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THE DEPRESSION OF REPTILE BIOMASS BY LARGE HERBIVORES

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I hypothesize that a large biomass of large wild herbivores in a habitat should severely depress the biomass of reptiles in that habitat. This is based on two somewhat distinct kinds of predation on reptiles by carnivorous birds and mammals, and, more indirectly, on two kinds of habitat modification by large herbivores. Habitat modification will receive little attention here because there is virtually no information on it in the current literature. Below, I first deal briefly with the hypothesized patterns and processes and then examine the African predator-prey literature for natural history information which suggests that these hypotheses are reasonable. I have been unable to locate any data to test directly the hypotheses that reptile density is lowered in the presence of large herbivores or that, if it is, the large herbivores are the cause. These hypotheses were prompted by the observation that, to me, Kenya, Uganda, and Cameroun reptile biomass appears much lower than that in comparable habitats in the neotropics.

HYPOTHESES ABOUT CARNIVORES

a) Specialized predators on reptiles, such as mongooses, small cats, secretary birds, and snake eagles, should be able to turn to carrion from large herbivore kills (and, occasionally, direct kills) during times when their usual prey is absent. Additionally, insects feeding on herbivore carcasses and dung may be usual prey for some of these predators. The availability of this food should mean that the specialists at dealing with reptiles will constitute a more omnipresent predator pressure the more abundant large herbivorous mammals are in time and space.

b) Predators that feed frequently on large herbivore kills and the carrion from them, such as jackals, hyenas, man, eagles, and vultures, may take reptiles as incidental food items throughout their lives. They should do this more frequently when large herbivores are scarce or when an individual has been excluded from its organized social unit, such as a pride of lions. The larger the biomass of herbivores in the habitat, the larger should be the biomass of such carnivores and the greater should be their incidental depressant impact on the reptile biomass.

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HYPOTHESES ABOUT HERBIVORES

a) Through intensive grazing, browsing, and trampling, especially near watercourses during severe dry seasons, large herbivores should greatly reduce the cover available for reptiles, the small vertebrate prey of snakes, and the insects available to reptiles.

b) To the degree that large herbivores maintain fire-susceptible grasslands, they may be viewed as partially responsible for the fires that annually reduce the cover for reptiles and kill many.

For all four causal relationships postulated above, the data of interest are not usually gathered by those who observe the participants. For example, those studying reptile specialists, such as snake eagles, focus on their more spectacular prey and on what is brought to the young, rather than on the role of carrion in adult survival during bad seasons or years. Those watching big carnivores focus on large and major prey items and on healthy predators in active social units. Biologists studying grazing and fire usually examine the consequences for plants and big mammals. My intent is to stimulate observation for a potentially dramatic side effect of processes that have been under scrutiny for many years.

For my purposes, there are three major types of data to seek in the literature. First, we need to know whether natural history observations suggest that carnivores behave in the manner postulated above; if they do not, then the suggested causal relationship can be summarily discarded. Second, we need to know whether the reptile biomass is indeed much lower where large herbivore biomass is extraordinarily high; if there is no suggestion of this, we need not worry about the first class of data, no matter what it suggests. Third, we need to know whether the reptile fauna of habitats rich in large herbivores displays traits suggesting exceptionally intense predator pressure. I will examine each of these in turn. I have chosen to focus on African animals for my baseline reference points because of the obvious value of Africa in a comparison such as that drawn in this paper.

CARNIVORES

Specialists on Reptiles

Do the carnivores thought to feed commonly on reptiles (and other small animals) take carrion from, and make fresh kills of, large herbivores? Especially, do they do it when their "regular" prey is scarce? The literature contains a few tantalizing bits of information on the former question and only one on the latter. Smeenk (1974) notes that "feeding on carrion [by tawny eagles (*Aquila rapax*)] seemed confined to the long dry season, when mortality among ungulates normally is heaviest." In the same study he recorded 10%–31% of the individual prey items at tawny eagle nests to be snakes, and 20%–40% to be live-caught ungulates.

Africa south of the Sahara contains at least four species of mustelids, three of

civets, seven of genets, and 17 of mongooses that are highly omnivorous and eat reptiles (Bourliere 1963; Dorst and Dandelot 1969; F. W. Fitzsimons 1919; V. F. W. Fitzsimons 1962; Hinton and Dunn 1967; Taylor 1969). While I expect a starving mustelid or viverrid to take carrion from big game, there are few records. The honey badger (*Mellivora capensis*) "is a deadly foe to snakes of all kinds. Their fangs cannot penetrate the leathern armour which completely encases it, nor, having regard to the easy fit of this covering, is it likely that even its perforation would be attended by any ill aftereffects. Consciously secure, therefore, the ratel [honey badger] does not hesitate to follow the justly dreaded mamba into the ant bear hole in which it has taken refuge, drag it out, and devour it with an air of supreme unconcern" (Stevenson-Hamilton 1947). Ewer (1973) reports one killing a 10-ft python. However, the honey badger occasionally eats "young and smaller antelopes, and also probably eats carrion" (Dorst and Dandelot 1969; see also color plate on p. 1507 of the *Encyclopedia of the Animal World* [1972] for a honey badger eating carrion). Stevenson-Hamilton (1947) describes the honey badger as a carrion eater, and Indian honey badgers apparently feed regularly on large animal carcasses (Brander 1934, 1936; Champion 1936; Hurst 1935; Toogood 1936). Indian mongooses have been recorded to eat fish carrion (Fernando 1913). Prater (1936) says that the Indian common mongoose (*Herpestes edwardsi*) eats rodents, reptiles, insects, and any other small animal, and that "it will eat carrion and is frequently seen feeding on the kills of large carnivores." African *Civetta civetta* eat lizards and frogs, and "carrion is eaten freely and they often come to leopard and other 'kill' in the absence of the rightful owners" (Stevenson-Hamilton 1947). African genets (*Genetta ludia*) eat snakes and lizards and are "also partial to carrion . . . and sometimes are caught in the large gins set at 'kills' for hyenas and leopards"; the slender mongoose *Gallerella canni* eats reptiles, including mambas, and carrion (Stevenson-Hamilton 1947). Zumpt (in Ewer 1973) reports the yellow mongoose (*Cynictus*) scavenging from carcasses, and Ewer (1973) says the white-tailed mongoose (*Ichneumia albicauda*) "searches the roads for the remains of traffic casualties."

Mustelid and viverrid populations are also aided indirectly by large herbivores. In Uganda, at least during the dry season, the common social banded mongoose (*Mungos mungo*) appears to feed primarily on dung beetles (Scarabaeidae) and millipedes found in elephant and buffalo dung, for which it searches carefully (Neal 1970). There is no way with the data at hand to know whether they are catching insects, eating carrion, or both, at large carcasses. M. Coe informs me that they can overnight clean a carcass of its dermestid population, and the ground around old carcasses is often littered with insect remains. I have watched a marabou stork catching flies on a hartebeast carcass in Nairobi National Park; yet it *appeared* to be taking carrion. Whatever the case with the mongooses, the effect on the reptiles should be the same whether the mongooses are eating carrion or the insects that feed on it.

Before leaving these small carnivores, I should note that some of them may be acting toward reptiles much as do the large carnivores. For example, Hinton and Dunn (1967), Neal (1970), and others stress that mongooses eat a large

number of insects. Perhaps mongooses should be regarded as highly oppor-
tunistic specialized predators on reptiles, predators whose activity will increase
when reptiles are locally abundant or when insects are scarce (which is, in-
cidentally, the dry season and most difficult time of year for lizards). Indeed,
Taylor (1969) observed of *Genetta* and *Herpestes* in Kenya that "while insects
form the major part of the diet during the rains, more rodents, insectivores and
reptiles are eaten during the drier seasons" (based on analysis of gut contents).
Incidentally, mongooses prey enough upon snakes that they have developed
considerable resistance to the venom of the slower cobras but not to the much
faster vipers (Grasset et al. 1935; Pillai 1960).

Hedgehogs are generally thought of as omnivorous, and Hinton and Dunn
(1967) mention in passing that "one of the favorite foods of the [African]
hedgehog is the viper" and that hedgehogs certainly eat frogs, lizards, and
snakes. Krishna and Prakash (1956) record captive Indian hedgehogs eating
live snakes. No mention is made of carrion eating, but, like the mongooses, a
starving hedgehog is unlikely to pass up the opportunity to forage for insects
and carrion in an ungulate carcass.

Small cats are generally thought of as predators on small birds and mammals.
This is probably due to their nocturnal habits and a shortage of reptilian prey
(see below) rather than to avoidance of reptiles. Stevenson-Hamilton (1947)
says of his pet *Felis ocreata cafra* that "he was very quick with snakes, and I
have often seen him consuming the remains of a night adder and such smaller
species in the early morning. Retribution eventually befell him, however, in
the jaws of a large python." Denis (1964) says the same of a semitame *Felis
libyca*. Fitzsimons (1919) describes his tame South African cat as a "standard
snake eater" and tells how it captured a puff adder. Broadley (1959) records a
3-ft *Calamelaps unicolor* (Colubridae) that was killed by a cat in southern
Rhodesia. Ewer (1968) notes that the serval cat (*Felis serval*) has a specialized
snake-killing technique in that "the snake's head was crushed by a downward
slapping blow of the outspread forepaw, delivered with quite surprising violence.
If, as sometimes happened, the first slap missed its mark, the blow was so hard
that the serval sometimes hurt its paw." Fitzsimons (1962) was of the opinion
that South African house cats probably eat as many snakes as do mongooses,
and Millet (1954) records a Siamese house cat that killed many snakes. Schaller
(1967) records the Indian jungle cat as eating lizards, and Vick (1930) records
a house cat killing an Indian cobra.

The secretary bird (*Sagittarius serpentarius*) is perhaps the most renowned of
the African reptile-eating raptors (Brown 1970; Fitzsimons 1962; Pitman 1935).
However, as Brown and Amadon (1968), Smeenk (1974), Pitman (1935),
Broadley (1974), and others emphasize, it feeds largely on lizards, rodents, and
insects. I suspect that the reason that it does not eat larger numbers of snakes
is because they are very scarce (see below) rather than because they avoid them.
Whatever the case, secretary birds "collect dead small mammals and insects
burned in grass fires" (Brown and Amadon 1968). While these authors state
that the secretary bird "does not eat carrion of large animals," Brown's studies
of secretary bird biology (1952, 1955) are too vague to substantiate this opinion.

Wright (1960) says equally vaguely that "the secretary bird has been observed to kill young Thomson's gazelles" and lists it as one of those predators and scavengers "in East Africa obviously obtaining a large part of their diet from large herbivores."

The African bateleur eagle (*Tetrathopius ecaudatus*) "is in all ways the most specialized of the Old World snake hawks" (Brown and Amadon 1968), is adept at stealing food from others (Brown 1970), "is largely a scavenger and carrion feeder" (Brown and Amadon 1968), and "becomes the commonest of all birds of prey in Kruger Park" (Brown 1970). However, it is also an active predator on snakes, lizards, and tortoises (Brown 1970; Smeenk 1974; Brown and Amadon 1968; Fitzsimons 1962; Broadley 1974; Pitman 1935; Steyn 1965, 1974). Stevenson-Hamilton (1947) says of the bateleur that "its favorite food seems to consist of reptiles and carrion. I have often noticed it coming down to kills with the vultures." Houston (1972) concludes that carrion is an important food for bateleur adults, but Snelling (1969) lists carrion as low in the prey recorded at nests (see later comments on food of nestling marabou storks).

If we examine only the prey brought to the nest, the African brown snake eagle (*Circaetus cinereus*) and other snake eagles are undoubtedly among the major threats to snakes in eastern and southern Africa. Steyn (1972, 1974) estimates over 90% of the prey to be reptilian and records 26 large snakes and one large varanid lizard brought into a Rhodesian nest. Broadley (1974) adds more snakes and a lizard to this list. However, adult snake eagles may also be taking carrion as alternate food, food that is inadequate for growth of juveniles owing to a lack of calcium and other nutrients found in whole prey. While it might be thought that such extreme specialists may not take carrion, even the rock hyrax specialist *Aquila verreauxi* (black eagle), which brings up to 100% hyraxes to the nest, may take carrion as adult food (Steyn 1974). Even the fish eagle (*Haliaetus vocifer*) has been recorded feeding on a dead rhino along with vultures (Steyn 1974). Steyn (1972) says that "there is an interesting record by Jackson . . . who saw a [snake eagle] in the early morning . . . at the carcass of a wild cat *Felis lybica* which was a road casualty." Brown (1963) also mentions that, in addition to snakes and lizards, brown snake eagles feed on mammals, but he is not explicit as to whether they are at carrion or fresh kills.

The kites (*Milvus* spp.), both migrant and resident in Africa, are well known for their carrion scavenging and food-stealing behavior (Brown 1970; Brown and Amadon 1968; Guggisberg 1963; Blondel 1967; Houston 1972; Lack 1946; Mackworth-Praed and Grant 1952; Stevenson-Hamilton 1947). Estes and Goddard (1967) describes kites as regularly encountered at wild dog kills, and in Tanzania one "successfully stole small pieces from the dogs by swooping, grabbing and mounting again to eat on the wing." Houston (1972) records kites as feeding at carcasses along with vultures. In addition, all but the last two authors list *Milvus milvus* and *M. migrans* as major predators on snakes and lizards.

Brown (1970) lists 36 species of diurnal African raptors as regularly taking lizards and snakes as prey, and Broadley (1974) lists lizard and snake prey for 38 species. Of the 62 diurnal African raptors (including migrants) discussed by

Mackworth-Praed and Grant (1952), 47% are recorded as snake and lizard eaters. However, such figures only tell us that African reptiles have a large number of species of avian predators. The data do not distinguish between what is fed to the young and what the adults eat and, even more important, never focus on what might be termed "starvation food" or on carrion as food. I suspect that close observation of the larger species would produce many records of the following type recorded for a North American northern red-shouldered hawk (*Buteo lineatus*), which is a regular reptile eater: in midwinter in Connecticut, Bent (1937) says that one "found a skinned deer's neck and a dead opossum, and it fed on the opossum every day for about two weeks."

Hawk and eagle biologists appear to have a strong aversion to recording in detail what adult birds are eating; references to carrion feeding are generally stuck on as an afterthought, as though it is of no importance to a bird or its prey. The same problem occurs with nonraptor reptile eaters, such as the southwestern U.S. roadrunner (*Geococcyx californianus* [see Sutton 1940; Bryant 1916]) and the African ground hornbills (Bucerotidae). "The birds are partly scavengers and also prey on small reptiles and snakes" in Uganda (Elliott 1967). African ground hornbills *Bucorvus cafer* eat snakes and tortoises (Pitman 1928, 1935; Stevenson-Hamilton 1947), and Kilham (1956) describes a casqued hornbill (*Bycanistes subcylindricus*) killing a lizard in Uganda. Broadley (1974) lists a number of snakes and lizards as prey of African hornbills. Hornbills other than African ground hornbills are generally frugivores (Moreau 1936, 1937), but Lowther (1942) shows an adult Indian hornbill (*Tockus birostris*) with a lizard in its beak, apparently using it to "entice young to leave the nest." On the other hand, corvids are well known to visit carcasses for carrion (e.g., Estes and Goddard 1967; Rowley and Vestjens 1973), but their reptile-catching abilities appear to be unexamined except for Broadley's (1974) records of snakes and lizards taken as prey and Barbault's (1973) mention of *Corvus albus* as a lizard predator in the Ivory Coast.

All of the above anecdotal information leads me to conclude that African animals that regularly take reptiles as prey also feed from carrion or fresh kills of large herbivores. Not even anecdotal information is available to determine how important the large herbivore food items are in maintaining these reptile eaters at a higher density than would be the case were they forced to survive only on small prey. However, it is logical that large herbivore food items would have this effect.

Specialists on Large Herbivores

Do the carnivores that seem to feed primarily on carrion and fresh kills of large herbivores also take reptiles? If they do, the African habitat, rich in large herbivores, certainly seems to support enough of them to have an effect on the reptile biomass; for example, Bourliere (1963) lists 25 species of mammalian carnivores in the Serengeti, all of which are potential consumers of carrion and of reptiles. Ewer (1973), in answer to her question "What do the Carnivora eat?"

says, "What they can get." A major difficulty with these questions is that it is commonplace to determine the food of large carnivores by locating them at their kill rather than by examining gut contents or feces. Small food items are likely to go unnoticed (Ewer 1973); Kruuk (1972) says that "when one hyena is eating a small Thomson's gazelle fawn, it may take less than two minutes for the victim to disappear completely, eaten in utter silence." How long would a lizard or small snake last? A second major sampling problem is that studies of large carnivores have been concerned almost entirely with healthy animals in stable social circumstances (e.g., Estes and Goddard 1967; Kruuk 1972; Schaller 1972). Sick, aged, juvenile, crippled, and socially outcast animals may take many more small prey items than would members of well-organized hunting groups such as a wild dog pack.

The healthy African lion (*Panthera leo*) clearly obtains most of its food from big herbivore carcasses and kills (Schaller 1972). However, Schaller (1972), Kruuk and Turner (1967), and Guggisberg (1963) all emphasize that lions are scavengers, and there are observations suggesting that they take reptiles when the opportunity arises. Stevenson-Hamilton (1947) says that "lions are quite partial to fish" and "will kill and eat pythons, and I have actually seen a lion in the act of consuming one of these large snakes." Guggisberg (1963) reports that "in the Kruger Park a lion was seen approaching a python which immediately attacked him. He cleverly avoided the attack, and when the snake once more went for him, he in turn jumped forward and almost bit it in two. He then ate part of the giant snake." Dorst and Dandelot (1969) list crocodiles and snakes among lion food items. Schaller (1972) describes unsuccessful attacks by lions on a leopard tortoise and a 3-ft-long monitor lizard, and says that when a lioness met a spitting cobra "she held her head down low and repeatedly sprang forward and recoiled with a 'woof.'. . . After doing this several times she withdrew, followed by a litter of several small cubs."

Lions that are not part of well-organized hunting prides may take more reptiles than do the group hunters. Stevenson-Hamilton (1947) describes four lion cubs trying to catch a large monitor lizard (which apparently avoided them by mimicking a snake with its long tail). If small lizards were readily available, lion cubs would probably hunt them. Guggisberg (1963) says solitary old lions forced to hunt alone supplement their diet with cane rats, porcupines, etc.; it seems unlikely they would pass up a reptile. Forced out of the pride, subadult males are probably in the same category. For a hint of what solitary lions may be eating, note that the Indian tiger preys "on whatever animals it can catch, including birds, reptiles, amphibians, fish, and even some invertebrates, but mammals—in particular hoofed ones—make up the bulk of its diet" (Schaller 1967). He then summarizes a literature that states that tigers eat turtles, crocodiles, lizards, snakes, and frogs. Tigers are not resistant to cobra venom (Editors 1925).

As leopards (*Panthera pardus*) are solitary hunters, their diets are little known. Leopards eat all sorts of small mammals and birds, in addition to large herbivores (Kruuk and Turner 1967; Stevenson-Hamilton 1947), and there is no

obvious reason why they would pass up reptiles. Kruuk and Turner (1967) list a python as leopard prey, and Dorst and Dandelot (1969) list tortoises as leopard food items.

There are no records of cheetahs (*Acinonyx jubatus*) taking reptilian prey (e.g., Graham 1966; Kruuk and Turner 1967; Schaller 1968), but there are so few long-term observations on their detailed hunting behavior that the possibility remains open. Graham (1966) says that they take mole rats and hares as prey and cautions that "animals such as hares would be eaten more rapidly by a cheetah and are consequently more likely to escape observation than larger kills. Small animals may therefore comprise a greater part of a cheetah's diet than generally recorded."

Spotted hyenas (*Crocuta crocuta*) are major predators (Kruuk 1972), but they are highly omnivorous scavengers as well. Kruuk (1972) records a puff adder (*Bitis arietans*) as prey and says they catch fish, tortoises, and pythons. Stevenson-Hamilton (1947) records a brown hyena (*Hyaena brunnea*) den containing a half-eaten boomslang. Kruuk (1972) says, "I am informed by East African residents that the diet of the solitary hyena (*Hyaena vulgaris*) contains many small creatures, even dung beetles, apart from what is scavenged from kills." As mentioned earlier, a hyena (and probably all the other large carnivores) can eat small prey items in a few seconds; thus the smaller reptiles are unlikely to be noticed. Hyenas are also prime examples of animals that, when foraging on their own, are likely to subsist on much smaller prey than are regularly taken by the pack.

African wild dogs (*Lycaon pictus*) have not been recorded to take reptiles, and the impression one gets from the literature is that they are specialists on large game (Estes and Goddard 1967; Kruuk and Turner 1967; Van Lawick–Goodall and Van Lawick–Goodall 1971; Wright 1960). However, Estes and Goddard (1967) state that "at this stage, when the hunt has started but before any common objective had been determined, individuals might forage for themselves. The observer would suddenly notice that a dog was carrying part of a gazelle fawn or a young hare (*Lepus capensis*) that must have been simply grabbed as it lay in concealment. Once during a moonlight hunt . . . individual dogs were seen to pick up at least two gazelle fawns and one springhare (*Pedetes surdaster*), a strictly nocturnal rodent, within one-half hour. Concealed small game such as this is apparently not hunted by the pack in concert." As stressed at the beginning of this section, these dogs may be taking reptiles in the same manner. There are even records of Asian dogs specializing at killing snakes (Wall 1906).

Of all the large mammals that commonly feed on big herbivore carrion and fresh fawn kills (Wright 1960; Wyman 1967), jackals are probably the most active predators on reptiles. In a description of a golden jackal (*Canis aureus*) killing and eating a large striped sandsnake (Van Lawick–Goodall and Van Lawick–Goodall 1971, fig. 9), the author says "at that time I believed that encounters between jackals and snakes would be rarely observed, but soon I found that snakes form a normal part of a jackal's diet." She even comments that jackals can distinguish poisonous from harmless snakes, killing the former

before eating them. A black-backed jackal (*Canis mesomelas*) was recorded as having eaten python (Stevenson-Hamilton 1947). In two surveys of Transvaal jackal gut contents, reptiles were recorded in 20 out of 563 jackals; the reptiles included five lizards, three small tortoises, and one young night adder (Grafton 1965), "two tortoises (*Psammobates*) and several unidentified specimens of Scincidae and Lacertidae (lizards), and some blind burrowing snakes (Typhlopidae). One stomach contained a small monitor lizard *Varanus exenthematicus albigularis*. Other stomachs contained some snakes, including a night adder *Causus rhombeatus*" (Bothma 1971). Schaller (1967) says of Indian jackals that "the remains of reptiles, most frequently lizards, were surprisingly prevalent in the feces"; of 119 droppings of Indian jackals, 29% contained lizard and snake remains (Schaller 1970). There is no way of knowing whether these reptiles were dead or alive when harvested. The relatively small number of Transvaal stomachs containing reptiles could suggest either that reptiles are scarce to the jackal or that they are of low preference. In addition to direct prey, large herbivores provide large amounts of food for *C. aureus* and *C. mesomelas* in the form of beetles in ungulate dung (Wyman 1967).

While the details of reptile predation by humans are poorly documented in tropical Africa, it obviously occurs (e.g., Wall 1906), and humans certainly are sustained in part by large herbivores. "Snake-eating in Uganda appears to be confined to the Bwamba of the northern Ruwenzori region. The members of this tribe eat any kind of reptile" (Pitman 1935). Pythons and gaboon vipers are highly marketable food items in Cameroun and Nigeria. Owing to their highly sedentary nature and generally protein-limited status, native peoples are probably severe predators on reptiles during times of shortage of other game. This is particularly relevant in view of the recent stress that anthropologists have been placing on the role of wild animal protein in limiting the density of subsistence agriculturalists (Gross 1974).

It is unclear how essential meat from small- to medium-sized herbivores is to chimpanzees (*Pan troglodytes*), but they do take bushpig, bushbuck, monkeys, and smaller mammals as prey (Goodall 1963, 1965; Van Lawick–Goodall 1965). From the way observations are made on these primates, small reptiles could easily be eaten without being recorded, and Van Lawick–Goodall (1965) says that "previously, scientists believed that chimpanzees were almost exclusively herbivorous, only rarely indulging in a rodent or a lizard."

Baboons clearly take small animals as prey. Strum (1975*a*, 1975*b*) and Dart (1963) give numerous cases of baboons hunting and killing reedbuck, duiker, birds, sheep, pigs, fawns of Thomson's gazelle, dikdik, steinbok, and impala (see Wright 1960). There is a good deal of local variation in the degree of big game hunting by baboons, and Dart (1963) observes that "the flesh protein needs" of South African baboons "may be met in some places adequately by the prevalence of insects, reptiles, rodents and other microfauna during that season." Hall (1962) notes that "it is reported by reliable observers in Southwest Africa that the baboons (*Papio ursinus*) catch and eat two of the common species of back-fanged sandsnake. . . . Snakes of this genus are immediately avoided by the baboons in the Cape, as has been observed by us from close

range on two occasions" (see also Hall 1963). Baboon predation on reptiles obviously contains a large learning component, and we can expect it to vary with the amount of innocuous reptile biomass in the region. Hall (1962) observes that a baboon (*Papio ursinus*) in captivity for 3 yr rejected live *Leptotyphlops*, two species of *Mabuya*, and one of *Eremias*, but a fresh-caught wild one ate a 25-cm *Leptotyphlops scutifrons* and bit the head off a lizard before letting it fall. In Uganda, Rowell (1966) recorded that *Papio anubis* occasionally caught and ate lizards, and "on six occasions, hares (*Lepus capensis*) were coursed by baboons after being flushed in open grass, and on four of these they were successfully caught and eaten" for a catch rate of one every 30 h. Altmann and Altmann (1970) record *Papio* as catching lizards but rejecting the opportunity to attack a large varanid (*Varanus niloticus*). Isemonger (1962) said of animals stranded when the Kariba Dam flooded the Zambesi that "starvation amongst baboons, monkeys and several other smaller mammals that had been stranded for a particularly long time, forced them to overcome their natural fear of snakes in such a desperate situation and they actually ate them, entirely or partially." Such carnivory probably did not require as great a change in behavior as Isemonger suggests. Even patas monkeys (*Erythrocebus patas*) eat *Agama agama* lizards in Uganda (Hall 1966). Field primatologists in Uganda state that some species of arboreal monkeys eat lizards when encountered (W. J. Freeland, P. Wasser, and R. Rudran, personal communication).

Wild suids have a wide reputation for eating reptiles, but their predatory and necrophagous behavior toward other herbivores is unknown. Johnson (1972) reports two wild Indian *Sus scrofa* eating the hindquarters of a moribund cow, and "wild boars are known to kill the newborn of the black-buck and the spotted deer." Dorst and Dandelot (1969) record bushpigs (*Potamochoerus porcus*) eating reptiles and carrion.

Adult marabou storks (*Leptoptilos crumeniferus*) are common scavengers on meat from large herbivore carcasses in East Africa (Pomeroy 1973; Kahl 1966). However, it is very significant for this discussion that they have to feed their nestlings a large number of entire small animals to provide calcium and other nutrients not found in meat (Kahl 1966). The large numbers of reptiles and other small animals brought to nestlings of raptorial birds may likewise not represent the adult diet; carrion may play a larger role in the diet of adults than appears to be the case when the bird's food is ascertained by what is brought to the nest.

While a number of species of vultures clearly feed primarily on carrion from big game (Attwell 1963; Houston 1974; Kruuk 1967), "vultures sometimes caught lizards and rats" (Kruuk 1967). Attwell (1963) records white-headed vultures (*Trigonoceps occipitalis*) catching frogs, a 14-ft python (*Python sebae*), and a 30-inch puff adder (*Bitis arietans*). Broadley (1974) records a python being killed by vultures in Kafue National Park, Rhodesia, and the hooded vulture *Neophron monachus* as taking small reptiles. Kruuk (1967) suspects that the "lappet-faced and white-headed vultures might take to killing for themselves." Brown (1970) records lammergeiers (*Gypaetus barbatus*) as primarily bone and carrion eaters but comments that "on Mruruanisigar in Turkana [northwestern

Kenya], my brother has seen a [lammergeier] carrying a monitor lizard, which was probably alive when taken." The problem with knowing whether vultures are predators on reptiles is that, as Houston (1974) points out, prey records are based on watching vultures descend to large carcasses and then observing them. What do they bring to the nestlings (see above discussion of marabou storks), and if it is sometimes small animals (including reptiles?), where do they catch them? Houston (1972) notes that a captive *Gyps africanus* chick died after 3 wk without a calcium supplement to a meat diet. Adults, however, need not catch small animals for calcium, as they selectively eat bone fragments (Grubh 1973).

The large eagles appear to pick up an even mix of birds, mammals, carrion, and reptiles. The tawny eagle (*Aquila rapax*) takes live mammals up to the size of lambs and calves (Brown 1963, 1970; Smeenk 1974; Stevenson-Hamilton 1947; Snelling 1969; Steyn 1973), feeds on big to medium-sized herbivore carcasses (Attwell 1963; Smeenk 1974; Brown 1970; Steyn 1972, 1973, 1974), and occasionally eats snakes and lizards (Brown 1970; Steyn 1974); Steyn (1973, 1974) says that, in addition to bringing mammals and birds to the nest, a tawny eagle brought in two puff adders (*Bitis arietans*), one *Causus rhombeatus*, one cobra, one *Varanus*, and 11 unidentified snakes. Broadley (1974) lists a boomslang and lizards as prey of the tawny eagle, and Smeenk (1974) found reptiles to constitute 10%–31% of the individual items brought to tawny eagle nests. Snelling (1969) says that the tawny eagle brings much more ungulate carrion to the nest than does the bateleur. Smeenk (1974) says that "when in Tsavo part of a larger prey is left behind by any predator, a tawny eagle or Bateleur is most likely to be the first scavenger on the scene." The martial eagle (*Polemaetus bellicosus*) takes live dikdiks, young antelopes, duikers, steenbok, and other similar-sized mammals (Brown 1970; Stevenson-Hamilton 1947; Smeenk 1974; Wright 1960), carrion (Brown 1970; Smeenk 1974; Wright 1960), and occasionally reptiles (Smeenk 1974; Brown 1970). Broadley (1974) records it taking varanid lizards and a cobra, and Snelling (1969) found its principal prey in Kruger National Park to be *Varanus*. Stevenson-Hamilton (1947) says "I shot one which was eating a large monitor lizard, and I put another up from the newly killed body of a big puff adder." The crowned hawk eagle (*Stephanoaetus coronatus*) is a predator and scavenger on large mammals (Brown 1970; Steyn 1974; Wright 1960), but Brown (1970) also states that they occasionally take reptiles.

REPTILE DENSITY

I have been unable to locate any habitat-wide quantitative censuses of reptile density or biomass conducted in comparable areas with widely differing biomasses of large wild herbivores and their accompanying carnivores. However, during recent fieldwork in Kenya (dry season, February 2–9, 1974), I saw not a single lizard or snake, and only one turtle, in about 1,000 miles of rural roads and 4 days of close scrutiny of four national parks, ranging from 3,000 to 10,000 ft elevation and from open grassland to deciduous thorn forest and

its contained riparian forest to evergreen forest (Mount Kenya, Samburu, Nairobi, and Nankuru Parks). I was not, however, expressly searching for reptiles but, rather, for animals in general. Covering similar terrain and vegetation during the dry season in Mexico, Costa Rica, Colombia, or Venezuela, I would have seen hundreds of lizards and some snakes with the same type of searching, and probably many more had I been looking as intensely for animals as I was in Kenya. The relatively low density observed in Kenya could be a large sample error, but I doubt it. Arnold Kluge (personal communication), an experienced herpetologist, remembers seeing extraordinarily few reptiles on his trip to East Africa, and James Karr (personal communication) noticed the same during ornithological surveys in Kenya.

Inspired by this observation, I decided to census reptiles during later field-work in Costa Rica, Uganda, and Cameroun during the 1974 rainy season. In all three countries I simply recorded the number of reptiles encountered per hour of nonraining fieldwork. I was careful not to search deliberately for them (or, if I did, to keep separate records) and not to count those pointed out by others. All sites were forested or semiforested and well away from villages (see Discussion section for reptile densities in villages). Road kills were not counted. In Costa Rica at three sites (Palo Verde, Guanacaste Province, 20 m elevation; Monteverde, Puntarenas Province, 1,600 m elevation; Finca Las Cruces, San Vito de Java, Puntarenas Province, 1,200 m elevation), I averaged 1.23, 0.38, and 2.07 lizards per hour (August 2–28, total of 66 h, average of 1.33/h). A total of six snakes were seen. During this same time period, I saw 13 large mammals, including seven monkeys. In Uganda, in the Kibale forest and its edges (near Fort Portal, 1,300 m elevation), and Ishasha, Queen Elizabeth National Park (900 m elevation), I averaged 0.08 and 0.06 lizards per hour (October 21–27, total of 55 h, average of 0.07/h). No snakes were seen. During this same period, I saw a minimum of 50 large mammals at Kibale and at least 1,000 at Ishasha. In Cameroun, in the forest around Lake Tissongo (southwest of Edéa, 50 m elevation), I averaged 0.1 lizard per hour (October 28–November 1, total 52 h) and found one snake. African records in Edéa and around houses were dramatically different and are discussed in a later section. Counting road kills, a total of eight mustelids or viverrids were seen in the Kibale forest area and 14 Carnivora that take reptiles were seen at Ishasha. One such mammal was seen at the Costa Rican sites. All the reptile biomass seen at the two African sites would not begin to add up to even one of the large iguanid lizards at the first-mentioned Costa Rican site.

I was able to locate only one other statement comparing African and neo-tropical reptilian biomass. Karr (1975) states that in Panamanian forests he has "been impressed by the abundances of lizards of a wide variety of sizes" and that "many of the hawks seem to specialize in feeding on these and other reptiles; by contrast, lizards seem less abundant and less diverse in African forest, and to my knowledge no forest hawk specializes on reptiles."

In contrast with these African records, the Australian reptile fauna is not only very rich in species (Pianka [1973] and references therein), but zoologists frequently comment on the very high density of reptiles in Australia (A. Kluge,

W. Freeland, personal communications). The absence of a large biomass of large herbivores, and especially their accompanying wild carnivores and scavengers, in Australian habitats needs no comment. Pianka (1973) concludes that "one reason the Australian deserts support such very rich lizard communities may be that competition with, and perhaps predation pressures from, snakes, birds, and mammals are reduced on that continent."

Rather than contrast numbers or absolute biomass of reptiles between the African and Central American tropics, we may ask what proportion of the vertebrate biomass is reptilian in these areas. Western (1974) estimates that reptile biomass in a highly seasonal site in northwestern Kenya (south Turkana) is 10%–15% of that of the large herbivores; no similar studies are available for Central or South America, but my personal sightings of large herbivores suggest to me that the figures would be reversed or much worse. In a total of some 7 yr of fieldwork in Central America, I have seen a total of about 26 large terrestrial wild herbivores (tapir, peccary, brocket deer, and white-tailed deer).

Perhaps the most thorough examination of reptile biomass in an African habitat is Barbault's (1967, 1973) study of the reptiles of lightly wooded savanna and adjacent riparian forest at Lamto, Ivory Coast. He records lizard numbers and biomass (1–56/hectare over the seasonal cycle, 2–240 g/hectare over the seasonal cycle) that appear to be similar to those found in Central American dry areas of similar physiognomy. However, there are virtually no large herbivores in the study area, their having been removed 30–40 yr before (Lamotte 1975). Barbault (1973) says that carnivorous mammals are too scarce to determine their importance as predators. The same may be said of snakes and their predators at the Lamto site. Unfortunately, these data cannot be used as a test of the hypothesized negative correlation of big mammal biomass with reptile numbers, since there are no comparative reptile data from a Lamto-like site with big mammals and their carnivores present.

It is tempting to expect the numbers of species as well as individuals of reptiles in carnivore-rich habitats to be depressed. However, there are two opposing relevant forces acting on reptile species richness. Their outcome is not obvious. On the one hand, we may expect predators to depress the density of superior competitors, thereby leaving more room for other species (e.g., Janzen 1970; Murdoch 1969; Paine 1966). On the other hand, intense predation may simply eliminate certain reptilian life forms (e.g., large foliage-eating Iguanidae) and prevent foraging in some of the more exposed habitats. In short, if lizard-rich Australian habitats (Storr 1964; Pianka 1969) were exposed to foraging by a normal East African carnivore fauna, I predict that a substantial number of the species would disappear immediately. Furthermore, since reptiles contain second-, third-, and fourth-order carnivores, such reductions in lizard species richness or biomass could easily lead to a simple reduction in snake species richness and biomass (Arnold 1972). Finally, if we are to ask whether the number of species of reptiles per unit area or habitat is different in East Africa compared with the neotropics, we need far more refined census data than those currently available (table 1).

In closing this section, I cannot help but note the confounding effect that a

TABLE 1

Numbers of Species of Snakes, Poisonous Snakes, and Burrowing Snakes in
Neotropical and African Faunal Lists

Locality	Area (Miles²)	Number of Species of Snakes*	% Poisonous to Man†	% Burrowers‡
Africa:				
Southern Rhodesia (Broadley 1959)......	150,354	59	24	9
Zambia (Broadley 1971)................	290,323	74	27	10
East and central Africa (Loveridge 1942).	?	73	26	15
Malawi (Loveridge 1953)...............	36,481	45	27	9
Eastern Africa (Loveridge 1937):				
10–1,000 ft elevation................	?	59	15	17
1,000–6,000 ft elevation.............	?	74	19	5
3,000–10,000 ft elevation............	?	38	40	13
Uganda (Loveridge 1957)..............	91,134	67	29	8
Kenya (Loveridge 1957)...............	224,960	82	28	16
Tanzania (Loveridge 1957).............	362,844	95	20	16
South of the Zambezi River (Stevenson-Hamilton 1947)	1,363,000	90	28	?
Southern Africa (Fitzsimons 1970).......	?	108	21	17
Gold Coast (Leeson 1950)..............	?	81	25	9
Kruger National Park (Pienaar 1966)....	7,340	44	21	16
West Africa (Villiers 1962).............	?	116	20	13
Western North America (Stebbins 1954)....	1,187,798	76	20	5
Sinaloa, Mexico (Hardy and McDiarmid 1969):				
0–1,000 ft elevation.................	?	46	14	5
1,000–6,000 ft elevation.............	?	48	15	2
Mexico (Smith and Taylor 1966):				
Chihuahua	94,806	40	25	0
Baja California......................	55,620	43	21	7
Sonora	70,465	41	29	0
Coahuila	58,052	36	17	6
Guerrero	24,880	70	13	1
San Luis Potosí.....................	24,411	48	15	4
Oaxaca	36,365	89	15	1
Tamaulipas.........................	30,726	38	13	5
Jalisco	31,298	52	13	5
Michoaçan	23,195	61	13	5
Yucatan	14,864	46	11	4
Veracruz	27,751	84	12	4
Chiapas	28,724	65	18	2
Costa Rica (Taylor 1951)...............	19,600	136	13	3
Costa Rica (Taylor 1951)...............	19,600	136	13	3
Venezuela (Roze 1966).................	352,143	119	17	9

* Including only terrestrial species.
† Including only the boomslang (*Dispholidas typus*) among the rear-fanged snakes.
‡ Including only Typhlopidae and Leptotyphlopidae.

low density of reptiles will have on understanding the processes referred to above. Animals that appear to eat very few reptiles might well eat very many if placed in a reptile-rich habitat such as Australia or Central America. I can imagine a troop of baboons or mongooses having a diet very rich in reptiles during the first few weeks of transplantation to a Central American lowland site.

CHARACTERISTICS OF THE PREY

Toxicity

If carnivorous vertebrates have generated much heavier predator pressure on reptiles in herbivore-rich Africa than in the neotropics and Australia, I expect the individuals of the surviving species of reptiles to be better protected in Africa than outside. Relevant data are circumstantial and at best suggestive.

a) Proportions of venomous snakes in samples.—There are two types of samples available, faunal lists and large collections. Large collections are essentially nonexistent for Africa. Pitman (1935) once collected "as many snakes as possible" during a period of a few weeks in the vicinity of Mabira Forest in Kyagwe, Uganda. He got 55 individuals, 44% of which were elapids and vipers. At 2,000–2,400 m elevation, in the Muko region of the Kigezi District, in 1 wk he examined 100 snakes (presumably brought in by native collectors), and 30% of these belonged to one poisonous species, an arboreal viper (*Atheris nitschei*). During a 22-mo period in 15 km of cocoa farm and secondary forest in Ghana, Leston and Hughes (1968) found (with the help of a rewarded work crew of locals) 176 snakes, 40% of which were elapids and vipers. In the same area, a later sample of 176 from mid-June 1967 to mid-January 1968 contained 49% elapids and vipers (Leston 1970b). In both of these samples, the night adder, *Causus rhombeatus*, was "far and away the snake most commonly seen" (Leston 1970a, 1970b). If indeed predation pressure is responsible for this apparent high proportion of venomous individuals, then it is probably due to such pressure generating a reptile community structure that persists even in the absence of carnivores, since Ghanian cocoa farm areas are probably not rich at present in either large herbivores or animals surviving on them. Wild animals also make collections, but, for example, it is very hard to know whether snake eagles collect an unbiased sample of what they see (e.g., poisonous snakes may make the fatal mistake of standing their ground while nonvenomous snakes may flee at the sight of the bird), but it is of interest that, of 26 snakes brought to a brown snake eagle nest in Rhodesia, 20 were poisonous (cobras, boomslangs, sand snakes, puff adders), and of the six unidentified, one was thought to be a cobra and another a puff adder (Steyn 1972). Similarly proportioned lists are given in a later study (Steyn 1974).

For contrast, there is only one large set of snakes collected in the neotropics. Dunn (1949) reports that of 10,985 Panamanian snake heads collected for reward, *in which more was paid for venomous snakes than nonvenomous*, only 21% were elapids and crotalids. In Heyer's (apparently unbiased) (1967) collection at four sites in Costa Rica (50–400, 400–700, 700–900, 500–600 m elevation), a total of 108 snakes contained 7%, 31%, 17%, and 20% elapids and crotalids. In my own brief census mentioned earlier, all Costa Rican snakes were colubrids while the Cameroun snake was an arboreal viper. In summary, elapids and vipers might make up a bigger proportion of the individuals in an African as opposed to a neotropical large sample, but the evidence is at best suggestive.

Faunal lists are equally difficult to interpret. In table 1, I calculate the percentage of some neotropical and African snake faunas that are highly poisonous

to man (and, by inference, to at least some other predators). The percentages are noticeably higher for the African samples. However, the reader should note that, aside from elapids and vipers, only the boomslang (*Dispholidus typus*) of the Colubridae is tabulated as venomous here; yet it is among the rear-fanged colubrids that we might expect intense predator pressure to select for venomous defenses, as well as merely favoring toxic families. Fitzsimons's (1970) comments in his field guide to snakes of southern Africa allow closer examination of this question. He lists 112 species, only 22% of which are venomous by the definition in table 1. However, the Colubridae may be subdivided into 35 Colubrinae with no venom fangs and 33 rear-fanged Boiginae. One Boiginae is the already mentioned *Dispholidus*. However, *Thelatornis* is lethal as well (it is irrelevant that bites to humans are very rare). He states that the others are not dangerous but makes the following comments on three common Boiginae. "The venom [of the spotted grass snake, *Psammophylax rhombeatus*] weight for weight has been shown to be more toxic even than that of the cobras." "Large specimens [of the sand snake, *Psammophis sibilans*] show considerable truculence when molested and can inflict quite a serious bite. Though seldom fatal, the venom can nevertheless induce most unpleasant and painful symptoms, such as excruciating pain, swelling, nausea, cold sweats, etc., for some days after a bite." "Although cases have been recorded where the bite of *Macrelaps microlepidotus* has caused several reactions, the results are seldom fatal." If we add these to the venomous total, the percentage becomes 27. As the rear-fanged snakes mentioned above are widespread in Africa, all the percentages of venomous snakes in the third column of table 1 could probably be adjusted upward in like manner.

The point is often made that rear-fanged snakes cannot get enough purchase on man to inject much of a venom dose, but obviously the fangs work on some part of an animal, and what is relevant here is whether the snake can bite the finger of a baboon, the paw or tongue of a mongoose, the nose of a jackal, etc. I know of no Central American rear-fanged colubrid that causes more than a mild swelling and tenderness or occasional continual bleeding when man is bitten. Of course, confusion is added by the obvious importance of snake venom in prey capture, but there is no obvious reason why the prey in Africa should require more venom for capture than the prey in the neotropics.

An Australian comparison is of little help. Since colubrids are apparently new arrivals and vipers have never arrived (Keast 1959), the cause is probably historical rather than ecological that most of the Australian snake fauna is toxic Elapidae (Storr 1964).

b) Aggressiveness of venomous species.—The bushmaster (*Lachesis muda*) is the only one of the neotropical poisonous snakes in table 1 that has a reputation for being aggressive toward humans (and, by inference, to other big animals); however, my experiences with bushmasters suggest that the snake is simply not afraid, rather than being aggressive, and is as likely to move in the direction of a person as in any other.

On the other hand, both cobras (*Naja* spp.) and mambas (*Dendroaspis* spp.) have a reputation for conspicuous warning displays and behavior and attacks

on humans (e.g., Pitman 1935). However, such tales have ample opportunity for exaggeration, and the spitting cobra (*Naja nigricollis*) is probably the only really indisputable case of a defensively aggressive African snake, since it certainly does not spit to capture prey. Cobra hoods may be viewed as directly analogous to rattlesnake rattles, with the latter probably serving as a warning to New World coyotes, cats, and mustelids if we may reason from the diets of their African analogues. Perhaps what is most striking about the large African elapids is their willingness to attack when they are the subject of attack. In a community rich in generalized reptile eaters, especially those with good brains, we may expect to find maximal development of "the best defense is a good offense." However, such an interpretation is confounded by the obvious fact that, to escape the specialized reptile eaters such as mongooses and snake eagles, the best strategy may be to flee. Since numerous African animals are obviously capable of killing and eating highly poisonous snakes, the absence of aposematic snakes in Africa (Gans 1961, 1965*b*) may support this point.

Crypticity

I expect the degree of cryptic behavior and morphology of a reptile fauna to reflect the intensity of predation on that fauna. Crypticity is very difficult to quantify without having worked with the predators and their prey, but there are a few suggestive traits.

a) Fossorial forms.—If we examine only that percentage of snake faunas that are in the Leptotyphlopidae and Typhlopidae, it is obvious that the African samples are richer in these two burrowing families than are the neotropical faunas (table 1). However, this is relatively uninteresting compared with asking what percentage of other families is fossorial or frequently burrowing. For example, a family-based tabulation as in table 1 misses forms such as the burrowing colubrids *Calamelaps unicolor*, *C. ventrimaculatus*, *Xenocalamus bicolor*, *Prosymna lineata*, *P. sundevallii*, and *Elapsoidea* sp. from southern Rhodesia. Unfortunately, not enough is published of the biology of African and neotropical snakes for me to ask what forms are regular burrowers; yet it is these groups rather than the Typhlopidae and Leptotyphlopidae that should differ in abundance between predator-rich and predator-poor habitats.

Amphisbaenids, a purely fossorial order probably derived from legless lizards, should be proportionately better represented among the reptiles in a predator-rich habitat. However, Africa has 61 species and South America has 64 (Gans 1967). Since the two land masses are about the same size, these data tell us little. It is of interest, however, that Gans's (1968) map of amphisbaenid distributions in the two continents shows all of South America east of the Andes (and a bit west of the Andes) to be occupied by amphisbaenids, but these animals are conspicuously missing from most of Tanzania, Uganda, Kenya, Congo, Central African Republic, Chad, Sudan, and Ethiopia. It is very tempting to postulate that their absence is due to extraordinary predator pressure which gets at them even underground, in view of Gans's (1965*a*) comment that, when collecting burrowing reptiles in the Somali Republic, he observed that

baboons and warthogs in acacia scrub "were responsible for much digging of
holes, turning of rocks and small logs, and rooting about. . . . The best localities
for burrowing reptiles soon proved to be sites where a thorn bush had decayed
and the ground was covered by a ten centimeter layer of interlocking multi-
radiate thorns, hard and sharp enough to penetrate the soles of my boots. . . .
Here and below very heavy logs (moved by towing with a truck) we took species
of *Mochlus* and *Typhlops*, [and] 2 species of amphisbaenids." He then comments
that "the quantity and diversity of reptiles within the city limits [of Mogadiscio]
were truly astonishing. . . . Most important, particularly for subterranean forms,
may well be the absence of the larger mammalian predators" (see also the
Discussion section below).

Likewise, fossorial lizards can be expected to constitute a larger part of the
total lizard biomass and species in a predator-rich habitat. It is of particular
interest in this connection that Pianka's (1973) lizard census by habitat gives
12.1% of 4,795 individuals in the Kalahari Desert as being subterranean, while
the comparable figures for North American and Australian deserts are 0.0%
and 0.5%, respectively. Pianka (1969, 1973) also reports an average of 10% of
the Kalahari lizard species to be fossorial in his 10 study areas (average of 15
species of lizard per plot), but only 4% of the average of 28 species in his eight
Australian study plots were fossorial; there were no fossorial species in his
North American desert study areas. However, not much importance can be
attached to these figures, as the African data are based only on two species of
Typhlosaurus termite eaters; their abundance may reflect little more than the
relative abundance of termites (Pianka 1973; Huey et al. 1974).

Increased predation pressure on reptiles need not necessarily increase the
absolute number of burrowing forms. Such an increase requires that the burrow-
ing guild not be "full" in some sense, and this should be so in an old fauna only
if there is intense underground predation pressure on the burrowers. To enter
a "full" habitat requires that the new burrower evolving into this microhabitat
will have to be in some sense better at escaping subterranean predators than
those already present, an idea that is untestable with the data at hand.

b) Nocturnal forms.—While Pianka (1973) records an average of 35% of the
lizard species in his African study areas as being nocturnal, in contrast to 17%
for his North American study areas, his Australian average is 36%. We might
expect the African nocturnal component to be largely arboreal (e.g., the more
arboreal geckos should be freer of nocturnal predation than would terrestrial
nocturnal lizards), but in fact Pianka (1973) found almost exactly the same
proportions of terrestrial to arboreal nocturnal lizards in Australian and African
study plots.

The African gecko fauna (largely nocturnal) appears to be much better
developed than that of the neotropics. A. Kluge (personal communication)
tabulated about 300 species of geckos for continental Africa, while all of Central
and South America (including its islands) have only about 150 species. Further-
more, about two-thirds of the neotropical geckos are in the Sphaerodactylinae,
which are almost entirely restricted to Caribbean islands. It is tempting to
postulate that this abundance of geckos in Africa is related to the conspicuous
absence of an analogue to the abundant and conspicuous diurnal neotropical

arboreal lizard *Anolis* (116 species [Peters and Orejas-Miranda 1970]). From
the standpoint of this discussion, the rare, highly cryptic, and species-poor
diurnal chameleons of Africa are in no way ecological analogues to *Anolis*. I
would even argue that excessive predator pressure has kept them from becoming
Anolis analogues. It is equally interesting that the Caribbean islands not only
contain the majority of the neotropical gecko species but also have many
Anolis species and a superabundance of individuals of these diurnal lizards;
this is expected since, in comparison with the mainland, the islands have very
reduced arrays of predators that take lizards (e.g., Rand 1954).

  c) Other defenses.—After watching African monkeys and baboons forage in
vegetation, I am convinced that the extremely cryptic nature of African
chameleons may well be due to much heavier predator pressure by arboreal
vertebrates than is found in the neotropics. I predict that *Anolis* lizards would
not last more than a few days if introduced into African vegetation. Humans
can easily catch *Anolis* with their hands, and they are far from cryptic to the
experienced collector; it seems likely that the superabundant African primates
and raptors (as compared with the neotropics) would quickly focus their
attention on them.

  Mimicry among African snakes (Gans 1961, 1965*b*) is difficult to examine in
the context of this discussion. In general, the more professional snake eaters
there are in a habitat (animals that can take poisonous as well as harmless
snakes), the fewer cases of mimicry I expect. On the other hand, the more
generalist predators that occasionally take a snake as prey (and then, usually,
the harmless ones), the more mimics I expect. Further, the more the venomous
snakes are involved in warning colors and behaviors, the better models there
are available for potential mimics. It is simply not clear how these different
forces are balanced in African predator-rich habitats, except that there is an
absence of very conspicuous warningly colored snakes that would have little
chance of escaping notice.

  There is even a turtle, *Malacochersus tornieri*, in East Africa that does not
rely on the usual chelonian defense. When attacked, it runs very fast for the
nearest rock crevice and, by virtue of its flexible shell, wedges itself out of harm's
way (Ireland and Gans 1972). Judging from the number of (apparently entire)
turtles recorded in the guts of jackals and secretary birds, small turtles and
tortoises in East Africa find their hard carapace next to useless for defense.

Life forms

  The ease with which leaf eating should evolve in a lizard fauna should
be decreased as predation intensity increases, since it appears that very
long periods of basking are an integral part of the digestive behavior of
leaf-eating lizards. Indeed, I have postulated that the appearance of herbivory
on Caribbean islands among lizard genera that are insectivorous on the main-
land is made possible by the absence of predators on the islands (Janzen 1973).
The total absence of a foliage-eating *Iguana* or *Ctenosaura* analogue from the
African tropics is very conspicuous. While *Agama agama* may eat a substantial
amount of vegetation during the African dry season (Chapman and Chapman

1964; Marshall and Hook 1960), they live in human habitations and are small enough to hide in very small holes in rock outcrops in nature. In his Kalahari Desert survey, Pianka (1973) records only 1.2% of the total volume of lizard gut contents to be plant matter, while in Australia it was 5.6% and in North America 8.3%. The latter two percentages are still much lower than would be found in the neotropics at a latitude comparable with East Africa. Since comparatively clumsy humans can catch the big neotropical iguanids with their hands, it seems that they would last no time at all in an African predator-rich community. Viverrids would have no difficulty eliminating the common large *Ctenosaura* from their nocturnal sleeping holes. Furthermore, *Iguana iguana* has been shown to have extraordinarily poor ability at sustained running (Moberly 1968), such as would be required to escape from a mongoose, baboon, or jackal. (Hunters in the rain forest at Tissongo, near Edéa, Cameroun, catch varanid lizards simply by running them down on foot [D. McKey, personal communication].) It may well be that for a warm-blooded carnivore, reptiles are the easiest of all medium-small prey to capture.

However, Australia complicates things in having virtually no herbivorous lizards (Pianka, personal communication).

DIRECT EFFECTS OF HERBIVORES

In addition to partly supporting a high density of carnivores, the big herbivores may also more directly reduce the reptile biomass and fauna.

Vegetation Cover

By grazing, browsing, and trampling, the East African large herbivores considerably reduce the density of standing vegetation during the year. This can be very important, as suggested by Brown's (1970) comment that, "hunting on the ground as they do, Secretary Birds cannot exist satisfactorily in areas where the grass grows tall. They are not common in places where the grass is more than, say, 16–20 inches high, and usually they like it shorter." Zebras even specialize at feeding during the dry season on the dense clumps of grass that should be important refuges for reptiles fleeing predators. Reptiles and small rodents should have about the same problems, and Sheppe (1972) points out that during the dry season Zambian (and presumably East African) small rodents are restricted to the bits of vegetation along waterways and to cracks in the ground, since the ungulates thoroughly graze and trample the vegetation during the dry season. In comparable neotropical sites, dry season wet spots are surrounded by dense semievergreen vegetation containing a high density of lizards, snakes, and their prey. The vegetation around East African wet sites during the dry season is heavily trampled, browsed, and alive with potential predators on reptiles. The shoulder-high dry season stands of grass and dense riparian vegetation at the big-mammal-free Lamto site mentioned earlier (Lamotte 1975) is in stark contrast to the barren East African dry season plains. There may also be some very complicated third-order interactions. Gans (1961) notes that a possible reason why *Causus* vipers have not invaded the drier

regions of Africa is that they feed exclusively on frogs and toads; however, the absence of frogs and toads from the drier parts of Africa may be due to the havoc wreaked on a waterhole and its associated aestivation sites by a herd of water buffalo or elephants during the dry season. If the lack of ground cover helps to reduce the small rodent population, then it may well reduce the snake biomass indirectly. Arnold (1972) emphasizes that the number of snake species in a habitat is probably related to the number of prey species in the habitat; by reducing the ground cover and thereby the prey density, the ungulates could be reducing the snake species richness in East Africa even if they were not supporting a large carnivore community.

Fires

Often set by man or his activities, fires should have a very depressing effect on reptile populations by directly killing them and by exposing them to predators. While avian predators are only rarely encountered feeding among the ashes of Central American fires, they are comparatively very prominent near East African fires. Pitman (1935) observed: "I have walked along several miles of a Kenya road in the Great Rift deep in dust, with a distant fire approaching, and seen the soft surface scored by the sinuous trails of countless fleeing snakes, while numerous Secretary Birds stalked up and down the high-way having a merry time." Vesey-Fitzgerald (1966) says of Zambian and Tanzanian rodents that "food seldom appears to be in short supply but shelter, especially in habitats which have been degraded by fire, may be a limiting factor." However, the reduction of reptile biomass in forested regions of East Africa and Cameroun (as contrasted with Central America) cannot be blamed on fire or on trampling of the vegetation by big mammals.

DISCUSSION

Two central themes are under scrutiny here: (1) Is reptile biomass actually lower in (apparently) predator-rich tropical African habitats than in comparable neotropical habitats? While there are no data in the literature on the subject, my admittedly brief field observations in Africa lead me to believe that there is a large difference in reptile biomass between comparable tropical African and neotropical habitats. However, all I can do at this point is plead for comparative estimates in future field studies. (2) Provided reptile biomass is lower in predator-rich habitats, is this due to some of their predators having alternate food sources during critical lows in reptilian prey density? Furthermore, can the exceptionally large biomass of large herbivores in tropical Africa be viewed as providing these alternate food sources and maintaining a large community of predators that take reptiles as incidental prey? The literature lacks information to answer these questions directly. However, it does contain enough anecdotes to suggest that *an affirmative answer is a possibility if sought with field studies.*

The answers to these questions are of relevance to studies of both productivity

and community structure. For example, an alternate explanation for the apparent low reptile biomass in Africa is that Africa is simply less productive from a reptile viewpoint. However, my impression is that, taking season into account, the African habitats I was in contain as many insects as the lizard-rich Central American habitats with which I am familiar. Certainly the lack of large folivorous lizards cannot be blamed on a lack of foliage in Africa, though it is conceivable that on average African arboreal foliage is more toxic to vertebrates than that in the neotropics.

At the level of community structure, it is useful to consider Pianka's (1971) conclusion that "the Kalahari supports proportionately more species of ground-foraging avian insectivores than does the Australian desert; this in turn implies that competition between birds and lizards is keener in the Kalahari than in Australia." The hypothesis advanced here would suggest that, on the contrary, the reptilian competitors have been removed by predators and therefore there is relaxed competition from the reptiles. Pianka (1973) notes repeatedly that overall niche breadths of the Kalahari Desert lizards are the broadest of his North American–African–Australian comparison; this is exactly what is expected in a habitat where the reptiles are subject to extraordinarily heavy predator pressure by fairly generalized predators.

Direct tests may become available for some of these ideas. We should expect, for example, that as the wild large herbivores and their associated carnivores are replaced by domestic animals, thereby greatly reducing the amount of carrion available to the community, the reptile biomass should increase. It is significant in this context that Western (1974) described his south Turkana study site as having what seemed to him a high density of reptiles and as having most of the wild herbivores replaced by domestic cattle, goats, sheep, donkeys, and camels under the care of herdsmen. I also expect reptiles to become much more abundant where carnivores have been directly eliminated, as in villages (as noted earlier by Gans [1965a]) and as stressed by M. Coe (personal communication). I found this to be the case in my African censuses as well. In the area of the Ugandan samples, I found three to 11 diurnal lizards in the two houses in which I lived; in walking from the boat landing to the center of Edéa, a distance of about six long urban blocks, I counted 62 lizards (three diurnal species) in 20 min. Similar phenomena are reported by Marshall and Hook (1960), Chapman and Chapman (1964), Harris (1964), Schmidt (1919), Romer (1953), Robertson et al. (1965), Grandison (1968), Cansdale (1951), Daniel (1961), and Leston (1970a). Reptiles should also be abundant where natural refuges are especially well developed, as on rock outcrops (e.g., Marshall and Hook 1960; Western 1974).

However, there is a major problem in testing the hypothesis by examining the increase of lizards and snakes in areas from which the large herbivores (and presumably the carnivores that feed on them) have been recently removed. I do not expect the missing life forms to suddenly appear. Second, lizard populations may have genetic traits leading to effective seasonal rarity. For example, Barbault (1973) documents the extreme fluctuation of wet season–dry season lizard density (many small species are effectively annuals, passing the worst

time of year as eggs). Such behavior could well have been selected for by a large carnivore community but will not immediately disappear when the carnivores are removed. Third, lizard populations may have genetic traits leading to spatial rarity. In a substantial portion of the habitat surveyed in the Kibale Forest area in Uganda, much of the large terrestrial mammal community had been eliminated; yet the diurnal lizards were still concentrated in the houses (*Agama* and Scincidae). Certainly the forest around Edéa no longer abounds in large mammals, nor does the forest around the habitations described as having high densities of lizards at the end in the previous paragraph. It appears that selection has produced lizard genotypes that attach themselves to human habitation. This hypothesis is substantiated by the observation that isolated houses recently built in virgin forest near Lake Tissongo do not attract the very rare but present forest lizards, but those a few miles away in ancient riparian settlements have numerous diurnal lizards living in them. I have never noticed a strong tendency for diurnal lizards to concentrate in houses or towns in Central America.

Errington (1956) comments that "predation, assuredly, *can* depress a prey population. Under special conditions, the impacts of a predator on its prey can be so severe that whole populations of a vulnerable prey species are wiped out. Predatory man has demonstrated this over and over again." Workers in biological control have long been well aware of the importance of alternate food sources that keep a predator population so high that it begins to act as soon as the prey population becomes more numerous following a temporary depression. Davis (1957) even showed that semiferal cats were much more effective at depressing rat populations is fed supplementary food when rats were in short supply. In discussing carnivore impact on microtine rodent cycles, Pearson (1966) concluded that "a limited but adequate amount of secondary prey permits the carnivores to survive longer and continue feeding longer on the vulnerable species. As a result, the primary prey becomes extremely scarce." However, most predator-prey studies, theoretical and field alike, have focused on the fate of the prey species that make up the bulk of the predator's diet. There may well be numerous cases where predators "incidentally" have a very depressant effect on prey species that do not constitute their main diet. On the other hand, numerous cases may be discovered where the predator has a very depressant effect on its "usual" prey simply because a marginal food source is available as supplementary rations when the primary prey is absent. These supplementary rations need constitute only a very small portion of the total annual food intake in order to have a very large effect on carnivore survivorship and standing crop. These ideas are not new to ecology, but their careful development is in short supply in the experimental ecological literature with wild animals. Such an analysis might, for example, be quite useful in understanding why certain shallow-water assemblages of tropical marine gastropods appear to be subject to substantially greater predation pressure than others (Vermeij 1974).

One cannot help but note that the phenomenon postulated here should apply to other predator-prey pairs as well. To what degree do the large predator

populations that build up periodically on arctic lemmings (e.g., Parker 1974; Pearson 1966; MacLean et al. 1974; Pitelka et al. 1955) reduce the biomass of, and have other effects on, small birds and other small animals during years of low lemming density? MacLean et al. (1974) note that, following an arctic lemming population crash, least weasels "must have maintained heavy pressure on the few remaining lemmings while sustaining themselves on alternative prey, especially the eggs and young of breeding birds."

There is a conspicuous absence of social Hymenoptera nests in African vegetation (unpublished field notes) as compared with the neotropics. For example, in the total of 5 wk that I have spent in the field in Nigeria, Cameroun, Uganda, and Kenya, I have seen only one social wasp nest (other than on houses); in normal Central American lowland to mid-elevation fieldwork I have encountered as many as 123 in 1 day while searching for other things. Social bee nests are likewise very rare in Africa; I have never found one there, but I regularly encounter several per day of fieldwork in the Central American forested lowlands. Is this due to the maintenance on other food sources of numerous vertebrates that are potential wasp and bee nest predators? The extreme aggressiveness of African honeybees (e.g., Thorp 1943; Michener 1975) certainly appears to be something that would be selected for by extreme predation. Tawny eagles congregate at termite swarms to eat newly emerging reproductives (Smeenk 1974); I would expect them to wreak havoc with the common nests of *Polybia* and *Polistes* in Central American lowland deciduous forest (as do the Costa Rican kites [D. Windsor, personal communication]). Baboons and mongooses should do the same. Is the extreme paucity of hole-nesting parrots and woodpeckers in African forests due to a similar cause? Bird nests on tree branches are conspicuously far rarer in African forests than in Central American ones, if we exclude from the comparison those that aggregate in huge numbers (e.g., *Quelea*). While I did not focus my attention on frogs or small rodents, it seems that the processes postulated here for reptiles should apply to these animals as well. African porcupines (*Hystrix*) have the longest quills of all porcupines, Africa appears to have the only porcupine mimic on earth (*Lophiomys imhausi*), and squirrels restricted to the ground are missing from the dry habitats of East Africa (e.g., the squirrel in Samburu National Park, Kenya, is highly arboreal; yet most of the vegetation is only a couple of meters high).

SUMMARY

I hypothesize that an apparent very low density of reptiles in a wide variety of African habitats is due to exceptional predation pressure on reptiles by a large array of carnivores that are maintained in two ways by the exceptionally large biomass of large herbivores in these habitats. First, there is anecdotal and circumstantial evidence suggesting that some of the regular predators on reptiles may take carrion or other products from big game in times of short supply of regular prey, thereby maintaining higher population densities than would

otherwise be the case. Second, there is anecdotal evidence suggesting that regular consumers of large game may take reptiles as the occasion permits. A brief examination of the reptile fauna of eastern and southern Africa, in search of traits expected of a reptile fauna under exceptional predator pressure, reveals little to support or deny this hypothesis. Additionally, but not developed in depth, it is postulated that African large herbivores may substantially reduce reptile biomass through habitat destruction, especially in more seasonal areas where local water sources and riparian vegetation are important to reptiles, their prey, and large herbivores.

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In equations (11), (12), (13), (15), (18), and (20), and in the first line of text following equation (11), $\hat{\bar{C}}$ should have been printed instead of $\bar{C}$, excluding the second $\bar{C}$ in (11); and $\dot{\bar{C}}$ should have appeared instead of $\dot{C}$, excluding $C_{ij,kl}$ in (11).