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The use of dormouse *Muscardinus avellanarius* nest boxes by two species of *Apodemus* in Britain

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The occupancy of *Muscardinus avellanarius* (Linnaeus, 1758) nest boxes by *Apodemus flavicollis* (Melchior, 1834) and *A. sylvaticus* (Linnaeus, 1758) was studied over a six-year period from five sites in southern Britain. *A. flavicollis* was a regular visitor to nest boxes, occupying them more frequently than *A. sylvaticus* or any other small mammal. Litters of *A. flavicollis* were uncommon in nest boxes suggesting these boxes were rarely used for breeding. It seems likely that nest boxes form temporary nesting places for individuals, pairs or small communal groups. *A. flavicollis* sometimes take over nest boxes occupied by *M. avellanarius*, usually constructing their own nests and sometimes removing old nest material. *M. avellanarius* may avoid nest boxes occupied by *A. flavicollis* earlier in the same year. Boxes favoured by *M. avellanarius* in one year tended to be reselected by them in the following year, but no such trend was apparent in box selection by *A. flavicollis*. Overall, there was little evidence to suggest that the presence of *A. flavicollis* had a significant impact on *M. avellanarius* occupancy of nest boxes.

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Introduction

For many years nest boxes have been used to supplement available breeding sites for certain insectivorous birds and bats. In continental Europe occupation of these boxes by rodents has been variously recorded (see Holišová 1969, Truszkowski 1974, Juškaitis 1995, 1997). In Britain, it is only relatively recently that nest boxes have been used for studying mammals, in particular for monitoring the elusive dormouse *Muscardinus avellanarius* (Linnaeus, 1758). Specially designed nest boxes are held by wire to trees at around 1.5–2 m above the ground and a rear facing hole (usually 35 mm diameter) allows access to climbing small mammals (see Morris *et al.* 1990). The National Dormouse Monitoring Programme now encompasses some 85 sites across Britain and uses 4000 nest boxes. Investigations into this species in Britain are well documented elsewhere (Bright and Morris 1990, Bright *et al.* 1994, Bright and Morris 1996), but considerable information has also been collected on other small mammals, including the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834). In Britain, at the western edge of its range, *A. flavicollis* is far less abundant than in mainland Europe and its ecology is comparatively poorly understood.

European studies involving a variety of nest boxes have provided data on *A. flavicollis* and other small mammals. In Poland, nest boxes sunk into the ground in forest and shelterbelt habitats were intensively used as food stores and as nests by *A. flavicollis* and bank voles *Clethrionomys glareolus* (Truszkowski 1974). In Lithuania the results from a large 'tit nest box' scheme showed that between 1984–1993 *M. avellanarius* and *A. flavicollis* were the dominant nest box occupants in autumn, representing up to 42% and 21% of captures respectively, with low numbers of *C. glareolus* and pygmy shrews *Sorex minutus*, also recorded (Juškaitis 1997). However, autumn nest box occupancy by *A. flavicollis* varied enormously between years; spring occupancy levels were consistently low.

Understanding *A. flavicollis* populations in Britain has been hampered by the problems associated with monitoring a small, agile and nocturnal woodland species at generally low population densities. Concerns raised over its current status in Britain (Morris 1993, Harris *et al.* 1995) have led to research into its habitat preferences (Marsh and Harris 2000) and to a national survey of this species (Marsh *et al.*, in press). However, within its range *A. flavicollis* is quite a common occupant of boxes in many *M. avellanarius* nest box sites. One particular advantage of nest box records over records from single-capture live-traps, such as the Longworth, is that more than one animal may be caught and hence anecdotal evidence can be gathered on intra-specific interactions. Very little is known about social structure among *A. flavicollis*, although some data showing group formation in autumn and winter has been presented (Fedyk 1971, Truszkowski 1974).

There is evidence from Lithuania that in the autumn *A. flavicollis* may take over nest boxes occupied by *M. avellanarius*, largely using them to store food (Juškaitis 1995). In Britain, the implications for *M. avellanarius* of nest box utilisation by *A. flavicollis* have not been considered. The presence of other small mammals in nest boxes is likely to inhibit their use by *M. avellanarius*, although whether direct competition for nest boxes takes place is unclear. This paper explores the potential of nest box records to provide information on *A. flavicollis* populations and examines the evidence, and implications for *M. avellanarius*, of competition with *A. flavicollis* for the nest box resource.

Material and methods

Data on nest box occupants were examined for five sites in southern Britain for the period 1993–1998. These sites were Siccaridge Wood, Gloucestershire; Ashford Hangers and Bramley Frith, Hampshire; Spong Wood, Kent and Coed-y-Cerrig, Gwent. The analysis of potential *M. avellanarius* and *A. flavicollis* interactions over the nest box resource is focused on the exceptional record set from Siccaridge Wood in Gloucestershire, south-west England. Very few nest box records of the wood mouse

Apodemus sylvaticus (Linnaeus, 1758) were made at this site and hence interactions between this species and *M. avellanarius* are not explored in the same detail.

The National Dormouse Monitoring Programme requires nest boxes to be checked at least twice a year (June and October). More frequent checks are made at some sites, often once a month, but not usually over winter when *M. avellanarius* hibernates underground or at the base of coppice stools where ambient temperatures are more stable than in nest boxes. For this reason, only spring (March, April and May), summer (June, July, and August) and autumn (September, October, and November) months were considered. All *M. avellanarius* found were weighed, sexed and assessed in terms of breeding condition. These same data were usually collected for *Apodemus,* although in some cases these data were not recorded and animals were simply classified as adults or juveniles based on pelage. For these analyses all *A. flavicollis* weighing less than 20 g were considered to be juveniles and where weights were unavailable adult/juvenile age classifications were accepted. Animals were not marked during these nest box checks and care must therefore be taken when interpreting the results; annual totals may count the same individuals several times. Indices were calculated for *A. flavicollis* and *A. sylvaticus* based upon the number of animals caught per 50 boxes in each season.

Results

Annual and seasonal trends

Numbers of *A. flavicollis* recorded in nest boxes at each site varied between seasons and between sites. Table 1 shows the total number of *A. flavicollis* recorded in nest boxes in spring, summer and autumn for each of the 5 sites between 1993 and 1998. Table 2 shows the comparable data for *A. sylvaticus*. Indices of abundance based on the number of animals recorded per 50 traps were also calculated for both species. The abundance indices varied between 0–30 mice/50 boxes for *A. flavicollis* and between 0–3.5 mice/50 boxes for *A. sylvaticus*. These figures include juvenile animals. Coed-y-Cerrig was the only wood where abundance indices for *A. flavicollis* were greater than 10 mice/50 boxes. Spong was the only wood where box occupancy by *A. sylvaticus* was recorded with equal or greater frequency than *A. flavicollis*, but this was not the case in all years. *S. minutus* were occasionally recorded in nest boxes but at such low frequency that they are not considered here.

The inter-annual abundance of *A. flavicollis* during the autumn peak (see Table 1) was compared for each site. The sites showed similar patterns of inter-annual abundance (with the exception of Coed-y-Cerrig), although inter-site differences in habitat quality and annual productivity may mask overall trends. The annual abundance of *A. flavicollis* and *M. avellanarius* in Siccaridge Wood is compared in Fig. 1 and possible interspecific relationships are considered later in these results.

Sex ratio

Where sufficient detail was available these data showed that male *A. flavicollis* tended to be found more often in nest boxes than females (Siccaridge, 51 males and 9 females, $\chi^2 = 29.4$, df = 1, $p < 0.001$; Ashford Hangers, 103 males and 39 females, $\chi^2 = 28.84$, df = 1, $p < 0.001$). However, at Coed-y-Cerrig, where the highest rates

Table 1. *Apodemus flavicollis* numbers recorded in nest boxes of *Muscardinus avellanarius* each season for 1993–1998. Actual capture numbers are shown outside the brackets and include juvenile animals. Indices of the number of animals per 50 nest box checks are given in italics. The number of nest boxes sampled and the number of checks conducted that season are shown in brackets.

Season	1993			1994			1995			1996			1997			1998		
Siccaridge																		
Spring	(111, 2)	4	*0.90*	(111, 2)	2	*0.45*	(111, 2)	0	*0*	(111, 2)	0	*0*	(111, 2)	2	*0.45*	(111, 2)	0	*0*
Summer	(111, 3)	0	*0*	(111, 3)	20	*3.00*	(111, 3)	0	*0*	(111, 3)	5	*1.13*	(111, 3)	16	*2.40*	(111, 3)	1	*0.15*
Autumn	(111, 3)	9	*1.35*	(111, 3)	9	*1.35*	(111, 3)	9	*1.35*	(111, 2)	21	*4.73*	(111, 2)	3	*0.68*	(111, 3)	10	*1.50*
Spong																		
Spring	(100, 3)	17	*2.83*	(100, 1)	2	*1.00*	(100, 3)	0	*0*	(100, 3)	2	*0.33*	(100, 2)	0	*0*	(100, 2)	8	*2.00*
Summer	(100, 3)	4	*0.67*	(100, 3)	0	*0*	(100, 3)	2	*0.33*	(100, 3)	4	*0.67*	(100, 3)	0	*0*	(100, 3)	7	*1.17*
Autumn	(100, 3)	4	*0.67*	(100, 3)	3	*0.50*	(100, 3)	0	*0*	(100, 3)	6	*1.00*	(100, 3)	1	*0.17*	(100, 3)	6	*1.00*
Ashford Hangers																		
Spring	(50, 3)	6	*2.00*	(62, 3)	1	*0.27*	(70, 3)	2	*0.48*	(70, 3)	4	*0.95*	(70, 3)	6	*1.43*	(70, 3)	4	*0.95*
Summer	(50, 3)	1	*0.33*	(62, 3)	2	*0.54*	(70, 3)	3	*0.71*	(70, 3)	9	*2.14*	(70, 3)	17	*4.05*	(70, 3)	5	*1.19*
Autumn	(50, 3)	1	*0.33*	(62, 3)	10	*2.69*	(70, 3)	7	*1.67*	(70, 3)	22	*5.24*	(70, 3)	11	*2.62*	(70, 3)	28	*6.67*
Bramley Frith																		
Spring	(139, 2)	0	*0*	(139, 2)	0	*0*	(189, 2)	0	*0*	(189, 2)	0	*0*	(189, 2)	0	*0*	(189, 1)	0	*0*
Summer	(139, 1)	0	*0*	(139, 3)	0	*0*	(189, 3)	0	*0*	(189, 3)	1	*0*	(189, 2)	0	*0*	(189, 1)	2	*0.53*
Autumn	(139, 2)	0	*0*	(139, 2)	0	*0*	(189, 0)	–	–	(189, 2)	3	*0*	(189, 2)	1	*0.13*	(189, 2)	2	*0.26*
Coed-y-Cerrig																		
Spring	(40, 1)	0	*0*	(40, 1)	4	*5.00*	(50, 0)	–	–	(50, 0)	–	–	(50, 0)	–	–	(50, 0)	–	–
Summer	(40, 2)	0	*0*	(50, 3)	3	*1.00*	(50, 1)	14	*14.00*	(50, 1)	30	*30.00*	(50, 0)	–	–	(50, 1)	14	*14.00*
Autumn	(40, 1)	1	*1.25*	(50, 2)	8	*4.00*	(50, 1)	11	*11.00*	(50, 1)	4	*4.00*	(50, 1)	≥ 14	*≥ 14.00*	(50, 1)	6	*6.00*

Table 2. *Apodemus sylvaticus* numbers recorded in nest boxes of *Muscardinus avellanarius* each season for 1993–1998. Actual capture numbers are shown on the left and include juvenile animals. Indices of the number of animals per 50 nest box checks are given in italics on the right. The number of nest boxes sampled and the number of checks conducted that season are the same as for Table 1.

Season	1993		1994		1995		1996		1997		1998	
					Siccaridge							
Spring	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*
Summer	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*
Autumn	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*	1	*0.15*
					Spong							
Spring	21	*3.50*	1	*0.50*	0	*0*	8	*1.33*	0	*0*	0	*0*
Summer	8	*1.33*	0	*0*	1	*0.50*	2	*0.33*	0	*0*	0	*0*
Autumn	2	*0.33*	12	*2.00*	2	*0.33*	11	*1.83*	1	*0.17*	0	*0*
					Ashford Hangers							
Spring	1	*0.33*	0	*0*	0	*0*	0	*0*	0	*0*	0	*0*
Summer	0	*0*	2	*0.54*	0	*0*	0	*0*	1	*0.24*	0	*0*
Autumn	3	*1.00*	0	*0*	0	*0*	1	*0.24*	0	*0*	0	*0*
					Bramley Frith							
Spring	0	*0*	0	*0*	0	*0*	0	*0*	1	*0.13*	0	*0*
Summer	*0*	*0*	0	*0*	0	*0*	2	*0.18*	1	*0.13*	3	*0.79*
Autumn	0	*0*	1	*0.18*	0	*0*	3	*0.40*	5	*0.66*	2	*0.26*
					Coed-y-Cerrig							
Spring	0	*0*	0	*0*	–	–	–	–	–	–	–	–
Summer	0	*0*	0	*0*	0	*0*	*0*	*0*	–	–	0	*0*
Autumn	0	*0*	0	*0*	0	*0*	2	*2.00*	0	*0*	0	*0*

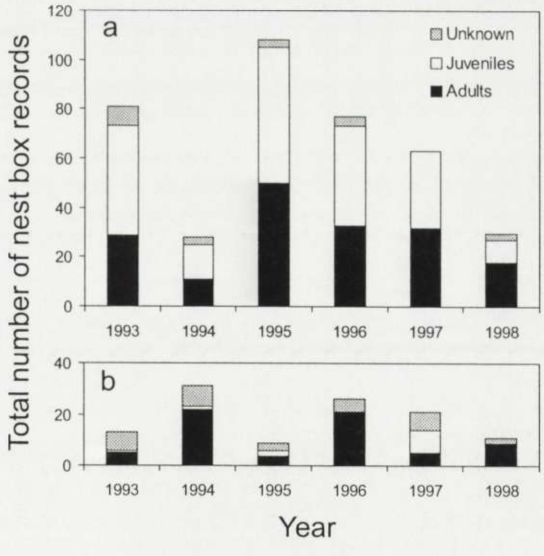

Fig. 1. Total number of nest box records each year of (a) *Muscardinus avellanarius* and (b) *Apodemus flavicollis* at Siccaridge Wood between 1993–1998. Each nest box record does not necessarily represent a different individual.

of box occupancy have been recorded, no significant difference was found between the occurrence of the two sexes (45 males and 35 females, $\chi^2 = 1.25$, df = 1, ns).

Breeding and social structure

Over the six year period investigated, adults accounted for 94.3% (n = 70), 85.2% (n = 128) and 83.5% (n = 79) of the records of *A. flavicollis* at Siccaridge, Ashford Hangers and Coed-y-Cerrig woods respectively, where age class could be determined. Litters of *A. flavicollis* were found in boxes infrequently at all three sites, in either the summer or autumn (Table 3). The largest litter came from Ashford Hangers, where four male and three female juveniles were found alongside an adult female in September 1998. The other litters (n = 9) varied from one to five animals. Observations of multiple captures for *A. flavicollis* were not uncommon (n = 38). Where two mice were caught in one box and both their genders were known, male-female pairs were most frequently recorded (n = 18), followed by captures of two males (n = 7) and only once two females. Adult groups of between three and six animals were also recorded, usually in summer or autumn. Only one inter-specific group was recorded, when a single *A. flavicollis* adult was found in a box on top of a nest containing a torpid *M. avellanarius*.

Table 3. Seasonal occurrence of group and pair captures of *Apodemus flavicollis* in nest boxes of *Muscardinus avellanarius*. Actual numbers are shown and are not corrected for the sampling effort used.

Season	Groups		Adult pairs			
	≥ 3 adults	Litters (≥ 2 juveniles)	Male and female	2 males	2 females	Genders unknown
			Siccaridge			
Spring	0	0	0	0	0	0
Summer	1	2	2	1	0	1
Autumn	2	0	2	4	0	5
			Ashford Hangers			
Spring	1	0	1	1	0	1
Summer	2	1	0	1	0	1
Autumn	6	3	10	0	1	2
			Coed-y-Cerrig			
Spring	0	0	1	0	0	0
Summer	3	3	3	0	0	2
Autumn	1	0	0	0	0	1

Implications for *M. avellanarius*

Patterns of nest box utilisation by *A. flavicollis* and *M. avellanarius* were examined more closely using data from Siccaridge Wood (Figs 1 and 2). Overall, *A. flavicollis* or *M. avellanarius* occupied between 21.6 and 31.5% of the 111 boxes in any one year. In the whole 6-year period, 24 boxes (21.6%) were never found to contain either species, suggesting that these boxes were unsuitable, perhaps due to their position within the wood. A core of 14.4% of the boxes were recorded as containing *M. avellanarius* in three or more years between 1993–1998, 62.5% of which were never found to contain *A. flavicollis*. The annual percentage of nest boxes occupied by each species closely resembles the nest box occupancy pattern shown in Fig. 1, suggesting a weak inverse relationship between the numbers of nest boxes occupied by the two species (even though overall occupancy levels were low).

Possible interactions between *M. avellanarius* and *A. flavicollis* can be explored using capture data and nest building data. At Siccaridge Wood, nests of *A. flavicollis* and *M. avellanarius* were routinely recorded, the former were usually constructed of loose dry oak or beech leaves and typically, the latter were woven honeysuckle bark or other material. Data for each year between 1993–1998 showed that while *A. flavicollis* nests were recorded as replacing or overlaying *M. avellanarius* nests that had been present in previous months ($n = 12$), the reverse was not observed. The results implied that *A. flavicollis* sometimes removed old nest material belonging to *M. avellanarius* prior to the construction of their own nests. However, even after the occasional removal of *A. flavicollis* nests *M. avellanarius* was only once found to have built a nest in such a box the same year. In addition,

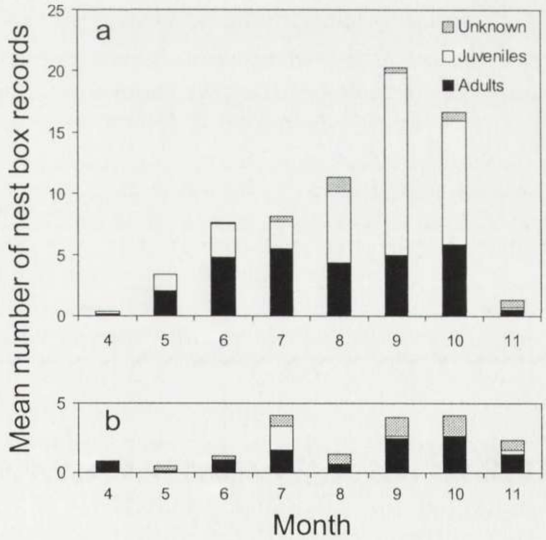

Fig. 2. Mean monthly numbers of nest box records for (a) *Muscardinus avellanarius* and (b) *Apodemus flavicollis* at Siccaridge Wood, calculated over the period 1993–1998. Each nest box record does not necessarily represent a different individual.

Table 4. Effects of nest box occupancy by *Apodemus flavicollis* and *Muscardinus avellanarius* for box use the following year (based on data from Siccaridge Wood between 1993–1998, $n = 555$).

Occupants the previous year	Occupants the following year			
	M. avellanarius	*A. flavicollis*	Both species	Neither species
M. avellanarius	53 (57.0%)	2 (2.2%)	6 (6.4%)	32 (34.4%)
A. flavicollis	7 (15.9%)	6 (13.6%)	0	31 (70.5%)
Both species	5 (33.3%)	1 (6.7%)	1 (6.7%)	8 (53.3%)
Neither species	41 (10.2%)	35 (8.7%)	5 (1.2%)	322 (79.9%)

actual capture data showed that while *A. flavicollis* was sometimes found occupying boxes formerly used by *M. avellanarius* in the same year ($n = 13$), the reverse was very uncommon ($n = 2$). Both of these last two records came from 1993 where one box was twice reoccupied by *M. avellanarius* after *A. flavicollis* had been found using it.

Table 4 explores the relationship between box occupancy in any given year on occupancy the following year. Taking the two columns for single occupancy by either *M. avellanarius* or *A. flavicollis* and excluding the row for former occupancy by both species a 2 × 3 contingency table is formed. Chi-square analysis shows that there is a highly significant difference between the occurrence of the two species ($\chi^2 = 29.1$, df = 2, $p < 0.001$). Post-hoc testing (using two separate 2 × 2 contingency tables) clearly shows that this difference is due to the variation in the pattern of occupancy seen for boxes previously occupied by *M. avellanarius* ($\chi^2 = 38.7$, df = 1, $p < 0.001$), rather than those previously occupied by *A. flavicollis* ($\chi^2 = 0.00$, df = 1, ns). It appears that a box used by *M. avellanarius* in the previous year was much more likely to be occupied by *M. avellanarius* the following year (57.0%) than by *A. flavicollis* (2.2%). Meanwhile, boxes previously occupied by *A. flavicollis* were no more likely to be occupied by them the following year (13.6%) than they were to be occupied by *M. avellanarius* (15.9%).

Discussion

A. flavicollis used nest boxes more often than any other small mammal, apart from *M. avellanarius*. *A. sylvaticus* was less common in nest boxes than its congener (with the exception of Spong Wood where *A. sylvaticus* were sometimes more abundant in boxes). This is in contrast to the general pattern of abundance seen in British woodlands, where *A. flavicollis* is normally much less abundant than *A. sylvaticus*. One possible explanation may be that *A. flavicollis* is more arboreal than *A. sylvaticus*, a mechanism for niche separation that has been suggested for sympatric populations of these species in Britain (Corbet 1966, Hedges 1966, Corke 1974). European studies have shown *A. flavicollis* is readily trapped in trees (Holišová 1969) and captive experiments have revealed a stronger tendency to climb than *A. sylvaticus* (Hoffmeyer 1973), although some field research has not supported these findings (Montgomery 1980a). The present paper offers additional anecdotal evidence that *A. flavicollis* may make greater use of the canopy than *A. sylvaticus*.

A. flavicollis was generally most abundant in nest boxes in the summer and autumn, reflecting their normal population cycle. Whether abundance in nest boxes reflects the population density is less clear. For example, Longworth trapping is regularly conducted at Bramley Frith and although *A. flavicollis* are often caught (A. Cleave, pers. comm.) they were not often found in nest boxes. Similarly, in October 1998, 40 Longworth traps were used to survey for *A. flavicollis* over two nights in Spong Wood. Five adults were caught in this period, equivalent to an index of 3.13 mice/50 trap checks, compared to the autumn nest box index of 1 mouse/50 box checks. These examples suggest that nest boxes are not an efficient means of sampling *A. flavicollis* populations, although nest box records may usefully indicate inter-annual population trends.

The reason for the male bias in sex ratio in *A. flavicollis* captures is uncertain. *Apodemus* males have much larger ranges than females (Wolton and Flowerdew 1985) and a male bias in adult captures is often reported from trapping studies (Montgomery 1980b). The relatively balanced sex ratio seen at Coed-y-Cerrig, was an exception to this and may be attributable to a high population density, a situation in which females might be caught more frequently.

Multiple captures suggest that, despite sometimes aggressive inter-specific interactions with *A. sylvaticus* (Montgomery 1978), *A. flavicollis* may show tolerance in intra-specific interactions, even forming social groupings. The increased occurrence of male-female pairs and multi-adult box occupancy in summer and particularly autumn may not simply be explained by mating behaviour. Any such behaviour should have been apparent in spring when breeding would already have started, while multiple box occupancy actually appeared to peak in the autumn after most mating has ceased. Thus, these data suggest that social ties may exist between individuals. Some pairings/groups may have represented first year sibling cohorts while the weights of animals in other groups clearly indicated older second year adults. It has been suggested that group formation over autumn and winter may be beneficial for thermoregulation purposes (Fedyk 1971) but this would not necessarily explain the groupings seen here over summer and autumn. Anecdotal evidence from trapping studies has tentatively suggested that *A. flavicollis* may sometimes forage communally (A. Marsh, unpubl.). Together these pieces of information indicate that understanding of social structure in *A. flavicollis* is far from complete. In nest boxes, the more regular occurrence of male pairs than female pairs is also intriguing and closer investigations of social behaviour in this species are desirable.

The results from Siccaridge Wood showed that the number of *A. flavicollis* found in boxes was lowest in 1995 when the number of *M. avellanarius* recorded was at its highest. Conversely, *M. avellanarius* numbers in 1994 were low while *A. flavicollis* numbers were high. A similar trend was apparent for each of these years in terms of the total number of nest boxes that were occupied by each species. However, it is not clear in which direction any cause and effect mechanism may be occurring, or even whether any such mechanism actually exists. Equally, the annual trends in autumn abundance in nest boxes from all five sites did not provide convincing evidence of an inter-specific effect.

M. avellanarius appeared to favour certain nest boxes, tending to use those selected by *M. avellanarius* in the previous year. However, it is unclear whether the same animals are using the same boxes since individuals were not marked. By contrast, *A. flavicollis* did not show any affiliation to specific boxes. The same tendencies were also apparent when indirect evidence from nest building was examined. Although *A. flavicollis* sometimes displaced *M. avellanarius* from nest boxes, there was no evidence that *A. flavicollis* took any specific interest in boxes occupied by *M. avellanarius*. Also, while *M. avellanarius* was not usually found in boxes where *A. flavicollis* had been caught the same year, there was no evidence of avoidance of those boxes by *M. avellanarius* in the following year. The apparent intra-annual avoidance by *M. avellanarius* of boxes that have contained *A. flavicollis* may be related to unwillingness by *M. avellanarius* to remove old material from the nest box. Boxes containing bird nests tend to be avoided until they are cleared out. It appears that where both species do show an interest in the same nest box at the same time, *A. flavicollis* is likely to prevail. However, a regular pattern of competition for nest boxes that could be detrimental to *M. avellanarius* populations has not been substantiated.

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