Naturwissenschaften (2001) 88:343–346
DOI 10.1007/s001140100245

SHORT COMMUNICATION

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Seasonal patterns in the orientation system of the migratory ant *Pachycondyla marginata*

Received: 11 December 2000 / Accepted in revised form: 8 June 2001 / Published online: 13 July 2001

Abstract Route directions of migrations by the neotropical termite-hunting ant *Pachycondyla marginata* at a forest reserve in Southeast Brazil were analysed by circular statistic. Colony movement patterns were compared between the rainy/hot and dry/cold seasons. Migrations during the dry/cold season are significantly oriented 13° with the magnetic North–South axis, while rainy/hot migrations do not exhibit a preferred direction. This result is discussed considering the hypothesis that *P. marginata* ants may use the geomagnetic field as an orientation cue for migrations in the dry/cold season. The presence of magnetic iron oxides in the head and abdomen of *P. marginata* is consistent with this suggestion.

The South American ant species *Pachycondyla marginata* (Roger) is widely distributed in several regions of Brazil (Kempf 1972). As several other members of the subfamily Ponerinae (see Hölldobler and Wilson 1990), *P. marginata* is an obligate termite predator. In Southeast Brazil, *P. marginata* conducts well-organised predatory raids toward nests of its only prey species: the termite *Neocapritermes opacus* (Leal and Oliveira 1995). The region in Southeast Brazil where Leal and Oliveira (1995) carried out their study has two well-defined seasons: a dry/cold season from April to September and a rainy/hot season from October to March. Target termite nests are up to 38 m from the ant colony. Raids on termite nests occurred both by day and by night, and could last for more than 24 h. *P. marginata* also presents a migratory behaviour, relocating the nest sites at irregular time intervals to distances of up to 97 m. The nest relocations last about 2 days and usually start in the afternoon and continue throughout the night until the next morning. Given that colonies resume nest relocation late in the afternoon of the second day, most of the migratory process takes place under darkness conditions.

Raiding and migratory activities appeared to be affected by seasonal factors (Leal and Oliveira 1995). Raids lasted significantly longer and covered significantly shorter distances during the rainy/hot season than in the dry/cold season. Colonies hunted more frequently in the dry/cold season. Migration distances were significantly shorter in the rainy/hot season. Group-raids and migrations by *P. marginata* colonies covered greater distances during the dry/cold season, and this may be related to a decrease in the availability of termites during this season (Leal and Oliveira 1995; see also Hölldobler et al. 1996).

Since magnetic nanoparticles have been found in *P. marginata* (Acosta-Avalos et al. 1999), the hypothesis of geomagnetic orientation can be raised, as in honeybees. Additionally, visual inspection of the multiple migratory diagrams of *P. marginata* colonies (Leal and Oliveira 1995; Hölldobler et al. 1996) suggests that their migratory routes follow directions near the magnetic North–South axis. This encouraged us to analyse the orientation migratory data collected in the study of Leal and Oliveira (1995). In this paper, statistical analysis was used to investigate orientation preferences in the migratory directions. Given that migratory movements presented a seasonal variation, we performed a detailed analysis of the route directions taken by migrating colonies during the year, and tested for differences between seasons.

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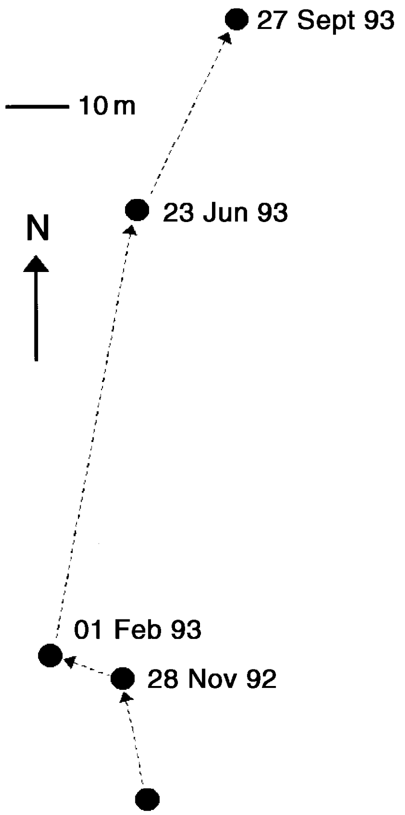

Fig. 1 Map showing the migratory (*dashed arrows*) routes of a marked colony of *Pachycondyla marginata*, from November 1992 to September 1993, in a forest area in SE Brazil. *Black dots* indicate nest sites

Fieldwork was carried out in a semi-deciduous forest of the Santa Genebra Reserve (22°49'S, 47°06'W) at Campinas, Southeast Brazil. From October 1992 to September 1993, 39 migrations from 25 marked colonies were followed. For each colony migration, the distance (metres) and the direction (degrees) were registered. Direction angles were measured with a compass, and were determined by a straight line linking the old with the new nest. No compensation was made for the local magnetic declination. Circular statistic of the migratory directions were performed using Oriana software (Kovach Computing Services). In this statistic, angular data can be of two types: unidirectional and bi-directional, which are known as vectorial and axial, respectively. To evaluate the significance of the circular statistic results, a Rayleigh test was performed.

During the observation period some colonies migrated just once whereas others migrated several times. Figure 1 shows an example of a colony migrating on different dates. It is reasonable to suppose that migrations

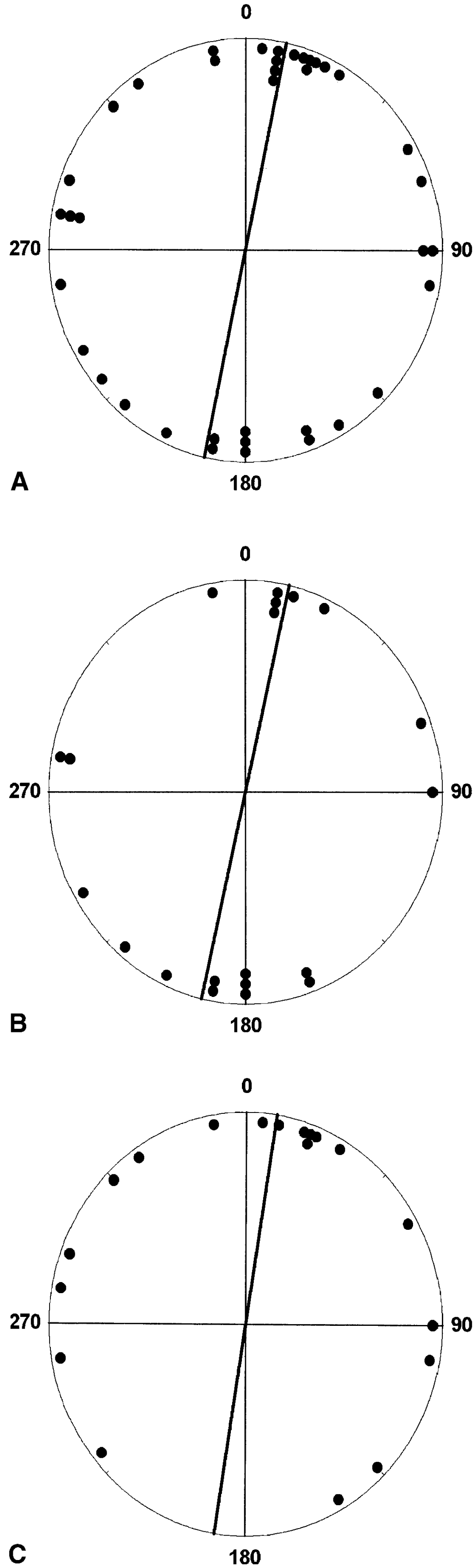

Fig. 2a–c Circular distributions of migratory data of marked colonies of *Pachycondyla marginata*, from November 1992 to September 1993, in a forest area in SE Brazil. *Line* indicates the mean axis direction. **a** All migratory data; **b** migrations during the dry/cold season; **c** migrations during the rainy/hot season

Table 1 Parameters of the axial circular analysis of the migration directions performed by *Pachycondyla marginata* colonies in SE Brazil, from November 1992 to September 1993. A Rayleigh test was used to evaluate the significance of the parameters *r* and μ. Symbols: *n* number of data; μ mean circular vector; *r* length of μ; *p* Rayleigh test parameter. Data are significantly oriented at *P*<0.05

	Migrations		
	All data	Rainy/hot season	Dry/cold season
n	39	19	20
μ	12°	9°	13°
r	0.29	0.11	0.46
p	0.04	0.76	0.01

should take ants to areas where they can still find termite nests to prey on and survive. In this study the data were considered as axial because migration routes in opposite directions on an axis would restrict ants to the specific location where their only termite prey lives. On the other hand, successive migrations in one direction would take them out of the termite-nest area. The distributions presented in Fig. 2a, b show data symmetrically arranged, which supports the axial analysis. The statistical analysis requires that the data from successive migratory events are independent of one another. The direction data from colonies that migrate just once fulfil this requirement, but the data from colonies that migrate more than once could not satisfy this condition. Worker ants of many species, including Ponerines, have their tasks determined mainly by age (see Hölldobler and Wilson 1990). We assume in this study that ant lifetimes are shorter than the average interval between migrations (5 months), and that different *P. marginata* scout ants would search for new nest sites at different dates. Migration events are therefore regarded as independent of each other.

The migratory data were classified as migrations during the rainy/hot season and migrations during the dry/cold season, because of the different raid and migration behaviours observed in both seasons (Leal and Oliveira 1995). The whole set of migratory routes was also analysed, combining both seasons' data. Table 1 and Fig. 2 show the results of the circular analysis. The whole set of migratory data shows a significant preferred migratory axis direction of 12° (p=0.04, SE=22°). Significant patterns were also detected for colonies migrating during the dry/cold season (p=0.01; mean direction=13°, SE=19°), but not for those migrating in the rainy/hot period (p=0.79; mean direction=9°, SE=83°).

These results show that this migratory species has a preferred direction for migrations during the dry/cold season only. Migration distances during the dry/cold season are also greater than those in the rainy/hot season (Leal and Oliveira 1995). Higher humidity levels during the rainy/hot season probably destroy food supplies in the nest, and force the ants to relocate the nest to avoid putrefaction**.** In this case a randomly oriented and short-distance nest relocation should not be considered as a typical migration, but rather as a nest relocation associated with poor sanitary conditions (Leal and Oliveira 1995). On the other hand, nest relocations in the dry/cold season can be considered as typical migrations.

Insects use different orientation cues for migration and homing, such as the position of the sun and the polarisation of UV-skylight (Wehner 1996), among others. Insects also use the geomagnetic field as a cue for orientation (Wiltschko and Wiltschko 1995; Vácha 1997). In particular, the wood ant species, *Formica rufa*, exhibits a magnetic compass response (Çamlitepe and Stradling 1995), and the fire ant *Solenopsis invicta* modifies its foraging behaviour when the local magnetic field direction changes (Anderson and Vander Meer 1993).

The present analysis shows that *P. marginata* maintains a preferred axis direction during migrations in the dry/cold season, which deviates about 13° from the magnetic North–South direction. This deviation is 12° and still significant if all migration data are considered. Since the directions were measured with a compass, the result is an angle relative to the geomagnetic field direction of the experimental zone. The geomagnetic declination map of 1990 elaborated by the National Observatory (ON/MCT/Brazil) indicates a declination angle of about 18° at Campinas, São Paulo, where the Santa Genebra reserve is located. Therefore, the migration axis is approximately 6° from the geographical North–South axis. But, how can *P. marginata* maintain their migrations around this axis? It is known that animal orientation relies on multiple cues, which may sometimes interact in complex ways (Able 1991). The most common cues are the azimuthal position of the sun, the skylight polarisation and the geomagnetic field, but local landmarks are also important for animals that live in restricted home ranges. The use of geomagnetic cues is more commonly associated with darkness conditions, as reported for mole rats (Marhold et al. 1997) and also proposed for bumblebees (Chittka et al. 1999). As *P. marginata* ants start the migratory process in the afternoon, they can use any of those cues in their orientation during the migratory journey. However, it is intriguing that they prefer an axis around the North–South axis to migrate. The only possible cue to give this information under all conditions is the one provided by the geomagnetic field. It is known that the geomagnetic field is used as a consistent reference system for animal travel (Wiltschko and Wiltschko 1995). This magnetic orientation hypothesis gains reliability considering that magnetic iron oxides have been found mainly in the head and abdomen of *P. marginata* ants (Acosta-Avalos et al. 1999) and that magnetic nanoparticles aggregates were inferred in their abdomen by EPR (Wajnberg et al. 2000). If *P. marginata* uses the geomagnetic field as a cue for migration, the ferromagnetic hypothesis can explain its behaviour (Kirschvink et al. 1985). To understand how the geomagnetic field can contribute to the orientation in one axis in the presence of other cues, an analogy with the problem of the drunkard on a slope can be useful. Bearing in mind that a drunkard does not walk in a straight line; if there is a slight slope in his way, the drunkard's random walk statistically results in a final downward tendency (Reif 1985). Similarly, the geomagnetic field breaks the isotropic random choice of directions resulting in a preferred direction.

This study, under natural conditions, stimulates further investigation on the seasonal pattern of the migratory behaviour of *P. marginata*. In particular, the cues used by the ants in the different seasons deserve a more detailed analysis. The environmental factors, which possibly account for seasonal differences in migration distances, should also be investigated. The current paper encourages additional investigation linking oriented migrations and ecological strategies in different ant species.

Acknowledgements D.A.A. acknowledges FAPERJ-Brazil, I.L. acknowledges FAPESP-Brazil, P.S.O. and E.W. were supported by CNPq-Brazil research grants.

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