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POGGIO ROSSO (UPPER VALDARNO, CENTRAL ITALY), A WINDOW ON LATEST PLIOCENE WILDLIFE

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ABSTRACT

The record of fossil mammalian remains from Poggio Rosso, Upper Valdarno, represents one of the richest samples for deciphering paleobiological information on latest Pliocene land faunas of central Italy. The taphonomic imprinting of this bone accumulation formed by *Pachycrocuta brevirostris* is investigated to determine the time-averaging of the assemblage, the structure of the paleocommunity from which it originated, and the interactions among some of the species represented in it, as well as the paleobiology and paleoethology of the hyenas. The bones were accumulated in a short time (within a year) during an episode of severe drought. The harsh environmental conditions debilitated the fauna and exposed it to predators. Harsh conditions also forced clans of *Pachycrocuta* hyenas, which under normal circumstances would have been primarily scavengers, to turn into killers of prey that now were easier to subdue. Thus portions of killed prey were added to the scavenged carcass parts usually taken to the dens. Furthermore, the remains at Poggio Rosso seems to add weight to the hypothesis that middle latitude *P. brevirostris* might have had seasonal breeding and parental care of cubs.

INTRODUCTION

A preliminary taphonomic study on Poggio Rosso, one of the richest paleobiological archives on Italian latest Pliocene faunas, was conducted by Mazza et al. (2004). In that analysis the authors ascertained that Poggio Rosso consists of bones accumulated in a den by the characteristic large-sized Upper Valdarno Villafranchian hyena *Pachycrocuta brevirostris* and that the carcass parts were amassed in a time of extreme drought. Mazza et al. (2004) also postulated that the hyenas were rearing cubs at the time and that the cubs possibly had some sort of parental care.

Important studies have decoded a large amount of invaluable paleobiological information on *P. brevirostris* (Turner and Antón, 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001a, 2001b). In fact, the site analyzed by Arribas and Palmqvist (1998) and Palmqvist and Arribas (2001a, 2001b), at Venta Micena, Spain, is the richest source of information on the activity and lifestyle of *P. brevirostris*. All these investigations, however, dealt with *P. brevirostris* performing under normal, unstressed circumstances. Poggio Rosso, in contrast, was formed during an unusual environmental situation. Its comparison with Venta Micena therefore unlocks unexpected new data on the ethology of this formidable bone-collector from the recent past.

In their extensive studies of the Venta Micena fauna, Palmqvist et al. (1996), Arribas and Palmqvist (1998), and Palmqvist and Arribas (2001a, 2001b) concluded that *Pachycrocuta brevirostris* was mainly a scavenging hyena, as are extant brown and striped hyenas, in contrast to modern spotted hyenas, which integrate scavenged food with actively hunted prey. The Venta Micena hyena was an Early Pleistocene *Pachycrocuta* that apparently lived in a normal, unstressed setting. In contrast, the Poggio Rosso hyena was a Late Pliocene *Pachycrocuta* that survived under very demanding environmental conditions. The paleobiological information drawn from the taphonomic imprinting of Poggio Rosso indicates that *Pachycrocuta* behaved differently than its Venta Micena relatives. Whether the species modulated its behavior in relation to its circumstances or changed its ethology through time is still unresolved.

Skeletal Parts

Unlike kill site accumulations, which generally abound in ribs and vertebrae, Poggio Rosso contains a low proportion of axial skeletal elements, with the site being almost entirely constituted by skulls and limb bones (raw data for the site can be found in Mazza et al., 2004). Teeth and antler remains are rare: MNI (minimum number of individuals) counts based on isolated teeth give significantly lower estimates than those based on bones ($\chi^2 = 33.3$; $p < 0.0001$; Fig. 1). Antler fragments belong entirely to *Pseudodama* (and none belong to *Eucladoceros*). The assemblage contains a low amount of complete longbones (4.3%), many of which were articulated (55.9%). All major limb bones are underrepresented ($\chi^2 = 374.43$; $p < 0.0001$), especially femora (Fig. 2). In longbones, the epiphyses outnumber the diaphyses ($\sim$2:1; $\chi^2 = 83.3$; $p < 0.0001$). Proximal epiphyses are less abundant than distal epiphyses in the humerus, metacarpal bone, femur, and tibia, while the opposite occurs in the radius and metatarsal bones (Fig. 2). The abundance of longbone epiphyses is related negatively to their flesh and fat content and positively to their marrow content, although the proximal epiphyses are markedly correlated with their marrow content, while the distal epiphyses are not (Fig. 3). In *Eucladoceros*, however, the relation between the number of proximal epiphyses and their marrow content is not statistically significant. There was also apparently a preferential destruction of epiphyses with low density, but the correlations in this case are rather dispersed (Fig. 4).

Juveniles

In kill-site assemblages, juveniles are present normally in very high numbers, often exceeding 25% of the total MNI counts. Palmqvist et al. (1996) established that the proportion of juveniles in any given ungulate population is independent of body size, ranging approximately between 30%–40%. Palmqvist et al. (1996) and Arribas and Palmqvist (1998) observed that the selection of predators induces a proportional increase of juveniles with the body mass of the prey. In contrast, in the Poggio Rosso assemblage, juveniles of all the species represent only 16.9% of the total MNI count, and their number is independent of size ($r = 0.2337$ with 7 df, $F = 14$, $p < 0.001$; Fig. 5). Size-independence of the proportion of juveniles is a typical feature of carcass accumulations formed during drought (Palmqvist and Arribas, 2001b). The proportion of juveniles rises, however, if one considers only the ungulate sample of the site (21.1% including subadults, 20% only juveniles); but again, the proportion of young to adult individuals does not relate to the sizes of the species.

Carnivore to Ungulate Index

As noted above, Poggio Rosso contains a high amount of carnivore remains. Their relative proportion grows even more if compared to the number of ungulates at the site: carnivore to ungulate index = 32.83%.

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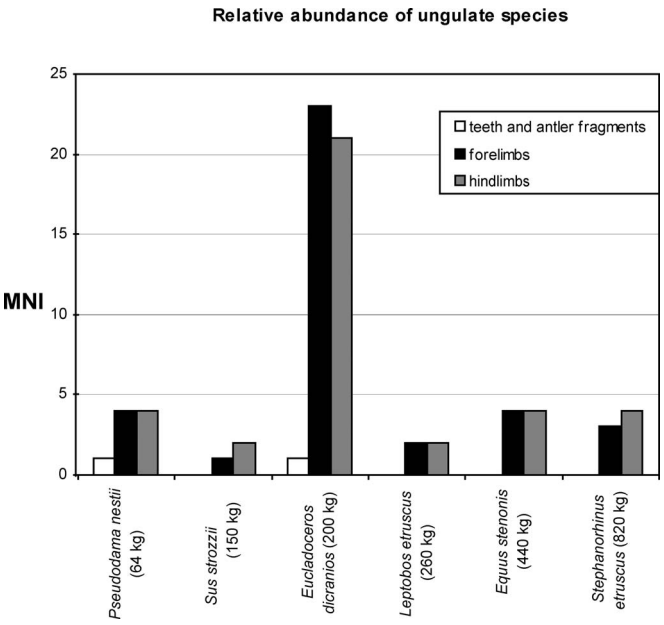

FIGURE 1—Relative abundance of ungulates in Poggio Rosso based on counts of teeth and forelimb and hindlimb longbones; size estimates obtained applying the allometric scaling of Schmidt-Nielsen (1984), Reitz and Quitmyer (1988), and Prange, Anderson, and Rahn (1979). The diagram shows a marked dominance of *Eucladoceros dicranios* in the longbone sample. MNE = minimum number of elements; MNE P = minimum number of proximal epiphyses; MNE D = minimum number of distal epiphyses.

Poggio Rosso calls to mind the bone accumulations formed by present-day *Parahyaena brunnea*, which normally abound in carnivore remains (35%–47%; Brain, 1981), although carnivores are numerous in kill sites as well (25%–50%; Palmqvist and Arribas, 2001b).

Richness and Body Size

Poggio Rosso includes a relatively high number of species (18) and a very wide spectrum of body sizes (<10 to >1000 kg). Normally, active hunters perform selective predation, killing a limited number of species that are usually approximately their own size. In contrast, accumulations formed by scavengers include a wide variety of species with the most diverse body sizes.

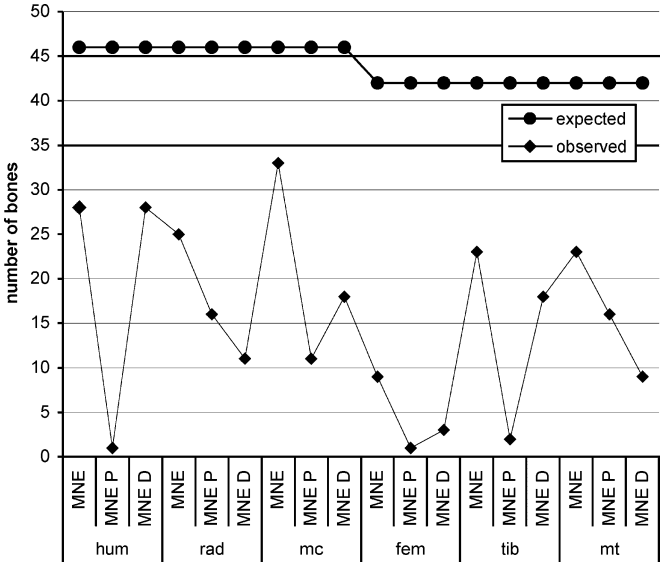

FIGURE 2—Expected versus observed number of longbones and of longbone epiphyses in *Eucladoceros dicranios*. The expected amounts are based on the MNI (minimum number of individuals) counts of the forelimb and hindlimb longbones. The diagram shows a marked underrepresentation of the proximal epiphyses of the humerus, metacarpal bone and tibia, distal epiphyses of the radius and metatarsal bone, and both epiphyses of the femur.

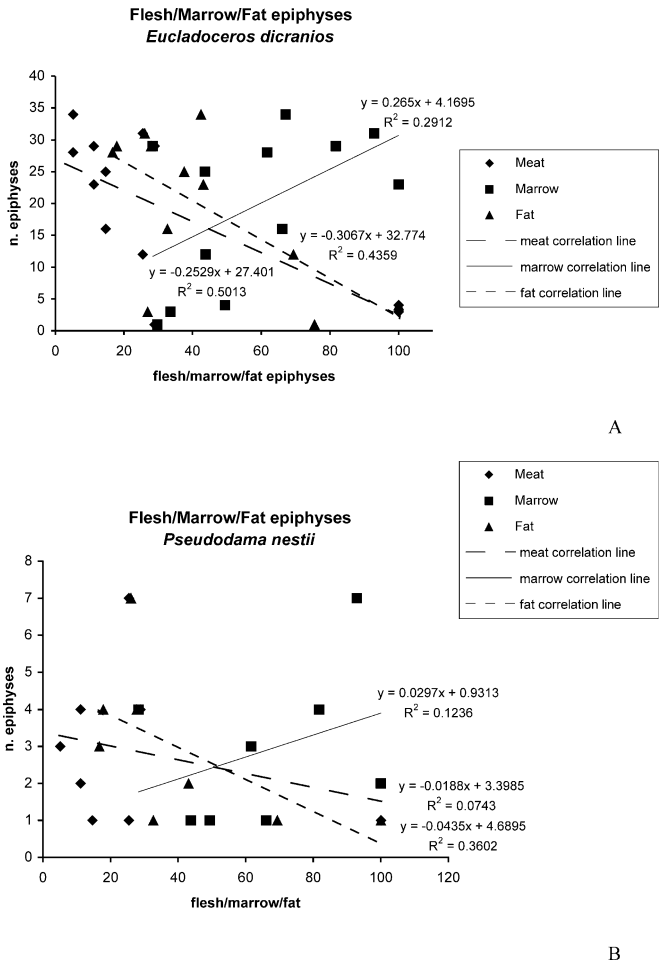

FIGURE 3—Scatterplots of the number of epiphyses of Binford's (1978) flesh, marrow, and fat content in deer. (A) *Eucladoceros dicranios*. (B) *Pseudodama nestii*. In both species there is an inverse correlation between the number of longbone epiphyses and their fat and flesh content and a positive one with their marrow content.

Mortality Profiles

The ages of several specimens of *Eucladoceros dicranios*, which outnumbers any other taxon in the assemblage, both in the NISP (number of identified specimens) and MNI counts, were estimated using tooth eruption in animals under 2.5 years of age and tooth wear in animals 2.5 years of age and older. The resulting age profile is U-shaped (Fig. 6). The two peaks in the diagram fall in the age classes of (1) juveniles and in those of individuals younger than 3 and (2) adults from 4.5 to 9 years. The least represented age class is that from 3–4.5 years, and there are no individuals older than 9 years. U-shaped patterns are normally given when there are relatively high numbers of young and very old individuals, the two age classes especially exposed to risk of death under stressed conditions. Extant cervids of equivalent size, such as the wapiti, are fully breeding animals from 4.5 to 9 years, and it is presumed that it was the same in *Eucladoceros*. Peaks in these age classes that have the lowest probability of death are unexpected. The absolute lack of very old *Eucladoceros* individuals also is anomalous. Specimens found in other Upper Valdarno localities that are older than 9 years of age prove that the species had a longer life expectancy than the specimens from Poggio

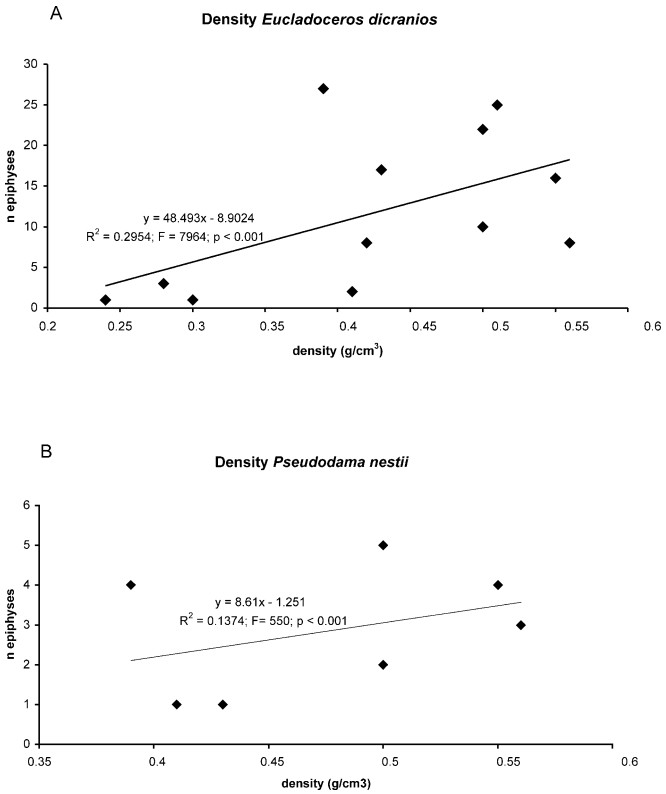

FIGURE 4—Scatterplots of the number of epiphyses of Lyman's (1994) density values in deer. (A) *Eucladoceros dicranios*. (B) *Pseudodama nestii*. In both species there is a positive correlation between the number of longbone epiphyses and their densities.

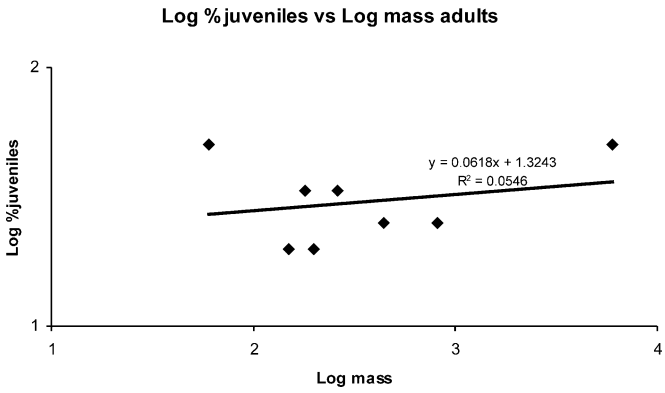

FIGURE 5—Scatterplot of the proportion of juvenile individuals (estimated from MNI counts) to adult body mass (in kg) for all the ungulate species of the Poggio Rosso assemblage. The diagram shows that the number of juveniles is independent of body size of species (the idea for this relationship was drawn from a similar regression analysis in Palmqvist and Arribas, 2001b).

Rosso. The remains at Poggio Rosso therefore attest to the death of animals least at risk of death.

KILLERS OR SCAVENGERS?

Poggio Rosso's taphonomic imprinting reveals a mixture of features both of kill site assemblages and of accumulations collected predominantly by scavenging carnivores. Similar to the situations in kill sites, Poggio Rosso has a large number of articulated elements, low proportions of epiphyses associated with large amounts of flesh and with high fat content, and, conversely, high proportions of epiphyses with high marrow content, as well as relatively high proportions of carnivore remains. On the other hand, as with scavenger-formed accumulations, the site contains: (1) elements of an array of species from a wide spectrum of body sizes; (2) an underrepresentation of all major limb bones; (3) low numbers of juvenile remains; (4) low proportions of ribs and vertebrae; (5) very few complete longbones; (6) high proportions of epiphyses in relation to diaphyses; and (7) preferential destruction of epiphyses with low density. At this point the task at hand is to establish whether the animals were killed by the harsh, inhospitable circumstances or if they were so debilitated that they were easy victims for the carnivores. If this second hypothesis is true, one must verify whether the animals were killed by *Pachycrocuta* or if they were overpowered by some other predator and later scavenged by *Pachycrocuta*.

Important information on the state of the carcasses at the time when the hyenas processed them can be drawn from the modifications of specific bones and body parts. Ripping entire limbs from a freshly killed carcass is not easy for modern-day hyenas, and it likely was similarly difficult for the powerful *Pachycrocuta*. Even after death the shoulder muscle masses as well as the sturdy hind muscles and tendons still resist the most powerful strains. Scapulae and femur heads are likely to remain attached to the body, while the limbs might break off at the middle of the humerus or at the femur neck. Putrefaction makes excisions easier by altering the nature and thus the resistance of muscles, tendons, and ligaments; in other words, rotting carcasses are easier to dismember. The proximal epiphysis of specific limb bones can reveal much about the state of the carcass when its limbs were ripped off.

At Poggio Rosso, only a few ungulate femurs and tibiae still preserve their proximal epiphysis, while all humeri and other femurs and tibiae systematically lack it. The proximal ends of most of these bones, with or without the epiphysis, rarely show bites or gnawing marks. This indicates that all forelimbs and most of the hindlimbs were ripped from freshly killed animals and that only a few hindlimbs and hindlimb parts were torn from rotting carcasses. It also rules out a proximo-distal consumption of the limbs. At kill sites, carcasses are normally processed from the pelvis and the abdomen toward the limbs, following distinct caudo-cranial

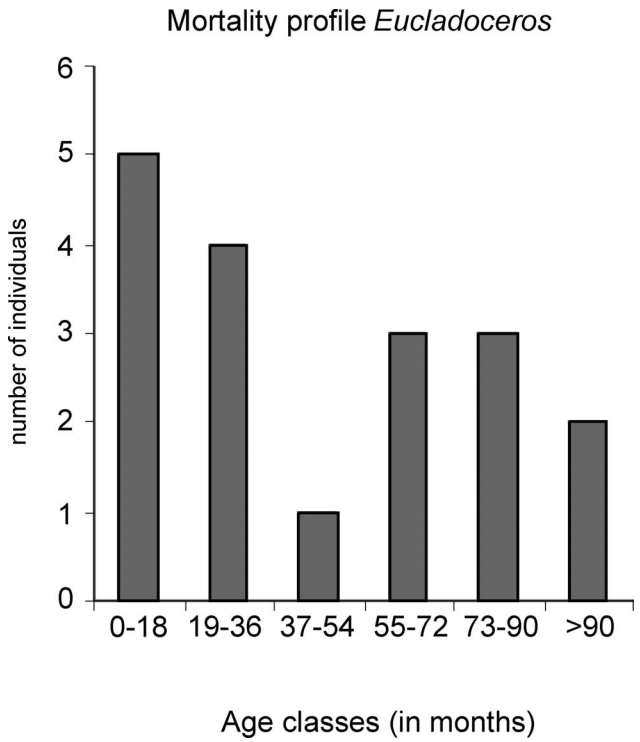

FIGURE 6—Mortality profile in *Eucladoceros dicranios*. The U-shaped pattern of this diagram is given by the relatively high numbers of young and of individuals 4.5 to 9 years of age. Note that there is a lack of specimens older than 9 years.

and proximo-distal consumption patterns. In contrast, the Poggio Rosso hyenas apparently processed the body parts taken to their den according to a less-rigid consumption scheme, or even without any scheme at all, although bites are mostly concentrated on distal epiphyses and diaphyses, and some bones, such as the radius/ulna and metatarsal bones, systematically lack their distal ends.

The conclusion that most of the Poggio Rosso carcasses were dismembered by the hyenas shortly after death is compatible both with the very limited weathering of the bones and the general lack of sediment in the bone porosities (Mazza et al., 2004). In fact, both these aspects exclude prolonged putrefaction and liquefaction of soft tissues. Carcasses were thus dismembered with large amounts of flesh still sticking to them. The scatterplots shown in Figure 3 indicate that the limbs were consumed primarily for their flesh and fat yields and probably not, or only secondarily, for their marrow content. Bones are consumed for their marrow when little flesh is left on them; in contrast the Poggio Rosso carnivores benefited greatly from sizable amounts of readily available prey provided by the unfavorable environmental conditions.

That hyenas fed on freshly killed carcasses is also indicated by the average annual mortality rate of *Eucladoceros dicranios*, which amounts to 0.6 (~2.4%; Mazza et al., 2004). At this pace the 25 *E. dicranios* carcasses at Poggio Rosso would have accumulated in ~40 years. Killing such a high number of deer takes time, even for a group of predators. This conflicts not only with the limited putrefaction and minimum exposure (and thus rapid burial) of the bones, but also with the rather high accumulation rates of the carcass parts indicated by the dense packing of the specimens, which frequently show bone-to-bone contacts. This evidence suggests that the time of accumulation and burial was far less than 40 years.

The life cycles of *Eucladoceros dicranios* are not only in accord with a short time of burial at Poggio Rosso but also reveal the time of the year when the accumulation might have formed. As all cervids, *E. dicranios* was a seasonally breeding animal. When mating and births occurred is unknown, but age-scoring based on the eruption and wear of cheek teeth in the Poggio Rosso *E. dicranios* indicates that 11% of individuals died within the first three months of life and that at least 28% of them died within six months of the season of birth. In the Poggio Rosso accumulation, young prey forms 21% of the total number of individuals represented, an amount comparable to the accumulation reached in the diet of the Serengeti and Ngorongoro hyenas in April (Kruuk, 1972). Worthy of note is the fact that, despite the occurrence of specimens of 25 individuals, no antler remains of *E. dicranios* were found among the Poggio Rosso material. Although this might relate to the difficulty of transporting cervid heads with exceptionally branched appendages, *Eucladoceros* antlers are reported in the Venta Micena material (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001b). An alternative possibility is that males were killed between the time of antler shedding and the appearance of new pedicles, which in modern-day, middle-latitude cervine deer falls between February and the end of March. Thus the site was formed in a very short time, seemingly between winter and spring. Poggio Rosso might have formed as seasonal perturbations in rainfall added their effect to a general drop in humidity recorded during this interval of time.

The large availability of prey was therefore a consequence of mass debilitation, annihilation, or both, induced by drought. The proportions of age classes represented in the Poggio Rosso assemblage reveal how much the carnivores profited from this aridity. The relatively low proportion of juvenile ungulates was shown to be independent of body size (Fig. 5) and thus related to drought. It was also shown that the mortality profiles of ungulates from the site (*Eucladoceros*, Fig. 6) show peculiar patterns with peaks in adult age classes that normally are least at risk of death. Comparison with extant hyenas may help explain this observation. Spotted hyenas living in the Serengeti National Park and in the Ngorongoro Crater show seasonal fluctuations in their diets (Kruuk, 1972). Kruuk (1972) observed that Serengeti National Park and Ngorongoro Crater

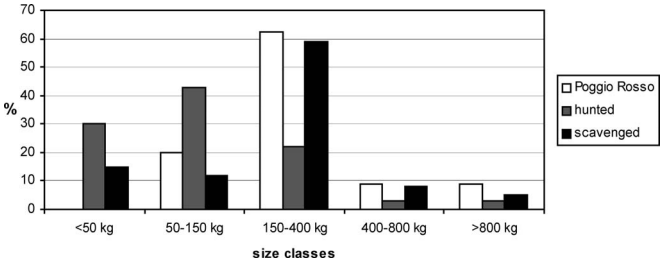

FIGURE 7—Bar diagram showing the relative abundances of ungulate size classes in the ungulate sample from Poggio Rosso and in the prey hunted and scavenged by modern spotted hyenas (*Crocuta crocuta*) in the Serengeti National Park (data from Kruuk, 1972; the idea of this diagram was drawn from a similar one in Palmqvist and Arribas, 2001b).

spotted hyenas concentrate on young ungulate prey during the wet periods of the year (~23% at Serengeti and >60% at Ngorongoro in February), but they favor adults during the dry seasons (young individuals total <10% in both areas from June to November). During dry seasons hyenas tend to move away from areas of wet-season range, opting instead to gather where ungulates tend to congregate, and they disperse again when the unfavorable conditions end (Kruuk, 1972). Consequently, drought concentrates abnormally high numbers of prey, thus causing unusually high concentrations of predators. In stratigraphical records formed under such environmental circumstances, very dry intervals could be singled out by larger accumulations of prey remains.

According to Palmqvist and Arribas (2001b), *P. brevirostris* was primarily a scavenger. The pattern of the size classes represented at Poggio Rosso actually resembles that of bone accumulations formed today by spotted hyenas (Fig. 7). The relative abundances of the Poggio Rosso ungulate size classes differ more from the frequencies of ungulates actively killed by modern *Crocuta crocuta* hyenas of the Serengeti National Park ($\chi^2 = 132$, $p < 0.001$) than from those of prey scavenged by the same hyenas ($\chi^2 = 22.3$, $p < 0.001$). Stating that the Poggio Rosso *P. brevirostris* largely fed on fresh carcasses does not contradict the opinion of Palmqvist and Arribas (2001b); on the contrary, it adds to our knowledge of the ethology of the hyena. The dominance of *E. dicranios* remains in the Poggio Rosso assemblage proves that *Pachycrocuta* performed killing of very weakened animals and that the cervid had the undesirable privilege of being one of the hyenas' most popular prey. Signs of *Pachycrocuta brevirostris* activity can also be found on ungulate remains from other Upper Valdarno sites. These are more frequently present on *E. dicranios* remains than on those from other taxa.

The conclusion from all the accumulated information is that the harsh environmental conditions pushed the hyenas to add killing to their customary scavenging. They presumably behaved as modern spotted hyenas do today in the same circumstances, acting mainly as population regulators by selecting the physically weakest or diseased animals and secondarily as scavengers of prey killed by other predators.

CLUES ON THE PALEOBIOLOGY OF THE POGGIO ROSSO *PACHYCROCUTA BREVIROSTRIS*

A great deal of information on the lifestyle of a living being can be deciphered from the remains of its meals, but its physical characteristics still need to be known. Turner and Antón (1996) made one of the best reconstructions of *P. brevirostris*. By plotting the condylobasal skull lengths and first molar lengths of Upper Valdarno *P. brevirostris* specimens comparable in size to those from Poggio Rosso on Van Valkenburg's (1990) regression equations, the latter can be inferred to weigh about 70 to 90 kg, in line with the average weight calculated by Turner and Antón (1996). Since an average-sized *Crocuta crocuta*, which weighs from 45 to over 70 kg, kills or scavenges from 2 to 3 kg per day (Kruuk, 1972), one can estimate that the theoretical amount of flesh ingested daily by a single *P. brevirostris* ranged from 3 to 4 kg (which includes the 3.5

kg of meat fed per day each of four adult spotted hyenas; Kruuk, 1972). This can be related to the proportion of *E. dicranios* material included in the assemblage in order to hypothesize the number of predators presumably involved in the formation of the bone accumulation. The 25 *E. dicranios* individuals consist of 18 adults, 2 subadults, and 5 juveniles. Using different methods listed in Mazza et al (2004), but especially the allometric scaling in Schmidt-Nielsen (1984), Reitz and Quitmyer (1988), and Prange et al. (1979), as well as the regression equations in Janis (1990) and Scott (1990), an adult Poggio Rosso *E. dicranios* was calculated as weighing in at ~200 kg, a subadult ~100 kg, and a juvenile ~40 kg. The site therefore attests to ~4000 kg of *E. dicranios* material available to the hyenas. Because skeletal weight is ~7.5 % of the total weight of artiodactyls (Reed, 1963), the hyenas could have consumed of ~ 3700 kg of *E. dicranios* flesh.

At the calculated death rate, the 25 *E. dicranios* individuals were said to take ~40 years to die by natural causes. On the other hand, a single *Pachycrocuta* would need ~2.5 to 3 years to consume the equivalent amount of flesh. *P. brevirostris*, however, might not have been a solitary carnivore. Modern *C. crocuta* forms groups of 30 to 80 individuals whose annual consumption varies from a minimum of 3,900 kg to a maximum of over 87,000 kg (East and Hofer, 2001; Hofer, 2002; Kruuk, 1972). The same number of *Pachycrocuta* hyenas, with the estimated daily ingestion of 3 to 4 kg of meat, would reach an annual intake of ~33,000 kg to almost 117,000 kg. Hence, it would take from 11 to 41 days for clans of 30 to 80 *Pachycrocuta*s to consume the calculated flesh of the 25 *E. dicranios* carcasses. Because of the rapid burial of the Poggio Rosso bones, one can conclude that *Pachycrocuta* might not have been a solitary predator. Turner and Antón (1996) reached the same conclusion. Examining limb proportions, Turner and Antón (1996) inferred that *P. brevirostris* was a large, sturdy animal, less adapted to running than any of its modern relatives, and not structured for the extensive wandering imposed by solitary scavenging. Despite its ability to overpower medium-sized prey due to its large size, *P. brevirostris* performed concerted group-hunting and perhaps aggressive cooperative scavenging (Turner and Antón, 1996). Moreover, concerted defense was certainly the most effective strategy for defending carcasses from other large carnivores and possibly from other *Pachycrocuta* clans as well. How large the *Pachycrocuta* clans were, however, is difficult to establish.

The Poggio Rosso accumulation contains a small number of *P. brevirostris* remains, a sign that a smaller number of individuals operated at Poggio Rosso, although another possibility is that there was reduced mortality in the hyenid population or a cannibal consumption of their own deceased. Kruuk (1972) observed that the number of spotted hyenas feeding on a carcass depends upon the weight of the carcass and that the relative density of both game and spotted hyena populations influences the amount of carcass remains left behind by the hyenas. The denser the hyena populations, the fewer the number of bones left over. If the same dynamic applied to the Upper Valdarno hyenas, the abundant, minimally consumed and rapidly accumulated large-size prey remains of the Poggio Rosso assemblage suggest a fairly dense *P. brevirostris* population and an unusually large amount of readily available food compared to normal circumstances.

It would be interesting to know if the *P. brevirostris* clans were stable or if they banded together only during dry seasons, as modern spotted hyenas tend to do today (Kruuk, 1972). To verify this, far richer samples accumulated over a range of environmental settings would need to be analyzed. Future comparisons of Poggio Rosso with other such sites will hopefully clarify this point.

Whether *Pachycrocuta brevirostris* had litters throughout the year or had specific breeding seasons is unknown. In many hyenas today, breeding is nonseasonal. *Parahyaena brunnea*, however, is a seasonal breeder. Females in the Kalahari desert were observed undergoing several estrus cycles throughout the breeding season. Mating occurs mainly between May and August, and births normally occur between August and November, with a gestation period of about 97 days (Mills, 1982; Nowak, 1999). In the subtropics, *H. hyena* has litters in the spring. Present-day brown and spotted hyenas sometimes have seasonal littering peaks (Kruuk, 1972; Skinner, 1976; Mills, 1990). Hyenas thus seem to have a latitudinal tendency toward seasonal breeding. The same may have applied to past hyenas as well, and it might be expected that in temperate Europe this tendency might have even been enhanced, with a peak of births in the spring (Turner and Antón, 1996). This timing of births in *Pachycrocuta brevirostris* agrees with the presumed time of formation of the Poggio Rosso bone accumulation and adds weight to the hypothesis of cub rearing (see Mazza et al., 2004) to explain the amount of small carnivore remains in the assemblage.

CONCLUSIONS

The Poggio Rosso vertebrate record represents one of the Upper Valdarno's largest samples for deciphering paleobiological information from the latest Pliocene communities of the area. The site was formed by *P. brevirostris* hyenas in a short time, possibly between a winter and the following spring, during an episode of severe drought. Less water-dependent taxa, such as equids and leptobovines, fled, while animals needing a more continuous water supply amassed in a few wetlands around shrinking water bodies. Predators thus found vast feeding opportunities in the drought-weakened animals and the great number of prey killed by the demanding environmental conditions or by predators themselves. *Pachycrocuta* was predominantly a scavenger, and it may have participated in cooperative rather than solitary scavenging. It was normally therefore an opportunistic carnivore, but the remains at Poggio Rosso suggest that in stressed situations *Pachycrocuta* clans transformed into deadly killers and became specialized feeders, pursuing herds of *Eucladoceros* deer in particular. Living at middle latitudes, *P. brevirostris* may have developed seasonal breeding and perhaps parental care of its cubs, feeding them with body parts of small carnivores as brown hyenas do today.

Hyenas certainly were one of the major bone-collecting agents. The accumulations they left behind are rich archives of information on ancient life. This study highlights the importance of a meticulous analysis of the taphonomic imprinting of fossil assemblages in order to unlock all possible paleobiological information on paleocommunities. Knowledge of population dynamics, paleocommunity structure, interactions between taxa, paleoethology, and the responses to large- and small-scale environmental change, greatly relies on and will greatly benefit from the comparative analysis of all hyena-formed accumulations presently known in Europe.

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