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

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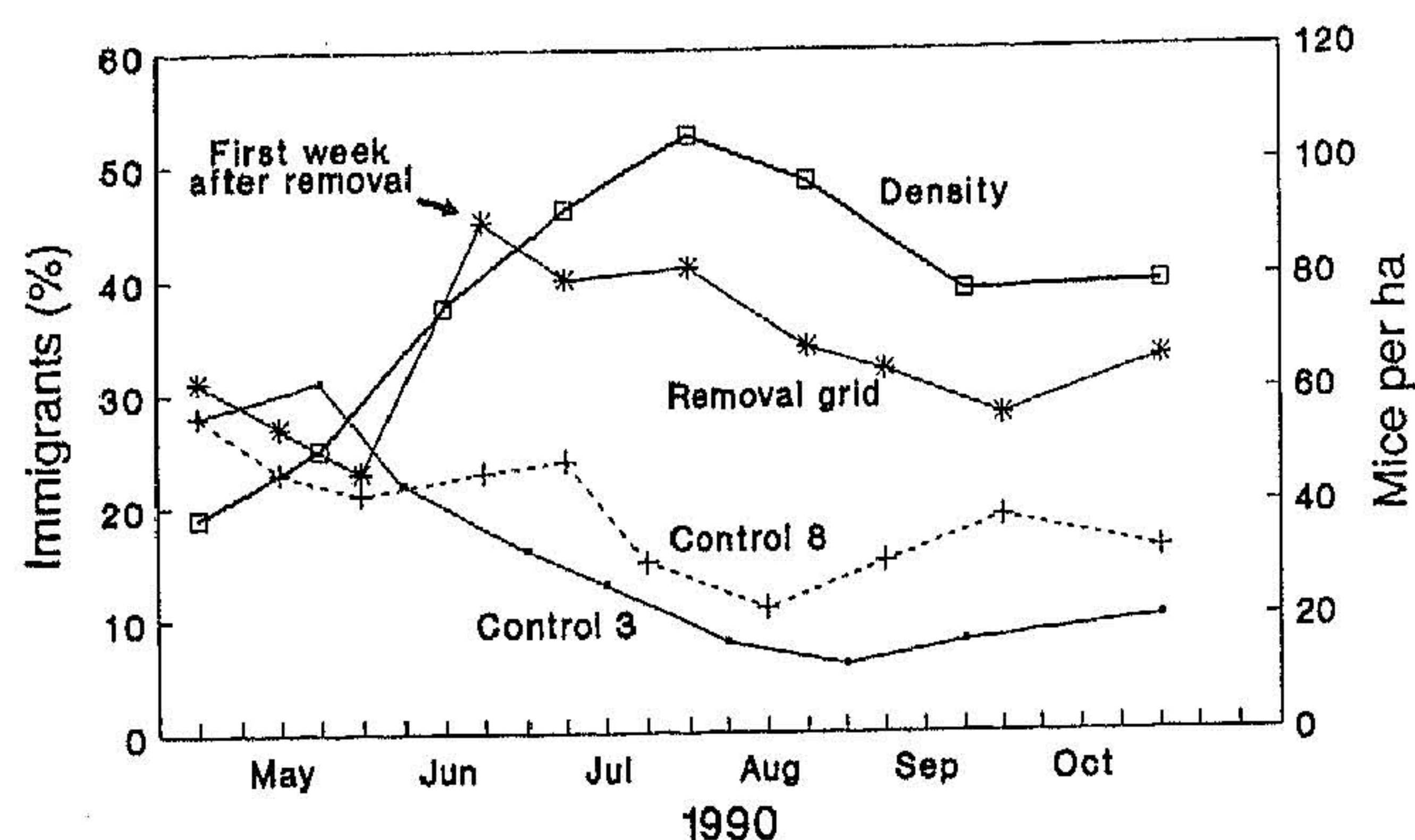


FIG. 2 The percentage of mice caught on one removal and two control grids during the 1990 high-density year that were new animals (presumed immigrants). Population density is the mean density on the two control grids.

control grids by the next trapping period. On the removal grid, 43% of juvenile males became sexually mature, compared to 8% on control grids ($\chi^2 = 9.519$, $P = 0.002$; Table 1). With almost 50% of the space being made vacant every two weeks, juvenile males apparently separated from their mothers and associated with non-relative females.

To determine whether the presence of parents of the opposite sex were the stimulus for sex-biased dispersal of juveniles, in 1991 I removed mothers from eight family groups and fathers from eight other family groups when the pups were 25–30 days old (weanlings). Sons remained significantly longer on natal home ranges from which mothers were removed than on those inhabited by mothers (medians 8.5 and 2 weeks, respectively; Wilcoxon medium test statistic = -3.386 , $n = 26$, $P = 0.0007$), and conversely, daughters remained longer on natal home ranges from which fathers had been removed than on those inhabited by fathers (medians 7 and 2 weeks, respectively; Wilcoxon median test statistic = -1.824 , $n = 22$, $P = 0.068$). The median residency for juveniles when both parents were present was two weeks, the same as when opposite-sex parents were present. I was unable to follow animals into the next breeding season; however, 8 of 14 sons remained for ≥ 7 weeks on home ranges from which mothers were removed, whereas none of 12 sons remained on home ranges inhabited by mothers (Fisher's exact test, $P = 0.002$). Also, 8 of 13 daughters remained for ≥ 7 weeks on the home ranges from which fathers were removed, whereas two of nine daughters remained on home ranges inhabited by fathers ($P = 0.099$). This confirmed previous observations that offspring tend toward philopatry when the parent of opposite sex is absent.

In conclusion, reproductive suppression results when juveniles are unable to separate from the parent of opposite sex. When population density is low, juvenile white-footed mice disperse to vacant habitats near their natal home ranges⁶, whereas they are apparently inhibited from dispersing when density is high, perhaps because the habitat is saturated with aggressive territorial neighbours that prevent immigration¹⁹. The consequence of this 'social fence'²⁰ is that juveniles remain philopatric and are reproductively suppressed if opposite-sex parents are present. Residency of adults and juveniles increases at high densities, and adults are not aggressive towards juveniles of the same sex¹⁶; thus sex-biased dispersal and reproductive suppression do not result from competition with same-sex parents. The presence of extended families of mothers and daughters raising litters together also indicates that resource competition and suppression of reproduction in juvenile females by their mothers and siblings are unlikely. My findings support the inbreeding-avoidance hypothesis for sex-biased dispersal^{6–10,21–26}. Any population regulation resulting from this reproductive suppression is possibly an artefact of daughters being unable to separate from their fathers. □

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No evidence for variable duration of sympatry between the great spotted cuckoo and its magpie host

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BROOD parasites and their hosts are thought to engage in a coevolutionary arms race in which parasitism selects for adaptive defences by the host (such as egg rejection), which in turn select for counter-adaptations by the parasite (such as egg mimicry)^{1,2}. Soler and Møller have tested whether the duration of coevolution (measured by the duration of sympatry at three different geographic areas) in a host–cuckoo system affected egg-rejection behaviour by hosts³. They found that the extent of both rejection and recognition of parasitic eggs covaried positively with the duration of sympatry. Here we show that, in the absence of strong historical evidence, field data do not support the existence of variations in the duration of sympatry at the two areas where the distributional ranges of the cuckoo and its hosts overlap. The reported differences in egg rejection by hosts might alternatively reflect flexible behavioural responses to the presence of the adult parasite near the nest.

Brood parasitic birds are becoming favoured examples in studies of coevolution². Experiment has shown that mimicry in cuckoo eggs has evolved as a counter-adaptation to egg discrimination by hosts, which in turn evolved as a behavioural defence against parasitism. Some have tested host responses towards real or model cuckoo eggs with different degrees of mimicry in areas where the host is sympatric with the parasite and in areas where the host has (presumably) never been parasitized. This work found that rejection rates were lower by hosts in

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TABLE 1 Reproductive parameters of great spotted cuckoos in Guadix and Santa Fe

	This study			Soler and Møller ^{3,8}		
	Guadix	Santa Fe	P	Guadix	Santa Fe	P
Nests parasitized* (n)	30.8 (130)	60.7 (242)	<0.001	42.0 (57)	50 (12)	n.s.
Nests containing more than 2 cuckoo eggs* (n)	20.0 (13)	38.0 (242)	<0.001			
Parasitized nests with more than 2 cuckoo eggs* (n)	65.0 (40)	62.6 (147)	n.s.	73.9 (23)	<73.9	
Nests with cuckoo eggs laid by more than one female* (n)	4.6 (130)	16.9 (242)	<0.001			
Parasitized nests with cuckoo eggs laid by more than one female* (n)	15.0 (40)	27.9 (147)	0.07	21.4 (28)		
Nests with multiple parasitism with more than one egg of the same female* (n)	53.8 (26)	83.1 (83)	<0.01	50.0 (18)	<50.0	
Cuckoo eggs per nest (mean \pm s.e.) (n)	2.02 \pm 0.17 (40)	2.44 \pm 0.12 (143)	n.s.	2.20 \pm 0.21 (23)	1.80 \pm 0.49 (5)	n.s.
Female cuckoos per nest (mean \pm s.e.) (n)	1.15 \pm 0.06 (39)	1.45 \pm 0.05 (134)	<0.01			
Fledgling cuckoos per nest (mean \pm s.e.) (n)	0.88 \pm 0.15 (41)	1.34 \pm 0.11 (127)	<0.05			
Cuckoo eggs that fledged* (n)	43.2 (81)	54.9 (295)	<0.05			

Nests were checked 2–6 times a week. Four clutches where we suspected that hosts had ejected cuckoo eggs before we detected them (as judged by the damage of host eggs⁹) were excluded from calculations of the number of cuckoo eggs per nest. The number of cuckoo females laying in each host nest was determined on the basis of egg characteristics and laying dates⁸. Ten clutches where the number of females could not be accurately determined were excluded from analyses. n, Number of nests; P, two-tailed probability levels in the comparison of proportions (Fisher's test) or means (Mann-Whitney test) between areas within studies; n.s., not significant.

* Values shown are percentages.

allopatry^{3,4}. In addition, hosts in sympatry were less likely to reject a mimetic model egg than a non-mimetic one^{3–7}.

Recently Soler and Møller³ provided a putative example of coevolution in action. They claimed that rejection of eggs of the great spotted cuckoo *Clamator glandarius* by magpie *Pica pica* hosts varied according to the duration of sympatry. In a population of presumed ancient sympatry (in Santa Fe, Spain), magpies readily rejected both mimetic and non-mimetic eggs; in an area of presumed recent sympatry (Guadix, Spain), 60 km away from Santa Fe, magpies were less discriminating, particularly of mimetic eggs; and in allopatry (Uppsala, Sweden), magpies showed no rejection at all. The key comparison here involves the areas of sympatry, which allows us to catch a glimpse of the dynamics of evolution and to test the view that cuckoos and hosts are engaged in a coevolutionary arms race, with cuckoos being one step ahead in areas of recent sympatry.

Soler argued that the higher altitude of the Guadix area (900–1100 m above sea level) had prevented cuckoos from colonizing it in the past, as the species seems to favour lowland below 500 m⁸ (but see ref. 9). However cuckoos are very abundant in the Santa Fe area, which is 700–800 m above sea level. We collected data on cuckoo parasitism from the Guadix area during 1982–1984, and from the Santa Fe area during 1985 and 1989–1991. Despite its altitude, local parasitization rates at Santa Fe were high (Table 1), actually among the highest ever recorded for any species of parasitic cuckoo².

In the absence of detailed historical information other than a claim made by local hunters that great spotted cuckoos were absent from Guadix until 1962 (ref. 8), Soler and Møller assumed that cuckoos had only recently colonized the Guadix area. Apparently, this conclusion is based on the fact that cuckoos were expanding their host niche and exploiting magpie hosts more successfully in the area of recent sympatry. They argued in favour of this possibility on the following grounds^{3,8}: (1) cuckoos “regularly parasitized three other corvid species in the Guadix area, whereas the magpie was the only commonly parasitized species in nearby areas of ancient sympatry, although all corvid species bred in both areas of recent and of ancient sympatry”³. This statement is erroneous. No study has been conducted in other areas in Spain where the cuckoo is sympatric with several potential hosts, and no corvids other than magpies have been observed to breed at Santa Fe. In fact, when describing the Santa Fe area, Soler⁸ explicitly states that “only magpies nest in this area”. (2) “The number of great spotted cuckoos laying in each host nest was larger at Guadix than in other areas”³. Although Soler⁸ did not provide any comparative evidence, our data show the opposite pattern. The number of female cuckoos laying in each nest, and the proportion of nests

containing eggs from more than one female, were both larger at Santa Fe (Table 1). (3) In the putatively recently colonized area, “individual female great spotted cuckoos frequently laid more than one egg in each host nest”³. Our estimate of the percentage of multiparasitized nests containing more than one egg of the same female at Guadix is close to that given by Soler⁸, but significantly lower than that obtained at Santa Fe (Table 1). (4) “The three [above] behavioural changes among great spotted cuckoos in the areas of recent sympatry all led to increased reproductive success of the parasite”³. As above, no comparative data were given⁸ but we found that cuckoos fledged more chicks both per nest and per egg laid at Santa Fe than at Guadix (Table 1).

Independently of whether such arguments have any bearing on the duration of sympatry between cuckoos and magpies, it is clear that with the larger sample sizes of our data, many of the trends oppose those claimed by Soler and Møller³. Even if Guadix is a recently occupied area, our data show that the supposed characteristics of a recent area do not apply. In any case, the differences between the two areas are probably unrelated to duration of sympatry. The occurrence of great spotted cuckoo parasitism on magpies was reported at Iznalloz (800–1,400 m above sea level, 40 km away from Guadix) as early as 1885 (ref. 10). Differences between the two areas may simply reflect the fact that the density of cuckoos relative to that of their hosts is larger at Santa Fe than at Guadix (Table 1).

This could in turn explain why a higher proportion of experimental eggs were rejected at Santa Fe than at Guadix, because hosts are known to be more likely to reject alien eggs when they are alerted by encounters with the adult parasite in the vicinity of their nest^{1,7}. Phenotypic flexibility might thus provide an alternative explanation for relatively low rates of rejection in allopatry found in other studies^{4,11,12}. □

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