Body Size Overlap, Habitat Partitioning and Living Space Requirements of Terrestrial Vertebrate Predators: Implications for the Paleoecology of Large Theropod Dinosaurs

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Ecological studies of extant tetrapod predators indicate that morphologically similar species which coexist in the same habitats routinely reduce interspecific competition for food by regular spacing of body size. The biggest predator species in the assemblage often differ more from one another in size than the smallest species. When coexisting carnivore species do not differ greatly in size, they commonly show morphological differences related to prey handling that may reduce dietary overlap. If carnivore species are very similar in both size and morphology, competition is avoided by habitat partitioning. Two tyrannosaurid species from the late Campanian Dinosaur Park Formation of western Canada are similar in both size and morphology, suggesting that they were segregated on the basis of habitat and/or biogeographic province. However, consideration of the living-space requirements of predator species of such large body size suggests that this kind of spatial separation would only have been possible had tyrannosaurids been more like ectotherms than endotherms in their metabolic rates. Distribution of different large theropod species across different, and surprisingly small (for the size of the animals) portions of Mesozoic landscapes may also account for the remarkably high diversity of morphologically similar large theropods in other dinosaur faunas.

INTRODUCTION

"Size does matter"
(Advertising slogan for the 1998 film *Godzilla*)

Large vertebrate meat-eaters lead difficult lives. Situated at the top of food chains, their numbers are constrained by trophic dynamics to a greater degree than those of other animals (cf. Carbone and Gittleman, 2002). Obtaining food may require killing dangerous prey, and once food is obtained it often must be defended from others of the predators kind as well as carnivores of other species (Palomares and Caro, 1999; van Valkenburgh, 2001; Creel and Creel, 2002). Consequently, both exploitation and interference competition are thought to be especially keen, both within and between species, among large carnivorous vertebrates. This expectation has led to considerable theoretical interest in the mechanisms by which predatory vertebrates mitigate potentially deleterious effects of competition, and in what factors enable carnivore species to coexist in ecological communities.

Two related mechanisms for reducing interspecific competition in sympatric species, which occur in the same geographic area, and syntopic species, which share the same habitat or microhabitat, have been proposed. Hutchinson (1959) suggested that the ratio of mouthpart sizes (larger/smaller) of closely related species has some minimum value that is necessary to permit ecological coexistence, and Hutchinsonian ratios have been implicated in the "assembly" of communities (Case *et al.*, 1983). Although the statistical validity of these patterns has been disputed (Grant, 1972; Horn and May, 1977; Grant and Abbott, 1980; Schoener, 1984; Pianka, 1994), ecologists now recognize 1.3 as a critical value of the Hutchinsonian ratio which commonly facilitates coexistence. Thus, species are deemed to be too similar to coexist if the ratio is below this value.

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Even if Hutchinsonian ratios do not reach this critical value, sympatric species may reduce niche overlap through ecological character displacement (Brown and Wilson, 1956). Morphological evidence of character displacement between closely related species is thought to be expressed in size regularities, such as equal size ratios of larger to smaller species, across the size range of co-occurring species, in trophically relevant morphological features. Such regularities are presumed to reflect an evolutionary response on the part of potentially competing species which spreads them out across the size spectrum, thereby reducing dietary overlap (Holmes and Pitelka, 1968). Body size differences among carnivore species often result in differences in prey size (cf. Karanth and Sunquist, 1995, comparing tigers and leopards). Thus, Hutchinsonian ratios may be interpreted as a special case of this more general phenomenon of ecological character displacement (Dayan et al., 1990).

In this paper, we will compare guilds of extant and extinct predators, so it behooves us to explain our use of the term. Root (1967, p. 335) defined an ecological guild as "a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." However, Root conceded that "the limits that circumscribe the membership of any guild must be somewhat arbitrary." The guild concept proved irresistibly attractive to ecologists, but the inherent imprecision of the term's definition has resulted in great conceptual fuzziness in its application (Simberloff and Dayan, 1991).

Van Valkenburgh (1985, p. 407) defined "the guild of large, land predators" as "the nonaquatic, nonvolant... mammal species within a community that take prey and potentially compete for food." This is a broad interpretation of the guild concept, for members of a guild of carnivorous mammals defined in this way could include hyaenids, canids, felids and ursids. These groups vary considerably in their morphological adaptations for killing their victims, which makes one wonder if these different kinds of predators should be regarded as exploiting vertebrate prey "in the same way" (Root, 1967, p. 335). Indeed, some authors (Dayan et al., 1989a; 1990; Dayan et al., 1992; Werdelin, 1996) have used the term "guild" more narrowly than van Valkenburgh in describing assemblages of carnivorans, perhaps staying closer to Root's original meaning.

In the present paper, we will use the guild concept as it was defined by van Valkenburgh, but we will also need a more specific term to describe potentially coexisting carnivore species whose morphology is similar enough that their prey handling methods are likely to be or to have been similar.

Rosenzweig (1966, p. 604) proposed such a term, the "hunting set", for a "group of species with similar body build and hunting strategy". He noted that within hunting sets "an increase in body size is correlated with an increase in prey size." Rosenzweig's "hunting set" is narrower than the "guild" as defined by van Valkenburgh. The "hunting set" seems to be equivalent to more restrictive versions of the guild concept that have been applied to coexisting carnivores by authors such as Dayan et al. (1989a; 1990; 1992) and Werdelin (1996).

To illustrate our use of the "hunting set" as opposed to the "guild", we would consider felids with conical teeth that occur together in an ecological community to be members of the same hunting set, as would coexisting canid species. Felids would not be members of the same hunting set as canids, but they would be members of the same guild.

Our object in employing hunting sets as well as guilds is to reduce terminological confusion. However, there will undoubtedly be cases where it will be difficult to decide whether potentially syntopic predators should be considered members not only of the same guild, but also of the same hunting set. This problem is particularly acute for extinct forms. For example, sabercats might arguably be assigned to a different hunting set from conical-toothed cats, given differences in their skulls and postcranial skeletons that appear to be related to prey handling. However, it is uncertain how much such differences would have affected the kind of prey they attacked (Antón and Turner, 1997).

We must also explain what we mean when we say that two predator species either do or do not coexist. Segregation of potentially competing predator species can be evaluated at several spatial scales. Species may share the same habitat, but occupy different microhabitats within it (e.g. arboreal vs. terrestrial species in a woodland setting). Species may occupy different sets of interspersed habitats in the same geographic region (e.g. more heavily wooded vs. grassland situations in a parkland), or abutting habitats along a large-scale environmental gradient (e.g. coastal vs. inland settings). On a still larger scale, species may occupy adjacent biogeographic provinces. Differences among these kinds of separation are obviously gradational.

In this paper, we first review case studies of several Recent and ancient hunting sets and guilds of predatory vertebrates, focusing on those morphological features that permit coexistence of species (at whatever spatial scale) in those communities. We will also examine cases in which species are too similar in size and morphology for syntopy.

We then consider the predator guild of one of the best-studied dinosaur faunas, that of the Dinosaur Park Formation from the Late Cretaceous of western

Canada (Eberth *et al.*, 2001). We will survey the size and shape of potentially coexisting Dinosaur Park theropod dinosaurs. This will reveal a paleoecological conundrum involving the largest theropod species of the Dinosaur Park Formation that has interesting implications for the interpretation of the paleoecology of these huge carnivorous reptiles.

SIZE OVERLAP, MORPHOLOGICAL DISPARITY AND COEXISTENCE OR HABITAT SEGREGATION IN PREDATORY VERTEBRATES

Australian Desert Varanid Lizards

Among extant vertebrates, varanid lizards provide the closest structural analog of typical non-avian theropod dinosaurs in such features as muzzle and tooth shape (Auffenberg, 1981; Molnar and Farlow, 1990). Varanid teeth are even serrated like those of most theropods. Consequently, functional comparisons of the varanid feeding apparatus with those of theropods are often made (Farlow *et al.*, 1991; Abler, 1992; Farlow and Brinkman, 1994). Most monitor lizards are active predators, foraging widely in search of prey (Losos and Greene, 1988; Pianka, 1994), and many are top predators in their ecological communities (Pianka, 1994). The way in which varanid species are packed in a hunting set therefore provides a useful starting point for thinking about how co-existing theropod species might have subdivided ecological space.

Six species of *Varanus* (Table I) occur at the Red Sands study site, 7 km west of Point Salvation, in the Great Victoria Desert (Pianka, 1968; 1969; 1970a,b; 1971; 1986; 1994). Each of these six species has its own distinct way of foraging. We briefly describe the ecology of each varanid, going up the size scale from the smallest to the largest species.

Varanus brevicauda is cryptic, spending most of its time inside tussocks of porcupine grass (James, 1996). It seldom moves, preying largely on insects but occasionally catching small lizards (Pianka, 1994).

The small terrestrial monitor, *Varanus eremius*, is a visual hunter that forages widely over large home ranges (Pianka, 1968). Fresh trackways often cover

distances of up to a kilometer, and they show that these lizards frequently reverse direction, looping back on their own trails (Farlow and Pianka, 2000). They are attracted to fresh holes and diggings of any sort, and will often visit a man-made digging within a day or two after it is made. In a typical foraging run, an individual *V. eremius* visits and goes down into several burrows of other lizard species, especially the complex burrow systems of the nocturnal skink *Egernia striata*.

Relatively little is known about the small arboreal species *Varanus gilleni*, but it appears to spend a lot of time in tree hollows. Its claws curve more sharply than those of terrestrial monitor species, presumably to facilitate climbing. Other lizards, especially geckos, constitute its major prey (Pianka, 1969). Stomachs of *V. gilleni* often contain just exceedingly fragile gecko tails, suggesting that these varanids may actually "harvest" the tails of geckos which would be too large to subdue intact (Pianka, 1969).

Varanus tristis drag the bases of their tails, leaving a very distinctive trackway with a wide, sinusoidal tail mark (Pianka, 1971; Farlow and Pianka, 2000). Trackways typically run more or less directly from tree to tree. These monitors climb most trees they visit, looking for food, primarily nestling birds and birds' eggs, but they also consume large arthropods and other lizards. Their claws are strongly recurved like those of *V. gilleni*. *V. tristis* are jet black. They appear to be active at lower body temperatures and earlier in the day than other varanids (Thompson *et al.*, 1999). *V. tristis* is highly seasonal in its activity, relying on fat reserves accumulated during times of plenty to get through lean periods (Pianka, 1971). Pianka once found an extremely emaciated *V. tristis*, literally skin and bones, hiding in a hollow tree, waiting for a drought to break!

The two largest monitors, *Varanus gouldii flavirufus* and *Varanus giganteus*, are both terrestrial, walking with their bodies and tails elevated well above ground. These two species cover extensive distances while foraging.

V. gouldii relies extensively on chemosensory cues to locate its prey. When foraging, these monitors hunt by smell, swinging their long necks and heads from side to side, constantly flicking out their long, forked tongues. They make as big an arc as they can, changing direction often, and covering as much ground as possible, searching for scent trails. Having located their prey, which are predominantly lizards and reptile eggs (Pianka, 1970a,b; 1994), *V. gouldii* dig their food up. Geckos, dug from their diurnal retreats, are important prey, but many diurnal species of lizards, especially skinks, are also captured. *V. gouldii* is cannibalistic and it also preys upon *V. brevicauda*, *Varanus caudolineatus* and *V. gilleni*. When a sleek, fast diurnal lizard like a skink is encountered, *V. gouldii* switches to visual

TABLE I   Mean head lengths of adult individuals of *Varanus* species from the Red Sands, Great Victoria Desert, Australia (Pianka, 1994)

Species	Head length (mm)
V. giganteus	120.9
V. gouldii	50.3
V. tristis	38.1
V. eremius	24.8
V. gilleni	24.5
V. brevicauda	14.0

hunting, lunging directly ahead to chase down and capture its prey. Very probably, these monitors will consume any other lizard that they can catch.

The largest monitor is the "perentie", *V. giganteus*. It forages over long distances, usually walking in a fairly straight line, hunting primarily by visual cues, although some prey are located by olfaction and dug up. Originally, their diet included small hare wallabies and other mid-sized marsupials, many of which have become extinct. Nowadays, perenties feed on other species of lizards (including *V. gouldii*) as well as introduced European rabbits. Several scats examined by Pianka contained large amounts of hair.

The six *Varanus* species that occur at the Red Sands site display an orderly, graduated progression of sizes (Table I). Interestingly, the two varanids most similar in size at this Great Victoria desert study site are *V. eremius*, which is strictly terrestrial and *V. gilleni*, which is semiarboreal. Head sizes of these two species are nearly the same, with a Hutchinsonian ratio of 1.01 (Fig. 1A). Coexistence of two species of the same size could be possible simply because one species is arboreal and the other is terrestrial. Size ratios among all other pairs of these sympatric species are equal to or greater than the critical minimum Hutchinsonian ratio of 1.3 (Fig. 1A; Pianka, 1994), and the size ratio is greatest between the two biggest species. Moreover, a null model analysis demonstrated significantly higher Hutchinsonian ratios among members of two real coexisting assemblages than was expected in random subsamples drawn from the species pool of all Australian varanids (Pianka, 1994). Such non-random size gradations suggest that size differences among species are necessary for coexistence (Schoener, 1984).
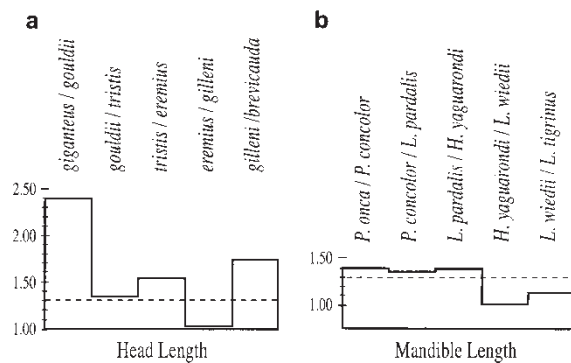

FIGURE 1 Length ratios based on heads or lower jaws (mandibles) for sympatric species in two hunting sets of carnivorous tetrapods. Each graph shows the ratio of the size of the larger species to that of the next smaller species; data from Tables I and II. Dashed lines in each graph show the minimum Hutchinsonian ratio deemed necessary for species coexistence (1.3). (a) Head lengths of *Varanus* lizards from the Red Sands study site, Great Victoria Desert, Australia. (b) Mandible lengths of Amazonian felids.

Crocodylians

Four crocodylian species (*Caiman crocodylus*, *Paleosuchus trigonatus*, *Paleosuchus palpebrosus* and *Melanosuchus niger*) occur in aquatic environments of the central Amazon basin (Magnusson, 1985; Magnusson, *et al.*, 1987). *M. niger* gets considerably bigger than the other species, which are similar in size. Although individual animals of these species do occur in the same habitats, the four species generally show distinct habitat segregation. *P. trigonatus* most commonly occurs in small streams that flow through dense tropical forest. *C. crocodilus* occupies lakes and large rivers, particularly those with shallowly sloping banks that are covered by mats of floating grass during seasons of high water. *M. niger* and *P. palpebrosus* are most common in bodies of water with steeply sloping banks that lack a mat cover of heavy floating grass. These differences in habitat affect the diets of the four species.

Two crocodylian species live along the northern fringe of Australia (Webb and Manolis, 1989). *Crocodylus porosus* occurs in a variety of habitats along the coast, in both saline and freshwater, while *C. johnstoni* is characteristic of more inland, freshwater habitats. In a transitional zone, both species can occur. Individuals of *C. porosus* occasionally wander well upstream into regions more typical of *C. johnstoni*, but individuals of the latter species seldom move downstream into the usual *C. porosus* habitat. There is a considerable size difference between adults of the two species. Male *C. porosus* generally reach total lengths of 4.6–5.2 m, and females 3.1–3.4 m; male *C. johnstoni* usually grow to about 2 m, and females to about 1.8 m. This should be a great enough difference to permit coexistence, but they are not commonly syntopic, probably because of the aggressiveness of *C. porosus* (Webb and Manolis, 1989).

Habitat partitioning of this kind seems to be the norm for sympatric crocodylian species: "Most crocodile habitats support only a single species, or, occasionally, a sympatric pair of species, but I know of no wild location where one could sit and expect to see three species in a day" (Ross, 2000, p. 1). Resource partitioning by occupation of separate habitats also seems to be common in many other groups of reptiles and amphibians (Toft, 1985).

Raptors

Schoener (1984) analyzed size ratios among the world's bird-eating hawks. Size ratios were computed among all possible pairs and triplets of the 47 species of short-winged *Accipiter* hawks. Schoener used wing lengths rather than beak lengths in his analysis. Frequency distributions of expected size ratios were generated for all possible

combinations of species. The resulting null model (Gotelli and Graves, 1996) was then compared with the much smaller number of *Accipiter* assemblages that are actually known to occur. Low size ratios were much less common among real than among hypothetical assemblages, strongly suggesting size assortment.

For more inclusive assemblages of birds of prey, segregation by habitat or time of foraging, as between diurnal hawks and nocturnal owls, seems to be important (Jaksic, 1985). However, such separation probably serves more to enable raptors to avoid agonistic interactions with members of other raptor species than to reduce exploitative competition for the same prey species.

Carnivorous Mammals

Mustelids kill using a canine bite, directed at the nape of the victim's neck. Consequently, canine diameter is thought to correlate closely with the size of the most common prey eaten by each species. Dayan *et al.* (1989a) and Dayan and Simberloff (1994) analyzed canine diameters among members of sympatric mustelid (in some cases viverrid) species in North America, the British Isles and Israel. Because these carnivorans show marked sexual dimorphism, males and females of each species were treated as separate morphospecies. Dayan and her colleagues demonstrated clear regularities in the size distribution of canine diameters of co-occurring morphospecies. These were interpreted in terms of "community-wide" (across the hunting set, in our usage) character displacement, serving to reduce competition for prey between sexes of a species and among species.

Canine teeth are less specialized for killing in canids, and sexual dimorphism is less pronounced in doglike predators than in mustelids. Dayan *et al.* (1989b; 1992) nonetheless observed regular size ratios among sympatric species of Israeli and Saharo-Arabian canids, using mixed sex samples of carnassial lengths across species. This too is suggestive of community-wide character displacement. In canid hunting sets throughout North America, Africa and Eurasia there are commonly three coexisting species: a large form (20 + kg) that specializes in killing ungulates, a medium-sized omnivorous species (10–20 kg), and a small, highly omnivorous species weighing less than 10 kg (Johnson *et al.*, 1996; Crabtree and Sheldon, 1999). Where two species are very similar in size and diet, there is often some habitat segregation between them (Johnson *et al.*, 1996).

East African jackals present an especially interesting instance of sympatry. Three species, *Canis adustus*, *C. aureus* and *C. mesomelas*, have overlapping geographic ranges (Fuller *et al.*, 1989; Wayne *et al.*, 1989; van Valkenburgh and Wayne, 1994). The three species are very similar in size. However, subtle differences in dental characters among these three jackal species suggest differences in emphasis between the slicing and grinding functions of the cheek teeth. These are related to differences in degree of omnivory as opposed to carnivory in the jackals' diets (van Valkenburgh and Wayne, 1994). Furthermore, the three species exhibit habitat differences, *C. mesomelas* preferring closed woodland, *C. aureus* grassland and *C. adustus* open *Euphorbia* woodland. The time of hunting activity also differs between *C. aureus* and its two congeners (Kruuk, 1972; Fuller *et al.*, 1989). Here, as in the case of *V. eremius* and *V. gilleni* in the Great Victoria Desert, and in that of Amazonian crocodylians, potential interspecific competition has been mitigated by differences in the locus of foraging.

However, separation of canid species on a landscape does not necessarily reflect habitat preferences. Partial spatial segregation of sympatric canids also results from avoidance of larger species by their smaller neighbors, as where coyotes avoid wolves (Crabtree and Sheldon, 1999).

During the Miocene, hyaenas took the role of doglike predators in Eurasia and Africa. Werdelin (1996) found evidence for "community-wide" character displacement among potentially coexisting hyaena species in the lengths of their lower carnassial teeth, analogous to results reported for Recent sympatric canids.

Kiltie (1984; 1988) recognized statistical regularities in the size distribution (ratio of larger/smaller species) of mandible lengths in tropical cat assemblages. Data for one of these are summarized in Table II. Interestingly, as in the Australian desert varanids (Fig. 1A), size ratios of the larger species pairs in this and other tropical felid hunting sets tend to be greater than those of smaller species pairs (Fig. 1B; Kiltie, 1988), and these ratios exceed Hutchinson's critical value of 1.3. However, *Herpailurus yaguarondi* and *Leopardus wiedii*, two of the smaller cats, have nearly identical jaw lengths. In this case, the latter species is more arboreal than the former (Sunquist and Sunquist, 2002), suggesting an interesting parallel with the relationship between

TABLE II   Mandible lengths of Amazonian felids

Species	Mandible length (mm)
Panthera onca	136.9
Puma concolor	98.1
Leopardus pardalis	71.7
Herpailurus yaguarondi	51.8
Leopardus wiedii	51.5
Leopardus tigrinus	45.3

Reported values are means of mean values for males and females of each species (Kiltie, 1988).

V. gilleni and *V. eremius* among the Australian desert monitor lizards.

Jaguar (*Panthera onca*) and puma (*Puma concolor*) theoretically differ enough in head size for coexistence (Fig. 1B), and they do occur in the same habitats (Emmons, 1987; Chinchilla, 1997). Even so, the two species differ in their intensity of use of those habitats. Jaguar prefer wetter, flatter areas, while puma are more abundant in drier, more irregular terrain. Along with differences in body size, this differential habitat use results in dietary differences between these two big cat species (Emmons, 1987; Chinchilla, 1997).

Dayan *et al.* (1990) did not observe even spacing of skull lengths in a hunting set ("guild" in their usage) of small Israeli cats. However, they did find (as in their earlier study of mustelids) size ratio regularities in canine diameters across felid morphospecies, treating males and females of each species as separate morphospecies. This is suggestive of community-wide ecological character displacement among members of the small felid hunting set. They also noted the possibility of habitat partitioning among the felid species in their study.

As with jackals, there is a case of possible geographic overlap of similarly sized species in large cats. Historically, the lion (*Panthera leo*) ranged across Africa, through the Arabian peninsula, and into the Balkans and central India (Nowak, 1991). During the Pleistocene its geographic range was even wider, including much of Europe and the Americas (Kurtén, 1968; Kurtén and Anderson, 1980). Asian lions persisted well into the 20th century (Heaney, 1943; Hatt, 1959; Harrington, 1977), but at present the species is extinct outside Africa, apart from a remnant population in the Gir Forest of Gujarat State, India (Prater, 1965; Joslin, 1984). Until recently, the geographic range of Asian lions would have overlapped that of the tiger, *Panthera tigris* (Kinnear, 1920; F.A. Khudsar, personal communication). Although information is largely anecdotal (e.g. hunters' accounts), Asian lions apparently occupied more open habitats than tigers in the area where their geographic ranges overlapped (Wynter-Blyth, 1949; Gee, 1964; Sankahla, 1978; F.A. Khudsar, personal communication). Thus, these two big cats of similar size, like the jackals already described, may have been largely non-syntopic. However, this may have been due in part to avoidance of lions by tigers, and not just different habitat preferences on the part of the two species (Sankahla, 1978).

Morphologically Diverse Mammalian Carnivore Guilds

The examples of extant predatory tetrapod assemblages surveyed thus far constitute hunting sets in our use of the term. We would expect size-related

ecological character displacement and associated Hutchinsonian ratios to be particularly distinctive in these examples.

If we now broaden our focus to consider more morphologically diverse carnivore guilds, including representatives of several distinct clades of meat-eaters, we can determine whether or not coexisting species still show regularity in size ratios between adjacent species in ranked size distributions.

This question can be addressed by comparing sizes of species in entire mammalian large-carnivore guilds (Table III), one from a tropical rainforest (Taman Negara, West Malaysia), and another (Serengeti-Mara, Kenya and Tanzania) from a dry savanna-woodland mosaic (van Valkenburgh, 1985; 1988). Species in these predator guilds include felids, canids, hyaenids, mustelids and viverrids. They differ in their hunting methods (ambush, pursuit, and digging for prey), diet (proportion of meat, bones, invertebrate prey and plant foods in the diet), and in some cases habitat (cf. Mills and Biggs, 1993). Habitat segregation reflects avoidance of some larger predator species by their smaller neighbors, as where African wild dogs avoid lions (Creel and Creel, 2002). It is not surprising to see that in most comparisons skull lengths do not differ by the expected 1.3 ratio (Figs. 2 and 3). Rosenzweig (1966) noted that size differences between species across different hunting sets do not necessarily result in

TABLE III Body sizes of species in two mammalian large-carnivore guilds

Species	Body mass (kg)	Skull length (mm)
Serengeti-Mara ecosystem, Kenya and Tanzania		
Panthera leo	179.9	257.0
Acinonyx jubatus	57.5	196.3
Crocuta crocuta	52.5	230.1
Panthera pardus	44.7	198.2
Hyaena hyaena	32.4	204.6
Lycaon pictus	21.9	185.4
Caracal caracal	16.6	110.9
Leptailurus serval	13.8	127.9
Civettictis civetta	10.7	138.6*
Mellivora capensis	10.0	125.6*
Canis adustus	7.6	141.0*
Canis mesomelas	7.3	140.9
Canis aureus	6.2	132.5*
Taman Negara, West Malaysia		
Panthera tigris	158.5	284.4
Panthera pardus	44.7	198.2
Neofelis nebulosa	20.0	164.8
Cuon alpinus	17.0	171.4
Catopuma temminckii	15.1	125.0
Arctictis binturong	10.5	147.4
Prionailurus viverrinus	8.9	129.4
Viverra megaspila	7.5	126.0*

For each guild, species are arranged in order of decreasing body mass (van Valkenburgh, 1985; 1988; van Valkenburgh and Ruff, 1987; Wayne *et al.*, 1989). Skull lengths measured by us are indicated with an asterisk. Measurements were made on available specimens, which did not necessarily come from Serengeti-Mara and Taman Negara—a possible limitation in the accuracy of our analysis.
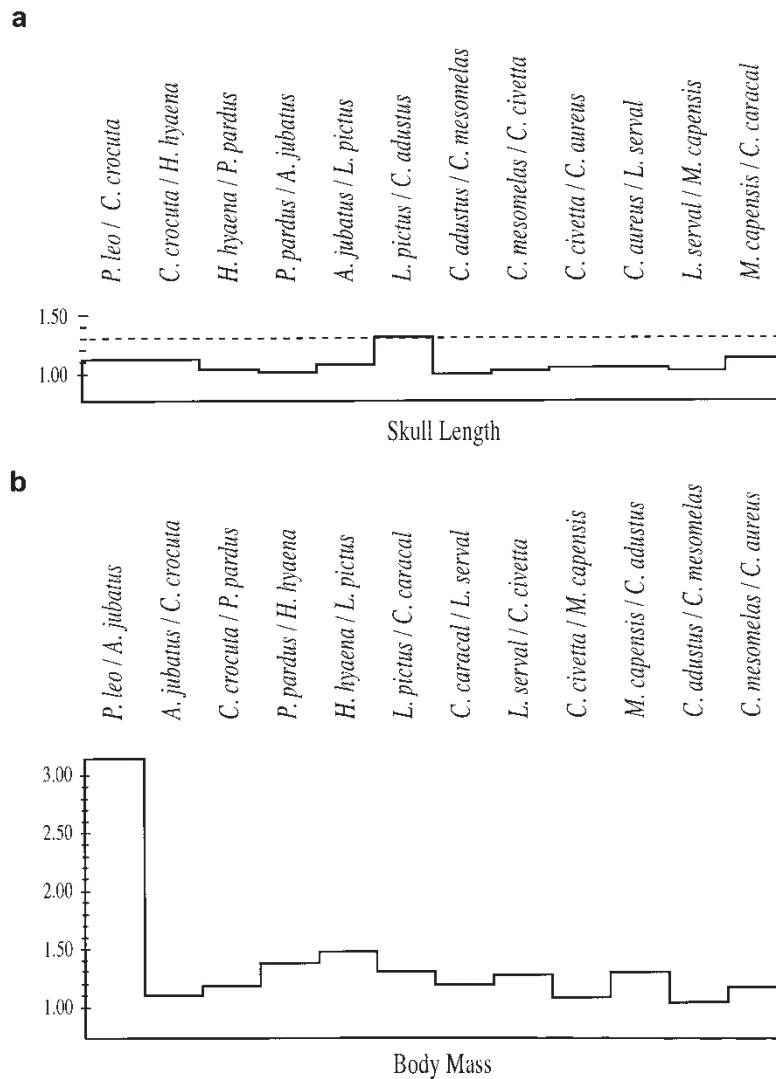
a

b

FIGURE 2 Size ratios of carnivorans from the Serengeti-Mara ecosystem, east Africa. Each graph shows the ratio of the size of the larger species to that of the next smaller species; data from Table III. Note that the rank order of species differs somewhat for the two size variables. (a) Skull lengths; dashed line indicates a Hutchinsonian ratio of 1.3. (b) Body mass.

differences in prey size. Most species of adjacent size in Table III are similar in body mass. However, note that the biggest species in both guilds are more different in size from the next smaller species than the remaining, smaller pairs of carnivoran species, a relationship which is analogous to that observed in our comparisons of head or mandible length in Australian varanids and Amazonian felids (Fig. 1).

If we restrict comparisons to a single hunting set that is well represented in both guilds (felids), skull length ratios of adjacent size pairs of species are closer to theoretical expectations (Fig. 4), but even here some cases require comment. Leopards (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) are similar in skull size, but they differ greatly in body proportions and hunting style. They also differ in habitat preferences. Cheetah prefer more open habitats than leopards (Schaller, 1972; Mills and Biggs, 1993). The Asian golden cat (*Catopuma temminckii*) occupies drier

habitats and hunts more terrestrial prey than the fishing cat (*Prionailurus viverrinus*) (Guggisberg, 1975; Nowak, 1991; Sunquist and Sunquist, 2002). The skull length ratio of leopards to clouded leopards (*Neofelis nebulosa*) is not quite 1.3, but these two cats differ considerably in body mass (Fig. 3B). The leopard generally hunts larger game and may be less arboreal than the clouded leopard (Guggisberg, 1975; Nowak, 1991; Sunquist and Sunquist, 2002). The caracal (*Caracal caracal*) prefers drier, more open situations than the serval (*Leptailurus serval*) (Guggisberg, 1975; Nowak, 1991). Thus, those sympatric felid species that are most similar in skull size do seem to be segregated on the basis of habitat.

Although the Serengeti-Mara ecosystem houses one of the highest-diversity large-carnivore faunas of the modern world, even this assemblage may be somewhat impoverished by extinctions. During the Plio-Pleistocene, east Africa was home to
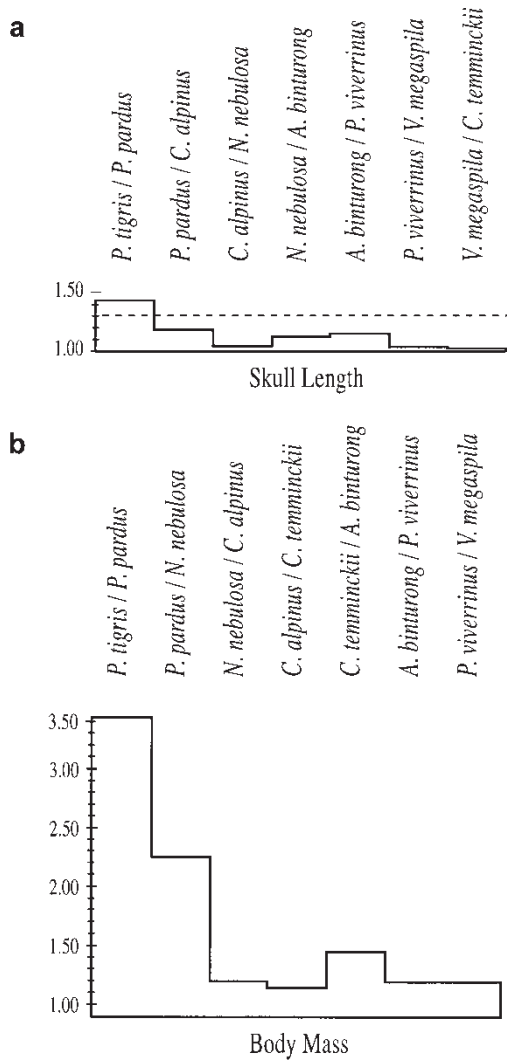
FIGURE 3 Size ratios of carnivorans from Taman Negara, West Malaysia. Each graph shows the ratio of the size of the larger species to that of the next smaller species; data from Table III. Note that the rank order of species differs somewhat for the two size variables. (a) Skull lengths; dashed line indicates a Hutchinsonian ratio of 1.3. (b) Body mass.

TABLE IV   Estimated body masses of large carnivore species in the Plio-Pleistocene of east Africa, excluding *Homo* (a possible hunter/scavenger)

Species	Body mass (kg)
Homotherium crenatidens	170
Panthera leo	170
Dinofelis sp.	150
Megantereon cultridens	95
Acinonyx jubatus	60
Crocuta crocuta	52
Panthera pardus	45
Hyaena brunnea	39
Hyaena hyaena	32
Canis sp.	30
Chasmoporthetes nitidula	21

The list does not include one or two additional species of *Panthera* and a bear that may have been present; data from van Valkenburgh (2001).

additional species of now-extinct carnivorans (van Valkenburgh, 2001; Table IV). Amongst these were sabercats (*Homotherium*, *Dinofelis*) that rivaled or exceeded the body mass of lions. Body mass ratios involving the biggest Plio-Pleistocene African cats were not larger than those of smaller-bodied carnivorans in the fauna (Fig. 5), unlike the pattern noted above for modern carnivoran guilds (Figs. 2 and 3). However, sabercats differed from lions in the jaw apparatus and overall body proportions, suggesting differences in killing style (Akersten, 1985; Biknevicius and van Valkenburgh, 1996; Biknevicius *et al.*, 1996; Bryant, 1996; Antón and Turner, 1997; Antón and Galobart, 1999). Whether or not these differences were related to differences in the kind of prey attacked, and whether or not there were habitat differences among the three biggest Plio-Pleistocene African carnivorans is unknown.
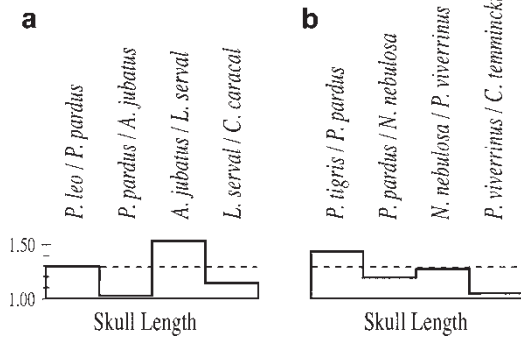

FIGURE 4   Ratios of skull lengths of felids from (a) the Serengeti-Mara ecosystem and (b) Taman Negara, West Malaysia. Each graph shows the ratio of the size of the larger species to that of the next smaller species; data from Table III. Dashed line indicates a Hutchinsonian ratio of 1.3.
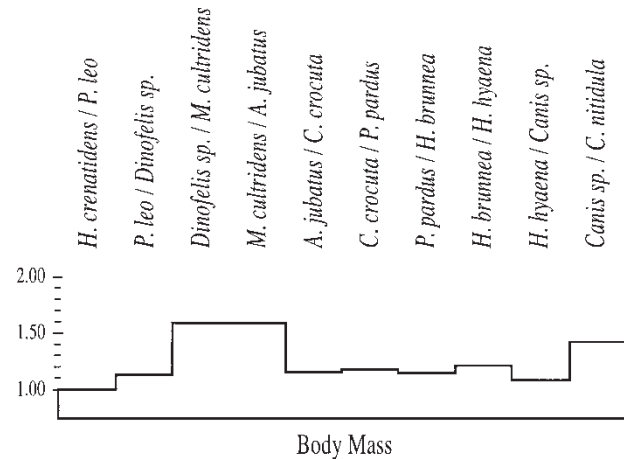
FIGURE 5   Ratios of estimated body masses of carnivorans from the Plio-Pleistocene of east Africa. The graph shows the ratio of the size of the larger species to that of the next smaller species; data from Table IV.

Conclusions about Carnivore Hunting Sets and Guilds

Several generalizations can be made, based on the preceding case studies of vertebrate carnivore hunting sets and guilds. (1) For morphologically similar carnivores, such as varanids, raptors, mustelids, modern (feline) felids or canids, species pairs coexisting in the same general habitat are separated by size, often with at least the 1.3-fold difference in head length between guild-members of adjacent size that was invoked by Hutchinson (1959). However, even when two morphologically similar species differ enough in size to theoretically permit coexistence in the same habitat, they may make differential use of distinct portions of those habitats, as in the case of jaguars and cougars. (2) Often, the biggest members of the hunting set or guild differ more from each other in the length of the feeding apparatus and/or body mass than do smaller members of the assemblage. (3) Where coexisting carnivores do not differ greatly in size, they show marked morphological differences related to prey handling, such as those which distinguish felids and canids, and possibly those of feline felids and sabercats. (4) Where sympatric carnivore species are very similar in size and morphology, they segregate themselves on the basis of habitat or microhabitat and/or geographic distribution, as in crocodylians, *V. gilleni* and *V. eremius*, jackals, and lions and tigers. Habitat segregation may be due either to different preferences of the species, or to avoidance of one predator species by another.

CARNIVOROUS DINOSAURS OF THE DINOSAUR PARK FORMATION

Composition of the Predatory Theropod Guild

During the late Campanian, western North America was a narrow appendage of Asia that has been called the Western American Peninsula (Lehman, 1997; 2001). The Western American Peninsula had a land area estimated at just under 8 million square kilometers (Lehman, 1997). It was at least intermittently in contact with Asia, and it shares several dinosaurian groups in common with eastern Asia, but Western American Peninsula dinosaur faunas are distinct from those of Asia at the species level. This suggests that a barrier prevented free exchange of animals between the Western American Peninsula and Asia (Le Loeuff, 1997; Carr and Williamson, 2000; Williamson and Carr, 2002). We therefore treat the Western American Peninsula as a separate landmass.

The late Campanian Dinosaur Park Formation of western Canada has yielded one of the best-preserved and most diverse dinosaur faunas in the world (Russell, 1967; Dodson, 1971; 1983; Eberth *et al.*, 2001; Ryan and Russell, 2001). As a result, this unit has figured prominently in efforts to reconstruct dinosaurian paleoecology (Dodson, 1971; 1983; Farlow, 1976; Russell, 1977; 1989; Béland and Russell, 1978; Brinkman, 1990; Baszio, 1997a; Brinkman *et al.*, 1998).

The Dinosaur Park Formation accumulated over only a few million years (Lehman, 1997), and its dinosaur species presumably coexisted in time. Some herbivorous species may not have lived in the same habitats (Brinkman, 1990; Brinkman *et al.*, 1998), but habitat segregation is not obvious from the taphonomic data, mainly shed teeth from micro-vertebrate sites, that are presently available for theropods. It is very likely that many of these carnivorous dinosaurs lived in close proximity.

At least 15 theropod species occur in the Dinosaur Park Formation (Eberth *et al.*, 2001; Ryan and Russell, 2001), representing several distinct clades. These dinosaurs may not all have been carnivores. Ornithomimids are small-headed, edentulous theropods that have variously been interpreted as consumers of small vertebrates and invertebrates, omnivores, herbivores, and even filter-feeders (Paul, 1988; Osmólska, 1997; Ryan and Vickaryous, 1997; Kobayashi *et al.*, 1999; Norell *et al.*, 2001). Since the three Dinosaur Park Formation ornithomimids (*Dromiceiomimus samueli*, *Ornithomimus edmontonensis*, and *Struthiomimus altus*) may not have been predators, they will not be considered further here. Therizinosaurs, represented in the Dinosaur Park Formation by cf. *Erlikosaurus*, are heavily built theropods whose morphology is reminiscent of that of prosauropods, suggesting that they were probably mainly herbivorous (Russell, 1997). So, these odd theropods will not receive further attention in this paper. Van Valkenburgh and Molnar (2002) excluded ornithomimids and therizinosaurs from their analysis of the Dinosaur Park (Judith River in their terminology) carnivorous theropod guild for similar reasons.

Oviraptorosaurs, represented in the Dinosaur Park Formation by *Chirostenotes* (*Caenagnathus*), were edentulous like ornithomimids, but with a stoutly built skull, so they are perhaps more likely than ornithomimids to have been carnivores (Ryan and Vickaryous, 1997). We include them in our analysis, but van Valkenburgh and Molnar (2002) did not include these dinosaurs in their study of Dinosaur Park predatory theropods.

Avimimus is yet another peculiar, toothless form (Norman, 1990; Currie, 2000). Little has been said about its likely diet. Although we suspect that it was no more likely than ornithomimids to have been a meat-eater, we have nothing firm upon which to base this notion, so we include it in our analysis.

Troodontids have a large claw on the hyperextensible second pedal digit and a manus designed for grasping, suggesting a carnivorous diet (cf. Ryan *et al.*, 2000). But, they also have fairly coarse tooth serrations like those seen on the teeth of presumed herbivorous dinosaurs. Conceivably these dinosaurs partook of plant matter as well as animal prey (Holtz *et al.*, 2000; Barrett, 2000), but we include them in our analysis. On the basis of theropod tooth assemblages, Fiorillo and Gangloff (2000) speculated that *Troodon formosus* may have been less characteristic of the Dinosaur Park region than of areas further to the north. If so, its geographic distribution, relative to that of other Dinosaur Park small theropods, may be analogous to that inferred by us for the two Dinosaur Park tyrannosaurids (see below).

The remaining theropod clades present in the Dinosaur Park Formation were unquestionably carnivores. The dromaeosaurids, *Dromaeosaurus* and *Saurornitholestes*, like troodontids, had a huge claw on the very flexible second digit of the foot, enlarged arms with grasping claws, and rather varanid-like teeth (Farlow and Holtz, 2002; Holtz, in press a). Tyrannosaurids, represented here by *Gorgosaurus* and *Daspletosaurus*, had absolutely and proportionally huge skulls with stout teeth (Farlow *et al.*, 1991; Holtz, in press a). Finally, one or more carnivorous small theropods of uncertain affinities, including *Richardoestesia*, are represented only by jaw fragments and isolated teeth (Currie *et al.*, 1990; Sankey *et al.*, 2002).

Before we proceed further, a brief comment on the nomenclature of one of the Dinosaur Park tyrannosaurids is necessary. Lambe (1914) named *Gorgosaurus libratus* on the basis of a beautiful skeleton from the Dinosaur Park Formation. However, Russell (1970) argued that *Gorgosaurus* was so similar to Osborn's (1905) previously named genus *Albertosaurus* that *Gorgosaurus* should be considered a junior synonym of *Albertosaurus*. Carr (1999 and pers. comm.) endorsed Russell's conclusions, on the grounds that phylogenetic analysis links Lambe's *G. libratus* and Osborn's *Albertosaurus sarcophagus* in a monophyletic *Albertosaurus* clade. Bakker *et al.* (1988); Currie (2000), and Holtz (2001, in press b), on the other hand, have resurrected *Gorgosaurus* for the Dinosaur Park species. We are neutral in this matter, but we will use *Gorgosaurus* rather than *Albertosaurus* here.

Head sizes and body masses can be estimated for some of the Dinosaur Park theropod species (Table V), although a note of caution must be inserted. For none of the dinosaur species does a large enough sample size of reasonably complete specimens exist to ascertain mean values. The discussion that follows necessarily assumes that those specimens for which estimates could be made are representative adults of their respective species.

There is an enormous gap in size between the two tyrannosaurids and the remaining members of the theropod assemblage (Fig. 6). This alone makes the theropod assemblage of the Dinosaur Park Formation very different from the carnivore hunting sets and guilds already discussed. Tyrannosaurids also differ markedly in morphology from the smaller Dinosaur Park theropods. Van Valkenburgh and Molnar (2002) characterized tyrannosaurids as "head-hunters" whose only significant organs for

TABLE V   Carnivorous dinosaurs from the Late Cretaceous Dinosaur Park Formation (modified from Eberth *et al.*, 2001; Ryan and Russell, 2001)

Taxon	Estimated body mass (kg)	Skull or lower jaw (LJ) length (mm)	Comments and sources of data
Gorgosaurus libratus	2500	1040	Skull length from Paul (1988); Christiansen (2000) estimated body mass of adults of this form at c. 1600 kg
Daspletosaurus sp.	c. 2300	c. 1040–1050	Assumed to be comparable in size to *D. torosus*; skull lengths from Russell (1970); Carr (1999)
Chirostenotes pergracilis (*Caenagnathus collinsi*)	50–75	208 (LJ)	Currie *et al.* (1993); a second species of the same genus, *C. elegans* (*C. sternbergi*), of about the same size may also be valid
Troodon formosus	50	c. 235?	Skull length estimated from model of reconstructed skull; Russell and Séguin (1982)
Dromaeosaurus albertensis	15	201	Skull length estimated from drawing (Colbert and Russell, 1969)
Avimimus sp.	22	c. 70?	Assumed to be comparable in size to *A. portentosus* (Paul, 1988); the estimated skull length is nearly a guess
Saurornitholestes langstoni	5	?	Sues (1978)
Richardoestesia gilmorei, R. isosceles, cf. *Paronychodon*	?	?	One or more small theropod species of uncertain affinities, based on teeth and/or jaw fragments (Currie *et al.*, 1990)

Ornithomimids and therizinosaurs are not included because these theropods are unlikely to have been predators (Russell, 1997; Norell *et al.*, 2001), but *Troodon*, which may have been omnivorous (Holtz *et al.*, 2000), is included. Skull or lower jaw lengths are based on particular specimens; see the cited studies for details. Body mass estimates from Paul (1988) or Seebacher (2001).
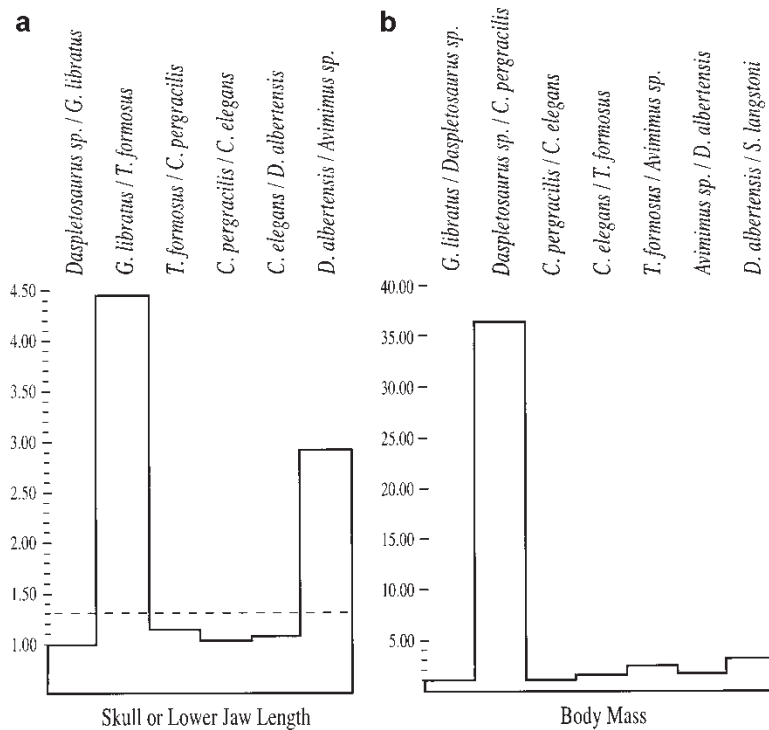
FIGURE 6 Size ratios of carnivorous theropods from the Dinosaur Park Formation. Each graph shows the ratio of the size of the larger species to that of the next smaller species; data from Table V. (a) Skull or lower jaw length; dashed line indicates a Hutchinsonian ratio of 1.3. (b) Body mass. Although *Gorgosaurus libratus* is treated here and in Table V as more massive than *Daspletosaurus* sp., individuals of the latter may have been more heavily built than *G. libratus* of comparable linear dimensions (Russell, 1970).

dispatching prey were their jaws, while at least some smaller theropods were "grappler/slashers" whose hands and feet assisted the jaws in killing their prey.

The data give no indication of regularly spaced size ratios, and among adjacent head size pairs of Dinosaur Park predatory theropods, most Hutchinsonian ratios are considerably less than 1.3. This last observation is partly explained by morphological diversity among the various clades of Dinosaur Park theropods, which is analogous to that seen in modern large mammalian carnivore guilds. As in the latter, this morphological diversity presumably permitted coexistence of species of comparable size.

However, some pairs of Dinosaur Park theropods undoubtedly were members of the same hunting sets. The two dromaeosaurids, *Dromaeosaurus albertensis* and *Saurornitholestes langstoni*, constitute one such pair. Although the skull length of *S. langstoni* is unknown, its estimated body mass is only 1/3 that of *D. albertensis*, suggesting that these dinosaur species differed enough in size to permit coexistence in the same habitat.

The two species of *Chirostenotes* (*Caenagnathus*) may be more problematic, if both species are in fact valid. They would be very similar in size.

However, the two largest members of the theropod fauna, *Gorgosaurus libratus* and *Daspletosaurus* sp., provide the biggest surprise. They do not differ dramatically in their feeding apparatus (Fig. 7).

Gorgosaurus and *Daspletosaurus* are not as different from each other in this respect as felids are from canids or hyaenids, or as sabercats are from feline cats. Nor do they differ in postcranial morphology. Consequently they must be considered members of the same hunting set. Nonetheless, they do not seem to differ significantly in skull length, assuming that skull length in *Daspletosaurus* sp. from the Dinosaur Park Formation was comparable to that of *D. torosus* (Table V), or in their postcranial dimensions. Femur lengths up to 1020 mm have been reported for *Daspletosaurus* and 1040 mm for *Gorgosaurus*
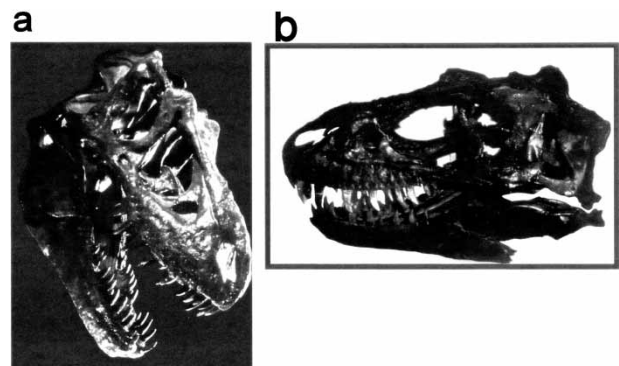

FIGURE 7 Skulls of late Campanian tyrannosaurids from western Canada. (a) *Daspletosaurus torosus* (Canadian Museum of Nature 8506; image reproduced with permission); skull length 1040 mm. (b) Immature individual (Carr, 1999) of *Gorgosaurus* (or *Albertosaurus*) *libratus* (Royal Ontario Museum 1247); skull length c. 750 mm.

(T. R. Holtz, Jr., pers. comm.). The adults of both species reached total body lengths of about 9 m (T.D. Carr and P.J. Currie, pers. comms.).

However, subtle morphological differences exist between the two species. *Daspletosaurus* was probably more heavily built than *Gorgosaurus* (Russell, 1970), but not enough so to result in a difference in body mass comparable to that between *Dromaeosaurus* and *Saurornitholestes*. This is surprising, given that these two tyrannosaurid species were the biggest members of the Dinosaur Park theropod guild. As noted above, the largest members of a hunting set or guild often show the greatest difference in size (Figs. 1, 2B and 3; Kiltie, 1988).

Henderson (2002) modeled the mechanical properties of skulls of various theropod dinosaurs. An immature individual of *G. libratus* had a "skull strength indicator" value about half that of an adult *Daspletosaurus torosus*, but Henderson (pers. comm.) suggests that skulls of equal length from the two species would have differed little in mechanical strength. On the other hand, *D. torosus* has a broader muzzle than *G. libratus*, which might indicate some feeding difference between the two genera.

Russell (1970) speculated that *Gorgosaurus* and *Daspletosaurus* may have concentrated on different kinds of prey, with *Gorgosaurus* preferring hadrosaurids, and the more massively built *Daspletosaurus* going after the presumably more dangerous ceratopsids. Tooth marks attributable to tyrannosaurids are much more common in hadrosaurid than ceratopsid bones (Jacobsen, 1997), but which tyrannosaurid was doing this biting is unknown. Perhaps more problematic for Russell's (1970) hypothesis, a specimen of *Daspletosaurus* from the Two Medicine Formation, which is coeval with and geographically adjacent to the Dinosaur Park Formation, preserves gut contents containing juvenile hadrosaurid bones (Varricchio, 2001). Also, a *Daspletosaurus* bonebed in Montana is associated with hadrosaurid bones (P.J. Currie, pers. comm.).

Habitat or Geographic Segregation of *Gorgosaurus* and *Daspletosaurus*?

By analogy with extant vertebrate predators, the similarity in shape and size of *Gorgosaurus* and *Daspletosaurus* suggests that these species usually did not coexist in the same habitat. We might suppose that the coastal setting in which the Dinosaur Park Formation accumulated was prime *Gorgosaurus* country, but marginal for *Daspletosaurus*. The relative abundance of the two species in the Dinosaur Park Formation is consistent with this hypothesis (Russell, 1970). *G. libratus* is presently known from 23 articulated or associated skeletons; *Daspletosaurus* sp. is known from only 7 skeletons (P. J. Currie pers. comm.). Furthermore, proportionately more juvenile

specimens of *Gorgosaurus* than young *Daspletosaurus* occur in the Dinosaur Park fauna (Russell, 1970; Béland and Russell, 1978; P.J. Currie pers. comm.), suggesting that *Gorgosaurus* commonly lived and nested in this area, but that *Daspletosaurus* did not do so.

Possibly the two tyrannosaurid species were geographically sympatric, but usually segregated by habitat, much like Amazonian crocodylians, jackals, and (on a smaller scale) *Varanus gilleni* and *V. eremius*. If so, the Dinosaur Park Formation accumulated in an area where more habitat existed for *Gorgosaurus* than for *Daspletosaurus*. However, because individual tyrannosaurids probably had very large home ranges (see below), it might have been difficult for populations of two tyrannosaurid species to find sufficient living space in patches of different habitat interspersed across the landscape (cf. van Valkenburgh and Molnar, 2002), particularly if the two tyrannosaurids had the space needs expected for carnivorous endotherms of the same body size.

A second possibility is that *G. libratus* and *Daspletosaurus* sp. were largely separated along a regional environmental gradient, albeit with some overlap, like the modern *Crocodylus porosus* and *C. johnstoni*. The most obvious potential gradient is distance from the Late Cretaceous seaway (cf. Brinkman *et al.*, 1998). Microfaunal data on the relative abundance of isolated teeth of different groups of herbivorous dinosaurs from the Dinosaur Provincial Park area show just this kind of environmental change, in that case associated with stratigraphic level (Brinkman *et al.*, 1998). Unfortunately, isolated tyrannosaurid teeth have so far not been identified to genus or species, so a comparable microfaunal data set is not available. However, skeletons of the two tyrannosaurid species known at present from Dinosaur Provincial Park do not occur at distinct stratigraphic levels. For six *Daspletosaurus* specimens from fossil quarries for which the elevation (meters above sea level) has been determined, elevations range 655–695 m (mean = 672.7 m); for 11 *Gorgosaurus* specimens, the elevations range 648–710 m (mean = 670.3 m) (P.J. Currie, pers. comm.).

Still further inland than the Dinosaur Park region was the coeval, neighboring environment represented by the Two Medicine Formation, where *Daspletosaurus* or a very similar form is known to occur (Horner, 1984; Horner *et al.*, 2001; Trexler, 2001). This suggests the possibility of a larger scale segregation of the two tyrannosaurids between formations, with *Daspletosaurus* dominant in the Two Medicine Formation, and *Gorgosaurus* in the Dinosaur Park Formation. However, even if the common Two Medicine tyrannosaurid is *Daspletosaurus*, it may not be the same species as its

Dinosaur Park congener (see below). Furthermore, two skeletons of *Gorgosaurus* and a *Gorgosaurus* bonebed have recently been found in the Two Medicine Formation (P.J. Currie, pers. comm.), indicating that *Gorgosaurus* may have been more common in that unit than first thought.

Failure to detect differences in relative abundance of the two tyrannosaurids, stratigraphically within the Dinosaur Park Formation, or between it and the Two Medicine Formation, may only reflect the very small sample size of large theropod skeletons, in contrast to the huge sample of ornithischian microfossils. However, for now there is no evidence that *Gorgosaurus* and *Daspletosaurus* were separated along a coastal-inland environmental gradient.

If the source of Dinosaur Park daspletosaurs was not a more inland setting in the same geographic region, these dinosaurs could have been strays from an adjacent biogeographic province. Late Campanian provinciality is hypothesized for herbivorous dinosaur taxa of western North America (Lehman, 1997; 2001). Carr and Williamson (2000) and T. D. Carr (pers. comm.) concluded that provinciality and/or habitat segregation also characterizes the distribution of late Campanian tyrannosaurids. There are at least two contemporary species of *Daspletosaurus*: one from the Dinosaur Park Formation and a second from the Two Medicine Formation. If *Daspletosaurus torosus* itself, from the slightly older Oldman Formation of the Dinosaur Park area, is specifically distinct from other members of the genus, and if it persisted somewhere in western North America after Oldman time, there would be yet a third contemporaneous *Daspletosaurus* species. Carr and Williamson (2000) assigned a new tyrannosaurid species from the Kirtland Formation of New Mexico to *Daspletosaurus*, but they now think that it represents a new genus (T.D. Carr, pers. comm.).

Holtz (in press b) combined the conclusions of these authors, proposing that albertosaurines like *Gorgosaurus*, along with lambeosaurines and centrosaurines among late Campanian herbivorous dinosaurs, were characteristic of a more northerly regional dinosaur fauna, while tyrannosaurines like *Daspletosaurus* were members of a more southerly fauna that also included hadrosaurines and chasmosaurines. We might therefore predict that the home range of the Dinosaur Park *Daspletosaurus* species will turn out to be south of Alberta, but north of New Mexico. The occurrence of *Daspletosaurus* along with *Gorgosaurus* in the Dinosaur Park Formation would then be analogous to the zone of geographic overlap in the historic distribution of lions and tigers, which were largely allopatric but occurred together in India.

If late Campanian tyrannosaurids did in fact show as much habitat specificity and/or geographic provinciality as is suggested here, this raises other questions about the paleoecology of these gigantic predators.

Gigantism, Habitat or Geographic Segregation, and Macroecology of Late Campanian Tyrannosaurids

The two Dinosaur Park tyrannosaurid species have skull lengths 5–10 times greater than *Varanus giganteus* or the biggest felids, and in life the tyrannosaurids were an order of magnitude or more bigger in body mass. Individual large animals require a great deal of habitat space (Owen-Smith, 1988; Brown, 1995; Calder, 2000; Kelt and van Vuren, 2001), and this constraint is particularly demanding for large endotherms and big carnivores (Flannery, 1991; Diamond, 1991; Farlow, 1993; McNab, 1994; Farlow *et al.*, 1995; Buskirk, 1999; Craighead *et al.*, 1999; Burness *et al.*, 2001; Carbone and Gittleman, 2002).

Consequently, the living-space requirements of truly enormous carnivores like tyrannosaurids should be mind-boggling. Farlow (2001) used regression equations linking size of home range to body mass in extant predatory lizards, birds and mammals (Peters, 1983) to extrapolate the home range needed by a single 2500-kg carnivorous dinosaur. If such an animal had the space needs of a huge meat-eating lizard, its home range might have covered hundreds of square kilometers; if it required as much space as a gigantic carnivorous mammal, its home range could have encompassed tens of thousands of square kilometers.

Although some overlap in home ranges of individual animals is inevitable, particularly if home ranges are large, only so many animals can be packed into a given area without degradation of their resource base. Coupled with the fact that an individual's living-space needs increase with increasing body mass, this means that population density (number of animals/area) must decrease with increasing body size (cf. Owen-Smith, 1988; Damuth, 1993; Ebenman *et al.*, 1995; Silva and Downing, 1995; Carbone and Gittleman, 2002). At the same time, however, animal species must maintain population sizes above some minimum number of individuals to avoid extinction (Calder, 2000). Consequently, species of very large animals can survive over long periods of time only on large landmasses (Marquet and Taper, 1998). Moreover, because of their higher metabolic rates, endothermic species require larger landmasses than ectothermic species of the same body mass to garner sufficient food to support their populations (McNab, 1994; 2002; Burness *et al.*, 2001). Similarly, because the biomass of animal prey is much lower than that of plant forage available in a given area, carnivore species will require larger landmasses to survive
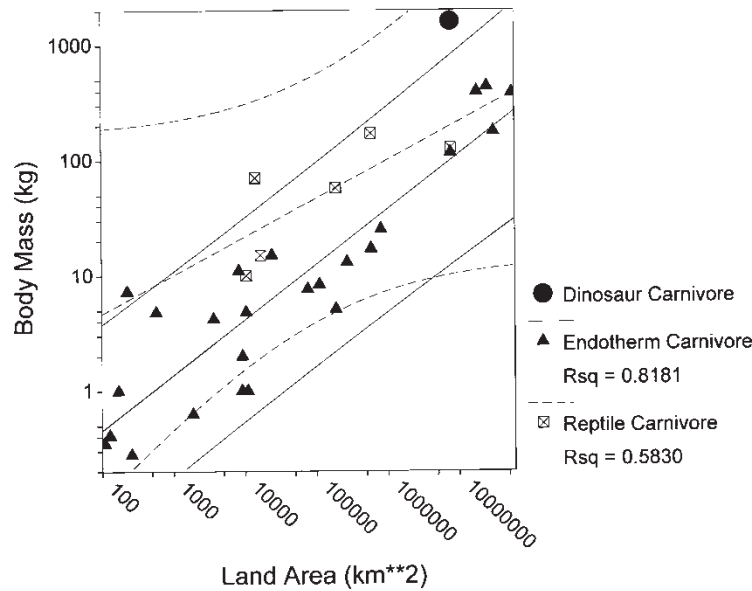
FIGURE 8 Body masses of the biggest species of carnivores (mammals, birds, and reptiles) on landmasses of a given area; data from Burness *et al.* (2001) with modifications from Wroe (2002). Regression lines and 95% individual prediction intervals are drawn for pooled Quaternary predatory birds and mammals ("endotherm carnivores"): $\log(\text{body mass}) = 0.479 \times \log(\text{land area}) - 1.300$; $r = 0.904$, $p < 0.001$, $n = 25$); and for Quaternary reptiles: $\log(\text{body mass}) = 0.333 \times \log(\text{land area}) + 0.372$; $r = 0.764$, $p = 0.077$, $n = 6$). Mass in kg, land area in km^2. The "dinosaur carnivore" point is for the late Campanian of the Western American Peninsula. It assumes the average mass of the largest tyrannosaurid species was about 1600 kg (Christiansen, 2000), unlike Fig. 6, where larger tyrannosaurid body masses were used (Table V). The smaller mass was used here so that any bias arising from different estimates of mass would act against the interpretation of tyrannosaurid metabolic physiology developed in the present paper. The land area of the Western American Peninsula is estimated at $7,671,000 \text{ km}^2$ (Lehman, 1997); the portion of Cretaceous Asia that may have been attached to the Western American Peninsula is disregarded for reasons discussed in the text. The tyrannosaurid point is outside the 95% prediction interval for the carnivorous endotherm regression line, but within the 95% prediction interval for the carnivorous reptile regression line. However, note the small sample size and high p value [>0.05] associated with the reptile equation.

than herbivore species of the same body mass (Farlow, 1993; Farlow *et al.*, 1995; Burness *et al.*, 2001).

Late Campanian tyrannosaurids of the Western American Peninsula are inconsistent with expectations based on the land area: body size relationship of predatory endotherms (Fig. 8). Even using a low estimate of adult body mass for *G. libratus* (Table V), and ignoring the possibility that individuals of *Daspletosaurus* were heavier than individuals of *Gorgosaurus* of the same linear dimensions, tyrannosaurids lie outside the 95% individual prediction interval for the expected body mass of an endothermic carnivore living on a landmass the size of the Western American Peninsula. Tyrannosaurids also plot above the regression line for carnivorous reptiles (cf. results of Burness *et al.*, 2001 for other large carnivorous dinosaurs), but within the 95% prediction interval associated with this line. However, this interpretation must be regarded as tentative on account of the small sample on which the reptile regression is based (Fig. 8).

A caveat must be noted, here. We excluded the portion of Asia to which the Western American Peninsula was at least occasionally attached from our estimate of landmass size, on the grounds that Asia and the Western American Peninsula had no dinosaur species in common. Thus, we assumed that Asia was unavailable as living space for Western

American Peninsula tyrannosaurids. Should this prove not to have been the case, we have greatly underestimated the land area potentially accessible to these huge predators. However, even if the exclusion of Asia from our analysis is unwarranted, another aspect of the distribution of Western American Peninsula tyrannosaurids suggests that these carnivores did in fact support themselves on surprisingly small geographic ranges.

As already noted, there may have been four or five species of these very big carnivorous dinosaurs living in the late Campanian of the Western American Peninsula. If tyrannosaurid species showed as much habitat specificity and/or provinciality as is suggested by the body size overlap between *G. libratus* and *Daspletosaurus* sp., implying ecological segregation at some spatial scale, and by recent systematic and biogeographic studies of tyrannosaurids, it follows that individual species of these gigantic predators were able to maintain viable populations on only portions of the landmass. Reconciling this with the hypothesis that these dinosaurs had metabolic rates comparable to those of extant birds and mammals is difficult. Indeed, it is hard enough to see how tyrannosaurids could have maintained populations large enough to ensure long-term viability, in particular habitats and/or geographic regions within the Western American

Peninsula, if they had metabolic rates and associated living-space requirements closer to expectations based on extant ectotherms.

Comparisons with other Theropod Faunas

Molnar (1978) illustrated a hunting set of four theropod taxa from the late Maastrichtian Hell Creek Formation: *Tyrannosaurus rex* (skull length c. 1371 mm), *Albertosaurus lancensis* (skull length c. 648 mm), the Jordan theropod, *Aublysodon* cf. *A. mirandus* (skull length very speculatively estimated at about 368 mm), and an unknown number of small theropod species roughly comparable in size to *Saurornithoides mongoliensis* (skull length c. 183 mm), which does not itself occur in the Hell Creek Formation. Molnar thought that a fifth form, intermediate in size between the Jordan theropod and the small species equivalent in size to *Saurornithoides* may also have been present.

Limiting consideration to the four skull sizes illustrated by Molnar, all six Hutchinsonian ratios are considerably greater than the minimal estimate of limiting similarity of 1.3. However, the animal Molnar (1978) called *Albertosaurus lancensis*, which was assigned to the new genus, *Nanotyrannus* by Bakker *et al.* (1988), could be a juvenile *T. rex* (Carr, 1999; Brochu, 2002). The Jordan theropod, called *Aublysodon molnaris* by Paul (1988), but placed in its own genus, *Stygivenator* by Olshevsky *et al.* (1995), may be an even earlier ontogenetic stage of *T. rex* (Holtz, 2001; in press b). If these putative species are immature individuals of *T. rex*, the overlap in skull sizes among adults of Hell Creek theropod species would be further reduced.

Unlike the Dinosaur Park Formation, which has two very large theropod species, the Hell Creek Formation has only *T. rex*. Any explanation for this difference is necessarily speculative. Possibly only one tyrannosaurid lineage survived into the late Maastrichtian, in western North America, for reasons unrelated to interspecific competition. Alternatively, the difference in number of tyrannosaurids may reflect the lower diversity of herbivorous dinosaurs in the Hell Creek, compared with the Dinosaur Park Formation (P.J. Currie, pers. comm.).

However, *T. rex* attained a body mass up to three times greater than those of the two Dinosaur Park tyrannosaurids (cf. Christiansen, 2000; Seebacher, 2001). Given the lower population density and greater required habitat space expected for *T. rex*, compared with the presumed requirements of *G. libratus* and *Daspletosaurus* sp., there may not have been sufficient ecological "space" for more than one tyrannosaurid species in the late Maastrichtian of western North America.

The Dinosaur Park and Hell Creek theropod guilds are representative of a distinct kind of predatory dinosaur assemblage (Foster *et al.*, 2001; Farlow and Holtz, 2002) that existed during the Late Cretaceous in western North America and in eastern and central Asia. These theropod guilds include a variety of small-bodied carnivore species, but only one or two very large species, which are always tyrannosaurids. In contrast, another kind of theropod guild characterizes Jurassic and Cretaceous dinosaur faunas over much of the world. These assemblages include considerable diversity of large-bodied theropods, representing several evolutionary lineages.

A good example of this other kind of theropod guild comes from the Late Jurassic Morrison Formation of the western United States. The Morrison has yielded nine (or more—depending on whose taxonomy one accepts) genera of theropods (Foster *et al.*, 2001; Foster and Chure, 2000). The Morrison dinosaur fauna changed in composition over time, but many theropod genera existed during the same time interval (Turner and Peterson, 1999). Indeed, a half-dozen or more theropod species can be found in the same fossil quarry (Miller *et al.*, 1991; 1996; Foster *et al.*, 2001).

Henderson (2000) analyzed shape differences between the skulls of two large Morrison theropods, *Ceratosaurus nasicornis* and *Allosaurus fragilis*, that overlap considerably in body size. In the latter species, he recognized two morphs, a typical *Allosaurus* form and an "*Antrodemus*" morph. The three morphs differ in their skull height/length, skull width/length, and maxillary tooth length/skull length ratios, as well as in other morphological features. Henderson suggested that these differences in shape might have translated into differences in dietary preference between *Allosaurus* and *Ceratosaurus* that would have permitted the coexistence of these big predators.

However, subsequent work indicated that the "*Antrodemus*" morph was based on an improperly mounted specimen (D.M. Henderson, pers. comm.). It actually falls within the range of morphological variation of normal *A. fragilis* (Smith, 1998). Furthermore, the differences in shape between skulls of *Allosaurus* and *Ceratosaurus* are not as marked as those between coexisting mammalian carnivores of very similar body size, such as canids and felids, or even sabercats and feline cats (van Valkenburgh and Molnar, 2002). Cranial shape differences between *Allosaurus* and *Ceratosaurus* may not have sufficed to permit coexistence of these taxa. On average, adult *Ceratosaurus* were smaller (van Valkenburgh and Molnar, 2002; J. R. Foster pers. comm.) than adult *Allosaurus*, however, and this presumably reduced dietary overlap.

Just as *Gorgosaurus* is numerically dominant in the Dinosaur Park Formation, so is *Allosaurus* in the Morrison Formation. *Allosaurus* (most specimens are

A. fragilis) comprises 60–70% of all Morrison theropod specimens (Henderson, 2000; Foster and Chure, 2000). By analogy with our hypothesis that *Daspletosaurus* was not routinely resident in the Dinosaur Park community, we suggest that *Ceratosaurus* and other rare large theropods of the Morrison (*Torvosaurus*, *Saurophaganx*) may not have been habitual residents of that geographic region, or they may not have frequented the same habitats as *Allosaurus*.

However, *Ceratosaurus* occurs together with *Allosaurus*, as skeletons and shed teeth, at a number of Morrison sites (Evanoff and Carpenter, 1998; J. R. Foster pers. comm.), so this taxon, at least, may indeed have been sympatric with *Allosaurus*. If *Ceratosaurus* was too similar to *Allosaurus* in size and morphology for complete syntopy, perhaps it occupied a different spectrum of less abundant Morrison habitats than *Allosaurus*. Bakker (1996) hypothesized that ceratosaurs and megalosaurs were characteristic of Morrison Formation habitats with wetter soils and denser vegetation, while allosaurs were typical of drier, more open habitats.

The apparent problem of housing viable populations of huge predators in different kinds of habitat that we have discussed in regard to the Dinosaur Park fauna presumably applies to that of the Morrison Formation as well (van Valkenburgh and Molnar, 2002). However, the problem might be partly mitigated if the per-animal space needs of large theropods in the Morrison fauna were less than would be expected for huge predatory endotherms, as we have suggested for the Dinosaur Park tyrannosaurids.

For theropod assemblages in general (including those of the Dinosaur Park and the Morrison Formation), van Valkenburgh and Molnar (2002) determined that species richness of theropod guilds often equals or exceeds that of modern predatory mammal guilds. They were surprised by these results, given the greater morphological similarity of the potentially co-occurring theropods, compared with carnivoran species, as well as the greater average body sizes of the theropods. They noted that "it is not unusual to find two or three similar-sized species of theropod in the same paleofauna that do not differ markedly in their locomotor or feeding anatomy. This contrasts with carnivoran guilds where similar-sized sympatric species usually do differ in either locomotor or feeding behavior" (van Valkenburgh and Molnar, 2002, p. 541). These authors doubted that such "over-packing" of predatory species could have occurred unless theropods had lower metabolic requirements than mammals. Lower trophic needs of ectothermic large carnivores would have permitted greater morphological overlap of coexisting forms than expected for large endothermic carnivores.

Although this conclusion is consistent with our speculations about large-theropod energetics, the fact that coexisting desert varanids show no more Hutchinsonian overlap than do carnivorans (Figs. 1–4) causes us to doubt that ectothermy itself necessarily allows tighter species packing of carnivores in the same habitat. The difference in living space required by ectotherms and endotherms suggests an alternative hypothesis. Ectothermy permits very large carnivores to subdivide landscapes more finely than would be possible for endothermic carnivores of equivalent body size. Allowing viable populations of huge predators to exist in relatively small geographic areas, ectothermy may enable species of big, morphologically similar carnivores to reduce competition by habitat partitioning. Huge carnivores that seldom occupied the same habitats or local areas would nonetheless be distributed fairly closely together on the landscape. Occasional wanderings of stray individuals of one species into regions routinely occupied by another, or taphonomic transport of carcasses, could then cause a diverse assemblage of huge predator species to share a common tomb in the same geologic formation.

Suggestions for Future Research

Our hypothesis that the two Dinosaur Park tyrannosaurid species were largely non-syntopic and/or non-sympatric is based largely on theoretical ecology, but it is potentially testable by paleontological data. Articulated specimens of tyrannosaurids are—unsurprisingly for such large predators—not abundant in the Dinosaur Park Formation, but isolated teeth are found considerably more often. Although criteria for identification of shed teeth of Dinosaur Park small theropods have been developed (Currie *et al.*, 1990), tyrannosaurid teeth have not been identified below the family level in microfaunal studies that have hitherto been undertaken (Dodson, 1983; Brinkman, 1990; Baszio, 1997b). While studying theropod tooth morphology (Farlow *et al.*, 1991), Farlow examined lateral teeth *in situ* in the jaws of *Gorgosaurus* and *Daspletosaurus*, recognizing subtle differences between the two genera. In *Gorgosaurus*, the proximal (basal) end of the mesial (anterior) serration carina makes a sharp lingual bend toward the inside of the base of the tooth, while in *Daspletosaurus* the base of the mesial serration carina does not curve so strongly in a medial direction. In addition, *Daspletosaurus* teeth often have tiny crescent-shaped ridges, perpendicular to the distal (posterior) serration carina, especially on the lingual side of the tooth. *Gorgosaurus* teeth do not have these ridges.

Using these criteria, tyrannosaurid lateral teeth in microfaunal assemblages of the Dinosaur Park

Formation and other late Campanian faunas could be identified at the genus level. If *Gorgosaurus* and *Daspletosaurus* lived in the same region, but in different habitats, this should be reflected by differences in the relative abundance of the two tooth types in contrasting sedimentary facies of the Dinosaur Park Formation. If instead the two tyrannosaurid species were segregated on a larger, regional or biogeographic scale, the two tooth forms should differ in relative abundance across coeval formations, as Fiorillo and Gangloff (2000) have shown for small theropods.

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