BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 40(5): 590–596 2008 10.1111/j.1744-7429.2008.00414.x

Rainfall Influences Ant Sampling in Dry Forests

Thibaut Delsinne[1,2,3], **Maurice Leponce**[1], **Laurence Theunis**[1,2], **Yves Braet**[1], and **Yves Roisin**[2]

[1]Royal Belgian Institute of Natural Sciences, 29 rue Vautier, Biological Evaluation Section, 1000 Brussels, Belgium

[2]Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral and Evolutionary Ecology – CP 160/12, 1050 Brussels, Belgium

ABSTRACT

The standardized 'Ants of the Leaf Litter' protocol aims to facilitate the use of ground-foraging and litter-dwelling ants in biodiversity assessment and monitoring programs. It was initially developed to characterize assemblages from tropical rain forests and is based on two main techniques: Winkler extractions and pitfall traps. Here, we tested to what extent this protocol was adapted to tropical dry forests and affected by the rainfall regime. Our 10 study sites were located along an aridity gradient (average annual rainfall: 350–1300mm) in the Gran Chaco. The number of species collected per sampling effort increased with aridity for pitfalls but followed an opposite trend for Winkler samples. This trend could be explained by the low daytime foraging activity in the leaf litter during drought periods. In arid and semiarid regions the good performance of pitfalls was probably related to their 24-h operation and to the attractiveness of the water they contained. Our results stress that the Winkler method used in the Ants of the Leaf Litter protocol may not be cost-effective during periods of drought and may lead to severe underestimations of litter ant diversity in tropical dry forests.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: A.L.L. protocol; conservation; Formicidae; Gran Chaco; rapid biodiversity assessment; sampling method evaluation.

AMONG INSECTS, ANTS APPEAR TO BE ONE OF THE MOST INFORMATIVE AND TRACTABLE GROUP for biodiversity evaluation and monitoring because of their ecological and numerical dominance (Folgarait 1998, Underwood & Fisher 2006), their perennial nests (Alonso & Agosti 2000), their quick response to environmental changes (Kaspari & Majer 2000), and their relative ease of identification (Brown 2000). The standardized 'Ants of the Leaf Litter' protocol (hereafter called A.L.L. protocol) for collecting ground-dwelling ants (Agosti & Alonso 2000) was established to allow a qualitative comparison of ant community structure at different localities, the basic information needed to design conservation policies (Fisher 1999, 2005). This protocol relies on 200-m transects, along which 1-m^2 litter samples are taken for Winkler extraction and pitfall traps are placed at 10-m intervals. These two methods are the most efficient for sampling litter-dwelling and ground-foraging ants in rain forest ecosystems (Delabie *et al.* 2000). Further techniques such as dead wood inspection or baiting may be added to collect more species, depending on the survey objectives (Agosti & Alonso 2000). The A.L.L. protocol has mainly been developed for tropical rain forests (Agosti *et al.* 2000) and it is still necessary to verify its applicability in a larger set of climates. To this purpose, Winkler and pitfall samples were recently compared in forests of Tennessee (Martelli *et al.* 2004), Florida (King & Porter 2005), and France (Groc 2006). In all these studies, the authors collected more species with Winkler than with pitfall traps, and advised to combine both methods to sample the ant assemblage.

Here, the A.L.L. protocol based on Winkler extractions and pitfall traps was carried out in dry forests along a gradient of aridity to test the effect of rainfall on: (1) the efficiency of both methods in terms of species richness and species occurrences collected; (2) their faunal complementarity; and (3) the fraction of the whole assemblage captured per A.L.L. transect. The Gran Chaco plains, divided into the wet Chaco (1000–1400 mm of average annual rainfall) and the dry Chaco (350–1000 mm), appear as ideal for such a study because of their flat topography and wide rainfall range spread along a regular gradient (Fig. 1).

In arid and semiarid ecosystems, rainfall occurs as sporadic pulse events separated by drought periods of variable duration (Reynolds *et al.* 2004, Schwinning *et al.* 2004). As rainfall is known to influence the activity of ant assemblages on a seasonal scale (Whitford 1978, Reddy & Venkataiah 1990, Lindsey & Skinner 2001), we hypothesized that rainfall pulses could have an immediate effect on ant foraging and, consequently, on the efficiency of the sampling protocol. In this paper, we tested this hypothesis by comparing samples taken during drought or after rainfall, and by simulating rainfall in experimental quadrats.

METHODS

STUDY SITES.—The study was conducted between 1998 and 2004 in the dry and wet Paraguayan Chaco and in the wet Argentinean Chaco. Ten localities, 20–800 km from each other and distributed along the aridity gradient (Fig. 1), were sampled at the end of the dry season, in September and October, when temperature and rainfall increased. This sampling period was selected in order to avoid the extremely high or low temperatures, which may occur during the dry or wet season, respectively (Ramella & Spichiger 1989), because extreme temperatures limit the foraging of some Chacoan ant species (Bestelmeyer 2000, Delsinne *et al.* 2007). The

Received 6 March 2007; revision accepted 21 January 2008.
[3]Corresponding author; e-mail: Thibaut.Delsinne@sciencesnaturelles.be

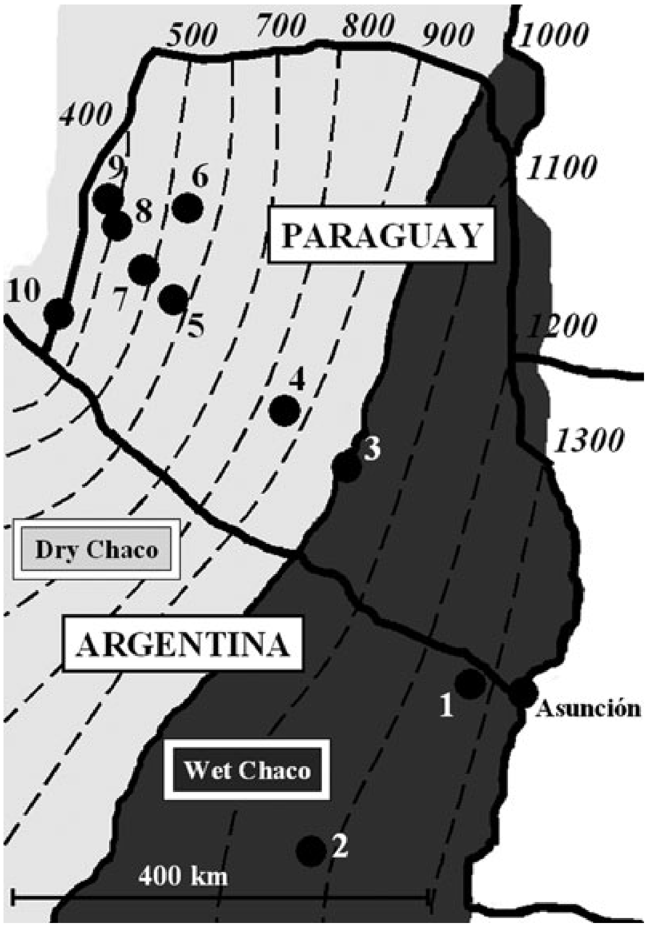

FIGURE 1. Study sites distributed along the aridity gradient of the Gran Chaco plains. Dotted lines are isolines of mean annual rainfall. Localities are: 1: Pilcomayo N.P.; 2: Chaco N.P.; 3: Río Verde; 4: Cruce de Los Pioneros; 5: Garrapatal; 6: Estancia María Vicenta; 7: Teniente Enciso N.P.; 8: Siracua; 9: Nueva Asunción; 10: Fortín Mayor Infante Rivarola.

habitats are a continuum of xeromorphic forests in the dry Chaco and mesoxeromorphic forests in the wet Chaco (Mereles 2005).

SAMPLING PROTOCOL.—Ants were sampled according to the standardized A.L.L. protocol (Agosti & Alonso 2000). Overall, 26 A.L.L. transects were carried out: six in localities 1 and 7, which were our reference localities for the wet and dry Chaco, respectively, three in localities 2, 5, and 10 and one in the other localities (Fig. 1).

The A.L.L. protocol consists of a line-transect of 20 sampling points spaced at 10-m intervals. One Winkler and one pitfall sample are taken at each point. For Winkler extractions, the leaf litter present inside a 1-m^2 quadrat is collected and sifted and its fauna is extracted with a mini-Winkler apparatus (Fisher 1998). The Winkler extraction is based on the passive desiccation of the leaf litter, forcing the ants to find a more favorable environment and their nest mates (Krell *et al.* 2005). Standard extraction time is 48 h. However, a preliminary test, consisting of the extraction of 100 Winkler samples for both 24 and 48 h, was conducted in the wettest locality (1 in Fig. 1) to determine if the extraction time could be reduced to 24 h. Pitfall traps consisted in 70-mm diameter drinking cups, containing water and a drop of detergent, operating for 24 h.

INFLUENCE OF A NATURAL RAINFALL PULSE.—In reference locality 7, three transects were sampled in September 2001 and three in September 2004. The data from this locality were used to study the influence of a recent rainfall event on the efficiency of the collection method. In September 2001, the mean ambient temperature at this locality was 28°C and six rainfall pulses (totaling 147 mm of precipitation) had occurred in the 40 d preceding sampling, one of them (a 15 mm pulse) occurring the day before. In September 2004, the mean ambient temperature was 26.5°C and no rainfall had occurred in the preceding 4 mo. In all other localities, no rainfall event occurred the day before sampling.

INFLUENCE OF SIMULATED RAINFALL PULSES.—In September 2004, 23 pairs of 1-m^2 quadrats were randomly selected in the dry Chaco (10, 8, and 5 samples in localities 7, 6, and 10, respectively; Fig. 1). In each pair, one quadrat was sprinkled with 2 L of water while the other, 1 m away, was used as a control. The leaf litter was collected and sifted 90 min after the beginning of the experiment and its fauna was extracted with a mini-Winkler apparatus for 24 h.

ANALYSES.—All workers were identified to species or morphospecies. Reproductives were excluded from the analyses because only workers certify the presence of an established colony (Longino *et al.* 2002). Species occurrences (*i.e.*, presence/absence) in samples were used as surrogate of abundance (*i.e.*, number of workers) because ants are spatially aggregated due to their sociality (Longino 2000) and because colony sizes may strongly vary among species (Hölldobler & Wilson 1990). As a consequence, a single trap may collect numerous individuals of a rare species (Longino 2000).

For each reference locality, a matched rank-occurrence plot (Longino & Colwell 1997) was computed to study the complementarity between pitfall and Winkler samples. The graph consisted of a standard rank-occurrence plot for pitfall traps (the reference method *sensu* Longino & Colwell 1997) and the corresponding occurrences of the species collected with Winkler extractors. This graphical method is efficient to reveal the degree of correspondence between two sampling methods and to detect species that are rare in samples from one method but common in samples from the other (Longino & Colwell 1997).

In addition, complementarity between pitfall and Winkler samplings was expressed by the complement of the NNESS index (Trueblood *et al.* 1994)

$$\begin{aligned}\text{Complementarity}_{PW/k} &= 1 - \text{NNESS}_{PW/k}\\ &= 1 - \{\text{ESS}_{PW/k}/[(\text{ESS}_{PP/k} + \text{ESS}_{WW/k})/2]\}\end{aligned}$$

where $\text{ESS}_{PW/k}$ is the expected number of species shared for random draws (without replacement) of k occurrences from pitfall samples (P) and k occurrences from Winkler samples (W). When

k is small, the index is highly sensitive to the occurrences of the most frequent ant species. When k increases, the influence of rarer species is emphasized. Complementarity was calculated for $k = 1$, $k = 64$, and $k = 128$. Complementarity ranges from 0, if pitfall and Winkler samples are not complementary (*i.e.*, they collect the same species) to 1, if species collected by the two methods are totally different. The software program BiodivR 1.0 (Hardy 2005) was used to compute the indices.

To investigate the sampling completeness of the A.L.L. transects in both the wet and dry Chaco, the number of species collected with 1–6 A.L.L. transects was compared with the total number of species recorded in the reference localities by a larger set of methods and at other sampling dates. These records corresponded to the minimum total number of species present at the reference sites and represented a thorough inventory based on a high number of samples (1943 samples in the reference locality of the wet Chaco and 3458 samples in the reference locality of the dry Chaco) from diverse methods (pitfall traps, Winkler samples, dead wood and soil inspections, hand collection, carbohydrate and protein baits).

RESULTS

CALIBRATION OF THE WINKLER EXTRACTION TIME.—A preliminary test showed that 93 percent (7048) of the individuals, 98 percent (532) of the species occurrences, and 100 percent (67) of the species collected after 48 h were collected in the first 24 h. After these results, a 24-h extraction time was adopted throughout the sampling program.

COMPARATIVE METHOD EFFICIENCY.—At the end of the dry season, the efficiency of both Winkler and pitfall samplings was related to the aridity (Fig. 2). A positive linear correlation existed between the number of species collected per Winkler transect and the annual mean precipitation (Pearson product moment correlation analysis; $N = 26$ transects, $r = 0.70$, $P < 0.0001$). The opposite trend was observed for pitfall transects ($r = -0.76$, $P < 0.00001$) while no correlation was obtained when both collection methods were combined ($r = -0.24$, $P = 0.24$). A similar result was obtained for species occurrences against rainfall (with Winkler transects: $r = 0.73$, $P < 0.0001$; with pitfall transects: $r = -0.74$, $P < 0.00001$; and with both methods combined: $r = -0.31$, $P = 0.12$).

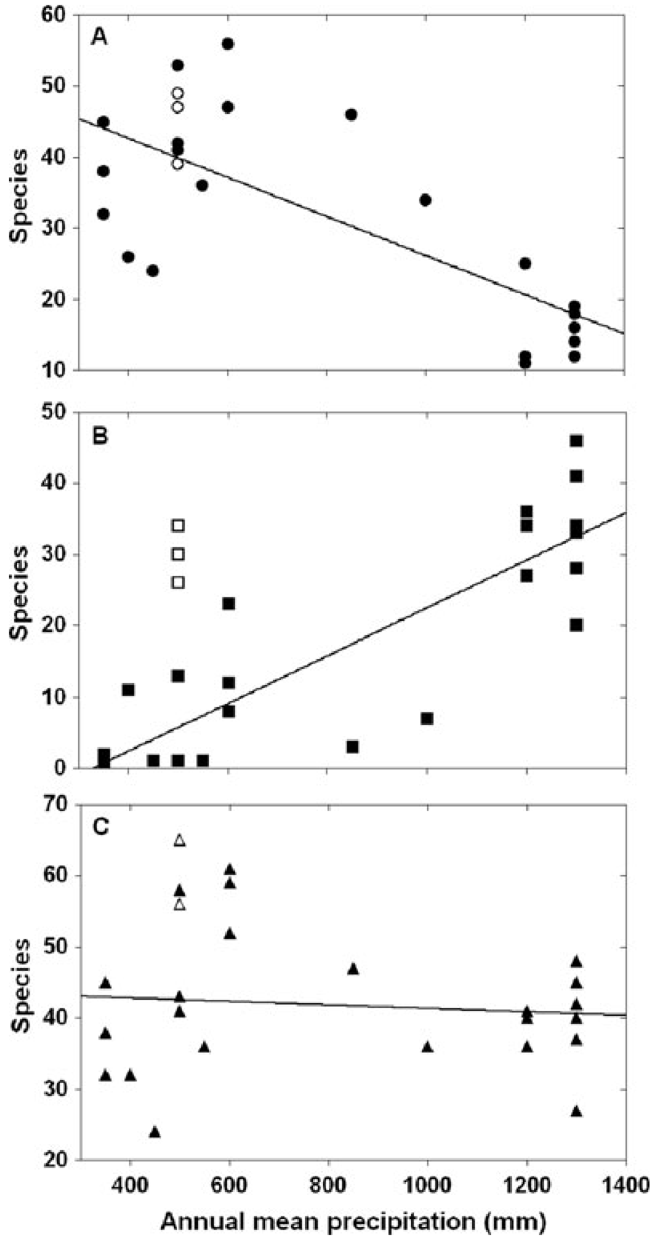

FIGURE 2. Number of species collected per A.L.L. transect by (A) pitfall traps, (B) by Winkler extractions, and (C) by both methods combined along the aridity gradient. Lines are the linear fitting of the plots. Empty symbols correspond to the three transects collected after a rainfall event at the dry Chaco reference locality.

INFLUENCE OF A RAINFALL PULSE ON METHOD EFFICIENCY.—In the dry Chaco (locality 7 in Fig. 1), when no rainfall occurred during the preceding 4 mo, a single A.L.L. Winkler transect collected only 5 ± 7 (mean ± SD) species and 9 ± 13 species occurrences. This was significantly less than previous collections after rainfall in 2001, where 30 ± 4 species and 87 ± 18 species occurrences were recorded (df = 4, $t = 5.41$ and 5.99, $P < 0.006$ and 0.004 for species and species occurrences, respectively).

In contrast, the rainfall pulse did not significantly influence the efficiency of a single A.L.L. pitfall transect in terms of species richness (wet year: 45 ± 5; dry year: 45 ± 7) and species occurrences (224 ± 44; 179 ± 14; df = 4, $t = -0.07$ and 1.69, $P = 0.95$ and 0.17 for species and species occurrences, respectively).

More species were collected with 60 pitfalls than with 60 Winkler but, for a similar common number of occurrences, Winkler extractions were as efficient as pitfall traps in terms of species collected (Fig. 3).

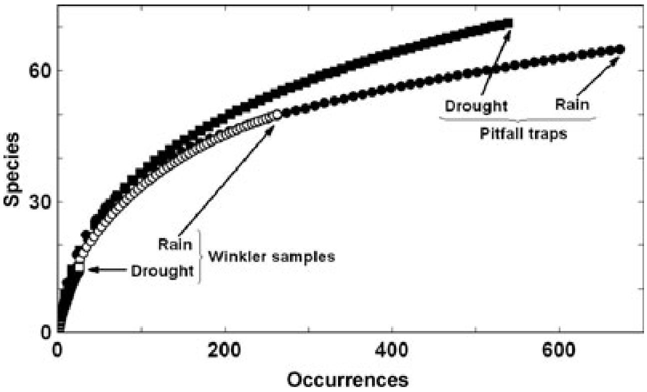

FIGURE 3. Occurrence-based rarefaction curves (Coleman method of EstimateS 7.5; Colwell 2004) of three pooled A.L.L. transects for Winkler and pitfall catches after a rainfall event (2001) and during a dry year (2004) at the dry Chaco reference locality (locality 7 in Fig. 1).

INFLUENCE OF A SIMULATED RAINFALL PULSE ON WINKLER EFFICIENCY.—For an identical number of samples, wet 1-m^2 quadrats collected nine times more species and 21-fold more occurrences than control quadrats (Table 1). Both the mean number of workers and occurrences per sample in the watered quadrats were higher than in the control quadrats (Table 1; Mann–Whitney rank sum test, $P < 0.001$).

PITFALL AND WINKLER COMPLEMENTARITY.—These analyses were restricted to the data sets of the reference localities 1 and 7. For the latter, only data from the rainy year were analyzed. In the wet Chaco, six A.L.L. transects yielded 90 ant species (Fig. 4A). Winkler samples alone recorded 76 species and pitfall traps alone 48 species.

TABLE 1. *Results of the artificial rainfall pulse experiment.*

	Watered quadrats ($N = 23$)	Control quadrats ($N = 23$)	Mann–Whitney rank sum test
Mean number of workers/sample (± SD)	29.6 ± 41.8	0.2 ± 0.5	$P < 0.001$
Total number of workers	681	5	
Mean number of occurrences/sample (± SD)	3.6 ± 2.0	0.2 ± 0.5	$P < 0.001$
Total number of species occurrences	83	4	
Total number of species	37	4	

In the dry Chaco, after rainfall, three A.L.L. transects yielded 91 ant species (Fig. 4B). Pitfall traps were more efficient (64 species) than Winkler extractions (51 species).

Pitfall and Winkler complementarity was higher in the dry Chaco than in the wet Chaco (26 percent and 35 percent of shared species, respectively; Fig. 4A, B; Table 2). In the wet Chaco, frequent ants were globally the same by either method, and rare species collected in pitfall traps were also found in Winkler samples (Fig. 4A). However, frequent ant species were different according to the sampling method in the dry Chaco (Fig. 4B).

SAMPLING COMPLETENESS.—To collect around 50 percent of the total ant fauna known from the reference locality so far, the minimum sampling effort is one A.L.L. transect combining both Winkler and pitfall traps in the dry Chaco during a rainy year. Two such transects would be necessary in the dry Chaco during a period of drought and up to five such transects in the wet Chaco (Table 2).

DISCUSSION

EFFECTIVENESS OF THE COLLECTION METHODS.—Winkler and pitfall sampling efficiency, in terms of both species and species occurrences per A.L.L. transect, was dependent of the rainfall regime with opposite trends for the two methods.

Ant species density is generally positively correlated with the leaf litter thickness (Kaspari 1996, Theunis *et al.* 2005). Although this factor could have influenced the Winkler sampling in this study, the drought occurring in the driest localities during and before the sampling campaigns seems to be the main cause of the Winkler inefficiency. This hypothesis is supported by the increased efficiency of the Winkler extraction in the dry Chaco reference locality after a natural or artificial rainfall. The absence of leaf litter nesting specialists may be an additional explanation. Indeed, in the dry Chaco reference locality, no ant colonies were encountered in the leaf litter even after careful searches (T. Delsinne, pers. obs.), probably because the microclimatic conditions inside the leaf litter were too stressful. All discovered nests were subterranean.

The overall better performance of pitfalls in dry environments may be explained by the fact that these traps also run during the night when temperature is less stressful. In addition, the water contained in the pitfall may actually attract workers. This would explain the strong negative correlation between pitfall efficiency and rainfall. In the Mexican Sonoran Desert (mean annual rainfall = 346 mm; Bestelmeyer & Schooley 1999), in the Argentinean dry Chaco (500 mm; Bestelmeyer & Wiens 1996), and in the Australian Gibson Desert (220 mm; Gunawardene & Majer 2005) ant assemblages were also collected by pitfall traps but their efficiency was not as noteworthy as in our study, possibly because the preservative used in these studies (*i.e.*, propylene glycol, a 70 percent mixture of ethylene glycol/ethanol, and ethylene glycol, respectively) neither attracts nor repels ants (Bestelmeyer *et al.* 2000). To our knowledge, whether ants possess the capacity to detect water sources from a distance

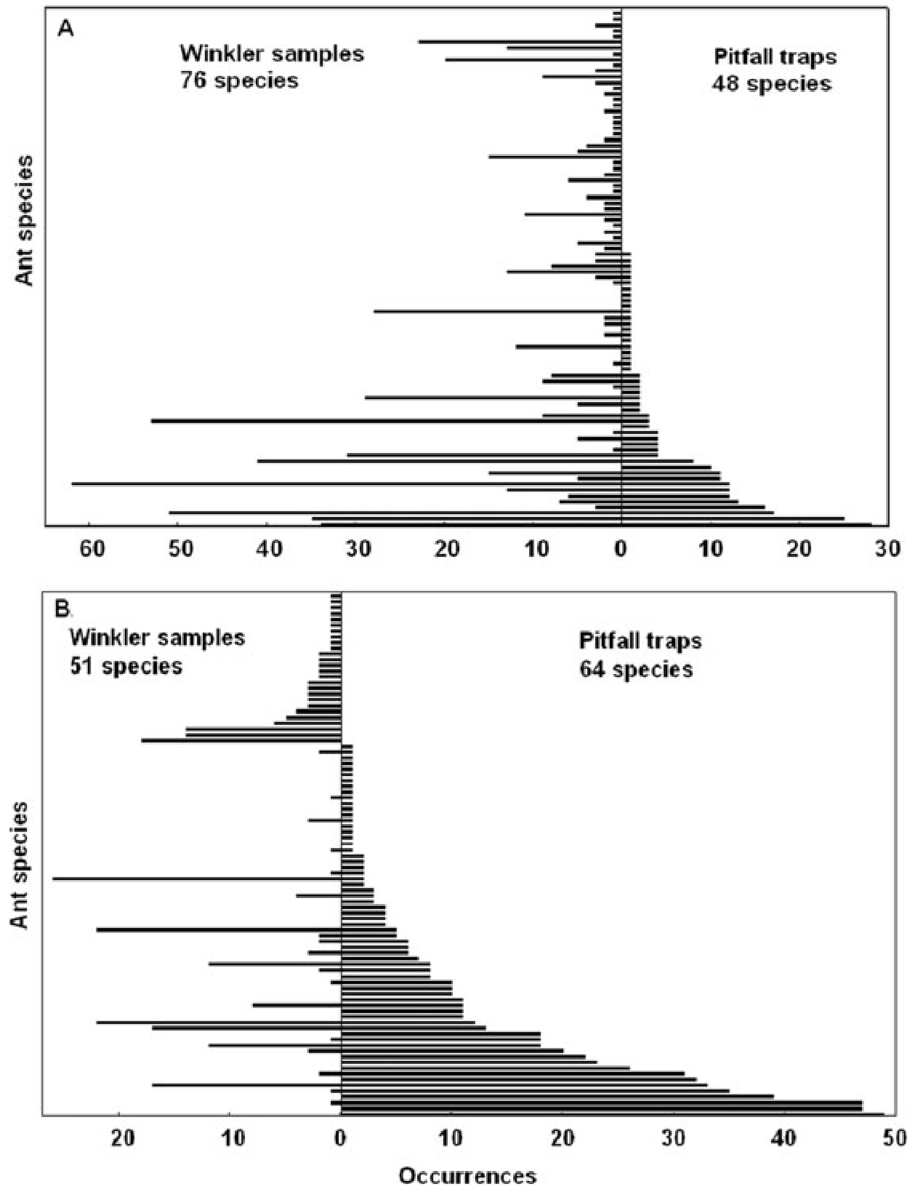

FIGURE 4. Matched rank/occurrence plots of ants collected with pitfall and Winkler samples (A) at the wet Chaco reference locality (mean annual precipitation 1300 mm; $N = 6$ transects; 90 species collected) and (B) at the dry Chaco reference locality after a rainfall (mean annual precipitation 500 mm; $N = 3$ transects; 91 species collected).

(*e.g.*, by detecting water vapor in a dry environment) is still unknown.

Pitfall traps generally perform better in habitats with a low leaf litter cover (Melbourne 1999) and in open rather than closed habitats (Parr & Chown 2001, Fisher & Robertson 2002). Dry Chacoan forests are seasonally deciduous (Ramella & Spichiger 1989). At the end of the dry season (*i.e.*, during the sampling period), the majority of trees and shrubs are without leaves. Consequently, at that time the leaf litter depth and the canopy openness were maximal. These environmental conditions may have influenced the pitfall sampling and may have contributed to the observed higher pitfall efficiency in the dry Chaco compared to the wet Chaco.

METHOD COMPLEMENTARITY.—Pitfall and Winkler complementarity was higher in the dry Chaco than in the wet Chaco. Diurnal and nocturnal differences in ant activity and ant assemblage composition may be more pronounced in the dry Chaco than in the wet Chaco due to stressful environmental conditions. It would be interesting to collect the leaf litter at night in the dry Chaco. We predict that the complementarity between methods would decrease. In a similar way, pitfalls could be operated at different times of the day to document the daily pattern of ant activity.

INVENTORY COMPLETENESS.—There are 150 ant species currently known from the dry subtropical forests of the wet Chaco reference

TABLE 2. *Pitfall and Winkler complementarity and A.L.L. transect completeness for reference localities of the wet and dry Chaco.*

	Wet Chaco Locality 1	Dry Chaco Locality 7, drought	Dry Chaco Locality 7, after rainfall
Winkler/Pitfall complementarity[a]:			
1 − NNESS ($k = 1$)	0.37	–	0.76
1 − NNESS ($k = 64$)	0.32	–	0.59
1 − NNESS ($k = 128$)	0.33	–	0.56
Total species richness[b]:	≥ 150	≥ 126	≥ 126
Mean percent of species collected with:			
1 A.L.L. transect	29	39	52
2 A.L.L. transects	38	52	64
3 A.L.L. transects	43	59	72
4 A.L.L. transects	48	–	–
5 A.L.L. transects	51	–	–
6 A.L.L. transects	54	–	–

[a]For the wet Chaco, six transects were used to compute the complementarity indices. For the dry Chaco after a rainfall, three transects were used. No indices were calculated for the dry Chaco during a drought because Winkler collected very few ants.

[b]Total species richness values represent the total number of species collected at the reference localities so far. Hence, they correspond to a minimal value of the ant fauna present in the reference localities.

locality 1. A single A.L.L. Winkler/pitfall transect collected 29 percent of them. This is slightly lower than the 36 percent obtained in the Atlantic region with the same methods (J. H. C. Delabie, pers. comm.; result obtained in 1 ha of cocoa plantation where 134 species were collected by a combination of 17 methods). By contrast, depending of the local rainfall history, a single A.L.L. Winkler/pitfall transect collected between 39 percent and 52 percent of the currently documented ant fauna of the dry Chaco reference locality 7. This good performance could illustrate the high complementarity between the fauna captured by pitfalls (active ground-foraging, thermophilic, or nocturnal species and also possibly ants attracted by water) and by Winkler after rainfall, when cryptic subterranean nesting species forage in the leaf litter. Nevertheless, this apparently good sampling performance could also be the result of underestimating local species richness and a longer-term collection effort at the reference locality would be required to discard this eventuality.

CONCLUSION.—Every sampling technique suffers from biases (Bestelmeyer *et al.* 2000, Longino 2000) and none allows the collection of the whole ant fauna locally present (Longino *et al.* 2002). Here, a single pitfall/Winkler A.L.L. transect collected at least one-third of the local assemblage. The A.L.L. protocol, which was initially developed for tropical rain forests, also seemed efficient for sampling ant assemblages in dry forests. Nevertheless, we have underlined the strong influence of rainfall on the efficiency of Winkler sampling in dry forests, and its consequences on the complementarity of methods and on the completeness of standardized A.L.L. transects. During drought periods, Winkler extractions are not cost-effective and pitfalls traps should be used in the context of rapid assessments of the ant fauna.

ACKNOWLEDGMENTS

We thank J. Kochalka, B. Garcete-Barrett, V. Filippi, J. Jara, C. Bénilez, C. Aguílar Julio, from the Museo Nacional de Historia Natural del Paraguay, the guards from Teniente Enciso National Park, and V. Olivier for their help during fieldwork or administrative procedures. A. Wild and J. H .C. Delabie supervised a part of the ant identifications. This study was made possible by financial support from the Fonds pour la Formation à la Recherche dans l'Industrie et l'Agriculture and the Fonds de la Recherche Scientifique — FNRS (Belgium). N. Gunawardene greatly improved the English version. T. M. Arias Penna translated the abstract into Spanish.

LITERATURE CITED

AGOSTI, D., AND L. E. ALONSO. 2000. The A.L.L. protocol. A standard protocol for the collection of ground-dwelling ants. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 204–206. Smithsonian Institution Press, Washington, DC.

AGOSTI, D., J. MAJER, L. E. ALONSO, AND T. R. SCHULTZ (Eds.). 2000. Sampling ground-dwelling ants: Case studies from the world's rain forests. Curtin University of Technology, Perth, Australia.

ALONSO, L. E., AND D. AGOSTI. 2000. Biodiversity studies, monitoring, and ants: an overview. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 1–8. Smithsonian Institution Press, Washington, DC.

BESTELMEYER, B. T. 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998–1009.

BESTELMEYER, B. T., AND R. L. SCHOOLEY. 1999. The ants of the southern Sonoran desert: Community structure and the role of trees. Biodivers. Conserv. 8: 643–657.

BESTELMEYER, B. T., AND J. A. WIENS. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecol. Appl. 6: 1225–1240.

BESTELMEYER, B. T., D. AGOSTI, L. E. ALONSO, R. F. BRANDÃO, W. L. BROWN JR., J. H. C. DELABIE, AND R. SILVESTRE. 2000. Field techniques for the study of ground-dwelling ants: An overview, description, and evaluation. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 122–144. Smithsonian Institution Press, Washington, DC.

BROWN, W. L. JR. 2000. Diversity of ants. *In* D. Agosti, J. D. Majer, L. E. Alonso, AND T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 45–79. Smithsonian Institution Press, Washington, DC.

COLWELL, R. K. 2004. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL: purl.oclc.org/estimates.

DELABIE, J. H. C., B. L. FISHER, J. D. MAJER, AND I. W. WRIGHT. 2000. Sampling effort and choice of methods. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 145–154. Smithsonian Institution Press, Washington, DC.

DELSINNE T., Y. ROISIN, AND M. LEPONCE. 2007. Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. J. Arid Environ. 71: 29–44.

FISHER, B. L. 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale Naturelle Intégrale d'Andringitra, Madagascar. Fieldiana Zool. (n.s.) 85: 93–108.

FISHER, B. L. 1999. Improving inventory efficiency: A case study of leaf litter ant diversity in Madagascar. Ecol. Appl. 9: 714–731.

FISHER, B. L. 2005. A model for a global inventory of ants: A case study in Madagascar. Proc. Calif. Acad. Sci. 56: 86–97.

FISHER, B. L., AND H. G. ROBERTSON. 2002. Comparison and origin of forest and grassland ant assemblages in the high plateau of Madagascar (Hymenoptera: Formicidae). Biotropica 34: 155–167.

FOLGARAIT, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodivers. Conserv. 7: 1221–1244.

GROC, S. 2006. Diversité de la myrmécofaune des Causses aveyronnais. Comparaison de différentes méthodes d'échantillonnage. DESUPS Diplôme d'Études Supérieures de l'Université Paul Sabatier.

GUNAWARDENE, N. R., AND J. D. MAJER. 2005. The effect of fire on ant assemblages in the Gibson Desert Nature Reserve, Western Australia. J. Arid Environ. 63: 725–739.

HARDY, O. 2005. BiodivR 1.0. A program to compute statistically unbiases indices of species diversity within samples and species similarity between samples using rarefaction principles. Université Libre de Bruxelles, Belgium.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The ants. Bellknap Press, Cambridge, Massachusetts.

KASPARI, M. 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76: 443–454.

KASPARI, M., AND J. D. MAJER. 2000. Using ants to monitor environmental change. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 89–98. Smithsonian Institution Press, Washington, DC.

KING, J. R., AND S. D. PORTER. 2005. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. Environ. Entomol. 34: 1566–1578.

KRELL, F.-T., A. Y. C. CHUNG, E. DEBOISE, P. EGGLETON, A. GIUSTI, K. INWARD, AND S. KRELL-WESTERWALBESLOH. 2005. Quantitative extraction of macro-invertebrates from temperate and tropical leaf litter and soil: Efficiency and time-dependent taxonomic biases of the Winkler extraction. Pedobiologia 49: 175–186.

LINDSEY, P. A., AND J. D. SKINNER. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. J. Arid Environ. 48: 551–568.

LONGINO, J. T. 2000. What to do with the data? *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 186–203. Smithsonian Institution Press, Washington, DC.

LONGINO, J. T., AND R. K. COLWELL. 1997. Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rain forest. Ecol. Appl. 7: 1263–1277.

LONGINO, J. T., J. CODDINGTON, AND R. K. COLWELL. 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. Ecology 83: 689–702.

MARTELLI, M. G., M. M. WARD, AND A. M. FRASER. 2004. Ant diversity sampling on the southern Cumberland Plateau: A comparison of litter sifting and pitfall trapping. Southeast. Nat. 3: 113–126.

MELBOURNE, B. A. 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Aust. J. Ecol. 24: 228–239.

MERELES, M. F. 2005. Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay. Rojasiana 6: 5–48.

PARR, C. L., AND S. L. CHOWN. 2001. Inventory and bioindicator sampling: Testing pitfall and Winkler methods with ants in a South African savanna. J. Insect. Conserv. 5: 27–36.

RAMELLA, L., AND R. SPICHIGER. 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44: 639–680.

REDDY, M. V., AND B. VENKATAIAH. 1990. Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. Int. J. Biometeorol. 34: 49–59.

REYNOLDS, J. F., P. R. KEMP, K. OGLE, AND R. J. FERNÁNDEZ. 2004. Modifying the "pulse-reserve" paradigm for deserts of North America: Precipitation pulses, soil water, and plant responses. Oecologia 141: 194–210.

SCHWINNING, S., O. E. SALA, M. E. LOIK, AND J. R. EHLERINGER. 2004. Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141: 191–193.

THEUNIS, L., M. GILBERT, Y. ROISIN, AND M. LEPONCE. 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. Insect. Soc. 52: 366–377.

TRUEBLOOD, D. D., E. D. GALLAGHER, AND D. M. GOULD. 1994. Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnol. Oceanogr. 39: 1440–1454.

UNDERWOOD, E. C., AND B. L. FISHER. 2006. The role of ants in conservation monitoring: If, when, and how. Biol. Conserv. 132: 166–182.

WHITFORD, W. G. 1978. Structure and seasonal activity of Chihuahua Desert ant communities. Insect. Soc. 25: 79–88.