the CD-PC index is examined in relation to weight class, craniodental remains are preferentially preserved in all weight classes compared with the expected frequency of occurrence (i.e., the CD-PC index is greater than 1.00) (Table 3). However, the results show that the proportion of craniodental remains is not uniform across the weight classes, with some weight classes (WC IV and WC V) being much more heavily skewed towards the preservation of craniodental remains (Table 3). The two extreme weight classes, WC I and WC VI, have the lowest CD-PC indices, implying that they have been less biased by taphonomic factors than have other weight classes. Given the assumption that carnivore scavenging is the primary contributor to discrepancies in the proportions of craniodental remains at Laetoli, we can conclude that these two weight classes have been significantly less influenced by carnivore activity than WC II–V. Possible explanations for these results are discussed below.

Table 3
Proportions of craniodental and postcranial elements in each weight class and the CD-PC index for each weight class

Weight class	NISP (*n*)	Craniodental (%)	Postcranial (%)	CD-PC index
I	906	44.15	55.85	1.54
II	267	74.91	25.09	2.62
III	265	56.60	43.40	1.98
IV	543	85.64	14.36	2.99
V	216	91.67	8.33	3.21
VI	176	39.77	60.23	1.39
All WC	2373	62.49	37.51	2.18

See text for how CD-PC index is calculated.

Discussion

Undoubtedly, the observed overrepresentation of craniodental remains in the Upper Laetolil Beds can be partly explained by the fact that teeth are the most resistant element in the mammalian skeleton (Hillson, 1986). However, the remarkably strong bias towards craniodental remains (compared with the Upper Ndolanya Beds, for example) suggests that other factors were involved in producing their overrepresentation. Given the clear evidence that the diverse carnivore guild at Laetoli had a significant impact on the fossil assemblage (as indicated by the association of bite marks and coprolites), it is reasonable to conclude that carnivore ravaging is an important reason for the strong skew in the representation of craniodental remains. Furthermore, it has been shown that when scavenging carnivores are the principal actors involved in the modification and destruction of a carcass, the head is often consumed last or left behind on the land surface (Kruuk, 1972; Klein and Cruz-Uribe, 1984; Blumenschine, 1986; Lyman, 1994; Lotan, 2000), resulting in an overrepresentation of craniodental elements. We infer, therefore, that the observed overrepresentation of craniodental remains at Laetoli among hominins and other large mammals is due primarily to the impact of carnivore scavenging on carcasses, given that postcranial elements have a much greater chance than craniodental remains of being completely destroyed during the processes of mastication, ingestion, and digestion.

It should be noted in passing that porcupines (Hystricidae) are another potential contributor to bone loss from assemblages in east African ecosystems; they can harvest and gnaw on very large bones, including those up to the size of giraffe limb bones (Tappen, 1995; Harrison, pers. obs.). However, fossil remains of hystricids are rare at Laetoli (Denys, 1987), and the size of the marks left by rodent incisors on fossils indicates that the observed damage on Laetoli bones was predominantly due to smaller rodent species. It seems likely that porcupines had a very limited impact on the Laetoli assemblage.

The carnivore guild at Laetoli is at least as diverse as the richest modern-day carnivore communities in Africa (Barry, 1987; Petter, 1987; L. Werdelin and R. Dehghani, pers. comm.) and includes a high diversity of large hyaenids and felids. *Australopithecus afarensis* was undoubtedly a suitable prey species for most of the larger carnivores, and competition among medium- and large-sized carnivores to scavenge hominin carcasses exposed on the paleoland-surface would probably have been especially intense. Most carcasses would have been destroyed completely by scavengers, but occasionally, carcasses or pieces of carcasses would avoid detection and end up scattered on the land surface (where they eventually would have been affected by a combination of weathering, trampling, rodent gnawing, and damage caused by insects and plant roots). Periodic ash falls at Laetoli would have been adequate in volume at times to cover the land surface to a sufficient depth to bury all of the dead organisms and parts thereof that remained on the surface. These would presumably have ranged from scattered, isolated, and fragmentary bones (very common) to entire fresh carcasses (very rare). This pattern is precisely the one that we find in the fossil record at Laetoli. Obviously, important and complex taphonomic processes come into play during the stages of burial, fossilization, and weathering out of the sediments, prior to collection. These could all potentially affect the survivability and preservation of animal remains, but generally, given the preservational circumstances, the fossil record at Laetoli appears to provide a close approximation to the types of skeletal assemblages that one might expect to find exposed on a modern-day land surface in east Africa. Basically, the Laetoli assemblage preserves a series of snapshots through time of the skeletal assemblages that littered the land surface (as well as organisms—such as termites and fossorial mammals—that were living just below it).

We collected comparative data on modern skeletal assemblages of ruminants in the Gadjingero Valley, just to the north of Laetoli, in which partial carcasses and individual bones ($n = 649$) were subjected to carnivore ravaging and trampling while laying on the land surface. The CD-PC index for these assemblages is 1.76, which demonstrates that modern-day skeletal assemblages exposed to carnivore activity show the same overrepresentation of craniodental remains as the Upper Laetolil Beds (although the fossil sample is more strongly skewed towards overrepresentation of craniodental remains).

In this model, carcasses, partial carcasses, and individual bones of different sizes should respond to two major variables that affect skeletal survivability: (1) the size and robusticity of the skeletal element, and (2) the size of the element in relation to the depth of the ash fall. As size and robusticity of the skeletal element increases, there is an inverse decline in the number of carnivore species that can destroy the specimen, until a certain size threshold is reached that largely exceeds the capacity (or motivation?) of scavenging carnivores to completely destroy it (Lyman, 1994; Lotan, 2000). For example, our comparative data on modern skeletal remains from the Gadjingero Valley show that only 15.7% of the sample belongs to ruminants in WC I and WC II, while 84.3% occurs in WC III to WC VI. Clearly, the bones of larger ruminants, with a body weight greater than 50 kg, have a much higher chance of surviving carnivore scavenging than do those of small ruminants. However, the ability of carnivores to completely destroy skeletons of relatively large animals should not be underestimated. We have observed fresh carcasses of zebras killed by lions that have been completely removed by hyaenas overnight (although we do not know that all of the bones were actually destroyed rather than simply removed to the den area).

The evidence supports the inference that, with increasing body size of the prey species, there is a greater chance that skeletal elements will survive complete destruction by carnivore scavenging. This results in a higher representation of postcranial elements relative to craniodental remains as body size increases. However, the converse means that species in the lower weight categories are increasingly susceptible to being entirely destroyed by carnivores. Hominins, which occur in the lowest end of the range for WC II, would be among those large mammals expected to be most heavily affected by the greatest number of species with the ability to completely remove skeletal elements from the skeletal assemblage at Laetoli. If this model is correct, then it is not unexpected that so few postcranial bones of hominins have been recovered. In fact, it is precisely what would be predicted at an open-air site with subaerial deposition in which the skeletal assemblage was readily accessible to carnivore scavengers.

If this is indeed a reasonable model to account for the fossil assemblage at Laetoli, then why is it that the smallest ruminants, those in WC I, have a relatively high representation of postcrania? This relates to the second variable governing survivability of skeletal remains, and one that is particular to the unusual preservational circumstances at Laetoli. In a sedimentary system in which primary tuffs are being deposited as ash layers of variable thickness (ranging from less than 1 mm to more than 30 cm), there is a direct relationship between the depth of the tuff and the size of the carcass or individual bone that will be buried. Obviously, smaller bones and carcasses are much more likely to be completely buried by substantial ash falls than are larger remains, and thus avoid detection from scavenging carnivores. Another factor that might be important here is the general relationship between the body size of ruminants and their ranging behavior. Larger ruminants were presumably much more likely and able to migrate from local eruptive events than were smaller species. For example, dik-diks, which are strictly territorial, are much more likely to hunker down and conceal themselves in dense vegetation within their established territory, as they do today when danger presents itself, rather than to flee the general area across unfamiliar space (Kingdon, 1997). In most cases, the ash fall would have covered the land surface in a thin dusting, and the local ecosystem and wildlife would have recovered quickly. Heavier ash falls would bury bones and carcasses already present on the land surface, but they might also contribute to an increased toll of fatalities among the smallest size classes of large mammals.

In this scenario, there is a much higher likelihood that bovid species in WC I (the neotragines *Madoqua* and *Raphicerus*) would be buried completely by ash falls before they could be discovered and destroyed by scavenging carnivores. With increasing size, the relative likelihood of the complete burial of carcasses decreases, and the chances that carnivores will discover them increases (as does their likelihood of exposure to weathering and trampling damage). However, given that primary tuffs in the Upper Laetolil Beds have a maximum thickness of 30–50 cm and the units of subaerially and fluvially reworked tuffs are typically 50–100 cm thick, those ruminants in WC I are of the size category most likely to be buried. This increased probability that partial and entire carcasses will be buried among WC I ruminants accounts for the lower CD-PC index compared to other weight classes. It is pertinent to note in this regard that LH 21, a partial skeleton of *Australopithecus afarensis*, which preserves the only postcranial specimens recovered by Mary Leakey's team, belonged to an infant individual, effectively placing it in WC I.

To test this hypothesis, we calculated the frequency by weight class of ruminant finds at Laetoli that consist of partial skeletons or associated postcranial remains (an indication that the carcass had been buried before it had been fully scavenged by carnivores). In the 1998–2005 Harrison collections from Laetoli, partial skeletons and associated postcrania of *Madoqua* in WC I account for 81.8% ($n = 9$) of all such finds for ruminants, while the craniodental remains of *Madoqua* only represent 29.9% of the total ruminant fauna. In support of this interpretation is the observation that the majority of partial skeletons of nonruminant taxa recovered from the Upper Laetoli Beds are those of lagomorphs ($n = 73$), rodents ($n = 19$), and herpestids ($n = 8$), all belonging to species less than 5 kg in body weight. These account for 89.3% of all partial skeletons and associated postcrania ($n = 112$) from the Upper Laetolil Beds.

Denys (1987) and Leakey (1987) suggested that fossorial rodent skeletons were preserved as a result of animals that died in their burrows after being buried by ash falls. This may be the case for some of the smaller fossorial rodents, such as *Heterocephalus*, but seems unlikely for large-bodied, powerful diggers, such as *Pedetes*, that are particularly common as partial skeletons ($n = 13$). There is also no evidence associated with any of the partial skeletons of sedimentary features that could be interpreted as tunnels or dens. Finally, the most common taxa found as partial skeletons and associated postcrania—*Madoqua*, *Serengetilagus*, and *Herpestes*—are nonfossorial taxa. The combined evidence supports the conclusion that the majority of partial skeletons in the fossil record at Laetoli were derived from animals of relatively small size (under 5 kg), preserved as carcasses lying on the land surface that were eventually buried by relatively shallow deposits of primary volcanic ash or subaerially and fluvially reworked tuffaceous sediments. Of the 112 partial skeletons and associated postcrania recovered from the Upper Laetolil Bed since 1998, only three (a suid and two bovids) belong to taxa with estimated body weights greater than 25 kg.

As a further indication of whether or not isolated remains of smaller ruminants were buried more quickly than those of larger ruminants, and therefore avoided the destructive influences of carnivore scavenging, we examined the degree of weathering of the bones by weight class. Comparisons of weathering stages (for definitions, see Behrensmeyer, 1978) in our sample of ruminant bones show that those of species in WC I are predominantly unweathered or very lightly weathered (93.6% are weathering stages 0–1), whereas those in larger weight categories (WC II–VI) show a significantly higher incidence of weathering (46.8% are weathering stages 2–3). This pattern implies that smaller bones were more likely to have been buried rapidly, while a greater percentage of larger bones remained on the land surface for up to several years prior to burial (even when secondary weathering of the surface-collected fossils is taken into account).

Based on our modern-day skeletal-assemblage data collected in the vicinity of Laetoli, similar weathering patterns occur according to size. Bones of larger mammals on the surface tend to exhibit a higher incidence of later stages of weathering, while bones of smaller mammals (including juveniles of large mammals) show little or no weathering. For example, our data on weathering of modern skeletal remains in the Gadjingero Valley shows that 71.9% of bones of ruminants in WC II fall into weathering stages 0–1, compared with only 53.1% in WC IV. Similarly, 80.3% of bones of immature individuals in adult WC IV fall into weathering classes 0–1, compared with only 53.1% of bones of adults in WC IV. Presumably, bones of the smaller-sized animals were more likely to be destroyed completely before reaching a late weathering stage. Of course, smaller bones may be more likely to be protected from weathering by low-lying vegetation, and heavily weathered bones of small animals may not have been easily seen by collectors and thus left unrecorded on the land surface.

It can be concluded from the findings and observations presented above that the fossil hominins at Laetoli, with an estimated body mass in excess of 25 kg, belonged to a size category of mammals in which the survivability of skeletal remains was not favored by the sedimentary and taphonomic setting at Laetoli. The Laetoli hominins fall into a weight class in which skeletal elements are too large to have had a high probability of being entirely buried, but one with a very high susceptibility of being completely destroyed by carnivores. Basically, taphonomic circumstances at Laetoli offer the worst possible conditions for the survivability of hominin remains, especially postcrania. The evidence accounts for why hominin postcrania are so underrepresented at Laetoli in relation to craniodental remains, and it further suggests that it is highly likely, due to the unique preservational and taphonomic circumstances at Laetoli, that hominins (and mammals in their weight class) are more markedly underrepresented at Laetoli when compared with mammals in other weight classes.

One now needs to ask whether such a taphonomic bias could produce the kind of difference seen in the frequency of occurrence of hominin fossils at Laetoli versus Hadar. The larger number of specimens from Hadar and the higher percentage of postcranial remains [55.1% of all hominin remains at Hadar (Johanson et al., 1982; Kimbel et al., 2004) compared with only 6.5% at Laetoli] would suggest that a taphonomic bias has played an important role in the relative underrepresentation of hominins at Laetoli. As discussed above, carnivore scavenging has probably resulted in a reduction in the relative frequency of hominins at Laetoli compared with their original proportion in the fauna, and this, along with other taphonomic and depositional processes, may account, in part, for their apparent rarity. However, the discrepancy between the hominin counts at Laetoli and Hadar are probably too great to be explained entirely as a consequence of taphonomic or preservational factors. First, although *Gazella janenschi* belongs to the same weight class as the Laetoli hominins, and would presumably have been affected by the same taphonomic and preservational processes, they are relatively common at Laetoli (6.8% of the fauna) compared to hominins. This pattern suggests that *A. afarensis* may have already been a relatively rare component of the original Laetoli faunal community. Second, the Hadar fauna, including hominins, has also been significantly affected by carnivore activity (Gray, 1980; Behrensmeyer et al., 2003) and the current assemblage is, in part, a result of its ravaging effects. Third, even though abundance data are not available for the entire Hadar large-mammal fauna, they are for bovids and cercopithecids (Bobe et al., 2007; K. Reed, pers. comm.). Because bovids are often the most common and best-represented taxon in fossil assemblages, relative proportions based on the bovid data may provide a reasonable guide to the potential relative abundance of Hadar hominins. Laetoli hominins are only 2.8% of the combined bovid-hominin assemblage, whereas Hadar hominins are 24.9% of the combined bovid-hominin assemblage (counts from Johanson et al., 1982; Kimbel et al., 2004; Bobe et al., 2007). In addition, fossil cercopithecids are 7.4 times more common at Laetoli than hominins, whereas at Hadar they are only 3.2 times more common (K. Reed, pers. comm.). These lines of circumstantial evidence all suggest that *A. afarensis* was relatively more common at Hadar than at Laetoli.

While we do not know the proportion of hominins in the original faunal community at Laetoli and Hadar, we can reasonably assume, based on the discussion above, that the discrepancy between the number of hominins at Laetoli and Hadar cannot be fully explained by depositional, taphonomic, and preservational factors. If this assumption is true, then we can deduce that hominins were rarer at Laetoli than at Hadar, presumably due to ecological factors. In order to explore the implications of this possible difference, we make comparisons with modern east African primate communities living in different habitats, and examine how paleoecological distinctions between Laetoli and Hadar might affect hominin density and relative biomass.

Ecological implications

Some insight can be gained into the ecological factors that might govern differences in hominin abundance in different habitats by making comparisons between modern-day primate communities. For example, African great apes, with their larger body size and extended life-history traits, are typically much less common than sympatric cercopithecids. In eight Ugandan forests, chimpanzees (*Pan troglodytes*) are 22.7 times less common on average than colobines and papionins combined,[2] but there is considerable variation (4.4–54.9 times) relating to forest composition and food availability (Plumptre and Cox, 2006). *Australopithecus afarensis* (which was similar to *Pan* in body size and life-history variables; Bromage and Dean, 1985; McHenry, 1992) appears to have a similar relationship in terms of its representation compared to that of cercopithecids, and it falls at the lower extreme of the variation seen in modern chimpanzees (cercopithecids at Laetoli are 7.4 times more common than hominins). We can be certain, however, that Laetoli was not comparable in ecology to modern Ugandan forests, so we might expect relatively fewer cercopithecids by comparison. Better models might be provided by comparing the Laetoli data with chimpanzee communities living in open woodland habitats, but unfortunately, primate census data are currently unavailable.

In addition, it important to point out that there are no modern-day analogues for the primate community at Laetoli, in which nonforested habitats support a hominoid (excepting humans) associated with four species of cercopithecid. Today, the only habitats in east Africa with a primate fauna that includes a hominoid, two species of papionin, and two species of colobine, as is the case for Laetoli, are evergreen and semievergreen forests, such as those at Kibale in Uganda and Mahale in Tanzania (Russak and McGrew, 2008). Nevertheless, we think that it is reasonable to infer from modern-day African primate communities that hominins at Laetoli were at least as rare as extant chimpanzees living in those forest and woodland habitats in which cercopithecid biomass is relatively low.

Extant chimpanzees occur at a wide range of population densities across equatorial Africa according to habitat. Densities range from 0.08–0.09/km^2 in open woodland (Ugalla, Tanzania; Mount Assirik, Senegal) to 3.1–4.7/km^2 in closed woodland and forest (Gombe, Tanzania) (Plumptre and Cox, 2006), an almost sixty-fold difference between marginal and optimal habitats. This observation gives us a better appreciation of how different types of habitat can influence the biomass of African hominoids. It can be assumed that similar levels of population-density variation would have characterized *A. afarensis* across its geographic range. Given this fact, if *A. afarensis* at Hadar is indeed more common than at Laetoli, then it would suggest that Hadar had habitats that were more optimal for sustaining higher population densities of *A. afarensis* compared to Laetoli. The magnitude of the difference between the specimen counts between Hadar and Laetoli are equivalent to the difference in population density between modern-day chimpanzees living in closed and open woodland habitats, respectively.

A number of different lines of evidence have been used to infer ecological distinctions between Hadar and Laetoli. During the late 1980s, the consensus view of the paleoecology of the Upper Laetolil Beds, based on studies of the geology, palynology, and fossil vertebrates, was that it represented an arid-to-semiarid grassland with scattered bush and tree cover, and patches of acacia woodland, much like the modern Serengeti ecosystem (Leakey, 1987; Hay, 1987; Harris, 1987; Denys, 1987; Bonnefille and Riollet, 1987; Watson, 1987; Walker, 1987; Verdcourt, 1987; Gentry, 1987). Subsequent work by Andrews (1989), Cerling (1992), Reed (1997), and Musiba (1999), using mammalian community structure and stable isotopes, has demonstrated that Laetoli was more heavily wooded than initially interpreted. Recent studies of the fossil plants (Bamford, 2005), vegetation (Andrews and Bamford, 2008), gastropods (Pickford, 1995; Peters et al., 2008), birds (Harrison, 2005), large mammals (Kovarovic, 2004; Su, 2005; Andrews, 2006; Kovarovic and Andrews, 2007; Su and Harrison, 2007), and stable isotopes (Kingston and Harrison, 2005, 2007) all indicate that Pliocene Laetoli had a higher density of woody vegetation cover than the modern-day Laetoli ecosystem.

Ecomorphological analysis of bovid postcrania by Kovarovic and Andrews (2007) suggests that Laetoli was predominantly covered by heavy woodland-bushland, with areas of lighter tree and bush cover and grassland. Although closed and open woodlands were probably more extensive at Laetoli during the Pliocene than today, overall the mammalian fauna indicates that drier shrubland-grassland habitats were still a significant component of the ecosystem (Su, 2005; Su and Harrison, 2007). Isotopic studies of the large mammals from Laetoli confirm that most ungulates were either browsers or mixed feeders, suggesting open woodland habitats with extensive areas of grassland (Kingston and Harrison, 2007). Thus, the balance of evidence suggests that the Laetoli paleoenvironment was predominantly open woodland, with significant portions of open bushland, shrubland, and grassland.

Paleoecological reconstructions of Hadar indicate that there were significant habitat changes through time, but in general, it was more wooded and more mesic compared to Laetoli (Bonnefille et al., 2004; Reed, 1997, 2008). Palynological evidence indicates that Hadar fluctuated throughout the sequence between forest-woodland and wet/dry grassland (Bonnefille et al., 1987, 2004). Analyses of the mammalian community structure indicate that Hadar was dominated by open woodland and shrubland, with forests around the margins of the lake and edaphic grasslands on floodplains (Reed, 1997, 2008).

Comparisons of the relative abundance of bovid tribes at Hadar and Laetoli highlight the ecological distinction between the two sites. Aepycerotini, Bovini, Reduncini, and Tragelaphini, which prefer more densely wooded and/or wetter ecological settings, are very common throughout the Hadar Formation, constituting over 75% of all bovids (Bobe et al., 2007; Reed, 2008). In contrast, the Laetoli bovid fauna is dominated by Alcelaphini, Antilopini, Hippotragini, and Neotragini, which represent more than 88% of the bovids and prefer drier bushland-shrubland-grassland habitats (Su, 2005).

Similarly, the taxonomic composition of the rodents and lagomorphs at Laetoli and Hadar provides further indication of important ecological distinctions. The micromammal fauna at Laetoli is dominated by *Serengetilagus* (hare), which constitutes 85% of all specimens. Among the rodents, *Pedetes* (spring hares, 70.0%), *Saccostomus* (pouched mice, 12.9%) and *Heterocephalus* (naked mole-rats, 6.3%), are the most common taxa. This rodent-lagomorph community indicates a mosaic of dry grasslands, bushland, and open woodland habitats. The occurrence at Laetoli of *Thallomys* (acacia rats) and *Paraxerus* (bush squirrels) indicates the presence of open woodland and dense woodland or forest, respectively, but these are not common taxa, together constituting less than 5% of the rodent fauna. Gerbillines are very rare at Laetoli, constituting less than 1% of all rodents. As a result, the Gerbillinae:Murinae ratio (G:M ratio), which has been shown to be correlated with percentage of woody vegetation cover (Reed, 2007), is low at Laetoli (G:M ratio = 0.13:1), most comparable to modern Serengeti ecosystems in which woody vegetation coverage is 25–30% (Reed, 2007).

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[2] Cercopithecins are excluded here because their radiation postdates the Pliocene, and they do not occur at Laetoli.

The rodent fauna from Hadar is strikingly different from that from Laetoli, and clearly indicates a marked ecological difference (Sabatier, 1979, 1982; Denys, 1985a,b, 1987). Of the 18 rodent genera represented at the two sites combined, only four genera occur at both Hadar and Laetoli. The most common taxa at Hadar, *Millardia* (soft-furred field rat) and *Golunda* (Indian bush rat), do not occur in Africa today, but are distributed primarily throughout southern Asia (Sabatier, 1979, 1982; Nowak, 1999). *Millardia* has a broad habitat tolerance, ranging from wet grassland to dry scrub-woodland, while *Golunda* prefers grasslands, swamps and habitats at the edges of moist forests (Nowak, 1999). Other common taxa at Hadar include *Saidomys* (an extinct murid) and *Oenomys* (rusty-nosed rat). The latter is a semiarboreal species that prefers clearings and secondary growth in tropical forest (Kingdon, 1997). Several taxa, such as *Acomys* (spiny mouse), *Xerus* (ground squirrel), *Gerbilliscus* (gerbil), and *Tachyoryctes* (root rat), imply the occurrence of somewhat drier bushland, savanna, and open woodland conditions, but these are a relatively rare component of the rodent fauna (constituting less than 10%). The G:M ratio for Hadar is 0.07:1, which suggests a higher percentage of woody vegetation cover than at Laetoli. Overall, the rodent fauna indicates that habitats at Hadar were dominated by closed woodlands set in a mesic environment (Sabatier, 1979, 1982; Denys, 1985a,b, 1987).

Reconstructed depositional environments and the absence of aquatic elements in the fauna and flora at Laetoli indicate that there were no permanent rivers or lakes. Water sources were apparently restricted to springs and small seasonal rivers, streams, and ponds (Hay, 1981, 1987; Harris, 1987; Bonnefille and Riollet, 1987). By comparison, fluvial and lacustrine sediments throughout the Hadar Formation indicate the occurrence of an extensive shallow lake and/or floodplain system (Aronson and Taieb, 1981; Campisano and Feibel, 2007). The lake and rivers supported a diversity of aquatic vertebrates.

Further detailed comparisons are needed to isolate more specific distinctions in the paleoecology between the two sites, but the habitat at Hadar appears to have differed quite markedly from that at Laetoli, being more densely wooded and more mesic, with permanent sources of water. Having permanent bodies of water at Hadar may have had a direct impact on hominin abundance through the availability of sources of drinking water, but it is much more likely that the relationship was an indirect one mediated through its influence on the vegetation. These inferred major ecological distinctions between Hadar and Laetoli are similar to the differences between modern-day chimpanzee habitats described above, in which comparable patterns of variation in population density and biomass are observed. The possibly higher frequency of occurrence of hominins at Hadar compared with that at Laetoli suggests that, just like chimpanzees, *A. afarensis* may have been more successful in habitats that were more densely wooded. In which case, Laetoli would have represented a somewhat marginal habitat for *A. afarensis*, and this is reflected in their presumed lower abundance, density, and biomass.

As noted by Plumptre and Cox (2006), forest composition and food availability are major determinants of variation in density and biomass among modern chimpanzee populations. As discussed above, comparisons of the mammalian faunas at Hadar and Laetoli have allowed us to infer that *A. afarensis* at Hadar may have lived in denser woodlands, and that these may have offered greater availability of preferred foods than were available at Laetoli, thereby permitting the species to attain higher population densities. Microwear analyses of the molars of *A. afarensis* provide important clues to understanding the nature of the relationship between diet and ecology at the two localities. Grine et al. (2006) demonstrated that the microwear on *A. afarensis* molars is remarkably uniform at Laetoli and throughout the Hadar sequence, and that there are no significant differences associated with spatial or temporal changes in ecology. As Grine et al. (2006) noted, *A. afarensis* must have consumed a variety of different foods with very similar mechanical properties (in this case relatively soft or tough food items, analogous to the diet of modern-day mountain gorillas) or it may have more narrowly tracked its preferred foods across different habitats. Unfortunately, current evidence does not allow us to decide between these two scenarios. Nevertheless, the microwear data do indicate that *A. afarensis* was probably restricted in the types of foods that it could process, and that it did not shift its dietary base or adopt fall-back food items with radically different properties in different habitats (see Marshall and Wrangham, 2007). Given these apparent constraints on the range of food items that were exploited by *A. afarensis*, it can be deduced that diet would have been an important contributing factor in determining the carrying capacity of *A. afarensis* across its geographic range. It seems likely that the more extensive coverage of forest and woodlands at Hadar, compared with Laetoli, was able to sustain higher population densities of *A. afarensis* because it offered more optimal habitats for their range of foraging and dietary behaviors.

It is important to note, however, that we are not making *a priori* assumptions about the inferred habitat preference of *A. afarensis*, but rather we are assuming that the density of *A. afarensis* relates directly to dietary behavior and foraging optimality, and that these in turn are related to differences in the ecology between Laetoli and Hadar. An important consequence of this study is that we are able to identify, for the first time, which components of the heterogeneous ecosystems occupied by *A. afarensis* were likely its most optimal (and presumably preferred) habitats. The ecological distinctions that we have isolated as potentially determining the differences in density of *A. afarensis* are quite coarse-grained, but we anticipate that with further refinement of the paleoecological settings at Hadar and Laetoli, as well as similar analyses at other contemporary localities, it will be possible to develop a more fine-tuned and nuanced assessment of the place of *A. afarensis* in east African ecosystems.

Conclusions

Hominins represent a very rare component of the large-mammal fauna at Laetoli, and, although there are no equivalent data available from Hadar to make direct comparisons, it can be presumed, from the much higher raw count and from the relative proportions of hominins to bovids and cercopithecids, that *A. afarensis* were much more common at the latter site. The lower frequency of representation of hominins at Laetoli may have important implications for the understanding of the ecology of *A. afarensis*. However, before we can draw ecological conclusions, it is important to assess the extent to which taphonomic variables might have been a contributing factor in the lower incidence of hominins at Laetoli. In this paper, we have shown that the hominins at Laetoli belong to a size class of large mammals whose bones are most likely to be preferentially removed from the assemblage prior to fossilization as a consequence of taphonomy. Using data from fossil ruminants, we have shown that two main taphonomic factors affect the survivability of carcasses and bones lying on the land surface at Laetoli—carnivore scavenging and subaerial burial by tuffaceous sediments. The pattern of preservation of fossil bones at Laetoli demonstrates that the diverse carnivore guild had a significant impact on the skeletal assemblage prior to fossilization through the differential destruction of carcasses and bones. The marked discrepancy in the representation of craniodental specimens compared to postcranial remains is associated with carnivore scavenging. The other factor that affects carcass and bone survivability at Laetoli relates to the potential for primary volcanic ash falls and tuffaceous sediments to completely bury skeletal material and thereby preserve it from scavenging and trampling. This taphonomic factor accounts for the much higher representation of postcranial remains and partial carcasses of mammals under 5 kg in body weight. Taking these data into account, we conclude that the rarity of hominins at Laetoli might be due, at least in part, to the influence of these two taphonomic factors. Hominin carcasses fall into a size category that is highly susceptible to total destruction by scavenging carnivores prior to burial and too large to have a high likelihood of being buried before being discovered by carnivores. Basically, taphonomic and sedimentary circumstances at Laetoli are unfavorable for the survivability of hominin remains, particularly postcrania.

Comparisons with modern African primate communities suggest that it is reasonable to assume that Laetoli hominins were about as rare as extant chimpanzees living in forests and woodlands in east Africa today. The highest population densities of chimpanzees occur in forest and closed woodland, with reduced densities in open woodlands. If similar levels of population-density variation characterized *A. afarensis*, the observed differences between hominin abundances at Hadar and Laetoli may relate to the quality or optimality of the habitats. Geological and paleontological evidence indicates that Hadar was, in general, much more densely wooded and more mesic than Laetoli, with evidence of permanent bodies of water. In contrast, Laetoli was predominantly an open-woodland-shrubland-grassland mosaic, with ephemeral streams and ponds. These major ecological distinctions between Hadar and Laetoli are comparable to the magnitude of differences seen in modern chimpanzees, in which comparable patterns of variation in population density and biomass are observed between different habitats. The apparently higher frequency of occurrence of hominins at Hadar compared with that at Laetoli suggests that, like chimpanzees, *A. afarensis* may have been more successful in more densely wooded habitats. Results from microwear analyses of the molars indicate that *A. afarensis* was restricted in the types of foods that it could process, and, as a consequence, dietary behavior would have been an important contributing factor in determining the density of *A. afarensis* in different habitats. The evidence presented here suggests that Laetoli represented a less optimal habitat for the foraging and dietary behavior of *A. afarensis*, and this is reflected in their inferred lower abundance, density, and biomass.

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