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# Exploitation competition between hole-nesters (*Muscardinus avellanarius*, Mammalia and *Parus caeruleus*, Aves) in Mediterranean woodlands

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## Abstract

Data from a long-term study (1993–2003) using artificial nest-boxes, were analysed to examine competition for nesting between blue tit *Parus caeruleus* and common dormouse *Muscardinus avellanarius* in Sicily. Occupation rates and the reproductive biology of the blue tit in sample woodlots outside the distribution area of the common dormouse were used as a control in sample areas where the two species were syntopic. A selection test showed that the two species, when living in syntopy, actively chose the small nest-boxes, thus overlapping in the use of the same spatial resource. The experimental exclusion of the common dormouse from nest-boxes caused an increase of blue tit occupation rate. Once the effect of nest-box density was removed, complementary density changes between the two species clearly appeared. The population cycle of both species in the areas of syntopy showed a swinging pattern, i.e. in areas or during years of common dormouse high abundance few blue tits bred and vice versa. The abundance of the blue tit was affected not only by common dormouse abundance, but also by some habitat and climate variables. Blue tits had low breeding success and a high percentage of nest failure (38% in syntopy vs 3% in control areas), owing to nest destruction and predation by common dormouse, as well as probably also by other rodents (23%) and *Martes martes* (15%). Another experiment, using stuffed models, showed that the blue tit recognized the common dormouse as an enemy, and behaved as if confronted by a competitor or predator species to protect their nests.

**Key words:** competition, coexistence, *Parus caeruleus*, *Muscardinus avellanarius*, Mediterranean woodlands

## INTRODUCTION

The global loss of biodiversity has led to a renewed interest in the underlying mechanisms that explain spatial differences and temporal change in diversity, through the study of interactions that enhance or diminish coexistence among competing species (Keddy, 1989; Sommer & Worm, 2002).

Acting mainly through resources, interspecific competition is one of the major factors that may limit the distribution and abundance of species. Experimental studies have so far been concerned mainly with congeners or within-taxon (i.e. bird–bird, mammal–mammal, etc.) interactions in temperate continental ecosystems (Connell, 1983; Schoener, 1983; Newton, 1998). The few studies on across-taxa interactions (Haemig, 1992; Christensen & Whitham, 1993) are generally related to the impact of herbivores on plant communities.

Tits of the genus *Parus* are one of the preferred models chosen for studying the population biology of passerines (see Krebs, 1970; Blondel, Goster *et al.*, 1990). Tits are

cavity-nesters in which competition for nest sites is often strong, with larger species usually evicting smaller ones (Newton, 1998). A complementary density change, i.e. a negative correlation, with the relative abundance of one species increasing as the other declines, is expected to occur when changes in the number of individuals depends on interspecific interactions (Tomialojc & Wesolowski, 1990). Conversely, if species abundance changes independently or species fluctuate in synchrony, other limiting factors rather than competition would lead to the observed interaction (Newton, 1998). Experimental manipulation, by altering the number of individuals of one species (Gustafsson, 1988) or the size of the nest-box holes (Dhondt & Eyckermann, 1980), further increases evidence of interspecific competition according to the Wiens' (1989) criteria.

Species living in Mediterranean islands are the result of evolutionary long-term responses that shape the insular communities and differentiate the ecology and diversity of island fauna with respect to that of the mainland (Blondel, Chessel & Frochot, 1988; Blondel & Vigne, 1993; Blondel, 1995; Massa, 1985, 1990; Sarà, 1998). Nevertheless, studies of interspecific competition in these areas are lacking and so far there is no evidence of across-taxa

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competition present in the area. Intensive long-term fieldwork (1993–2003) in sample areas of Sicily gave us a large body of raw data on the colonization and use of artificial nest-boxes by hole-nesters in Mediterranean woodlands. Among the dozen species using, more or less regularly, the nest-boxes, only the blue tit *Parus caeruleus*, a small insectivorous passerine, and the common dormouse *Muscardinus avellanarius*, a small arboreal mammal, gave us enough data and preliminary and circumstantial evidence of overlap in the spatial resource they used in syntopy.

Moreover, reports in continental Europe (see review in [Juskaitis, 1995](#); [Vaughan, 2001](#)) indicate that common dormice occupy artificial bird nest sites, where they are suspected, with some conflicting evidence, of destroying nests and clutches and eating eggs, nestlings and even adult birds.

For these reasons, the interactions between these two hole-nesters were carefully examined. An asymmetric relationship ([Keddy, 1989](#)) between the two species was assumed, i.e. the dominance of the common dormouse, and whether the breeding density of the blue tit was limited by the exploitation competition for the nest-sites was questioned. Initially the positive selection (*sensu* [Johnson, 1980](#)) of the same resource was checked for, i.e. for the preference in both species of nest-boxes with small hole size. Then checks were made for the presence of complementary density changes throughout the study period and for related changes in some parameters of the blue tit's reproductive biology. These analyses were intended to give us the following information: (1) the species overlap in resource use; (2) whether resource use by one species reduces the availability of the same resource for the other. The two field experiments then tested: (3) if the abundance of one species is reduced by the other; (4) whether the blue tit perceives the common dormouse as a danger (competitor and/or predator).

## STUDY AREAS

The main study area in northern Sicily was in the Madonie mountain range, a Natural Regional Park of some 40 000 ha, in northern Sicily. The 13 sample areas being studied can be arranged along altitudinal belts by vegetation type ([Pignatti, 1997](#)). Three sample areas were in a beech forest (*Anthriscus-Fagetum aceretosum*) within the sub-Atlantic belt. Seven of them were in a holly forest (*Ilici-Quercetum petraeae*) within the Colchic belt; two were in a mixed evergreen oak wood (*Erico-Quercion ilicis*) in the Mediterranean belt, as was the last one, which was in a hazel orchard. The Colchic belt is a localized pre-glacial association of evergreen plants (*Ilex aquifolium*, *Daphne laureola*, *Taxus baccata*, *Buxus sempervirens* and *Ruscus aculeatus*) mixed with temperate deciduous oaks (*Quercus petraea* and *Q. robur*); within this forest also lie a pure chestnut stand (Mad8). The hazel wood represents a special case of *Quercion ilicis* woodland, where hazel cultivation formerly replaced the original Mediterranean vegetation, but it is now for the most part abandoned.

Further description of the sample areas is in [Sarà, Spinnato et al. \(2000\)](#), [Sarà, Casamento & Spinnato \(2001\)](#) and in Appendix 1. From 1996 to 2003, these 13 sample stands were studied by mounting a variable number of small (20 × 15 × 15 cm, hole size 32 mm) artificial nest-boxes to monitor the common dormouse populations. In seven of these areas (Mad5–6, Mad9–13, see Appendix 1) grids containing 25 large (20 × 20 × 30 cm, hole size 50 mm) nest-boxes per ha for the fat dormouse *Glis glis* were also present ([Milazzo, Falletta & Sarà, 2003](#)).

The second study area in south-western Sicily was in the Sicani Mountains, outside of the common dormouse distribution range in Sicily ([Sarà, 2000](#)). This is a woodland of 1600 ha belonging to the Agriculture and Forestry Department, and divided in three main woodlots: (a) 700 ha of mixed natural wood dominated by broad-leaved *Quercus virgiliana*, evergreen *Q. ilex* oaks and other deciduous trees such as *Acer* spp. and *Pirus* spp.; (b) 700 ha of reforestation by *Pinus halepensis* and *Pinus* spp.; (c) 200 ha of pine reforestation in the process of being turned to natural woodland. Fifty standard artificial nest-boxes were set in 1993 and checked until 2002 in both natural and reforestation stands; a further group of 50 nest-boxes was mounted in the third stand in 1997 and checked until 2002. Further details on the study area are reported in [Massa & Lo Valvo \(1996\)](#) and [Massa \(2002\)](#). All the studied stands in the Madonie (except for Mad9 and Mad10, see Appendix 1) and in the Sicani mountains were located in woodlands not older than 40–50 years, where snags are removed by forestry management and natural holes in branches or trunks of trees are very rare. Natural cavities are therefore a limiting resource for breeding.

## MATERIAL AND METHODS

Due to the location of the 2 study areas, with respect to the distribution range of the common dormouse in Sicily, the occupation rate and breeding biology of the blue tit was analysed comparatively to check for interspecific competition. The 3 sample stands in the Sicani Mountains therefore represented a group of control areas (dormouse absent), where data on tit breeding, without the presence of the small dormouse, were recorded; whereas the 13 stands in the Madonie (dormouse present) furnished data on the syntopic presence of both species.

### Data collection and analysis of complementary density change

The common dormouse and the blue tit easily colonize artificial nest-boxes where they build clearly distinguishable nests of vegetable matter: a woven round ball of leaves, grasses, bark strips by the small mammal, and a cup of moss replenished with feathers, horse-hair, fur, etc., by the bird.

In the Sicani, from 1993 to 2002 (see [Massa & Lo Valvo, 1996](#); [Massa, 2002](#)), as in the Madonie, from 1996 to 2003, nest-boxes were checked monthly during the year

and every 7–14 days from the end of March to early June. This allowed recording of all the species living in the nest-boxes and the basic parameters of the reproductive biology of the blue tit (number of nest-boxes occupied, number of eggs laid, of nestlings, of fledglings, of failures) and determining the fate of each tit nest.

The presence of the common dormouse inside the nest-boxes was recorded according to the following scheme: (a) attempts or beginnings of colonization = faeces and/or stored food and/or very little vegetable matter; (b) empty nests = a badly woven cup with some leaves as roof and/or perfectly woven round nests; (c) occupied nests = dormice present in the above (a) and (b) categories or, rarely, even in empty nest-boxes.

For both species in both areas, raw data were used or a simple occupation rate (OR) derived per each study year and per each sample stand. For each a–c category of occupation (e.g. number of empty nests/number of nest-boxes, etc.), the sum of all categories gave the total OR per year and per sample area (Appendix 1).

In the Madonie, the common dormouse has a bimodal reproductive season, in spring and autumn, peaking respectively in June and December (Sarà, 2000). The blue tit in the same sample areas begins to visit nest-boxes in March and starts laying and incubating eggs from mid April to early May. Three months (March, April and May) in which the reproductive periods of both species coincide were studied because it was assumed, in the light of the putative interspecific competition, that the presence of the common dormouse would have affected the breeding of the blue tits. Therefore, a number of direct (i.e. dormice in March vs blue tits in March, etc.) as well as indirect (i.e. dormice in March vs blue tits in April, etc.) negative regressions between the number of common dormice and the number of blue tits was expected.

The previous aims of our investigations on the common dormouse in the Madonie Regional Park created 2 methodological constraints to the present study. First, nest-box density changed (from 5 to 75, Appendix 1) on per area and per year basis, because in the first years small groups were mounted to explore the main woodland typologies in the Park. Later, in some other areas/years, larger groups of 40–75 nest-boxes were mounted for specific reasons. Therefore, nest-box density was corrected for and the residual of regressions were used to check for the complementary density changes.

Second, the 13 stands in the Madonie covered different habitats varying in altitude, type and structure of wood, exposition and climate. This made it necessary to distinguish the role and weight of the environmental variables and that of common dormouse presence in determining the abundance of the blue tits. We therefore explored, by multiple regression techniques, the relationship between the blue tit OR and 11 independent variables which physically and ecologically describe these woodlands: common dormouse OR plus 10 other variables (altitude, exposition, tree canopy, understorey coverage, tree height, specific richness of trees and of understorey species, average annual minimum and maximum temperatures, Thornthwaite humidity index). The effect of other

species was not checked because of their low ORs (Appendix 2).

Finally, data on the tits' reproductive biology and ORs in the Sicani and Madonie ranges was statistically compared to check for differences owing to the presence/absence of the competitor.

### Selection test for the same resource

First the overlap of the same resource use was tested by comparison of their usage and availability (Johnson, 1980; Manly, McDonald & Thomas, 1993). We took advantage of the contemporary presence of seven sample grids in the Madonie, in which a comparable number of both small (hole size: 32 mm) and large (hole size: 50 mm) nest-boxes was present. Six years of sampling in 7 areas (Mad5 from 1999 to 2001, Mad6 in 2000–01, Mad9 and Mad10 in 2002–03, Mad11 and Mad12 in 1998, Mad13 in 1999) were available for the test. To analyse the selection of the spatial resource represented by nest-boxes with small and large holes, the index of selection  $B_i$  was used (Manly *et al.*, 1993).

### Field experiments

Two field experiments were planned for the 2002 and 2003 seasons to test further for the presence, if any, of exploitation competition between the 2 species.

The first was a classic exclusion experiment. In the best studied sample area of the Madonie, observed since 1996, the common dormouse was excluded by closing the holes of 25 nest-boxes in 1-ha grid from November 2001 to mid March 2002. Another adjacent 1-ha grid was used as a control, allowing the dormice to enter the nest-boxes. ORs and reproductive parameters in both grids were recorded for both species in April and May.

The second field experiment was carried out during the 2002 and 2003 breeding seasons in 5 sample areas of the Madonie. An in-progress study was used on the variation in nest defence intensity and on the related assumption of risk by parent tits (i.e. test of the feedback hypothesis; see Halupka & Halupka, 1997; Pavel & Bures, 2001). Multiple stuffed specimens were presented to blue tit nests for 10 min (78 experiments in 48 nests with broods), throughout different nestling stages. The stuffed models were chosen for eliciting a response by parents to the known threat represented by: a general intruder (black cap *Sylvia atricapilla*); a competitor (blue tit and great tits *P. major*); a predator (weasel *Mustela nivalis*) and the unknown threat represented by the common dormouse. In addition, the response towards a new species not present in the study area (the Spanish sparrow *Passer hispaniolensis*) or a new object (orange tennis ball, Marlboro cigarette packet was checked). After a preliminary inspection and because they elicited a similar response, experiments with the Spanish sparrow were pooled together with those using the black cap.

The aims of these experiments were: (1) to get preliminary information about the neophobic response

of tits to new species or new objects appended in front of the nest; (2) to place the common dormouse in the right position along a gradient of nest defence intensity, by means of the blue tit's parental response to the known models. In other words, a check on whether the common dormouse would elicit an indifferent, competitive or anti-predatory response was attempted. To detect the variations in nest defence intensity and risk assessment by blue tit parents, which are pertinent to this study, the frequency of parental trips to the nest and the time of first and second entrance into the nest without (natural rates) and with any given model was measured. All the responses of blue tits dependent from different nestling stages, as well as the presence and frequency of other behaviours towards the models, were not considered.

### Statistical analysis

The index of selection  $B_i = (u_i/m_i)/\Sigma(u_i/m_i)$ ; where  $u_i = n$  of units in category  $i$  in the sample of used units;  $m_i = n$  of available units in category  $i$  in the sample (where  $i = 1, 2, \dots, I$ ); and the related statistic (Manly *et al.*, 1993):  $\chi^2_L = 2\Sigma u_i \log_e(u_i/u + \pi_i)$ , were run and calculated by a macro routine in Excel<sup>®</sup>. Origin 6.1 and STATISTICA 6.0 allowed running the linear and multiple stepwise regressions, to calculate the related statistics, and all the non-parametric and parametric tests. All statistical tests were two-tailed and set at a statistical significance  $\alpha = 0.05$ . The stepwise multiple regressions were started from a null model (forward, i.e. initially adding variables) and from a saturated model (backward, i.e. initially removing variables). This produced alternative regression models with variables showing significant relationships, in order to obtain the largest significance increase in the explained variation ( $R^2$ ) at each step, until the addition (or subtraction) of further variables resulted in only minor increases to  $R^2$ . This routine approach (e.g. Bellamy, Hinsley & Newton, 1996) resulted in a regression model which included as few variables as possible, but retained the strongest statistical significance and explained most of the variation in blue tit OR.

## RESULTS AND DISCUSSION

Throughout the 13 stands of the Madonie, the blue tit and the common dormouse were the most regular and abundant nest-box dwellers (Appendix 1). The blue tit started colonization in March, in coincidence with a low abundance phase of the common dormouse population. April and May, while the common dormouse was recovering until the peak of June, were the months of highest co-presence in the sample areas. During this period, nest-box turnover from one species to another was rather low, a median value of 2 nest-boxes per area (min–max: 0–10), which corresponds to a mean frequency of 7% (min–max: 0–25%) of the available nest-boxes, changed owner. Occupation of apparently abandoned nests of the common dormouse by blue tits was much more common than the reverse.

Some other facultative or obligate hole-nester species colonized, more or less regularly, nest-boxes in the Madonie and Sicani ranges and their spring ORs are reported in Appendix 2. The great tit was a regular breeder in the Sicani stands with relatively high frequencies in the reforestation and in the reforestation turning to natural woodlots (Massa, 2002). Great tits were rare and localized nest-box dwellers in some of the Madonie areas, as were the other two bird species recorded (tree creeper *Certhia brachydactyla*, nuthatch *Sitta europaea*) and the woodmouse *Apodemus sylvaticus*. Reptiles (wall lizards *Podarcis sicula* and *P. wagleriana*, and gecko *Tarentola mauretana*) colonized nest-boxes only in the mixed evergreen woodlots, while the fat dormouse proved to be localized only in some of the Madonie high altitude stands. This species was found within small nest-boxes only accidentally (youngsters during dispersal) in late summer, but from late June to early December, successfully colonized, grids provided with large nest-boxes (Milazzo *et al.*, 2003).

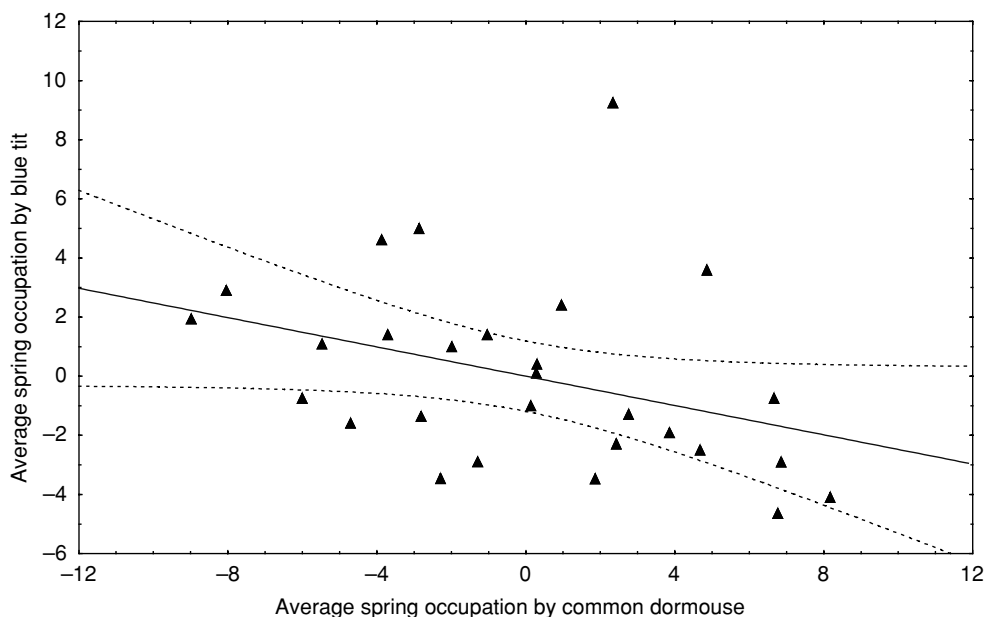
### Selection test for the same resource

The 6 years of monitoring in the seven 1-ha grids of the Madonie yielded year-round occupation data for a total sample of 492 nest-boxes; 300 of which had a small and 192 had a large hole size. Records of the blue tit and the common dormouse (tracks, nests, individuals, etc.) inside these nest-boxes gave the usage rate for these two kinds of spatial resources. Both species positively selected for small nest-boxes and hole sizes. The index of selection for common dormice was  $B_i = 0.63$  for small and 0.37 for large nest-boxes and this difference is highly significant ( $\chi^2_L = 13.05$ ,  $P < 0.001$ ). Blue tit preference was even stronger with a  $B_i = 0.80$  for small and 0.20 for large ( $\chi^2_L = 21.41$ ,  $P < 0.001$ ).

The outcome of positive selection for small nest-boxes with small hole-size, in areas where natural hole-trees are limiting, was neither surprising nor unexpected, since it is widely known that the choice of the precise hole size is highly recommended in research projects that use nest-boxes, to favour the desired species colonization and to discourage others (Dhondt & Eyckermann, 1980; Morris, Bright & Woods, 1990). Nevertheless, the selection test allowed us to state that the two species under investigation in the Madonie sample areas actively chose the small nest-boxes, thus overlapping in the use of the same spatial resource. This experimental evidence was the starting point for later analyses of exploitation competition.

### Complementary density changes

The positive correlation between the number of tit breeding pairs and the nest-box availability was already known (Minot & Perrins, 1996) and proved to be present in both species also in the Madonie areas (blue tit:  $R^2 = 0.28$ ,  $P = 0.004$ ,  $n = 28$ ; common dormouse:  $R^2 = 0.78$ ,  $P = 0.0001$ ,  $n = 28$ ). Once corrected for nest-box density,



**Fig. 1.** The complementary density change of blue tit *Parus caeruleus* and common dormouse *Muscardinus avellanarius* as expressed by the linear fit (straight solid line) and upper and lower 95% confidence limits (dotted lines) among residual of correlations of the average occupation rates (no. of nests/no. of nest-boxes) during March–May.

**Table 1.** Results of the regression models between the residuals of spring occupation rates (OR) of blue tit *Parus caeruleus* (*P.c.*) and common dormouse *Muscardinus avellanarius* (*M.a.*)

Model	Linear fit	$R^2$	$P$	$n$
OR <i>P.c.</i> March – OR <i>M.a.</i> March	$y = 0.335 - 2.096x$	0.449	0.0002	25
OR <i>P.c.</i> April – OR <i>M.a.</i> April	$y = 0.0000001 - 0.703x$	0.234	0.009	28
OR <i>P.c.</i> May – OR <i>M.a.</i> May	$y = 0.102 - 0.487x$	0.143	0.052	27
OR <i>P.c.</i> April – OR <i>M.a.</i> March	$y = 0.130 - 0.117x$	0.025	NS	26
OR <i>P.c.</i> May – OR <i>M.a.</i> April	$y = 0.000001 - 0.178x$	0.075	NS	28

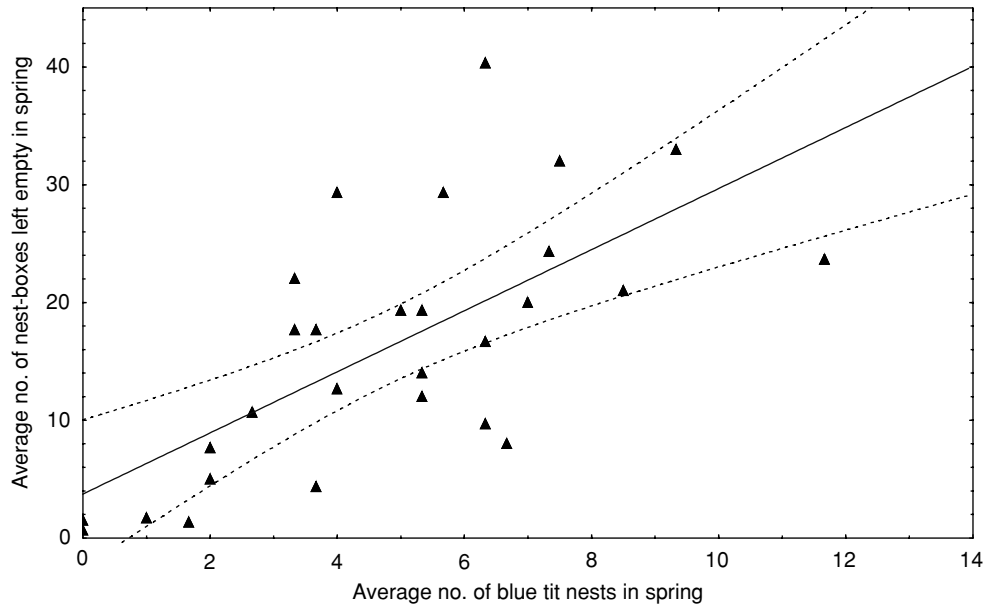
the regressions of blue tit and common dormouse ORs in each couple of months gave the results reported in Table 1 and that of regression averaging for the three spring months is in Fig. 1. All the direct regressions were statistically significant, but we did not find significant correlation between the indirect regressions, e.g. among the residuals of common dormouse abundance in March and those of blue tit occupation in April (Table 1). This would probably mean that the negative effect of the common dormouse abundance on blue tit colonization was direct and not delayed (i.e. the abundance of the common dormouse in March did not affect breeding of the blue tit in April or May, and so on). Accordingly, the direct correlation values decreased from March to May, because the competitive effect of dormice was probably stronger at the start of the breeding season, when the birds visited the nest-boxes and began establishing their territories.

A set of significant regressions was also found between the number of blue tit nests and the number of nest-boxes left unoccupied by the common dormouse in March ( $R^2 = 0.22$ ,  $P = 0.02$ ,  $n = 25$ ), April ( $R^2 = 0.36$ ,  $P = 0.0001$ ,  $n = 28$ ) and May ( $R^2 = 0.33$ ,  $P = 0.002$ ,  $n = 27$ ). Therefore, in each month the blue tit occupied only the space left available to it for breeding. The result of

regression averaging for the season ( $R^2 = 0.46$ ,  $P < 0.0001$ ,  $n = 28$ ) is shown in Fig. 2.

The population cycle of both species in the Madonie showed a swinging pattern with a negative correlation throughout the study period (all stands confounded during 1996–2003:  $R = -0.64$ ,  $P = 0.08$ ,  $n = 8$  years). As a result of this complementary relationship, in areas or during years of common dormouse high abundance, few blue tits bred; whereas when the common dormouse decreased, the abundance of the small passerine increased.

We wondered whether the presence of common dormouse was really an exclusive limiting factor in the abundance of blue tit nests, which is why the 13 stands in the Madonie range were spread over different habitats, from sclerophyll woods at *c.* 400 m a.s.l., to temperate beech forest at 1500 m a.s.l. It therefore seemed logical to assume that ecological or climatic factors would also influence blue tit abundance. A control test was thus conceived, using a stepwise multiple regression analysis, with a set of 10 independent environmental variables plus the common dormouse OR, to determine their contribution to the blue tit OR. The tested models converged rather well. The understorey species richness was removed and the remaining 10 variables were entered or removed with



**Fig. 2.** The linear fit (straight solid line), upper and lower 95% confidence limits (dotted) between the average no. of blue tit *Parus caeruleus* nests in March–May and the average no. of nest-boxes left unoccupied by the common dormouse *Muscardinus avellanarius*.

**Table 2.** Main parameters (mean  $\pm$  SD) of blue tit *Parus caeruleus* reproductive biology in the two studied areas

	Madonie range (common dormouse present)	Sicani range (common dormouse absent)	Statistical significance
Average laying date (first egg)	27 April ( $\pm 8$ days, $n = 99$ )	23 April ( $\pm 12$ days, $n = 337$ )	$t_{[434]} = 3.11$ , $P = 0.002$
Average clutch size	$7.57 \pm 1.75$ , $n = 103$	$8.05 \pm 2.89$ , $n = 243$	$t_{[444]} = 2.2$ , $P = 0.03$
Average no. of fledglings	$4.68 \pm 3.47$ , $n = 83$	$6.87 \pm 2.57$ , $n = 204$	$t_{[285]} = 5.86$ , $P < 0.0001$
Average OR (all stands)	$0.28 \pm 0.19$ , $n = 28$	$0.29 \pm 0.22$ , $n = 23$	$t_{[49]} = 0.17$ , $P = \text{NS}$
Average OR (only oak stands)	$0.29 \pm 0.20$ , $n = 20$	$0.53 \pm 0.13$ , $n = 9$	$t_{[27]} = 3.18$ , $P = 0.004$
Average no. of nests (all stands)	$15.04 \pm 9.87$ , $n = 28$	$14.44 \pm 10.89$ , $n = 23$	$t_{[49]} = 0.20$ , $P = \text{NS}$
Average no. of nests (only oak stands)	$8.78 \pm 4.51$ , $n = 20$	$26.6 \pm 6.58$ , $n = 9$	$t_{[27]} = 8.17$ , $P < 0.0001$
Frequency of nest destruction ( <i>Martes martes</i> excluded)	38% (23%)	3% (not recorded)	$\chi^2_{[1]} = 43.1$ , $P < 0.0001$

different weights. Three variables (in order of highest contribution: common dormouse OR, species richness of trees, altitude) had statistically significant  $\beta$ -coefficients and accounted for a forward model with an  $R^2 = 0.55$ ,  $P = 0.00004$ . Common dormouse OR again, canopy coverage, species richness of trees and the Thornthwaite humidity index were selected by the final backward model with  $R^2 = 0.69$ ,  $P = 0.00001$ .

The breeding biology of the blue tit in the Madonie range and in the control areas of the Sicani range was different (Table 2). In the Madonie, the average laying date was significantly postponed by 4 days; and delayed by 1 week (29 April vs 22 April) if the median values were considered. This difference depended, however, on the different bioclimatic conditions, since in the Madonie the date of first egg laying was significantly correlated to altitude a.s.l. ( $R = 0.44$ ,  $P < 0.0001$ ,  $n = 99$ ), and moving from lower (430 m a.s.l.) to higher (1450 m a.s.l.) altitude, the average date moved up from 16 April ( $\pm 10$  days) to 1 May ( $\pm 7$  days).

The average clutch size and the average number of fledglings were also statistically different, since in the Madonie range, the blue tit performed worse than in the Sicani. These differences, however, did not depend on bioclimatic conditions, because both the average clutch size ( $R = -0.05$ ,  $P = 0.61$ ,  $n = 96$ ) and the average number of fledglings ( $R = -0.01$ ,  $P = 0.53$ ,  $n = 81$ ) of the Madonie blue tits were not correlated to altitude.

The lowest reproductive success in the Madonie was determined by heavy predation and nest destruction. Thirty-eight per cent of the 87 nests recorded during the study period were destroyed in the Madonie range; 15% of these were destroyed in one area by a marten *Martes martes* that learned to open the lids of nest-boxes; the other 23%, in all the sample areas, by small predators that entered nest-boxes. The figure in the Sicani was much lower, with only 3% out of 343 recorded nests destroyed (Table 2).

The annual average OR of blue tits or the annual average number of nests found inside the nest-boxes in

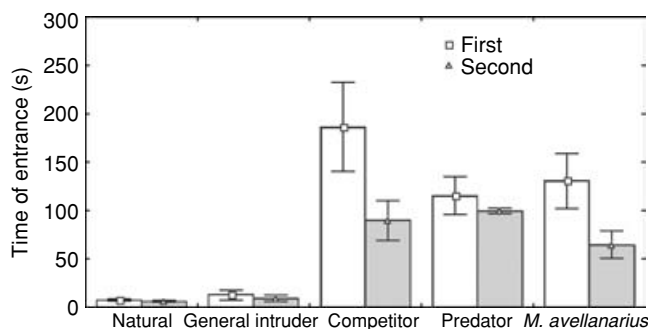
the two ranges did not show any statistically significant differences. But these gross mean values came from several factors which independently affected blue tit density, such as the kind of woodland management (natural vs reforestation) in the Sicani and the bioclimatic heterogeneity of the Madonie sample areas. In fact, if the comparison is restricted to the similar oak habitats of the Madonie (annual mean blue tit OR =  $0.23 \pm 0.20$ ,  $n = 18$ ) and of the Sicani ( $0.53 \pm 0.13$ ,  $n = 10$ ), a statistically significant difference is obtained ( $t_{[26]} = 4.11$ ,  $P = 0.0003$ ), which correlates, with the presence/absence of the common dormouse.

### Field experiments

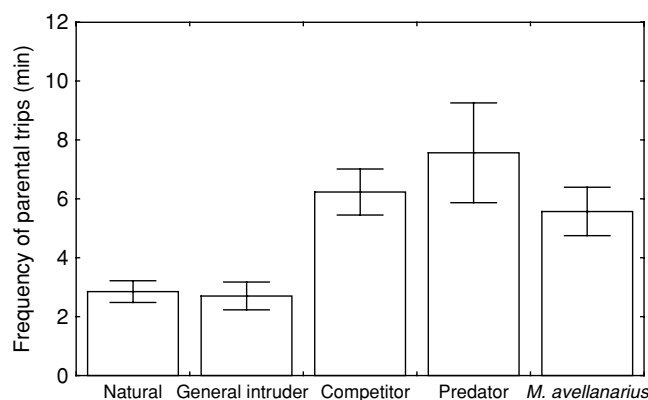
The exclusion experiment in the Mad5 grid led, as expected (Newton, 1998), to a decrease of common dormouse colonization and to an increase of blue tit occupation rate, with respect to the adjacent control grid (Mad6). The frequency of empty nest-boxes was equal in the two grids; meaning that the available space for nesting was well saturated. The  $2 \times 2$  contingency table, however, did not give a significant value (Fisher exact test  $P = 0.19$ ), this was probably owing to the small sample of nest-boxes used. None the less, the blue tit OR, in the experimental grid (0.56), reached values comparable to that ( $0.53 \pm 0.13$ ) in the similar oak habitat of the Sicani where the common dormouse was absent. The average blue tit OR in all the Madonie stands was  $0.27 \pm 0.18$ , which was significantly lower ( $P = 0.038$ ) than that reached in the experiment grid, as occurred with the common dormouse OR (average value =  $0.52 \pm 0.20$  vs experiment value =  $0.16$ ,  $P = 0.009$ ).

Owing to the partial lack of statistical significance in the exclusion experiment, a second field experiment was extracted from a behavioural study on the variation in the nest defence intensity and the assumption of risk of the tits. The following are some preliminary results of these experiments carried out in sample areas of the Madonie. The first question was how were tits able to know what a dormouse looks like, since tits are diurnal and dormice are generally active in the dark. An investigation in this direction was begun by checking the neophobic response to a new species/object, because this would exclude the observed response to the stuffed dormouse model as elicited by neophobia. When an object (orange tennis ball, Marlboro® cigarette package) was presented, we did not notice any reaction in the time of first entrance (mean =  $6.50 \pm 4.0$ ,  $n = 4$ ), which was not significantly different from the time of natural entrance ( $t_{[26]} = 0.29$ ,  $P = \text{NS}$ ). Also, the reaction to a species not present in the sample areas, such as the Spanish sparrow did not elicit a different response with respect to the natural rate or to that in the presence of the black cap.

Figure 3 shows the average time of first and second entrance into the nest in presence of the series of stuffed models. The hypothesis to test here was that the time of parent entrance would increase from the natural condition (without any model) to the competitor or predator presence



**Fig. 3.** The average time (Mean  $\pm$  SE) of blue tit *Parus caeruleus* first and second entrance into the nest-box in presence of stuffed models. The statistical pairwise comparison, in both cases, follows this scheme: natural rate vs general intruder model = not significant; natural rate and general intruder vs predator, competitor and common dormouse *Muscardinus avellanarius* models = significant; predator and competitor vs *M. avellanarius* = not significant.



**Fig. 4.** Frequency (Mean  $\pm$  SE) of parental trips of blue tits *Parus caeruleus* to the nest, in presence of the stuffed models. The statistical pairwise comparison is the same as in Fig. 3.

(Duckworth, 1991). Parents normally fly directly to the nest or to a 'stop-over' roost situated some metres away from the nest-box. This entrance is very fast, lasting only a few seconds (mean first entrance =  $7.42 \pm 5.96$ ,  $n = 24$ ; mean second entrance =  $6.05 \pm 4.81$ ,  $n = 22$ ). When a general intruder model (Spanish sparrow and black cap pooled together) was presented to the nest, this time was equivalent ( $t_{[30]} = 1.37$ ,  $P = \text{NS}$ ), but it increased in a significant way when an intra- or interspecific *Parus* competitor ( $t_{[40]} = 3.95$ ,  $P = 0.0003$ ) or a weasel ( $t_{[31]} = 6.57$ ,  $P < 0.0001$ ) was presented. The stuffed common dormouse elicited a significant delay in the time of the parents' entrance with respect to the natural rate ( $t_{[40]} = 4.74$ ,  $P = 0.00002$ ) or to the general intruder models ( $t_{[24]} = 2.59$ ,  $P = 0.016$ ), and this delay was similar to that showed in presence of the competitor ( $t_{[34]} = 1.14$ ,  $P = \text{NS}$ ) or the predator ( $t_{[25]} = 0.005$ ,  $P = \text{NS}$ ).

The frequency of parental trips to the nests was altered in the same way (Fig. 4) and showed the same scheme of pairwise statistical significance as above. In the areas studied, a blue tit rearing its young made a trip to the nest, on average, every  $2.34 \pm 1.84$  min.



This trip frequency was analogous ( $2.70 \pm 1.34$ ) when a general intruder model is put in front of the nest ( $t_{[31]} = 0.50$ ,  $P = \text{NS}$ ), but became significantly lower when *Parus* spp. ( $6.23 \pm 3.75$ ,  $t_{[41]} = 4.38$ ,  $P = 0.00008$ ) or weasel models ( $7.56 \pm 5.08$ ;  $t_{[32]} = 4.33$ ;  $P = 0.0002$ ) were presented. The trip frequency in the presence of the common dormouse was analogous ( $5.57 \pm 3.49$  min) to that of a predator ( $t_{[25]} = 1.15$ ,  $P = \text{NS}$ ) or a competitor ( $t_{[34]} = 0.53$ ,  $P = \text{NS}$ ).

This was only part of the behavioural response of the blue tit parents to avoid the localization of their nest or to defend it. The recorded behaviours of the blue tit included nest guarding, alarm calls, distraction flights, direct attacks (to *Parus* spp.) and mobbing (to the weasel), that changed in frequency and intensity according to the nestling stage and to the model. These experiments opened also the question of whether the blue tit recognizes the nocturnal dormouse for itself or if it perceives only the shape of a 'rodent-like' intruder. None the less, the experiments with stuffed models clearly demonstrated that the blue tit recognized the common dormouse as a dangerous intruder species. The blue tit altered its normal behaviour, delaying both the time of entrance into the nest and nest attendance (Figs 3 & 4).

At this stage of analysis, whether the blue tit distinguishes the dormouse as a competitor or as a predator could not be determined. This yet unsolved question turns on the longstanding debate regarding whether or not common dormice predate small birds and their nests (see review in Juskaitis, 1995; Vaughan, 2001). This is worth briefly discussing, because when comparing the reproductive biology of the blue tit, we have found meaningful lower reproductive success (Table 2) in the syntopy range (Madonie) than in the control (Sicani). This depended not only on the heavy predation of adults and nestlings (i.e. average number of fledglings), but also on the predation or, at least, the disturbance of laying females (i.e. decrease in average clutch size caused by the nests abandoned with few eggs).

The only difference in the qualitative composition of competitor and predator species, between the two ranges, is the Gliridae presence in the Madonie. Automatically, this does not mean that only the common dormouse is responsible for nest destruction and predation. In the Madonie, in fact, predation (15% of destroyed nests) by martens was recorded, a species also present in the Sicani sample areas; and other species present in both areas, such as *A. sylvaticus* (or even the greater spotted woodpecker *Picoides major*), could also be responsible for all or part of the remaining (23%) predation. However, the signs and tracks of predation in this quota of nests were typical of small rodents, easily entering the nest-boxes. Large for dormouse adults start activity during the late blue tit breeding season and, in our field experience, they only entered large nest-boxes in summer; however, incursions inside nest-boxes occupied by the blue tit cannot be excluded. The woodmouse occasionally colonized nest-boxes during spring (see Appendix 2), more frequently in the rest of the year; none the less giving evidence of its arboreal activity in the study areas. In conclusion, apart

from the woodmouse and the fat dormouse, the common dormouse seems to be the other main suspect.

Our study dealt with exploitation competition, but the analysis of reproductive parameters led us to record some evidence for interference or even for probable predation on blue tits. It is possible that during competitive interactions for the spatial resource, common dormice entered nest-boxes containing blue tit eggs and destroyed the nests, or even that the defence response of the owner triggered direct attacks. Adults and nestlings killed for interference competition later became a food resource.

These interactions relate to the use of artificial nest-boxes, because they provide additional holes for nesting, supplying more of a limiting resource, and for this, nest-boxes may alter the population densities and add complexity to the ecosystem in an unpredictable way. For instance, the pine marten learned to open the hooks of the lids, raided one grid in 2002, and in 2003 began using some nest-boxes for food caching. Therefore, the addition of nest-boxes can change the direction, intensity and strength of ecological interactions occurring in a given woodland ecosystem and the results from these studies are better considered as a helpful insight and a practical way for modelling the true interactions.

Nevertheless, adding nest-boxes may have simulated a situation in which a limiting resource suddenly increases. The investigation, therefore, may have shown the response of the two hole-nester species when they are no longer constrained by breeding space. In a short-term (1–7 years, according to the sample areas), released from such limiting factor, the two species increased in density and showed an adjusting phase, i.e. the complementary density change. Both populations were probably interacting for the establishment of a new level of density or awaiting for a new limiting factor. In conclusion, nest-boxes may stir up the ghost of interspecific competition (Connell, 1980), always dormant in community ecology, and their use can lead to unwanted results (see Vaughan, 2001).

## CONCLUSION

Exploitation competition for the breeding space proved to be an important ecological force, which dynamically structures bird–mammal interactions in woodlands of a large Mediterranean island, also working across phylogenetically unrelated taxa and without leading to competitive exclusion.

Today, communities are considered as free assemblages (Simberloff & Dayant, 1991), where the dynamic and the course of the coexisting populations are largely independent. In this view, several models such as the lottery of Chesson & Werner (1981) or the dynamic equilibrium of Huston (1994) explain the local coexistence of competing organisms. Hubbel (2001) proposed one of the last advances in the direction of neutral theories that try to explain how niche differences are not essential for coexistence of species. In our study case, according to Huston (1994), seasonal or annual predictable fluctuations in mast crop abundance (in the Colchic and sub-Atlantic

woodlands) and the unpredictable fire perturbation regime (in the evergreen woodlands of lower Madonie), can prevent blue tits and common dormice from reaching equilibrium densities. This would alter the relative competitive abilities of such organisms and thus prevent the occurrence of competitive exclusion.

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**Appendix 1.** General features of the sample woodlots in the Madonie (common dormouse *Muscardinus avellanarius* present) and in the control Sicani range (common dormouse absent)

Sample area	Year	Altitude a.s.l.	Type of wood	Natural holes/ha <sup>a</sup>	No. of nest-boxes	Blue tit			Common dormouse		
						Total OR March <sup>b</sup>	Total OR April <sup>c</sup>	Total OR May <sup>d</sup>	Total OR March <sup>e</sup>	Total OR April <sup>e</sup>	Total OR May <sup>e</sup>
Mad1	2000	430	Mixed cork oak	0.5	52	0.04	0.08	0.12	0.40	0.46	0.44
Mad1	2001	430	Mixed cork oak	0.5	51	0.06	0.12	0.16	0.49	0.41	0.37
Mad2	1998	775	Mixed cork oak	1	20	0.10	0.35	0.35	0.00	0.10	0.00
Mad3	1996	960	Mixed hazel	0	43	0.00	0.05	0.19	0.58	0.72	0.47
Mad3	1997	960	Mixed hazel	0	43	0.12	0.26	0.14	0.53	0.40	0.37
Mad3	1998	960	Mixed hazel	0	25	0.08	0.36	0.20	0.40	0.40	0.52
Mad4	1996	1125	Mixed holly	0.5	16	0.00	0.00	0.00	0.94	0.88	NR
Mad5	1996	1225	Mixed holly	1	28	0.00	0.00	0.29	0.82	0.46	0.57
Mad5	1997	1225	Mixed holly	1	28	0.00	0.00	0.21	0.82	0.79	0.57
Mad5	1998	1225	Mixed holly	1	28	0.00	0.25	0.43	0.86	0.64	0.46
Mad5	1999	1225	Mixed holly	1	50	0.00	0.08	0.22	0.66	0.64	0.54
Mad5	2000	1225	Mixed holly	1	75	0.04	0.09	0.12	0.51	0.45	0.43
Mad5	2001	1225	Mixed holly	1	50	0.00	0.34	0.36	0.72	0.48	0.38
Mad5 <sup>f</sup>	2002	1225	Mixed holly	1	25	NR	0.12	0.56	NR	0.16	0.16
Mad6	2000	1225	Mixed holly	1	58	0.00	0.07	0.10	0.60	0.62	0.64
Mad6	2001	1225	Mixed holly	1	56	0.02	0.23	0.25	0.54	0.38	0.32
Mad6 <sup>f</sup>	2002	1225	Mixed holly	1	28	NR	0.11	0.39	NR	0.29	0.29
Mad7	1998	1250	Mixed holly	1	10	0.20	0.90	0.90	0.40	0.10	0.10
Mad8	1996	1280	Pure chestnut	0	8	0.00	0.00	0.38	1.00	0.88	0.50
Mad8	1997	1280	Pure chestnut	0	8	0.00	0.13	0.50	0.88	0.88	0.75
Mad8	1998	1280	Pure chestnut	0	5	0.00	0.00	0.00	1.00	1.00	0.60
Mad9	2002	1300	Mixed holly	4	25	0.12	0.16	0.16	0.44	0.20	0.24
Mad9	2003	1300	Mixed holly	4	25	0.20	0.24	0.32	0.36	0.44	0.20
Mad10	2002	1300	Mixed holly	4	25	0.00	0.20	0.28	0.72	0.24	0.52
Mad10	2003	1300	Mixed holly	4	25	0.00	0.32	0.32	0.68	0.28	0.60
Mad11	1998	1350	Pure beech	0	10	0.00	0.30	0.30	0.60	0.60	0.30
Mad12	1998	1350	Pure beech	0.5	9	0.33	0.44	0.44	0.56	0.56	0.44
Mad13	1999	1450	Pure beech	0	50	NR	0.16	0.14	0.38	0.32	0.38
OR Mean ± SD						0.05 ± 0.09	0.19 ± 0.19	0.28 ± 0.19	0.61 ± 0.23	0.49 ± 0.25	0.49 ± 0.17
n Mean ± SD					31 ± 18	1.24 ± 1.64	5.18 ± 4.19	7.36 ± 4.08	18.08 ± 11.0	14.54 ± 10.3	13.33 ± 9.58
Sic1	1993	900	Mixed deciduous oak	1	50			0.44			
Sic1	1994	900	Mixed deciduous oak	1	50			0.64			
Sic1	1995	900	Mixed deciduous oak	1	50			0.72			
Sic1	1997	900	Mixed deciduous oak	1	50			0.42			
Sic1	1998	900	Mixed deciduous oak	1	50			0.34			
Sic1	1999	900	Mixed deciduous oak	1	50			0.70			
Sic1	2000	900	Mixed deciduous oak	1	50			0.52			
Sic1	2001	900	Mixed deciduous oak	1	50			0.54			
Sic1	2002	900	Mixed deciduous oak	1	50			0.46			
Sic2	1993	900	Pine reforestation	0	50			0.18			
Sic2	1994	900	Pine reforestation	0	50			0.06			
Sic2	1995	900	Pine reforestation	0	50			0.12			
Sic2	1997	900	Pine reforestation	0	50			0.06			
Sic2	1998	900	Pine reforestation	0	50			0.06			
Sic2	1999	900	Pine reforestation	0	50			0.14			
Sic2	2000	900	Pine reforestation	0	50			0.08			
Sic2	2001	900	Pine reforestation	0	50			0.08			
Sic3	1997	900	Reforestation turning	0	50			0.12			
Sic3	1998	900	Reforestation turning	0	50			0.12			
Sic3	1999	900	Reforestation turning	0	50			0.18			
Sic3	2000	900	Reforestation turning	0	50			0.16			
Sic3	2001	900	Reforestation turning	0	50			0.26			
Sic3	2002	900	Reforestation turning	0	50			0.24			
OR Mean ± SD								0.29 ± 0.22			
n Mean ± SD					50 ± 0			14.43 ± 10.9			

<sup>a</sup> Median value.<sup>b</sup> Tracks, i.e. feathers, faeces, etc.<sup>c</sup> Tracks and beginning or already active nests.<sup>d</sup> Active or abandoned nests.<sup>e</sup> Corresponds to the three preceding columns (see Material and Methods).<sup>f</sup> Exclusion experiment: Mad5, control; Mad6, treatment grid.

NR = not recorded.

**Appendix 2.** Occupation rate (March–June) of other species found inside the nest-boxes in the Madonie and Sicani ranges. Number of nest-boxes is the same as that in Appendix 1. The mean OR of *Parus major* in the Sicani is  $0.20 \pm 0.08$ , equivalent to an average of  $10.22 \pm 4.24$  nests. In this range the year frequencies of *P. caeruleus* and *P. major* are positively correlated ( $R = 0.53$ ,  $P = 0.009$ ,  $n = 23$ )

Sample area	Year	<i>Podarcis</i> spp.	<i>Tarentola mauretanicus</i>	<i>Parus major</i>	<i>Certhia brachydactyla</i>	<i>Sitta europaea</i>	<i>Rattus rattus</i>	<i>Apodemus sylvaticus</i>	<i>Glis glis</i>
Mad1	2000	0 <sup>a</sup>	0.02	0	0	NP	0	0.02	NP
Mad1	2001	0.02	0.04	0.10	0.02	NP	0 <sup>c</sup>	0.02	NP
Mad2	1998	0	0	0	0	0	0	0	NP?
Mad3	1996	0	0	0	0	0	0	0	NP?
Mad3	1997	0	0	0	0	0	0	0	NP?
Mad3	1998	0	0	0	0	0	0 <sup>c</sup>	0	NP?
Mad4	1996	0	NP	0	0	0	NP	0.13	0 <sup>b</sup>
Mad5	1996	0	NP	0	0	0	NP	0.04	0 <sup>b</sup>
Mad5	1997	0	NP	0.04	0	0	NP	0.04	0 <sup>b</sup>
Mad5	1998	0	NP	0	0	0	NP	0.11	0 <sup>b</sup>
Mad5	1999	0	NP	0	0.02	0	NP	0	0 <sup>b</sup>
Mad5	2000	0	NP	0.01	0.01	0	NP	0	0.04
Mad5	2001	0	NP	0.02	0.02	0	NP	0	0.06
Mad5	2002	0	NP	0.04	0.04	0	NP	0	0
Mad6	2000	0	NP	0	0	0	NP	0	0 <sup>b</sup>
Mad6	2001	0	NP	0.02	0	0	NP	0.02	0 <sup>b</sup>
Mad6	2002	0	NP	0.04	0	0	NP	0.04	0 <sup>b</sup>
Mad7	1998	0	NP	0	0	0	NP	0	0 <sup>b</sup>
Mad8	1996	0	NP	0	0	0	NP	0.13	0 <sup>b</sup>
Mad8	1997	0	NP	0	0	0	NP	0	0 <sup>b</sup>
Mad8	1998	0	NP	0	0	0	NP	0.20	0 <sup>b</sup>
Mad9	2002	0	NP	0	0	0	NP	0	0 <sup>b</sup>
Mad9	2003	0	NP	0.04	0	0	NP	0	0 <sup>b</sup>
Mad10	2002	0	NP	0	0	0	NP	0.04	0 <sup>b</sup>
Mad10	2003	0	NP	0.04	0	0	NP	0	0 <sup>b</sup>
Mad11	1998	0	NP	0	0	0	NP	0.10	0 <sup>a</sup>
Mad12	1998	0	NP	0	0	0	NP	0	0 <sup>a</sup>
Mad13	1999	0	NP	0	0	0.02	NP	0	0 <sup>a</sup>
Sic1	1993	0	NP	0.30	0	NP	NP?	0	NP
Sic1	1994	0	NP	0.22	0	NP	NP?	0	NP
Sic1	1995	0	NP	0.36	0	NP	NP?	0	NP
Sic1	1997	0	NP	0.28	0	NP	NP?	0	NP
Sic1	1998	0	NP	0.40	0	NP	NP?	0	NP
Sic1	1999	0	NP	0.20	0	NP	NP?	0	NP
Sic1	2000	0	NP	0.22	0	NP	NP?	0	NP
Sic1	2001	0	NP	0.30	0	NP	NP?	0	NP
Sic1	2002	0	NP	0.16	0	NP	NP?	0	NP
Sic2	1993	0	NP	0.18	0	NP	NP?	0	NP
Sic2	1994	0	NP	0.24	0	NP	NP?	0	NP
Sic2	1995	0	NP	0.12	0	NP	NP?	0	NP
Sic2	1997	0	NP	0.16	0	NP	NP?	0	NP
Sic2	1998	0	NP	0.08	0	NP	NP?	0	NP
Sic2	1999	0	NP	0.16	0	NP	NP?	0	NP
Sic2	2000	0	NP	0.12	0	NP	NP?	0	NP
Sic2	2001	0	NP	0.08	0	NP	NP?	0	NP
Sic3	1997	0	NP	0.24	0	NP	NP?	0	NP
Sic3	1998	0	NP	0.24	0	NP	NP?	0	NP
Sic3	1999	0	NP	0.22	0	NP	NP?	0	NP
Sic3	2000	0	NP	0.18	0	NP	NP?	0	NP
Sic3	2001	0	NP	0.14	0	NP	NP?	0	NP
Sic3	2002	0	NP	0.10	0	NP	NP?	0	NP

NP, not present in that area.

<sup>a</sup> Recorded later, during July–October.

<sup>b</sup> Recorded later during July–December.

<sup>c</sup> Recorded only in November.