Seasonal Trends in the Social Composition and Inside-Trunk Distribution of *Kalotermes flavicollis* (Isoptera: Kalotermitidae) Colonizing Grapevines

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ABSTRACT The polyphagous drywood termite *Kalotermes flavicollis* (Fabricius) can establish its colonies inside living trees, causing a progressive debilitation that ends with the death of the plant. For this reason, it is considered one of the major pests of Sherry vineyards in Andalusia, SW Spain. To analyze the trends of colonization of this termite, a detailed investigation was performed during 16 mo in seven districts of the Sherry area, cutting randomly selected grapevine trunks into six sections, from which all individuals were collected and counted according to their developmental instar or caste. The results detected variations in the social composition of the groups colonizing grapevines according to the spatial distribution inside the vine trunk and in the numerical trends over the seasons. A pattern of seasonal migrations of the termites inside the trunk was inferred, with upward movements from spring to autumn and downward movements from autumn to winter. During winter, when termites were mainly located in the medium-basal sections of the trunk, a higher proportion of eggs and larvae was detected. Going from spring to summer, when the majority of the termites was located in the medium-upper sections of the trunk, there was an increase of nymphal instars followed, during autumn, by the appearance of alates, mostly located in the upper sections of the grapevine. Pseudergates and reproductives maintained their proportions and locations almost unchanged during the year.

KEY WORDS termites, colony composition, caste location, seasonal variations, vineyard pest

Kalotermes flavicollis (Fabricius 1793) is a xylophagous termite species living in regions across the Mediterranean basin (Harris 1970). Its colonies are small (1,000–1,500 individuals), develop slowly, feed in the piece of wood initially selected by the founder couple, and produce alates 3–4 yr after colony founding (Grassi and Sandias 1893, Grassé and Noirot 1958). Information on proportions of the different developmental instars and castes in wild colonies is scarce and is usually restricted to termites found in dead trees (Mazzantini 1953, Grassé 1986). However, this termite has been the subject of many experimental studies because of the extraordinary flexibility of its postembryonic development that makes it particularly difficult to characterize the different castes (Lebrun 1967, Lüscher 1961, Noirot and Bordereau 1991, Roisin 2000). A "normal" imaginal development ending with the dark winged imagoes (initially alates, than becoming dealate primary reproductives of the newly founded colonies), consists of at least seven instars, where the first four are designated as larval and the following three as nymphal (with visible wing buds) (Noirot 1985). Pseudergates, functionally behaving as workers, are large individuals, similar to nymphs in size but with extremely short or no wing buds at all, which maintain a prolonged ability to molt into other caste forms, in response to the colony needs (Noirot and Pasteels 1987, Thorne 1996). All individuals after the fourth larval instar (or even the third in young colonies) have the potential to develop in any of the terminal castes: alate, soldier, neotenic.

As in most Kalotermitids, *K. flavicollis* can feed on wood of living trees (Lee and Wood 1971) and has been reported to occasionally attack a wide variety of ornamental and fruit trees such as poplar, elm, cork, pine, olive, chestnut, fig, and pear (Monastero 1947, Prota 1965, López et al. 1996, Ferrero 1973, Kervina 1972), as well as grapevine (Grassi and Aloi 1885, Mayet 1907, Springhetti 1957), where it has been recognized as a serious pests in some Spanish and Portuguese vineyards (Pérez 1982, Lebrun 1976, López et al. 2000). When infesting trees, this termite occupies the portions between necrotized and sound areas (Grassi and Sandias 1893) amid bark and pith or bark and cambium, and can gradually penetrate in the living wood (Mazzantini 1953) actively contributing to the desiccation and progressive death of the tissues of the tree trunk. In grapevines it appears that it can enter as dealate imagoes into the epigeal part of the vine

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through wounds and holes, such as pruning cuts, and, as the colony gradually increases and expands its galleries, it progressively debilitates the vine causing the sequential loss of the arms and finally the death of the whole stock (López and Ocete 1999).

Despite the importance of *K. flavicollis* as a potential pest of living trees, no study has yet been performed on plant-invading colonies. The present research was carried out in Sherry vineyards, where these termites are considered a major pest (López et al. 2003b), as a part of a survey aimed at investigating the ecological features of grapevine occupying termite groups to provide suggestions for their management. In a previous paper (López et al. 2006) the occurrence, size and social composition of the vine inhabiting colonies were reported. In the present work the natural proportions of different developmental instars and castes and their location inside the vine trunks across the four seasons were investigated to obtain the trends over time and space of grapevine colonizing groups.

Materials and Methods

Study Sites and Vineyard Features. Sherry vineyards grow in Andalusia (SW Spain), where temperatures oscillate between 0 and 40°C, with an average of 17.07°C. Annual average precipitation is ≈600 liters/m^2. Because of the proximity to the Atlantic Ocean, relative humidity is high, with an average value of 60%. For this study, samples were collected periodically from vines of the "Palomino fino" variety in seven districts (Balbaina, Burugena, Carrascal, Cuartillo, Macharnudo, Torrecera, Berbén) belonging to the Sherry area, in plots situated inside the area with coordinates 6° 08′ 10″ W (longitude) and 36° 41′ 10″ N (latitude). The kind of pruning was a variety of guyot, locally denominated "*jerezana.*"

Sampling. This study was performed for a period of 16 mo in succession, during which samples were taken every 15 d. For each sampling date, considering the relative availability of differently aged grapevines, one 4-, 6-, 9-, 15-, and 20-yr-old vine and two to four 30-yr-old vines were randomly selected for sampling in each of seven different sites. The total number of collected vines (198) was limited to conserve plants in productive plots. Each grapevine trunk was sectioned in situ by means of electric and manual saws in six parts (named sectors A, B, C, D, E, F), according to Fig. 1. Each section was independently placed in a plastic bag and afterwards carefully opened in the laboratory. Collected termites were placed in vials with 70° alcohol for later examination. Sawdust, debris, and termite excrements were passed across two sieves of 1 and 0.3 mm, to concentrate the eggs. Under a binocular microscope, the different instars and castes of *K. flavicollis* were recognized, separated (to distinguish larval instars and pseudergates, the head capsule width was measured) and counted according to the following classification: eggs (EGGS), larvae (LA_{1-2}), older larvae (LA_{3-4}), pseudergates (PSE), nymphal instars (N_1, N_2, and N_3), presoldiers (called also white soldiers, WS), soldiers (SOL), alates (ALA), and reproductives (REP) (males and females primary or secondary reproductives).

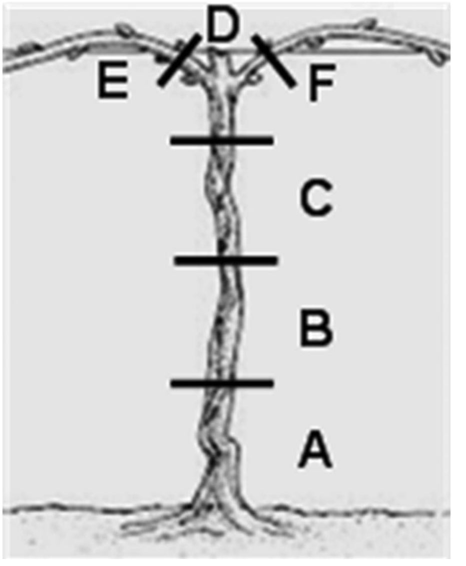

Fig. 1. Scheme of the cuts performed in each grapevine trunk to obtain six parts, named sectors A (rootstock), B, C, D, and E, F (lateral branches).

Statistical Analysis. Only the vines in which at least one section had some *K. flavicollis* specimens were considered for the statistical analysis. Since no infestations were detected in vines aged between 4 and 9 yr old, only those aged 15–30 were subjected to the analysis. Data for this study were reported as number of individuals for each instar/caste found in each grapevine trunk sector and in the whole vine trunk. Samples of the same age from the different districts were pooled. Months of sampling were grouped in seasons based on average temperatures (Winter = December, January, February; Spring = March, April, May; Summer = June, July, August; Autumn = September, October, November). Initially, to see if the number of termites in the whole vine trunks was affected by the season and/or by the age of the vine (15, 20, 30 yr), a 2-way ANOVA was performed on the total number of individuals and a 2-way MANOVA (multivariate analysis of variance, sigma-restricted parameterization, using a full factorial method for between effect design) was performed on the number of individuals belonging to the different instars. A Pearson Correlation analyses was also performed between the total number of termites in the whole trunk and the age of the vine. Next, to see if the number of termites in each grapevine sector was affected by the season and/or the sector location (=position of the trunk section in the sampled grapevine, Fig. 1), a 2-way ANOVA was performed on the total number of individuals (per sector) and 2-way MANOVA was performed on the number of individuals belonging to the different instars. Results of the MANOVAs were reported as multivariate tests of significance for all effects (Wilks test) and a summary table for uni-

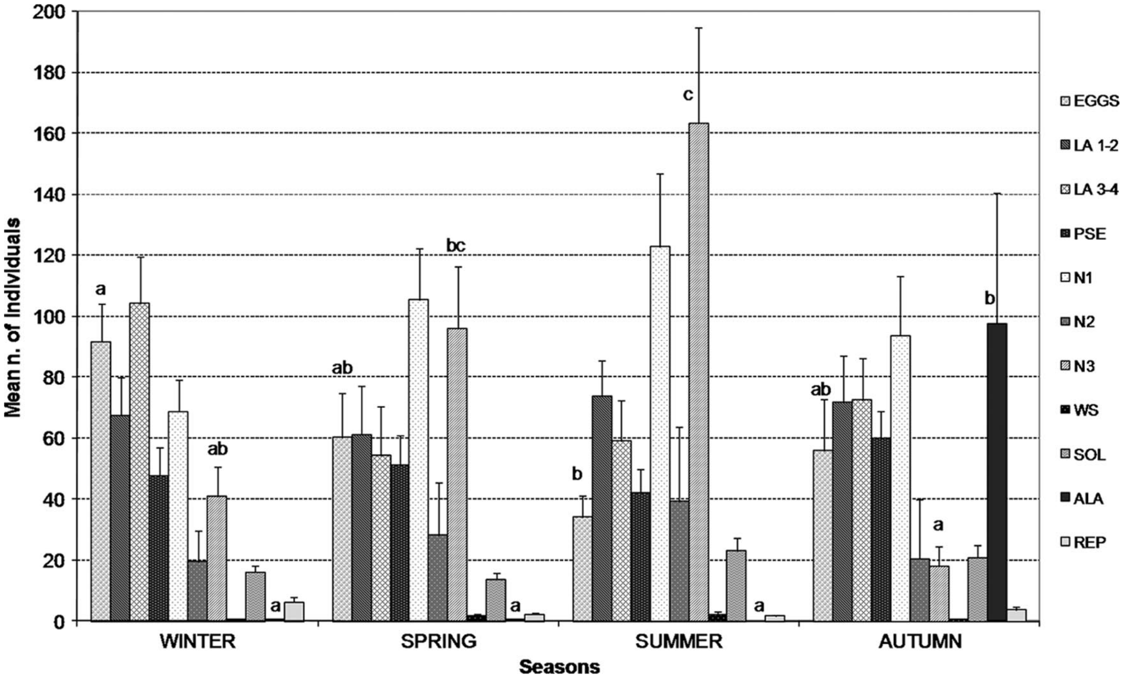

Fig. 2. Average seasonal composition of *K. flavicollis* grapevine colonizing groups (mean number of individuals of each developmental instar +SE). For each one of the instars EGGS, N_3, and ALA, columns marked by the same letter are not significantly different at the 0.05 level determined by the Tukey HSD tests after MANOVA. LA_{1-2}, larvae; LA_{3-4}, older larvae; PSE, pseudergates; N_1-N_2-N_3, nymphal instars; WS, white soldiers; SOL, soldiers; ALA, alates; REP, reproductives.

variate results for each dependent variable. Data on eggs were analyzed separately. For all analyses, Tukey honestly significant difference (HSD) tests were performed to separate the means. All the analyses were performed using Statistica 7.0 (StafSoft Inc., Tulsa, OK).

Results

For this study, 198 grapevine trunks were examined and *K. flavicollis* was detected in 95 vines (47.9%), which were always aged 15 yr or older. The initial analysis showed that the total number of termites detected in the grapevine trunks was not significantly affected by the season (F (3, 83) = 1.25; P = 0.30) or by the age of the vine (F (2, 83) = 0.94; P = 0.39) and no correlation was detected between the age of the vine and the total termite population inside the trunk (Pearson r = −0.075, r^2 = 0.006; P = 0.47). Data on the size (n. of individuals) of the vine colonizing groups are as follows: means ± SE = 431.75 ± 35.43; median = 360, min = 2, max = 1692. However, inside vine trunks significant variations were detected in the number of individuals of each instar in different seasons (MANOVA: Wilks lambda = 0.30, F (33, 239.35) = 3.60; $P < 0.001$) and univariate results showed that significant differences were found for three instars: EGGS (F (3, 91) = 3.61; P = 0.016), N_3 (F (3, 91) = 12.65; $P < 0.001$), ALA (F (3, 91) = 6.55; $P < 0.001$). Figure 2 shows the average seasonal caste composition of the grapevine colonizing groups.

The number of individuals and eggs varied significantly among vine sectors (F (5, 546) = 9.58; $P <$ 0.001) and results from Tukey HSD test indicate that the highest number of termites was found in sectors B (137.72 ± 31.85), D (112.49 ± 37.17), C (92.84 ± 24.47), that significantly lower numbers were detected in sector A (83.11 ± 21.90) and the lowest in the vine branches (E = 37.69 ± 14.75, F = 40.17 ± 14.57). Although no significant differences were detected for the factor season (F (3, 546) = 0.53; P = 0.66), interesting trends in the total number of individuals detected on each sector during the year can be noted (Fig. 3). In both the basal sectors (A and B) there was a high presence of termites in winter, the numbers reached their peak in spring and then declined in summer and autumn. In the middle sectors (C and D) the lowest number of termites was detected during winter and spring and the peak was reached in summer. In the lateral branches (E ad F) termite numbers were lowest in winter and spring, increased during summer and reached a peak in autumn.

The MANOVA performed on the number of individuals for each *K. flavicollis* instar showed highly significant differences for both season and vine sector location as well as the interaction between the two factors (Table 1). Results for each instar are represented in Table 2 and Fig. 4 for the factor season and in Table 2 and Fig. 5 for the factor sector. A summary of the results for each instar/caste follows:

Eggs. A significantly higher number of eggs was found during winter, especially in sectors B and A. The

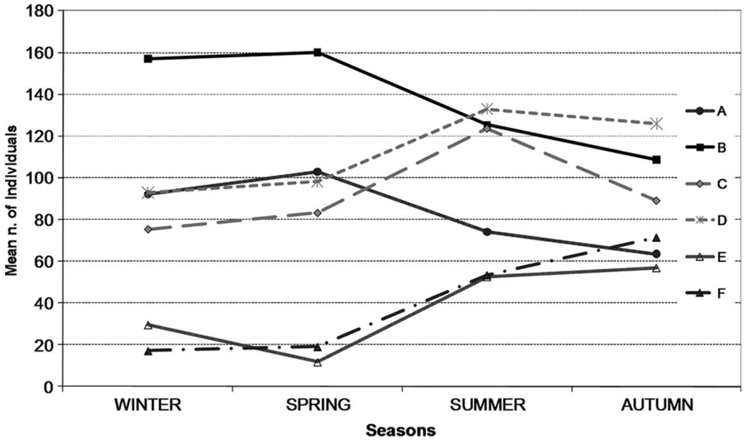

Fig. 3. Average total number of individuals of *K. flavicollis* found in each grapevine sector during each season.

lowest presence of eggs was in summer, in the lateral branches (E and F).

Larvae (LA $_{1-2}$). The number of younger larvae was similar throughout the whole year; they were found particularly in sector B and D and significantly less in the lateral branches.

Older Larvae (LA $_{3-4}$). The number of older larvae was similar during almost all year, with a slight peak in winter. Most of them were found in sector B and very few in the lateral branches.

Pseudergates (PSE). Pseudergates were found in similar numbers during the whole year, mostly in the central sectors of the vine (B, C, D).

Nymphs (N_1-N_2-N_3). Most of the nymphs found in Sherry vineyards belonged to the earlier instar or the later instar (the one just before the metamorphosis to become alates). All nymphal instars showed a similar pattern, with a peak during summer (particularly remarkable for N_3) and lowest numbers during autumn and winter. All nymphs were found especially in sectors B and D and significantly less in the lateral branches.

White soldiers (WS). Presoldiers were detected at very low numbers, with a significant peak during summer, and significantly more in sector D.

Soldiers (SOL). The presence of soldiers was significantly higher during summer and autumn in all vine sectors, except for the lateral branches.

Alates (ALA). They were found only during autumn in the upper sectors of the vines.

Reproductives (REP). They were detected in all vine sectors with a significantly higher number in winter, compared with summer.

Table 1. Results for the multivariate tests of significance on all dependent variables after VGLM MANOVA performed on the no. of individuals for each *K. flavicollis* instar

Factors	df (effect, error)	Wilks lambda	*F* values	*P* values
Intercept	11, 536	0.65	26.80	<0.001
Season	33, 1579.86	0.70	6.16	<0.001
Sector	55, 2484.61	0.82	1.99	<0.001
Season × Sector	165, 4810.20	0.69	1.26	0.015

Discussion

As a part of an investigation aimed at describing the patterns of colonization of the termite *K. flavicollis* in an arboreal crop, the grapevine, the current study is unique in providing details on the social composition, localization, and fluctuation over the seasons of its castes/developmental instars in different parts of the plant. From this survey it emerged that termites were detected in grapevine trunks aged 15 yr or older, with different degrees of infestation, ranging from a single pair of reproductives to almost 1,700 individuals. Previous analyses (López et al. 2006) that categorized the colonizing termite groups on the basis of the total population and its social composition, showed that the majority of grapevines (64%) were occupied by groups with 50–700 individuals, ≈13% of the vines had small groups with <50 individuals and ≈23% of the vines were colonized by the biggest groups (700–1,700 individuals). The present work revealed that the size of the infesting termite groups was independent from the age of the occupied vine trunk, indicating that grapevines of any age beyond 15 yr choice held colonies at different degrees of maturity and therefore

Table 2. Summary for univariate results for each dependent variable after VGLM MANOVA performed on the no. of individuals for each *K. flavicollis* instar

Instar/caste	Season (df = 3, 546)		Sector (df = 5, 546)	
	F values	*P* values	*F* values	*P* values
EGGS	3.74	0.01	7.75	<0.001
LA_{1-2}	0.17	0.91	6.00	<0.001
LA_{3-4}	3.41	0.02	3.36	0.005
PSE	0.75	0.51	5.50	<0.001
N_1	3.23	0.02	8.03	<0.001
N_2	4.31	0.005	5.51	<0.001
N_3	22.86	<0.001	3.90	0.002
WS	3.07	0.03	3.77	0.002
SOL	2.57	0.05	9.08	<0.001
ALA	15.42	<0.001	1.38	0.23
REP	4.32	0.005	1.48	0.20

LA_{1-2}, larvae; LA_{3-4}, older larvae; PSE, pseudergates; N_1-N_2-N_3, nymphal instars; WS, white soldiers; SOL, soldiers; ALA, alates; REP, reproductives.

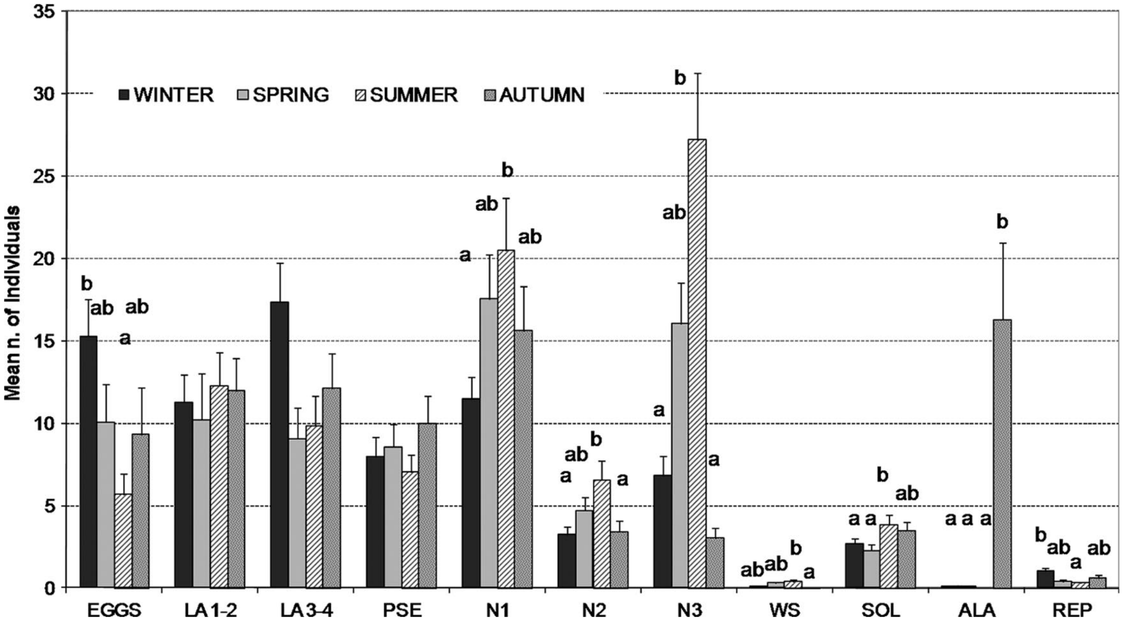

Fig. 4. Mean number of individuals (+SE) of each developmental instar/caste of *K. flavicollis* found on each season, independently of the vine sector. Columns marked by the same letter within a group (or with no letters) are not significantly different at the 0.05 level determined by the Tukey HSD tests after VGLM MANOVA. For abbreviations see Fig. 2.

that, at least in the sampled area, the choice of the founding couples was driven by the age of the vine only by discarding the youngest ones (those below 15 yr). Possibly this might be related to biochemical and/or structural features of the younger vines (up to the age of 9 yr) that make them less attractive than older ones; such features change over time and after a certain threshold, vines appear to termites all equally acceptable and "colonizable." On the other side, when the "best" nesting site is not available (e.g., extremely

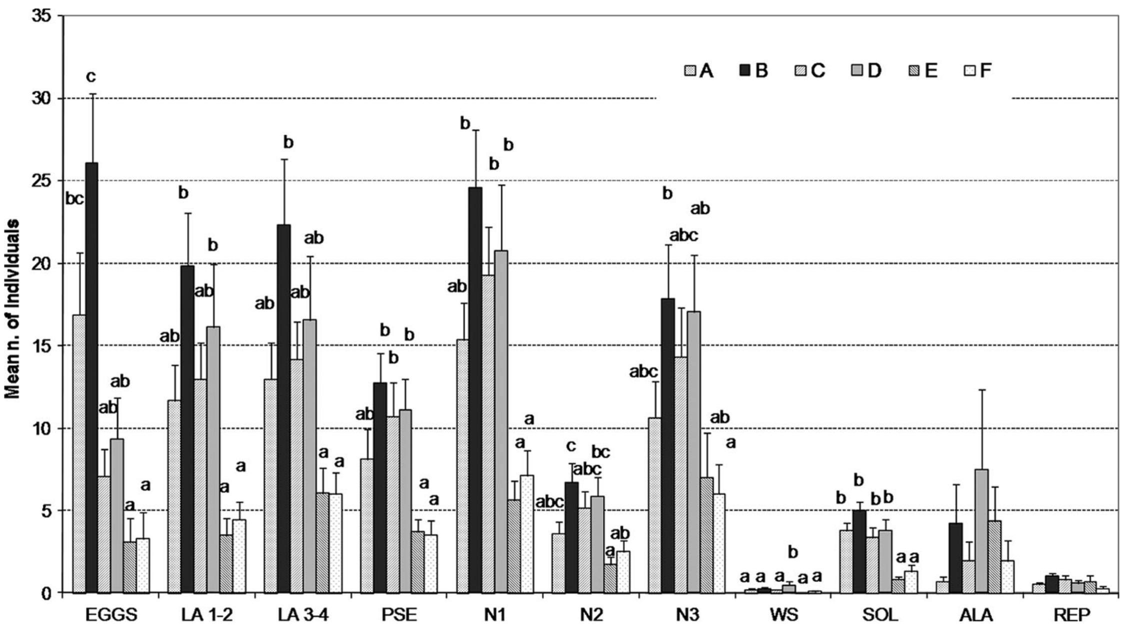

Fig. 5. Mean number of individuals (+SE) of each developmental instar/caste of *K. flavicollis* found on each vine sector (A, B, C, D, E, F), independently of the season. Columns marked by the same letter within a group (or with no letters) are not significantly different at the 0.05 level determined by the Tukey HSD tests after VGLM MANOVA. For abbreviations see Fig. 2.

high population densities), termites can attack even younger grapevines. In facts, another survey in a different district of Sherry vineyards (López et al. 2003b) showed that termites were present in 100% of vines older than 15 yr, in 60% of the 10 yr old ones and in 45% of those aged 5 yr.

The average size of the groups occupying the grapevine trunks appeared similar in different seasons, however, variations in their social composition occurred, especially for eggs, mature nymphs, and alates, whose seasonal peaks were, respectively, detected during winter, summer, and autumn. During winter and spring almost all the individuals were found in the basal regions whereas in summer there was a higher number of termites, occupying the upper sector and the external branches, where a peak was reached during autumn. These data seem to indicate a pattern of seasonal migrations of the termites inside the vine trunk, which is upward from spring to autumn and downward from autumn to winter. During this movements, the intermediate vine area (sector C) represents a transition area from the lower to the upper part and vice versa, according to the season, explaining the lower numbers detected in this sector for most of the castes/instars (Fig. 5). Such seasonal migrations could be the combination of the response of the termites to climatic changes during the year together with some biological constraints of their natural life cycle. *K. flavicollis* is a drywood termite with a typical "single wood piece life type" (Abe 1987), nesting and feeding in the wooden substrate initially selected by the founding pair of reproductives, whose members never forage outside. It is possible that during autumn the transfer to the basal region of the vine, closer to the ground, can offer termites a greater insulation and protection from the lower winter temperatures. On the other side, the upward migration during summer seems to be correlated to the annual swarming of the alates, which, for this species in these regions, takes place between September and October (López et al. 2003a,b). This was further supported in our study considering the different developmental instars and castes. During late autumn and winter, when most of the termites were found in the basal regions, the number of eggs and larvae reaches its peak, indicating that colder seasons are likely to represent the most important period for egg production and for the care of the younger developmental instars. The fact that egg numbers peak during winter and yet larval numbers are similar throughout the year could indicate either a longer time of development for eggs laid in colder months, a poorer survival of winter eggs or it might eventually be associated with a drop in reproductives' fecundity and/or fertility. For most termite species, egg-laying may fluctuate over season and with changes of environmental conditions (Nutting 1969, Grassé 1986).

During spring and summer, when most of the termites were observed especially in the upper vine regions, a remarkable increase in the number of nymphs was observed, and this period of the year might represent a period of general growth of the colony and development of alates, in preparation to the swarming phase. From our study it emerged that N_2 were always present in much smaller numbers than N_1 and N_3. Such a situation might suggest that the length of the N_2 instar is much shorter than the other two nymphal instars or might be related to the possibility that some of the N_1 regressed to pseudergates (Noirot 1985). The peak in the number of mature nymphs (N_3) in summer was immediately followed by the peak in the number of alates during autumn (simultaneously with the abrupt drop of N_3), mostly found in the upper vine regions, indicating that swarming was taking place. The number of soldiers, which are dependent on other nestmates to be fed, was higher during summer and fall and this might be related to the necessary protection of emerging alates (Howard and Haverty 1981, Luykx 1986) and this same need might also explain the higher number of presoldiers detected in summer in the upper sector, as they are the instar immediately preceding the soldier one. Presence of soldiers in the upper part of a tree was observed also in the mangrove inhabiting Kalotermitid *Incisitermes schwarzi* (Banks), where they occupied the more deteriorated part of the wood acting as a defensive barrier against the invasion of predators, to protect the bulk of the colony, which was found in the more suitable wood at the bottom of the tree (Luykx et al. 1986). Pseudergates and reproductives were almost ubiquitous in the medium-basal regions of the vine, avoided the external branches and were found throughout the year with no significant changes in their numbers. This situation might be related to their role inside the termite society: labor/care of nestmates and reproduction are essential for the life of a colony. Pseudergates represent the major work force and their presence is required all year round for taking care of the nest and all needy nestmates (Noirot and Pasteels 1987). A similar more ubiquitous distribution of the workers inside a tree, compared with that of nymphs, was observed also in the mangrove inhabiting *I. schwarzi* (Luykx et al. 1986). Reproductives are the only individuals with developed and functional gonads, and they are responsible for the colony increase. The peak in the number of reproductives detected during winter was because of the presence of de-alates trying to colonize the grapevine trunks to develop incipient colonies. This was confirmed by the fact that during winter samplings it often occurred to find a single vine occupied in different areas by different couples of reproductives surrounded by only eggs and young larvae, and these pairs sometimes shared the trunk with an established colony. It seems that as far as galleries from different families remain separated, more colonies can develop in the same trunk. Because in a vineyard grapevines are the only available potential nest sites for the new colony founders, it is very likely that more than one couple can settle in the same vine, where possibly there may be also an already developed colony. Coexistence of 2–3 colonies and co-occurrence of fully developed and incipient colonies, always inhabiting separate sections of the wood, was also detected in *I. schwarzi* occupying mangroves (Luykx 1986, Luykx et al. 1986). Lower numbers of reproductives were found in spring and summer, when almost all sampled trunks were inhabited by established colonies with only one royal couple (López et al. 2006). A possible explanation is that after a few months from colony foundation, termites from different families occupying the same trunk came in contact and intraspecific competition occurred, resulting in the death of the reproductives. Indeed, this was already hypothesized for *I. schwarzi* (Luykx 1986) and has been experimentally demonstrated in another lower termite species, *Zootermopsis nevadensis* (Thermopsidae), where synchronous settling in the same piece of wood by multiple royal pairs commonly occurs in natural conditions (Thorne et al. 2003). They showed that staged encounters between unrelated similar size incipient colonies resulted in the death of reproductives and merging of the surviving members into one colony, whereas in encounters with between established colonies and incipient ones, the larger ones had a competitive advantage and decimated the younger ones.

The present work, originally performed to investigate the patterns of infestation of a termite as a pest of vineyards, revealed interesting details on the social structure, seasonal adaptations and development of *K. flavicollis* colonies. Similar studies performed on those termite species that threaten or cause real damages to crops or economically important trees, besides representing a contribution to the understanding of termite biology, may be of crucial importance for the development of management strategies of pest species.

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