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Factors influencing the responses to nest damage in the African weaver ant. *Oecophylla longinoda* (Latreille)

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Abstract. Responses of the African weaver ants (*Oecophylla longinoda*) to nest damages were studied in the field in Nigeria. During the wet season, the ants responded to nest damages almost unexceptionnally by a quick onset of nest-repairing behaviour. The latencies to the start of nest-repairing activities (L_N) did not depend on the size of the damage, but they were significantly shorter during the night, and positively correlated with ambient temperature. During the dry season, the ants responded to large nest damages mainly by abandonning the nest. In the case of medium size damages, the onset of nest-repairing behaviour was equally rapid as during the wet season, but in the case of small damages it was sometimes greatly delayed (up to three hours). The values of L_N did not differ between the nighttime and the remaining times of the day, and they were not correlated with ambient temperature.

Key words: nest, season, daily pattern, temperature, *Oecophylla longinoda*, Formicidae

INTRODUCTION

Weaver ants of the genus *Oecophylla* are highly evolved formicine ants famous for their habit of using their own larvae as shuttles to weave together living leaves into large nests (Doflein 1905, Hingston 1927, Ledoux 1950, Way 1954, Hemmingsen 1973, Hölldobler and Wilson 1983). Presently, the genus *Oecophylla* consists of two living species only: the green tree ant, *Oecophylla smaragdina* (F.) of south-eastern Asia, Melanesia and Australia, and the African weaver ant, *Oecophylla longinoda* (Latreille) of tropical Africa. Societies of these ants are monogynous (there is a single queen in each colony), but they are usually highly polydomous (a single colony occupies numerous nests). Large societies of *O. longinoda* occupy hundreds of nests spread over an entire tree crown or even over a group of several trees (Way 1954, Vanderplank 1960, Hölldobler 1983, Hölldobler and Wilson 1990, Dejean and Beugnon 1991).

Nest-building and nest-repairing behaviour of ants of the genus *Oecophylla* is often considered as one of the peaks of the ability for cooperative behaviour in all animal kingdom (Hölldobler and Wilson 1983, 1990). It was investigated in numerous studies, focused mainly on details of nest-constructing behaviour, and on division of labour between the workers engaged in that process (Doflein 1905, Cole and Jones 1948, Weber 1949, Ledoux 1950, Chauvin 1952, Way 1954, Hemmingsen 1973, Hölldobler and Wilson 1977, 1983, 1990). As revealed by these studies, nest-repairing activities involve two main stages: first, pulling edges of leaves together, and then, binding them into place with thousands of strands of larval silk. Drawing leaves together may involve the cooperation of several hundreds of workers, which form living chains of up to twelve individuals to bridge the gap between the leaves, each ant gripping with its mandibles the petiole of the ant in front. Then, all parallel chains are pulling together, often in a strikingly coordinated manner. When the leaves have been manoeuvred into a proper, tentlike configuration, some of the ants remain on them holding them in place, and other workers bring to that building site nearly mature larvae to use them subsequently as sources of silk to bind the leaves together (Doflein 1905, Ledoux 1950, Way 1954, Hemmingsen 1973, Hölldobler and Wilson 1977, 1983).

Although the details of nest-building and nest-repairing behaviour of *Oecophylla* ants are already described in a fairly detailed way, factors controlling that process remain still relatively little known. In our present study, we report the results of an experiment carried out in the field in Nigeria in order to throw some light on factors influencing in *O. longinoda* the latency to the onset of cooperative nest-repairing behaviour. In particular, we investigated the effects of size of the damage, season and temperature. In addition, we were carrying out our tests according to a temporal schedule permitting us to collect also some preliminary data concerning the daily pattern of the investigated phenomena (i.e. speed of onset of nest-repairing behaviour, and temperature). We were particularly interested in possible differences between the responses of *O. longinoda* to nest damages during the night and during the remaining times of the day. The existence of nocturnal peak of readiness to display nest-building behaviour is controversial in the case of *O. smaragdina*, and in the case of *O. longinoda* the daily pattern of readiness to display nest-building and nest-repairing activities is so far almost totally unknown (Hemmingsen 1973, Hölldobler and Wilson 1990, see also Discussion).

METHODS

The study was carried out in the field in Nigeria, in the garden of the campus of the University of Nigeria in Nsukka. The tests were carried out during two periods: during the wet season (5-20 August 1982), and during the dry season (2-18 February 1983). As subjects, we used the ants of a very large polydomous colony of *O. longinoda* spread over a group of eight cashew trees (*Anacardium occidentale* L.), each about 6-8 m high. For our tests, we choose the nests of similar size (each about 10 cm in diameter, and constructed of 2-3 leaves). They were all situated approximately 2-2.5 m from the tree trunk, and 1.5-2 m above the ground.

The nests were subjected to three types of damages: (1) opening the nest along its external seam to about 1/4 of its length (small size nest damage); (2) opening it to about a half of its length (medium size nest damage); lastly, (3) opening it along its full length (large size nest damage). To make these damages, we were first cutting lengthwise the external seam of the nest by means of a small but very sharp knife made of a razor blade mounted on a wooden shaft, and then we forced the external leaves apart to form an about 1-1.5 cm wide gap.

Altogether, 72 nests were damaged. During each season, 12 nests were subjected to each of the three types of nest damage. In such a way, the following six experimental groups were created:

Group 1 (small size damage, wet season);
Group 2 (medium size damage, wet season);
Group 3 (large size damage, wet season);
Group 4 (small size damage, dry season);
Group 5 (medium size damage, dry season);
Group 6 (large size damage, dry season);

To collect at the same time preliminary data on the daily pattern of investigated phenomena, the nests were damaged at four times of the day, labelled, respectively, as "morning", "noon", "evening" and "midnight": between 6.00 and 8.00, between 12.00 and 14.00, between 18.00 and 20.00 and between 0.00 and 2.00. To reduce to some degree the potential variability of our results related to varying degree of exposure of damaged nests to sun radiation, out of 3 nests damaged at the same time of day one was always situated on the eastern side of the tree crown, one on its southern side, and one on its northern side. Finally, to avoid possible interfering effects of simultaneous damaging of two nests situated too close one to another, nests damaged simultaneously were always situated on different trees.

In each case, we recorded:

(1) the latency to the onset of cooperative nest-repairing activities, i. e. to the beginning of drawing together of leaves forced apart by the experimenters, by more than one ant (L_N), and

(2) ambient temperature measured in the shadow in the immediate proximity of the damaged nest (T).

In the cases in which the ants did not respond to nest damage by nest-repairing behaviour, we checked whether the nest in question was still occuppied by them or deserted on subsequent days. The nests abandonned by the ants can be very easily distinguished from those occupied by them, as their leaves start to die very soon.

In the statistical analysis of our results we used Fisher exact probability test, two-tailed Mann-Whitney U test, and Spearman rank correlation test.

RESULTS

As shown in Fig. 1, *O. longinoda* most often (in 86.1 % of the cases) responded to nest damage by nest-repairing behaviour. However, in 10 cases (13.9%) the ants abandonned the damaged nest (Fig. 1*C* and *F*).

The decision whether to repair a damaged nest or to abandon it depended on two main factors: size of the damage and season. Nests subjected to small or medium size damage were never deserted (Fig. 1 *A*, *B*, *D* and *E*). Moreover, 9 out of 10 recorded cases of abandonning of a damaged nest (90%) took place during the dry season (Fig. 1*C*).

During the wet season, the responses of *O. longinoda* to nest damages showed high uniformity: with a single exception, the ants responded to nest damage by relatively rapid onset of cooperative nest-repairing activities (Fig. 1*A*-*C*). The latency to the onset of nest-repairing behaviour (L_N) ranged from 5 to 37 minutes, and it was not influenced by the size of the damage: it did not differ significantly between any of the three groups corresponding to various categories of damages (two-tailed Mann-Whitney U test: NS).

During the wet season the values of L_N showed, however, significant positive correlation with ambient temperature (ranging from 27^o to 32^{o}C) (Spearman rank correlation coefficient rho=0.339, P<0.05).

The values of L_N obtained during the night were also significantly shorter than those obtained at all

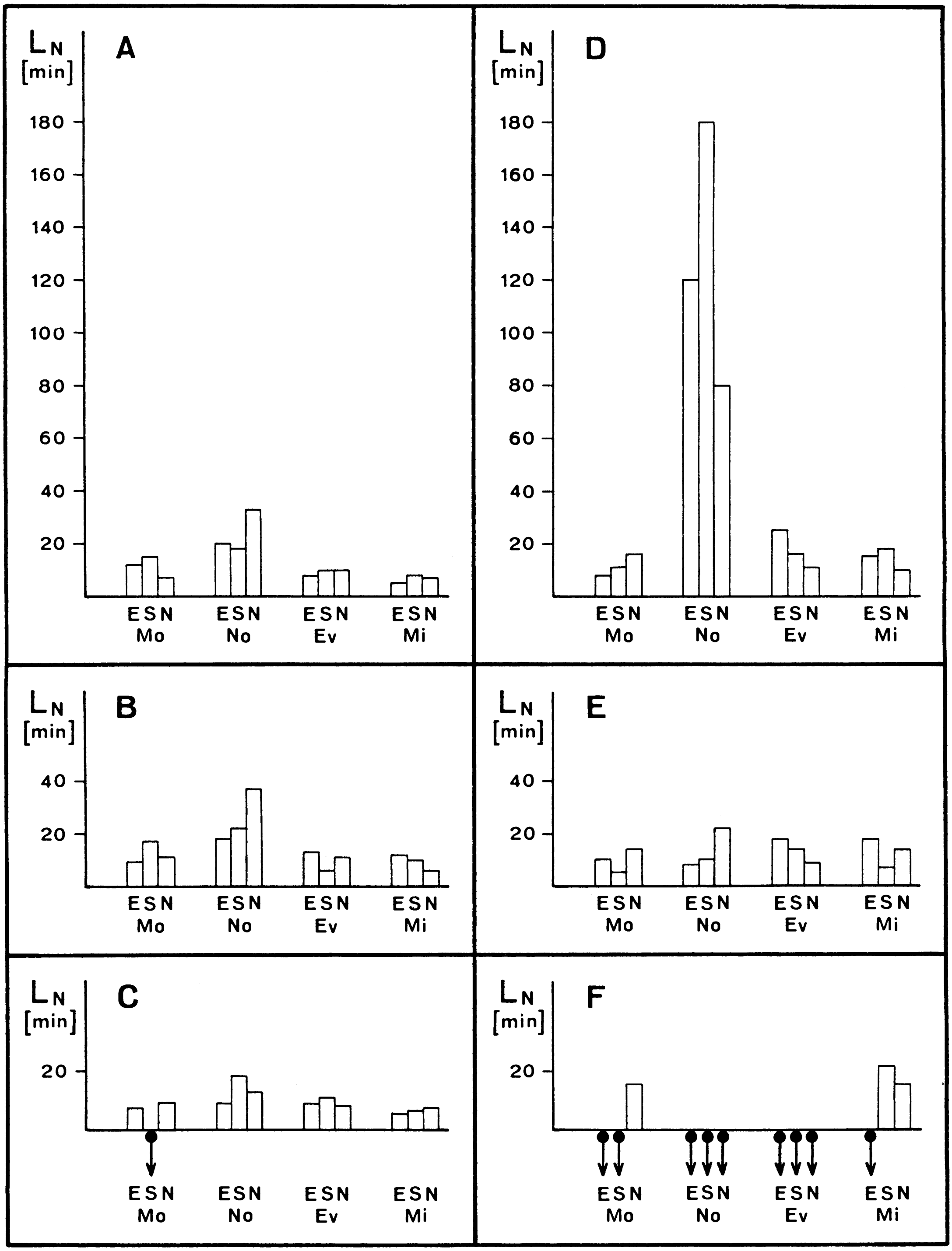

Fig. 1. The latencies to the onset of cooperative nest-repairing behaviour (L_N) shown by workers of the African weaver ant (*Oecophylla longinoda*) in response to nest damages of various sizes carried out during the wet and dry seasons. *A*, responses to small nest damages recorded during the wet season; *B*, responses to medium size nest damages recorded during the wet season; *C*, responses to large nest damages recorded during the wet season; *D*, responses to small nest damages recorded during the dry season; *E*, responses to medium size nest damages recorded during the dry season; *F*, responses to large nest damages recorded during the dry season. Mo, No, Ev, Mi: respectively, morning (6.00-8.00), noon (12.00-14.00), evening (18.00-20.00), and midnight (0.00-2.00). E, S, N: respectively, eastern, southern and northern exposure of the damaged nest. Arrows pointing downwards indicate the deserting of the damaged nest.

remaining times of the day (two-tailed Mann-Whitney U test: $P<0.01$) (Fig. 2). Significant shortening of latency to the onset of nest-repairing behaviour observed during the night might have been related to nocturnal decrease of ambient temperature, also significantly lower during the night than at the remaining times of day (two-tailed Mann-Whitney U test: $P<0.01$) (Fig. 2).

During the dry season, the responses of *O. longinoda* to nest damages were much more variable than during the wet season, and their character was strongly influenced by size of the damage (Fig. 1*D-F*). Whereas small and medium size nest damages always triggered the onset of nest-repairing behaviour, large damages have been repaired only in 3 out of 12 cases (25%). Interestingly, in two out of these three cases the nest was damaged at night, at relatively low ambient temperature (22°C and 23°C, respectively), and in the remaining case nest damage was carried out in the morning, at still lower ambient temperature (20°C; the nest in question was situated on the northern side of a cashew tree) (Fig. 1*F*). In the majority of the cases (9 out of 12; 75%), large nest damages carried out during the dry season led, however, to deserting the nest by the ants. In three out of these cases ambient temparature was equally low as in the case of the nests which have been repaired by the ants (22°C); however, in the majority of the cases (6 out of 9) it was much higher, ranging from 27°C to 37°C. None of the nests subjected to large size damage at about noon or in the evening has been repaired (Fig. 1*F*).

The ratio of the cases in which nest damage triggered the onset of nest-repairing activities to those in which it was followed by the abandonning of the nest did not differ significantly between any of the groups tested during the wet season (Groups 1 - 3), nor between any of these groups and Group 4 and 5 (small and medium size nest damages carried out during the dry season, respectively) (Fisher exact probability test: NS). In contrast, that ratio differed highly significantly between Group 6 (large size nest damage carried out during the dry season) and all remaining groups (Fisher exact probability test: $P=0.0014$ for the comparison between Group 6 and

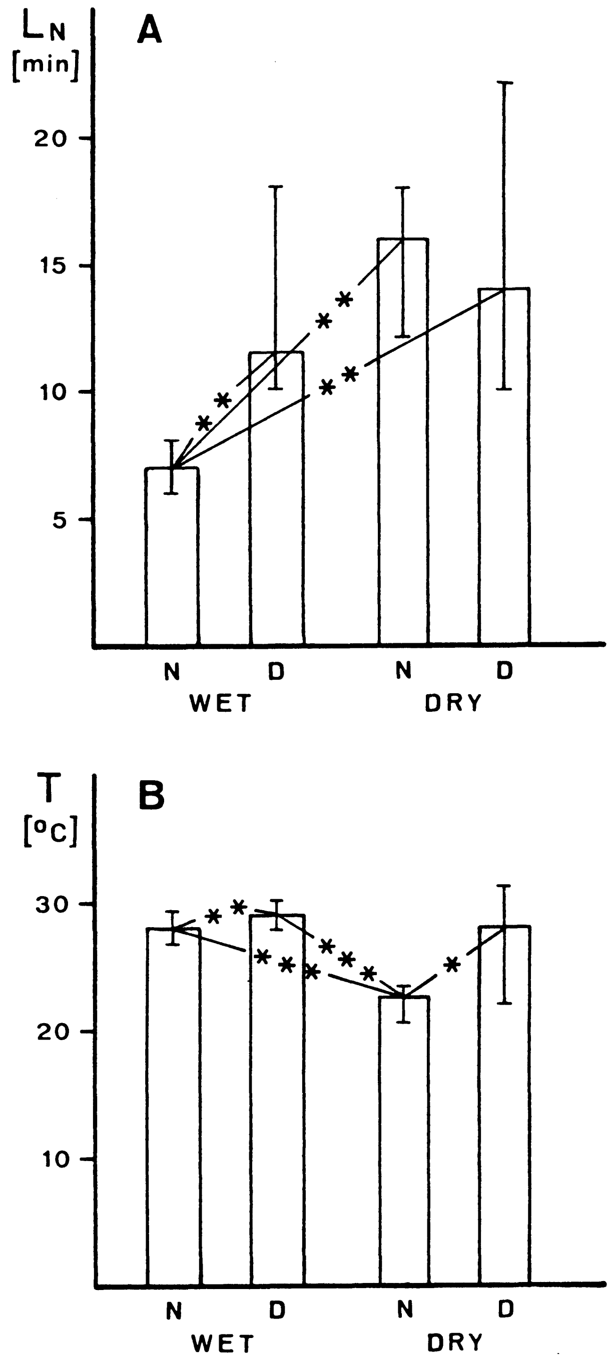

Fig. 2. *A*, median values (± upper and lower quartiles) of the latency to the onset of cooperative nest-repairing behaviour (L_N), as recorded during the night (N) and at all remaining times of day (D) during the wet season (WET) and during the dry season (DRY). *B*, median values (±upper and lower quartiles) of ambient temperature (T) as measured in shadow close to each of the damaged nests. Lines joining pairs of bars indicate statistically significant differences as calculated by means of the two-tailed Mann-Whitney U test: $*P<0.05$; $**P<0.01$; $***P<0.001$.

Group 3, and $P=0.0002$ for all remaining comparisons (1 vs. 6, 2 vs. 6, 4 vs. 6 and 5 vs. 6)).

During the dry season, the latency to the onset of nest-repairing behaviour took values within much wider range than during the wet season (5-180 min, as compared to 5-37 min during the wet season). Although the latencies to the onset of nest-repairing behaviour did not differ significantly between the two groups in which the nests have been subjected, respectively, to small and medium size nest damages (Group 4 and 5, respectively), they were nearly significantly higher in Group 4 than in Group 5 (two-tailed Mann-Whitney U test: $P=0.06$). The values of L_N obtained for Group 4 (small nest damages carried out in the dry season) were also significantly higher than those obtained for Group 1 and Group 3 (respectively, small and large nest damages carried out in the wet season) (two-tailed Mann-Whitney U test: $P<0.05$ and $P<0.01$, respectively). There were, however, no significant differences between Group 4 (small nest damages carried out during the dry season) and Group 2 (medium size nest damages carried out during the wet season) (two-tailed Mann-Whitney U test: NS). The differences between Group 4 and Groups 1, 3 and 5 arose as a consequence of exceptionnally high values of L_N recorded for the three nests of Group 4 damaged at about noon. Whereas in all remaining cases L_N ranged from 5 to 37 min, in these three cases it ranged from 80 to 180 minutes (Fig. 1*D*).

In contrast to that, no significant differences were found between the values of L_N obtained for Group 5 (medium size nest damages carried out during the dry season) and any of the three groups tested during the wet season (two-tailed Mann-Whitney U test: NS). Lastly, the values of L_N obtained for Group 6 (large size nest damages carried out during the dry season) were not compared with the values of that index obtained for the remaining experimental groups, as in that group the ants responded to nest damage by nest-repairing behaviour only in three cases.

In the dry season, ambient temperature (T) took values within a wider range than during the wet season (20-36^{o}C, as compared to 27-32^{o}C during the wet season). However, contrary to the wet season, in the dry season L_N and T were not correlated (Spearman rank correlation coefficient rho = 0.244; NS).

Also contrary to the wet season, during the dry season the values of L_N recorded at night did not differ significantly from those recorded at all remaining times of day (two-tailed Mann-Whitney U test: NS), in spite of the fact that, similarly as in the wet season, the ambient temperature (T) was significantly lower during the night than at the remaining times of the day (two-tailed Mann-Whitney U test: $P<0.05$) (Fig. 2). No significant differences were found between the values of L_N recorded during the night in the dry season, at the remaining times of day in the dry season, and at the remaining times of day in the wet season (two-tailed Mann-Whitney U test: always NS). However, all these values were significantly higher than those recorded during the night in the wet season (two-tailed Mann-Whitney U test: $P<0.01$ for all three comparisons) (Fig. 2).

DISCUSSION

Our present data demonstrate, as far as we know for the first time, that the repertoire of responses of African weaver ants (*Oecophylla longinoda*) to nest damages involves at least three alternative tactics: (1) rapid onset of nest-repairing behaviour, (2) delayed onset of nest-repairing behaviour, and (3) abandonning of the nest. Our results show also that the choice between these tactics depends mainly on two groups of factors: on one hand, size of the damage, and on the other hand, season and time of day. The most frequent response to nest damage consisted in relatively rapid (up to about 30 minutes) onset of nest-repairing activities. The deserting of damaged nests was observed solely during the dry season, being a typical response to large nest damages carried out during the daytime. Finally, the important delay of the onset of nest-repairing activities was also observed solely during the dry season, being a typical response to small nest damages carried out at about noon.

As far as we know, factors influencing the decision whether to repair a damaged nest or to abandon it were so far never investigated in *Oecophylla* ants. However, nest-repairing behaviour of these ants was already studied by numerous authors (see Introduction). In particular, Chauvin (1951) made some preliminary measurements of latencies to the onset of nest-repairing behaviour during a field experiment carried out in Ivory Coast. In his experiment, the arrival of the first worker starting to pull together the edges of damaged leaves occurred on the average after 1.9 minutes following the damage. However, as he kept removing these ants to record subsequently the latency to the arrival of the second worker engaged in leaf pulling, he could not measure the latency to the onset of cooperative nest-repairing, as we did in our study.

The phenomenon of nest deserting is also known in the African weaver ants. According to Ledoux (1950), *O. longinoda* abandon a part of their nest or the whole nest when the leaves of which it was built start to die, because such leaves cease to produce enough vapour to maintain a sufficiently high level of relative air humidity inside the nest to assure the survival of larvae. Way (1954) carried out a long-term observation of a large colony of *O. longinoda* in Zanzibar, and discovered that the ants of that colony were occupying each of their nests only during 85 days on the average, and then deserted it in response to the death of the majority of its leaves. Vanderplank (1960) described also the deserting of nests by *O. longinoda* in response to certain insecticidal treatments.

Our results demonstrate that in *O. longinoda* in Nigeria the tendency to abandon damaged nests depends in a very important degree on the season. As reported by Way (1954) and Vanderplank (1960), in Zanzibar abandonning of nests by *O. longinoda* and their choice of sites for building new ones is also highly influenced by seasonal factors. Colonies of these ants keep shefting their nests alternatively to the northern and southern sides of trees just after each equinox, most probably to keep them better exposed to the sun. This is one of the most known examples of regular seasonal migrations of ant colonies (Hölldobler and Wilson 1990).

Another important finding provided by our experiment is that in *O. longinoda* not only the overall choice of the tactic of response to nest damage, but also the speed of the onset of nest-repairing behaviour is highly influenced by seasonal factors. During the wet season, the latencies to the onset of nest-repairing behaviour were positively correlated with ambient temperature, and they were significantly lower during the night, possibly also in response to decreased ambient temperature. No such phenomena were observed during the dry season. High uniformity and temperature-dependence of the speed of the onset of nest-repairing behaviour observed during the wet season, and the absence of these phenomena in the dry season, may be interpreted hypothetically in terms of relative uniformity and stability of other weather factors during the wet season, as opposed to their much higher variability in the dry season. It must be remembered that although the workers of weaver ants are thermophilous and fairly resistant to dessication (Greenslade 1972), the larvae of *O. longinoda*, used as sources of silk during the final stages of nest-repairing process, are both highly susceptible to dessication (Ledoux 1950) and much less resistant to high temperature than adult ants: according to Vanderplank (1960), already at 33.3°C they fail to develop and die. From the point of view of temperature and humidity requirements of weaver ant larvae, in the wet season weather conditions are as a rule much more favourable for nest-repairing activities on the surface of the nest than during the dry season, mainly because relative humidity of the air is high and relatively stable, and direct exposure of nests to sun radiation is absent or rare. High uniformity of responses of *O. longinoda* to nest damages observed during the wet season is thus most probably related to relatively high uniformity of these two meteorological factors. Similarly, the variability of responses of these ants to nest damages, and the absence of their significant temperature-dependence in the dry season may be related to prevailing masking influence of fluctuations of these factors. Such interpretation of our results is, however, hypothetical, and should be tested experimentally.

The results of our study provide not only further important evidence that seasonal factors are of major importance in controlling the behaviour of *O. longinoda*, but also some preliminary data on the daily pattern of readiness of these ants to carry out nest-re-pairing activities. Circadian activity rhythms of *Oecophylla* ants are relatively well known: it is commonly agreed that these ants are active during both day and night, but that they tend to show diurnal peaks of activity (for a review see Dejean 1990). At the same time, daily patterns of nest-building and nest-repairing activities of these ants remain so far relatively little known [for reviews see Hemmingsen (1973) and Hölldobler and Wilson (1990)]. As observed by Hemmingsen (1973), *O. smaragdina* in Thailand are very rarely weaving on the surface of their nests in the daytime, but that behaviour occurs frequently at night. However, in Queensland (Australia) *O. smaragdina* are frequently engaged in exterior weaving during the day (Hölldobler and Wilson 1990). Frequent exterior weaving in the day time was also observed in a captive colony of *O. longinoda* kept in a well lit laboratory; however, the daily pattern of weaving activities of *O. longinoda* in the field remains so far largely unknown (Hölldobler and Wilson 1990).

Our present data show that in *O. longinoda* in Nigeria the readiness to start the initial stage of nest-repairing process (pulling together edges of leaves separated by the experimenters) tends to be higher at night than at the remaining times of day. In the wet season, the onset of these activities was fairly rapid during both day and night, but we observed, nevertheless, a significant nocturnal shortening of the latencies to the start of nest-repairing process. During the dry season, large nest damages carried out in the daytime were practically never repaired, and the repairing of small damages carried out at about noon was very considerably delayed. However, our data on daily patterns of readiness to start nest-repairing process must be considered as preliminary, and they should be supplemented by further experimental evidence before drawing any ultimate conclusions.

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