The Termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and Their Role in Determining a Potential Keystone Species[1]

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ABSTRACT

The role of the termitaria of *Cornitermes cumulans* in the ecology of the Brazilian *cerrado* was examined. The mounds of *C. cumulans* were studied to determine density per hectare, rate of mound abandonment, structure, and other inhabitants, and were compared with four other sympatric mound-building termite species. Predation on *Cornitermes* was also examined. The average termitaria density for all five mound-building species was 323 per hectare. *C. cumulans* mounds averaged 55 per hectare. In comparison with the mounds of other termites, a higher proportion of those built by *Cornitermes* were inhabited by the mound-building species. The large size and unique bipartite structure of *C. cumulans* mounds make them excellent nesting locations for ant and termite inquilines. At least 17 species of termites and 10 species of ants were found nesting in different *Cornitermes* mounds. Only one percent of the mounds were found uninhabited by any ant or termite species. Armadillos had attacked 36 percent of the mounds; there was a strong correlation between such attacks and the absence of a *Cornitermes* colony. The frequency with which the large and abundant *Cornitermes* mounds are inhabited by inquilines and used by other animals gives these structures an important part in the ecology of the Brazilian *cerrado* and contributes to the role of their builders as a keystone species.

RESUMO

O papel dos termiteiros de *Cornitermes cumulans* na ecologia do cerrado brasileiro foi examinado neste estudo. Os termiteiros de *C. cumulans* foram estudados para determinar densidade por hectare, taxa de abandonamento de ninhos, estrutura e habitantes adicionais, e foram comparados com outras quatro especies que constroem ninhos de barro. Foi também examinada a predação sobre *Cornitermes.* A densidade média de cupinzeiros, para todas as cinco espécies, foi de 323 por hectare. Ninhos de *C. cumulans* foram econtrados com uma média de 55 por hectare. Em comparação com ninhos de outras espécies, uma proporção maior dos contruidos por *Cornitermes* estavam habitados pela mesma espécie que construiu o ninho. O tamanho grande e a estrutura bipartida dos termiteiros de *C. cumulans* fazem deles excelentes ninhos para formigas e outros cupins. Pelo menos 17 espécies de cupins e 10 espécies de formigas foram encontradas nidificando em diferentes termiteiros de *Cornitermes.* Em somente um porcento dos ninhos, não foi detectada a presença de formigas e outras espécies de cupins. Trinta e seis porcento dos termiteiros foram atacados por tatus. Foi encontrada uma forte correlação entre ataques por tatús e ausência da colônia de *Cornitermes.* A frequência com que os grandes e abundantes ninhos de *Cornitermes* são habitados por inquilinos e utilizados por outros animais faz com que estas estruturas tenham um papel importante na ecologia do cerrado brasileiro, e através delas, contribui para que *Cornitermes* seja considerada uma espécie-chave.

Termite mound densities average 323 per hectare in the open vegetation formations of central Brazil. This abundance suggests that the termitaria are a significant component of the ecology of these areas. The most noticeable of the termite mounds are those constructed by *Cornitermes cumulans.* Araujo (1970) states that "*Cornitermes cumulans* is perhaps the commonest and most successful species in its group in pastures, cultured lands, and savannas of middle and south Brazil as well as Paraguay and Argentina." The large size, abundance, and unique bipartite structure of their mounds make *C. cumulans* a potential keystone species (*sensu* Gilbert 1980) of the region. The purpose of this study was to explore the role played by *C. cumulans* and its mounds in the ecology of central Brazil.

This study examines the ecological role of *C. cumulans* with emphasis on termitaria of this species and compares *C. cumulans* mounds with those of other termites common in the area. Five aspects of the termitaria were examined, focusing principally on the mounds of *C. cumulans*: the density of mounds, the frequency with which mounds were found without a colony of the mound-building species, the structure of the mounds, the commensal ant and termite fauna, and predation on mounds.

METHODS

Research was conducted from April 1980–October 1981, in and immediately adjacent to Emas National Park, Goias

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TABLE 1. *Mound densities in open grassland (converted to number of mounds/hectare).*[a]

Site	*Cornitermes* live and dead	*Veloci-termes*	*Armitermes*	*Syntermes*	*Orthognathotermes*	
					Live	Dead
Sq 1 (50 × 50) (1)	32	40	16	0	4	668
Sq 1 (100 × 100) (1)	25	—	—	—	—	—
Sq 11 (50 × 50) (1)	84	4	12	4	0	140
Sq 11 (100 × 100) (1)	69	—	—	—	—	—
Sq 111 (100 × 100) (1)	43	0	4	8	97	171
Tr (20 × 100 m) *N* = 7 (2)	59	11	31	1	36	14
LTr 1 (100 × 4) *N* = 10 (3)	43	158	0	10	3	8
LTr 11 (4 × 100) *N* = 10 (3)	85	55	15	5	13	73
	55	44.7	13	4.7	35.5	179
	(22.9)	(59.6)	(10.8)	(3.9)	(37.5)	(248.4)

[a] Numbers in parentheses refer to methods described in the text.

State, Brazil (18°19′S and 52°45′E). This 131,000-hectare park located within the *cerrado* vegetation zone of central Brazil (Eiten 1972) consists of open grassland (*campo limpo*), grassland dotted with shrubs (*campo sujo*), scrub forest (*cerrado*), and gallery forest. The open grassy areas occupy approximately 60 percent of the park. The park, which ranges in altitude from 650 to 1000 m, contains the divide between LaPlata and the Amazon River basins. Approximately 1500 m of rain falls during the September to May wet season (Anon. 1981). During the rest of the year virtually no rain falls and the temperature can exceed 35°C during the day. At night it can be cold, and every few years the park experiences a frost that kills most of the foliage. Fires are common within the park, burning virtually the whole area every several years. In 1980, at least six separate fires burned 90 percent of Emas Park. Grazing still occurs in some areas of the park, though it is much lighter than in areas outside. Vegetation outside the park is strongly affected by grazing, and fires are set twice yearly to improve grazing quality.

I examined over 900 large (phase 3 of Grassé 1958) *Cornitermes* mounds in the course of this study. Although *C. cumulans* occurs in other vegetation types, only the mounds found in open grassy areas were considered (Fig. 1). A total of 106 mounds were completely excavated and all ant and termite species inhabiting them were recorded. In all mound surveys, the first mound was chosen in an undisturbed area and then its nearest neighbor was examined.

To determine the density of termite mounds in the open grassy areas of the park, surveys of three types were run. In addition to *C. cumulans*, the other common mound-building species are *Velocitermes heteropterus*, *Syntermes dirus*, *Orthognathotermes gibberorum*, and *Armitermes euamignathus*. Since the habitat containing the mounds of these species appeared homogeneous, an area was chosen at random and the quadrats for estimates were placed 100 m away from the road.

Mound densities were calculated in three ways. 1. Two 2500 m² areas were marked and all termite mounds within these areas sampled. These squares were then expanded to 10,000 m² and only the *Cornitermes* mounds were counted. A third 10,000 m² area was marked and all mounds within it counted. The results are presented in Table 1. 2. Seven 20 × 100 m transects were run in one area of the park. Transect directions were chosen at random and transects were not allowed to overlap. The total area sampled was approximately 15 hectares. 3. Ten 100 × 4 m transects were run in two open grassland areas in the park. The transect directions were chosen randomly, but no transects were allowed to overlap. The total area sampled was approximately 10 hectares.

RESULTS

MOUND DENSITIES.—The most abundant mounds were those constructed by *O. gibberorum*, averaging 204.5 mounds per hectare. However, only 12.5 percent of these were occupied by *Orthognathotermes*. The large standard deviation around the mean density of *O. gibberorum* mounds reflects the observation that the mounds of this species are clumped.

Cornitermes cumulans mounds, averaging 55 per hectare, were second in abundance. In open grassland these tall mounds are visible even above the unburned grass. Although found in other vegetation types, *C. cumulans* mounds are most common in grassland.

Velocitermes heteropterus, in addition to being a common inquiline, also builds freestanding structures which were classified as "mounds" if they contained nymphs to differentiate them from structures which contained mostly communited grass (Table 1). However, the comparatively large number of mounds ($\bar{x}$ = 44; SD = 60) recorded in the density surveys is misleading because many of these were small, interconnected structures. It is possible that some recorded colonies were in fact part of a polydomous colony.

Armitermes euamignathus mounds are relatively rare ($\bar{x}$ = 13 per hectare) and seem to be patchily distributed and generally more common in the grassy areas near gallery forests. *Syntermes dirus* mounds, on the other hand, are restricted to the drier areas of grassland, and their mound density averaged only 4.7 per hectare. Mounds of *Grigiotermes* sp., *Cornitermes bequaerti, Nasutitermes kemneri, Anoplotermes* sp. and an unidentified soldierless termite occur much less frequently in the open grassy areas of Emas Park.

MOUND ABANDONMENT.—As already mentioned for *Cornitermes* and *Orthognathotermes,* not all of the mounds built by a species still contain colonies of that same species. When possible, mounds of the five termite species were examined to determine whether or not they contained a colony of the mound-building species. Of 592 *C. cumulans* mounds examined 58.6 percent were dead, no longer containing a *C. cumulans* colony. This compares with 53.4 percent (*N* = 191) dead mounds for *Orthognathotermes* mounds in one survey and 87.5 percent dead mounds (*N* = 1227) in another survey. In contrast, 73 *Syntermes* mounds examined all showed signs of active *Syntermes* colonies.

Because of their extreme softness, *Velocitermes* mounds apparently do not survive once abandoned by the original colony, and no dead mounds of this species were found. *Armitermes* mounds, however, are quite hard and were frequently found unoccupied by *Armitermes.*

MOUND DESCRIPTIONS.—Of the mounds examined, *C. cumulans* were the only ones divided into two distinct portions—an outer shell or "wall" and an inner core or "hive." The shell is an extremely hard soil matrix (see Coles de Negret and Redford 1982 for quantification) which, in mature mounds, usually houses very few *C. cumulans* individuals. It serves both to help regulate humidity and temperature within the colony (Parra *et al.* 1974) and as a form of colony defense (Fig. 2). The termite colony lives in the core of the mound, which is soft, crumbly carton mostly made from fecal material, some soil, and woody material (Fig. 3).

The relative proportion of the two mound components varies during the different phases of mound construction (Grassé 1958). Until the mound grows to about 30 cm in diameter (phase one of Grassé 1958) it remains below ground. During the second phase it is only partially subterranean, while in the third phase the mound is fully developed with a strong soil wall and a large carton nest center, which exists both above and below the ground.

Mature mounds can reach 2 m in height, though in a survey of 35 mounds located in grassland the average height was 77.7 cm (SD = 28.3). The same mounds averaged 65 × 72 cm in their minimum and maximum dimensions at ground level. The interior carton in these mounds averaged 39.6 cm height above ground (SD = 21.7), with a ground-level width and length of 29.3 cm (SD = 7.8) and 30.9 cm (SD = 6.4), respectively. The carton in these mounds varied in distance from the mound exterior from 8 to 52 cm, with the average greatest distance 24.4 cm (SD = 7.5) and the average least distance 14.3 cm (SD = 5.4).

Velocitermes heteropterus mounds are pyramidal, very soft and crumbly, and less than 15 cm in height. *Armitermes euamignathus* mounds are mushroom-cap shaped, averaging 24.7 cm high (SD = 5.1; *N* = 10) and 57.5 cm (SD = 8.8) across. *Syntermes dirus* mounds are low, dome-shaped, and free of vegetation; they average 14.3 cm in height (SD = 6.9; *N* = 20) and 178 cm (SD = 42.6) across (maximum diameter at ground level). *Orthognathotermes gibberorum* builds low, circular, domed mounds averaging 14.8 cm in height (SD = 5.7; *N* = 30) and 42.9 cm (SD = 17.1) across (maximum diameter at ground level). Live mounds of this species are usually built around live grass stems which protrude from the surface. The mounds of these four species are structurally relatively homogeneous throughout, lacking the distinct inner and outer sections characteristic of *C. cumulans.*

MOUND COMMENSALS.—Many species of termites do not actually build mounds themselves; instead, they inhabit mounds built by other species. The invading termite species converts the galleries of the "host" mound in characteristic fashion, and it is often possible to deduce the identity of the invader by examining the galleries. The thick soil shell of a single *Cornitermes* mound can contain the nest of up to five other species of termites. To determine the abundance of these inquiline termite species, 106 *Cornitermes cumulans* mounds in four randomly chosen areas were thoroughly examined for inquilines and scored "*Cornitermes* absent" (dead) or "*Cornitermes* present" (live). Of the *Cornitermes* mounds examined, 55 percent lacked

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FIGURES 1–3. 1. A view of the open grassland in Emas Park with *Cornitermes cumulans* mounds. 2. Exterior of a *C. cumulans* mound (darker portion on upper left is recently added). 3. Sagittal section through *C. cumulans* mound showing inner core of carton and hard soil exterior (ruler is 45 cm long).

1

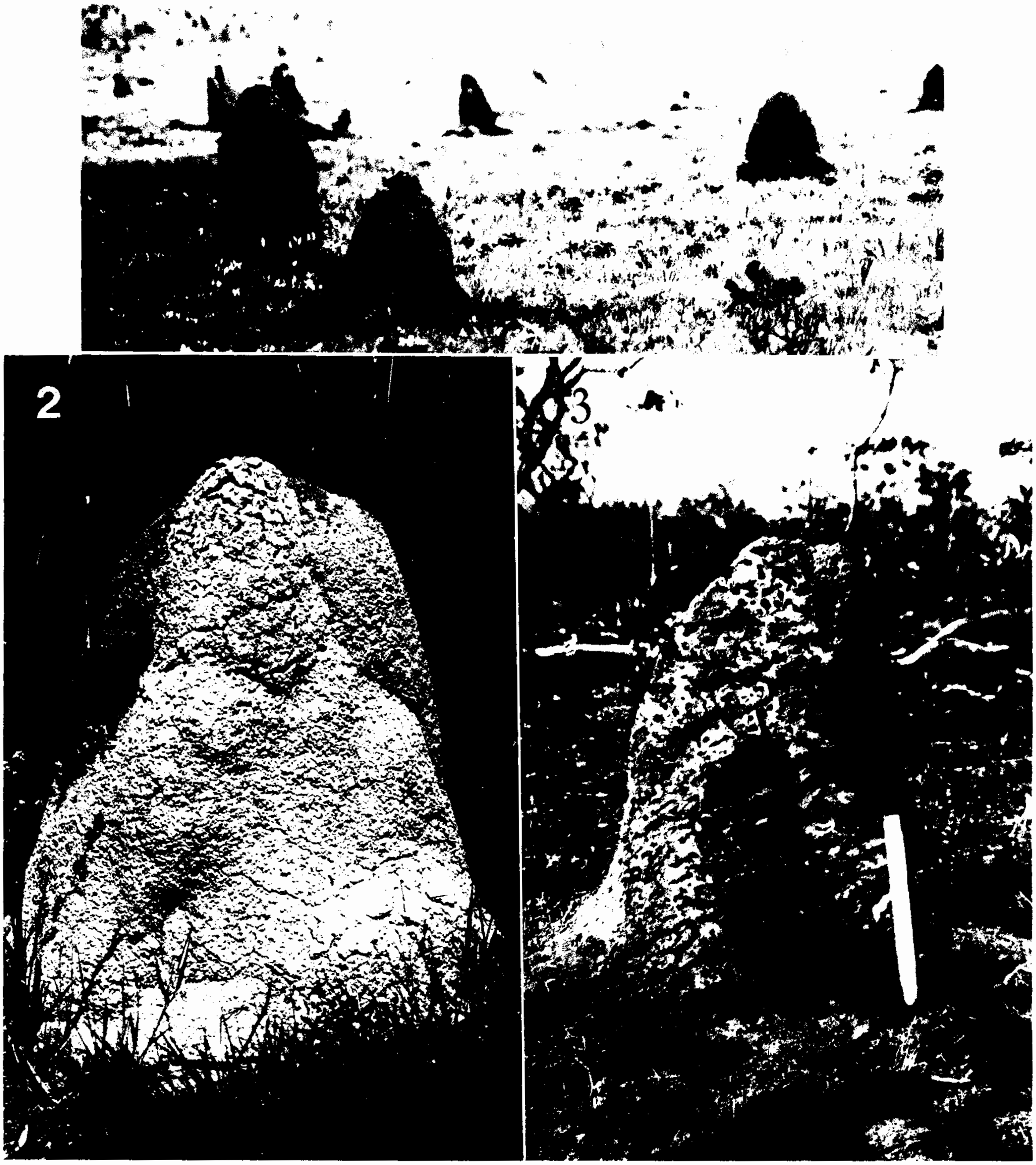

TABLE 2. *The number of inquiline termite colonies in 106* Cornitermes *mounds.*

Number of commensal species	*Cornitermes* Present	Absent
0	16	2
1	11	15
2	7	15
3	10	11
4	2	9
5	2	6
	48	58

TABLE 3. *Frequency distribution of inquiline termite species in 64* Cornitermes *mounds.*

Velocitermes heteropterus	38
Armitermes ?festivellus	29
Anoplotermes spp.	23
Spinitermes robustus	22
Grigiotermes sp.	10
Orthognathotermes gibberorum	8
Curvitermes planioculus	7
Neocapritermes parvus	7
Spinitermes bispinosus	4
Heterotermes tenuis	3
Armitermes sp.	3
Cavitermes parmae	2
Subulitermes sp.	2
Ruptitermes sp.	2
Armitermes sp.	2
Syntermes molestus	1
Angularitermes orestes	1

colonies of *Cornitermes* (Table 2). A total of 144 colonies of inquiline termites were found in the mounds without *Cornitermes* and 73 in the mounds with *Cornitermes.*

In one-third of the live mounds *Cornitermes* was the only termite species present. Only 2 of the 105 mounds examined contained no termites at all. Live mounds also had fewer cases of many species of inquilines than dead mounds: 8 percent of the live mounds had four or more inquiline species as compared with 26 percent of the dead mounds, a significant difference ($\chi^2 = 14.54$, $P < 0.01$).

Seventeen species of termite inquilines representing 14 genera were found in 64 *Cornitermes* mounds. *Velocitermes heteropterus* was the most common inquiline, appearing in 54.9 percent of the mounds. The high organic content of its nest material is commonly seen on the outside of *Cornitermes* mounds. *Armitermes ?festivellus* was the second most common, in 45.3 percent of the mounds (Table 3).

To test whether the presence of *Velocitermes* was correlated with the presence of a colony of *Cornitermes* in a *Cornitermes*-built mound, 205 *Cornitermes* mounds were scored "*Velocitermes* present" or "*Velocitermes* absent" and "*Cornitermes* present" or "*Cornitermes* absent." All *C. cumulans* mounds encountered in two surveys were examined. A contingency table analysis ($\chi^2 = 0.02$, $P >$ .09, n.s.) shows that the presence of a colony of *Cornitermes* in a *Cornitermes* mound does not affect the presence of *Velocitermes.* Of the 205 mounds examined, 70 percent contained *Velocitermes. Velocitermes* virtually always nests in the outer soil shell of the *Cornitermes* mounds, an area that contains few *Cornitermes* individuals.

A survey of 85 *C. cumulans* mounds examined for termite inquilines produced at least 10 species of inquiline ants in eight genera. Ants were found in 60 percent of the mounds examined. *Pseudomyrmex termitarius* was the most common, occurring in 47.1 percent of the mounds. The two other genera of ants most commonly found were *Camponotus* and *Solenopsis.* The presence or absence of *Cornitermes* had little significant effect on the presence or absence of inquiline ant species ($\chi^2 = 3.4$, $0.1 > P > 0.05$).

In contrast to *Cornitermes,* the presence of an *Orthognathotermes* colony in an *Orthognathotermes* mound seemed to inhibit the presence of inquilines: no live mound was ever found to contain other termite or ant species. Fewer inquilines were present in *Orthognathotermes* mounds without *Orthognathotermes* (dead mounds) than in *Cornitermes* mounds without *Cornitermes.* In 168 dead *Orthognathotermes* mounds, 68.5 percent were totally unoccupied by ants or termites. In the other 53, ants (principally *Camponotus* sp.) occurred 22 times, while termites (principally *Grigiotermes* spp., *Armitermes* sp. and *Anoplotermes* sp.) occurred 46 times. In other areas of the park, *Velocitermes* was a common occupant of old *Orthognathotermes* mounds, occurring in 11.7 percent of 171 dead mounds examined.

None of the *Velocitermes* mounds contained other species of ants and termites, while small colonies of both ants and termites were found at the edges of large *Syntermes* mounds. Live *Armitermes* mounds frequently contained small colonies of ants and other termite species, while dead *Armitermes* mounds were often inhabited by ants.

PREDATION AND MOUND ATTACK.—Despite its very hard, large mound, *C. cumulans* is vulnerable to numerous predators: those that consume termites outside the mound, those that can successfully attack the mound, and those that prey on *Cornitermes* once the mounds' defenses have been breached.

Cornitermes workers and soldiers that forage above ground are preyed on by many animals including foxes, rodents, birds, lizards, arachnids, ants and other arthropods. The principal vertebrate predators of *C. cumulans,* armadillos and anteaters, often consume soldiers and workers outside the nest (Mathews 1977; Redford 1983, in press). However, each of these mammals has a method of feeding on *C. cumulans* in the mound.

Armadillos characteristically dig holes more than 10 cm in diameter in or near the base of a mound. To assess the relationship between armadillo holes in *Cornitermes* mounds and the presence or absence of a *Cornitermes* colony, four surveys of 592 large mounds were conducted. All *Cornitermes* mounds encountered were scored *C. cumulans* absent or present and "with hole" or "without hole." The absence of *C. cumulans* was associated with a hole in the base of their mound ($\chi^2 = 156.24$, $P < 0.01$). Of the 215 mounds with armadillo holes, 90.2 percent were without a *Cornitermes* colony. A much lower percentage (40.6) of the 377 intact mounds had no *Cornitermes* colony. Only 3.5 percent of the 592 mounds examined had both a colony of *C. cumulans* and a hole in the base.

Anteaters usually scrape at the surface of *C. cumulans* mounds. Damage from such attacks was apparent on only 15 percent of 385 mounds examined. However, this must be considered an underestimation because anteater scrapings are obliterated fairly rapidly either by the repair efforts of the termites themselves or by erosion of the mound.

Cornitermes colonies are more vulnerable to mammalian predation when they are just emerging above ground level—64 percent of the mounds surveyed had been damaged or destroyed. Also, 25.8 percent of the 592 mounds surveyed contained no holes at the base yet were uninhabited by a colony of *Cornitermes.* Obviously there are other sources of mortality which play important roles.

The third group of *Cornitermes* predators attack the termites in the mound only after the mound has been damaged by another predator. Ants, the major predators within this category, are generally ineffective against an undamaged *C. cumulans* mound, yet once the exterior shell has been breached they appear within 30 seconds and begin carrying away workers and occasionally soldiers. Such ants either nest in the termite mound or forage on or near the mound. On one occasion I even found army ants (*Labidus*) removing *Cornitermes* from a mound recently breached by an armadillo. Other invertebrates such as wasps, spiders, flies, and beetles and vertebrates such as caracaras and giant anteaters have also been observed taking termites from damaged mounds.

Data on rates of attack of mounds built by other species were taken only for *Syntermes* and *Orthognathotermes.* Of 73 *Syntermes* mounds, 86 percent showed sign of anteater or armadillo attack. In contrast, only 34.7 percent of 193 live *Orthognathotermes* mounds were found to have been breached by these predators.

DISCUSSION

Both live and dead *C. cumulans* mounds together with the other termite mounds play a very important role in the ecosystem of Emas Park. The average mound densities from Table 1 yield an average figure of 323 termite mounds per hectare—a total of over 25 million termite mounds in the open vegetation formations of Emas Park. Previous investigators have often identified mounds as being characteristic of a certain species, counted these mounds, and then assumed that this reflected the abundance of the species. However, as is clear from this study, many mounds may be unoccupied by the original mound builders—58.6 percent for the 592 *C. cumulans* mounds examined.

In addition to their abundance, the size and nature of construction make *C. cumulans* mounds the most important termitaria in Emas Park. Unlike the more common mounds of *Orthognathotermes,* those of *Cornitermes* are large and extremely hard, representing a larger, more permanent nesting location for potential commensals. The importance of the durability of an empty mound to obligate inquilines can be seen by comparing the rapidly disintegrating, soft mound of *Orthognathotermes* with the similar sized, much harder (see Coles de Negret and Redford 1982) mound of *Armitermes.* Dead *Orthognathotermes* mounds frequently are found devoid of inquilines while those of *Armitermes* are often occupied by ants or other termites. Another factor which makes *Orthognathotermes* mounds, dead or alive, less suitable for inquilines than *Cornitermes* (and *Armitermes*) mounds is the difference between the food habits of the two mound-building species. *Orthognathotermes* is primarily geophagous and constructs its mound largely with fecal material. *Cornitermes,* on the other hand, eats grass and herbaceous material which is incorporated into the mound in the form of carton. Thus, for humivorous species, an *Orthognathotermes* mound represents a very poor source of food in contrast to a *Cornitermes* mound. Mathews (1977), corroborating this fact, found eight species of termites in a decaying *C. snyderi* mound and stated that many humivorous species are "more or less restricted to the niche of secondary decomposers with the mounds of other species."

The bipartite structure of *C. cumulans* mounds, with a carton interior and a hard soil exterior, also contributes to their suitability as sites for potential inquilines. The outer shell contains galleries made by *Cornitermes* as the mound was being constructed which serve as inquiline nest sites in both live and dead mounds. In mounds with or without a *Cornitermes* colony, this shell is virtually unpopulated by *Cornitermes.* It is in this shell, for example, that most of the *Velocitermes* colonies were located, and up to five species of termites and four species of ants were found in the shell of one *C. cumulans* mound.

The presence of at least one of these obligate inquiline ant or termite species in 99 percent of the 106 *Cornitermes* mounds examined means that there is rarely a truly dead *Cornitermes* mound.

Inquilines can provide some benefit to *Cornitermes*. A mammalian predator attempting to break into a termite mound inhabited by several species of social insects is confronted with a marbling of species possessing a variety of defensive behaviors. These can provide the mound with "an integrated defense system" (Coles 1980) against mammals. For example, 70 percent of 206 *C. cumulans* mounds surveyed were occupied by *V. heteropterus*. A giant anteater breaking into a *Cornitermes* mound in search of *Cornitermes* would frequently be confronted with *Velocitermes* soldiers and their apparently repellant chemical spray.

Inquilines can also provide distinct drawbacks to *Cornitermes*. As Deligne *et al.* (1981) have pointed out, most ants are unable to get through the defenses of an intact termite mound. But as observed for *Cornitermes*, after the mound defenses have been breached, ants that lived previously as inquilines can become very efficient predators. Ants nesting in the mound and outside the mound are probably the major source of mortality for *C. cumulans* colonies. However, this would not be the case if mounds were not first opened by armadillos and perhaps anteaters.

Cornitermes workers can rapidly repair a hole that penetrates to the carton. However, the low frequency of repaired holes indicates how rarely a *Cornitermes* colony is able to perform repairs after a major break has been made and before ants or other factors kill the colony. The successful repairing of a hole probably depends on what proportion of the colony the mammalian predator killed and whether or not the queen was killed. If the colony is killed, the mound may be recolonized by another colony of *C. cumulans* (pers. obs.) or may begin the slow process of erosion, a process hastened by humivorous termites.

In addition to the approximately 30 species of obligate inquiline ants and termites, other types of obligate inquilines inhabit *C. cumulans* mounds. These include many species of termitophiles (Kistner, pers. comm.; Newton, pers. comm.) as well as several different species of beetle larvae (Tenebrionidae, Cincindelidae, and Elateridae) and fly larvae (Asilidae) found in the soil shells (Costa 1982). Of particular interest are abundant larvae of the genus *Pyrearinus* (Elateridae) which live in the shells of *Cornitermes* mounds and produce light in the body segment immediately behind their heads. These larvae luminesce only during the first weeks of the rainy season, apparently attracting ant and termite alates which they then consume (Redford 1982).

Because of their distinctive structure, size, and abundance, the *C. cumulans* mounds almost certainly increase the number and diversity of ants, termites, and other obligate inquilines found in an area. In this regard they are what Gilbert (1980) terms a keystone species.

C. cumulans mounds also undoubtedly increase the diversity of facultative inquilines. The cracks in and under mounds serve as homes for opilionids, scorpions, centipedes, spiders, and myriapods; bees, wasps, mice (*Zygodontomys* sp.), lizards, and snakes (*Bothrops* sp.) live in old armadillo holes in the mound base. On one occasion I found a lesser anteater (*Tamandua tetradactyla*) asleep in a hole, a habit that the park guards also ascribe to jaguarundi (*Felis yagouaroundi*) and grison (*Galictis cuja*).

Several birds were seen to nest in holes in *Cornitermes* mounds—kestrels (*Falco sparverius*), peach-fronted parakeets (*Aratinga aurea*), and monjita (*Xolmis* sp.)—and park guards report a similar behavior for campo flickers (*Colaptes campestris*).

Other animals use *Cornitermes* mounds for a variety of purposes. Tiger beetles, ponerine ants, and lizards search the mound surfaces for food; birds of many species, most commonly caracaras (*Polyborus plancus*) and burrowing owls (*Athene cunicularia*), sit on the elevated spots to scan the surroundings. Seriamas (*Cariama cristata*) stand on *Cornitermes* mounds to sing their territorial songs, and giant anteaters use the rough surface as a place to rub their backs. For many of the animals in Emas Park, *C. cumulans* mounds serve as functional equivalents of trees.

In the structural simplicity of open grassland the large, long-lived *C. cumulans* mounds, both occupied and unoccupied, are an important feature of the ecology of many animals. In addition, the termites themselves are an important source of food for species ranging from ants to armadillos. Their omnipresent mounds are a vivid reminder of the importance of this keystone species in the grasslands of central Brazil.

Finally, it is interesting to note that the areas in which *Cornitermes* mounds appear to be most abundant are those most heavily grazed by cattle—both inside and outside the park. Cattle grazing or the presence of fire may serve to make such habitat more suitable for *C. cumulans*. The current policy of the park is to exclude both fire and grazing. It may, however, be advisable to practice controlled burning so as not to decrease the populations of *C. cumulans*. As Gilbert (1980) has pointed out, the loss of a keystone species would precipitate a cascade of local extinctions of obligate inquilines and would undoubtedly also severely affect those animals which use *C. cumulans* mounds more opportunistically.

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