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Nest plasticity of *Cornitermes silvestrii* (Isoptera, Termitidae, Syntermitinae) in response to flood pulse in the Pantanal, Mato Grosso, Brazil

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ABSTRACT. Nest plasticity of *Cornitermes silvestrii* (Isoptera, Termitidae, Syntermitinae) in response to flood pulse in the Pantanal, Mato Grosso, Brazil. The Pantanal is one of the largest wetlands in the world. Since many areas in Pantanal are flooded during part of the year, it is expected that plants and animals would have mechanisms for their survival during the flooded period. This study investigated the existence of differences in nest shape and inquilines of *Cornitermes silvestrii* in areas influenced by the flood pulse. We measured the volume, height, width, and height/width ratio of 32 nests in flooded areas and 27 in dry areas, and performed an one-way-Anova with the quasi-Poisson distribution to determine if there were differences in the nest measurements between the points. To analyze the relationship of nest inquilines to flood pulse and nest shape, we performed a regression with a Poisson distribution with the inquiline richness and flood pulse, and the above measurements. The nests of *C. silvestrii* in flooded areas were significantly higher than nests in dry areas, and had a larger height/width ratio. Colonies in periodically flooded areas would probably make a larger effort to extend their nests vertically, to maintain at least some portion of the structure out of the water and prevent the entire colony from being submerged. Neither the size of the nest nor the flood pulses influenced the assemblage of 11 species found in nests of *C. silvestrii*.

KEYWORDS. Insecta; inundation; nest shape; termites; wetland.

The Pantanal is a floodplain in the Paraguay River basin, in the center of the South American continent. It covers an area of 147,574 km^2, mostly in Brazil, but also partly in Bolivia and Paraguay (ANA 2013). It is one of the world's largest tropical wetlands (Junk & Da Silva 1999), and since the fauna and flora of the Pantanal are influenced by the Amazon, Cerrado (Brazilian savanna), Chaco and Atlantic Forest biomes, this is a region of extreme importance for biodiversity and conservation (Alho 2005).

The rainy season in the Pantanal extends from October through April, and concentrates 70% to 80% of the mean annual rainfall. However, the flood dynamics is much more variable, and some areas can remain submerged longer than six months. In Cáceres, Mato Grosso state, Brazil, the highest streamflow and flooding normally occur in March, near the end of the rainy season. In this region, the terrain is flooded during 29% of the year on average, mainly by the Paraguay River overflow (ANA 2013; Tucci 2004).

The flood period in the Pantanal is caused by the increase in groundwater level and river overflows that flood the lowlands and profoundly affect the local fauna and flora (Junk & Da Silva 1999). Mobile organisms can seek refuge from harsh conditions such as the Pantanal inundations. However, sessile organisms must remain in place, and a flood may be lethal to them (Begon *et al.* 2006). Because sessile organisms must tolerate the flood period or become locally extinct, mechanisms that allow them to survive during the flood period are expected (Adis 1997).

Termites (Isoptera) are eusocial organisms that live in colonies, and many species build hard nests to protect their colonies against predators and environmental disturbances (Noirot 1970). These colonies can be considered almost analogous to sessile or sedentary organisms, at least for moderate periods of time (5–10 years or more). The species of the genus *Cornitermes* are known for their conspicuous epigeal (above-ground) nests that are abundant in many environments, including the Pantanal (Emerson 1952; Cancello 1989). The members of this genus are considered keystone species in some ecosystems (Redford 1984), since their nests can harbor many animals, such as certain vertebrates and many other invertebrates (including other species of termites, here called inquilines). Therefore, the abundant presence of nests of *Cornitermes* increases the termite species richness of an area (Redford 1984).

Many of the species that are found in the nests of *Cornitermes* are facultative inquilines, and some may even build their own nests (Costa *et al.* 2009). Thus, it is a plausible hypothesis that the facultative inquilines would search for protection more often in areas with harsher conditions, such as the annually flooded areas of the Pantanal (Plaza 2013).

The nests of *Cornitermes* are typical for each species, although they display some intraspecific plasticity in their shape (Cancello 1989, 1991). The nests of *C. silvestrii* Emerson, 1949, for instance, are normally wide and low (Mathews 1977; Cancello 1989). This species is quite abundant in the Cáceres region, in both areas that flood and areas that do not flood (Plaza 2013). Our hypothesis was that both nest shape (or size) and inquiline species richness would differ in areas that flood, from those in areas that do not flood. This study aimed to investigate this hypothesis.

MATERIAL AND METHODS

The study was carried out in the municipality of Cáceres, Mato Grosso state, Brazil, in the Upper Pantanal micro-region (IBGE 2005). According to Köppen´s classification, the region has a Tropical Savanna (Aw) climate, with dry winters and rainy summers. The annual precipitation is 1,000–1,400 mm, with a maximum in January and a minimum in July (Brasil 1997).

The sampling was conducted between March and May 2012, in six areas near the Paraguay River. The six areas have the same flood pattern, including locations that flood annually (flood points) and locations that are not flooded by the river overflow (dry points). All areas were composed of dry and flood-prone pastures, and also by flood-prone savannas; only one area contained no dry savanna. The minimum distance between areas is 50 km, and the areas are located on farms at least 10 km^2 in size.

A total of 58 nests of *Cornitermes silvestrii* were measured and sampled for inquiline termite species, including 32 in flood-prone and 27 in dry areas. The height and base width of nests were measured, and used to calculate the approximate volume (semi-ellipsoid volume = $[(4/3*(\pi*\text{Height}*(\text{Width\textasciicircum 2})))/2]$) and height/width proportion (H/W) of each nest.

We used generalized linear models (GLMs) to summarize the relationships between the flood and dry points. To determine if there were differences in the nest measurements between the points, and if there was a difference in the inquiline species richness between the points with different flood patterns (dry and flood), we used a one-way-Anova with the quasi-Poisson distribution to correct the error distribution. To determine if any nest measurements affected the richness of inquiline termites, we used a regression with a Poisson distribution to relate the inquiline species richness (y) to the explanatory variables: x1, nest height; x2, width; x3, volume; and x4, H/W proportion. To detect whether the model was overdispersed, we calculated the dispersion coefficient, i.e., the ratio of the deviance over the residual degrees of freedom (Matthiopoulos 2011).The statistical analyses were performed with the software R v.2.15, using the “GLM” function of the package “stats” to fit the generalized linear models (R Development Core Team 2012).

RESULTS

At the flood points, the nests of *Cornitermes silvestrii* were, in average, 22.1 cm higher, 1.61 cm narrower (smaller width), and 0.024 m^3 larger in volume than at the dry points. However, only the height difference was significant (Fig. 1A; Table I). Consequently, the H/W proportion was also significantly higher at flood points than at dry ones (0.63 times higher) (Fig. 1D; Table I), however nest width and volume was not significantly (Figs. 1B-C; Table I).

Only five of the 32 nests of *C. silvestrii* at flood points had a H/W proportion less than 1 (one), i.e., 84.4% of the nests affected by inundation were higher than wide. At dry points, the number of higher-than-wide nests was also relatively large, but only 10 (37%) out of the 27 nests measured.

Eleven species of termites were collected as inquilines from the 58 nests. The species *Silvestritermes euamignathus* (Silvestri, 1901) was found exclusively at flood points, and *Cornitermes bequaerti* Emerson, 1952 and *Diversitermes diversimiles* (Silvestri, 1901) only at dry points (Table II). However, the inquiline species richness in nests of *C. silvestrii* showed no significant difference between the flood and dry points (Table I). Similarly, the inquiline species were not related to any of the nest variables: nest height (p = 0.41), width (p = 0.74), volume (p = 0.98) and H/W proportion (p = 0.20).

Table I. Means of variables of the nests of *Cornitermes silvestrii* (59 nests) and significance value (p-value) between flood and dry points in the Cáceres region of the Pantanal, Mato Grosso, Brazil.

	Height (cm)	Width (cm)	Volume (m^3)	Height/Width proportion (H/W)	Inquiline richness
Flood points	64.840	45.000	0.088	1.570	2.220
Dry points	42.740	46.620	0.064	0.940	1.850
p-value	>0.001	0.743	0.473	>0.001	0.779

Table II. Species list of inquiline termites found in nests of *Cornitermes silvestrii* in the Cáceres region of the Pantanal, Mato Grosso state, Brazil.

Family	Subfamily	Species	Flood	Dry
Rhinotermitidae	Coptotermitinae	*Coptotermes* sp. 1	3	1
Rhinotermitidae	Coptotermitinae	*Coptotermes* sp. 1	7	4
Termitidae	Apicotermitinae	*Anoplotermes* sp. 1	3	3
Termitidae	Apicotermitinae	*Anoplotermes* sp. 2	6	1
Termitidae	Apicotermitinae	*Anoplotermes* sp. 3	4	2
Termitidae	Apicotermitinae	*Anoplotermes* sp. 4	4	5
Termitidae	Nasutitermitinae	*Diversitermes diversimiles* (Silvestri, 1901)	–	6
Termitidae	Syntermitinae	*Cornitermes bequaerti* Emerson, 1952	–	3
Termitidae	Syntermitinae	*Silvestritermes euamignathus* (Silvestri, 1901)	3	–
Termitidae	Termitinae	*Amitermes amifer* Silvestri, 1901	7	5
Termitidae	Termitinae	*Termes nigritus* (Silvestri, 1901)	8	1

DISCUSSION

Nests of *C. silvestrii* are commonly described in the literature as wider than high, normally in comparison to another species of the same genus, *C. cumulans* (Kollar, 1832), which occurs in extensive sympatry with *C. silvestrii*, but has nests that are normally higher than wide (Cancello 1989; Fernandes *et al.* 1998). Nevertheless, the colonies of *C. silvestrii* established at points that are flooded annually had significantly higher nests and, consequently, a higher H/W proportion than the nests of those colonies that established themselves in places where there is no influence of inundation, in the Cáceres region. Although some nests at dry points had the same pattern, they comprised a significantly smaller proportion of the total than at the flood points.

Grassé (1958) described three phases of nest development in *C. cumulans*: 1) hypogeous (entirely subterranean), 2) hypogeous with external mound, and 3) hypogeous-

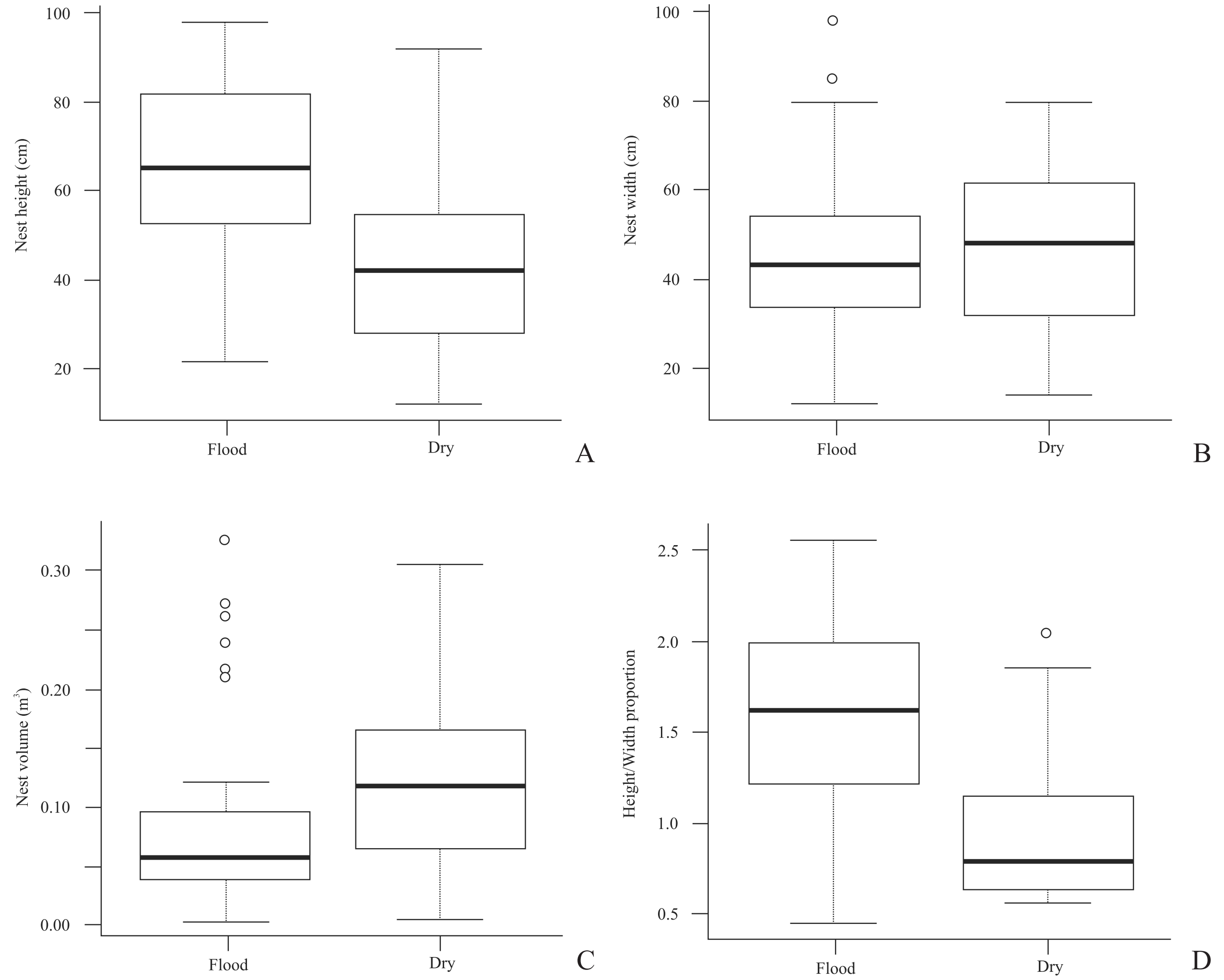

Fig. 1. Boxplot with flood and dry points by nest of *Cornitermes silvestrii* (59 nests measured) for (A) nest height ($p < 0.001$), (B) nest width ($p = 0.734$), (C) nest volume ($p = 0.197$) and (D) height/width proportion ($p < 0.001$) in the Cáceres region of the Pantanal, Mato Grosso state, Brazil.

epigeous (below and above ground). The nests of the colonies of *C. silvestrii* also pass through these three phases (Mathews 1977, under the name *C. snyderi* Emerson, 1925), with the first two being the most critical for colonies established at points that are annually flooded.

The durations of these phases are not well known, but it is unlikely that a colony would pass through the first two phases rapidly enough to prevent the colony from spending at least one rainy season underwater in this part of the Pantanal. The beginning of streamflow and flooding in the Cáceres region normally occurs in December/January (ANA 2013), and the dispersal flights of *Cornitermes* normally occur at the beginning of the rainy season (Bourdereau *et al.* 2011), in October/November in the states of São Paulo and Goiás, Brazil. Thus, the colony would need to pass through foundation and phases 1 and 2 in less than three months, or it is likely that at least those nests in phases 1 and 2 have some kind of waterproofing mechanism. Mathews (1977) described the nest of *C. silvestrii* in phase 2 with a subterranean "cylinder of hardened mineral earth... lined with stercoral material … and surrounded by a narrow air space separating it from the surrounding soil". It is possible that this stercoral material functions as waterproofing.

The nests of *C. silvestrii* at flood points tended to be higher than wide. Thus, even with a subterranean waterproofing mechanism, this increase in height is probably a local adaptation of this species in phase 3. With higher nests, the colony can maintain at least part of the nest structure out of the water during the flood period, preventing the entire nest in phase 3 from becoming completely submerged.

Nest plasticity has also been documented for other termite species, and is normally related to a combination of factors ranging from environmental, such as thermoregulation or adaptation to the soil type, to factors such as gas exchange between the nest and the outside air, or even as the result of self-organized behaviors (Roisin & Korb 2011). For instance, Cancello (1991) described two kinds of nests for another species of the same genus, *C. bequaerti*, with one kind of nest with many narrow chimneys or open channels, and another with only one wide and tall chimney.

Termite nest plasticity influenced by the colonization of flood-prone areas has also been documented in Australia. *Amitermes laurensis* (Mjöberg, 1920), *A. vitiosus* (Hill, 1935) and *A. meridionalis* (Froggatt, 1898) are the so-called "magnetic termites", which build wall-shaped nests in which the main axis is oriented north-south. The first two species (*A. laurensis* and *A. vitiosus*) build this kind of nest in flood-prone areas, but in dry areas they build normal semi-ellipsoid nests (Gay & Calaby 1970).

Studying *A. laurensis*, Ozeki *et al*. (2007) tested the hypothesis that colonies with a similar nest format would also be genetically closely related. However, they found that the genetic distance was related only to the geographic distance, not to the nest format. This means that genetically related colonies can build different types of nests depending on where the colony establishes itself (Ozeki *et al.* 2007). Their results reinforce the idea that the plasticity in nest construction seems to be much more related to the environment itself than to any presumed genetic differences between different populations (such as those from dry and flood areas, in the present case, for instance), although we have not investigated this matter.

In the Cáceres region of the Pantanal, in addition to the Paraguay River overflow, the groundwater also rises during the flood period (Junk & Da Silva 1999), which may prevent termites from finding refuge in the soil. Therefore the termites must find refuge in other ways, such as changing the nest structure or, as shown in the present study, making their nest taller, with at least part of it above the water level in the flood period.

Regarding the inquiline species richness in nests of *C. silvestrii*, we hypothesized that it would differ in areas that flood, from those in areas that do not flood. Although the inquiline species richness showed no significant difference between the flood and dry points (Table I), one may consider the different biology of the 11 species found as inquilines. The facultative inquilines *C. bequaerti* and *S. euamignathus* were collected in different situations, the former only in dry areas and the latter exclusively in flood areas. Importantly, *C. bequaerti* always construct their own nests, and some individuals collected inside other nests may represent only a foraging group. Therefore it is expected that *C. bequaerti* would be collected only in the dry area, as this species does not build nests in flood areas. *Silvestritermes euamignathus* is known to build their own nest, but can also be inquiline, "remodeling" the host nests (Rocha *et al.* 2012), and was found exclusively at flood points. This suggests a particular strategy of this species in flood areas, to live as an inquiline rather than constructing its own nest. *Diversitermes diversimiles* was found at dry, but not at flood points, and as the species is usually collected from abandoned nests of other species or in the litter, it would be more plausible to find it in dry areas.

It is not possible to say anything about the members of Apicotermitinae, as the species were not identified and the biology of this group is little known. *Termes nigritus* was found eight times at the flood points, but only once at a dry point. The taxonomy of the genus is presently confused, and a revision is necessary to understand the limits of the species. For this reason, it is not possible at present to state whether this species may construct its own nest or not. The case of *Amitermes amifer* is similar, as the species was never recorded previously in the Pantanal, and Constantino (2005) did not mention this species for the cerrado formation in MT. A more comprehensive survey with careful observations on the biology of the termites from the Pantanal would be necessary to discuss in depth the relationship of the inquilines, including the facultative inquilines, and the flood pulse.

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