Juvenile dispersal in relation to adult densities in wood mice *Apodemus sylvaticus*

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Two alternative hypotheses explaining low densities of juvenile wood mice *Apodemus sylvaticus* (Linnaeus, 1758) early in the breeding season were compared: the Adult Aggression Hypothesis and the Habitat Saturation Hypothesis. They predict different ratios between adult and juvenile densities, which were tested using trapping data from mixed deciduous woodland and from lowland arable field margins. According to the Adult Aggression Hypothesis, juveniles have a poor persistence rate early in the breeding season as a result of aggressive behaviour shown by the adults. As the breeding season progresses, a drop in adult aggression levels results in increased juvenile persistence, which, in turn, leads to increased densities. The Habitat Saturation Hypothesis proposes that juveniles disperse from their parents' territories until the surrounding habitats are saturated and that this gradual saturation results in increased densities as the breeding season progresses. The observed correlations between adult and juvenile densities both in woodland and on field margins were consistent with the predictions of the Habitat Saturation Hypothesis.

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Introduction

A large proportion of the literature on population dynamics and animal dispersal deals with the dispersal of juveniles and attempts to answer the following basic questions: why do juveniles disperse, which individuals disperse and under which particular conditions? The emerging answers have tended to fall into two broad categories:

(1) Juveniles disperse because they have to.

They are forced to disperse by their parents or other resident adults, when they are perceived by these as becoming a threat in the competition for resources (eg food, shelter and mates). Those that are not strong or fit enough to resist eviction are forced to leave.

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(2) Juveniles disperse because they can.

By leaving their natal home range they may increase their chances of breeding successfully and perhaps avoid inbreeding. They do this if suitable areas are available to disperse into, and if they are fit enough to compete for a new home range. In other words, the fitter juveniles disperse.

These two categories of answers represent two fundamentally different scenarios and form the base for hypotheses offering very different, even opposing predictions.

The two categories roughly correspond to the Resident Fitness Hypothesis and the Emigrant Fitness Hypothesis respectively, defined in Andersons monograph (1989) with special reference to rodents, which deals with adult as well as juvenile dispersal. According to the former hypothesis, favoured by Anderson, juveniles are fundamentally philopatric, settling on their natal sites if permitted to do so. Dispersal is driven by the aggressive behaviour of adults (Anderson 1989).

Explanations of patterns of seasonal variations in rodent population structure have traditionally been based on this assumption. Phenomena such as the disproportionately slow increase in juvenile densities observed at the beginning of the breeding season in, for example, the wood mouse *Apodemus sylvaticus* (Linnaeus, 1758) have been attributed to the effects of adult aggression (especially that of males) being particularly high at this time of the year and resulting in either death or expulsion of the juveniles (Watts 1969, Flowerdew 1974, Gurnell 1978, 1985, Montgomery and Gurnell 1985). This hypothesis, which will hereafter be called the Adult Aggression Hypothesis, corresponds largely to the Resident Fitness Hypothesis while dealing exclusively with juvenile dispersal. Aggression displayed towards juveniles in behavioural trials (Garson 1975, Gurnell 1977, Lambin 1988) has been cited in support of the view that breeding male wood mice are responsible for the low recruitment rate of young and immigrants. The sudden increase in juvenile densities observed at the end of the summer has been correlated with a decrease in the aggression levels amongst adult wood mice and the death of overwintering males (Gurnell 1978). During the winter, the level of aggression between individuals is believed to be very low and the social organisation aggregative (Green 1979, Montgomery and Gurnell 1985, Wolton 1985, Lambin 1988). However, doubts about this mechanism have recently been voiced by, amongst others, Montgomery (1989a), Wilson *et al.* (1993a) and Wolff (1993, 1994) and I will return to their arguments in the discussion.

The alternative Habitat Saturation Hypothesis, corresponding to Andersons (1989) Emigrant Fitness Hypothesis but again dealing exclusively with juvenile dispersal, gives a different explanation for the observed slow increase in juvenile densities at the beginning of the breeding season. The Habitat Saturation Hypothesis was originally formulated to explain co-operative breeding in birds (Selander 1964, Brown 1974). The term has since been adopted by researchers on population dynamics of small mammals (eg Wolff *et al.* 1988). It proposes that by dispersing from their place of birth whenever possible, juveniles may reduce competition and

avoid inbreeding (pre-saturation dispersal; Lidicker 1975), and that the increase in densities as the breeding season progresses is due to the saturation of surrounding habitats, leaving the juveniles with no other option than to remain within their parents territories and forfeit breeding (Wolff 1986 cited in Wolff 1992, Wolff *et al.* 1988).

Two different predictions result from these alternative hypotheses regarding the expected proportion of juveniles at different densities of adult males: (1) Since the Adult Aggression Hypothesis proposes that mature adults, and especially males, suppress juvenile survival at the beginning of the breeding season, lower proportions of juveniles are expected at higher densities of adult males in May and June for a given habitat. (2) The Habitat Saturation Hypothesis, on the other hand, predicts lower proportions of juveniles at lower adult male densities, on the assumption that low densities of adult males (and of adults in general) in the study area reflect low densities in the surrounding habitats which are therefore not saturated, thereby providing juveniles with opportunities to disperse away from their parents' territories. The proportions of juveniles should be high at high adult male densities, because saturation of surrounding habitats prevents juvenile dispersal.

The breeding season in wood mouse populations usually begins in March with the first females giving birth in late April or early May (Miller 1958). The two predictions are here tested using data collected over a number of years in Wytham Great Wood, a mixed, deciduous woodland, in June (early in the breeding season) and December (outside the breeding season). Further comparisons were drawn with data collected from a different habitat type, namely hedgerows and field margins on a nearby arable farm.

Methods

The predictions of the two hypotheses were tested using data collected on the same site in Wytham Great Wood, Oxfordshire, UK, for 10 consecutive years (between 1982 and 1992) in June (early in the breeding season) and December (outside the breeding season) as well as data collected in 6 trapping sessions in spring and early summer and 5 sessions in winter over 4 consecutive years (between 1988 and 1991) from nearby arable field margins (Oxford University Farm, Wytham, Oxfordshire, UK). The ratio of trappability between adults and juveniles was assumed constant across both seasons and years.

The trapping data from Wytham Great Wood were collected with Longworth live-traps, placed in 2 trapping grids in oak-ash-sycamore woodland. The 2 grids each consisted of 15 trap points ca 21 m apart with 5 traps at each point, bringing the total to 150 traps. The traps were pre-baited with wheat for 48 hours and then set. They were examined on the evening of the same day and on the following morning. Since captured animals were not individually marked, and morning sessions yielded the largest number of captures, only data from mornings were used in the analysis. Captured animals were weighed and sexed. For further details of the trapping regime for Wytham Great Wood see Southern (1973).

The trapping regime on the Wytham Farm field margins involved 256 pairs of traps placed 10 m apart on experimentally expanded margins (for description of field margin project see Smith *et al.*

1993). The traps were baited with wheat for rodents and fly pupae (*Calliphora* sp.) for shrews and were filled with hay for bedding. Each trapping session lasted 4 days and nights with no pre-baiting and the traps were checked every 8 h (except during the hottest part of the summer, when the maximum interval during the hottest part of the day was 4 h). On initial capture the mice were numbered using fur-clipping (Twigg 1975), and at each capture they were weighed, sexed and classified as either adults or juveniles according to weight and breeding condition. Females were classified as adults if they were perforate, pregnant, lactating or weighed more than 17 g. Males were classified as adults if they had scrotal testes or weighed more than 19 g. No distinction was made between juveniles and sub-adults for the purposes of the analysis.

The correlation between adult wood mouse numbers and the arcsin-transformed proportions of juveniles captured was determined with a regression analysis (PROC GLM, SAS Institute Inc. 1988). Since data were collected on the same site over a number of years, a runs test (Sokal and Rohlf 1981) was performed to test for independence of successive observations.

On the grounds that higher proportions of juveniles might be a function of higher proportions of adult females occurring at high densities, the correlation between the arcsin-transformed proportions of adult females and overall densities in the woodland trapping grid was also investigated for June and December. Due to insufficient detail in the information on breeding status in the woodland trapping data, the proportions of pregnant females could not be determined. However, for the mice captured on the field margins, neither the proportions of all adult females nor of pregnant or lactating females captured in June were correlated with total densities of adult wood mice.

Results

In June, which is early in the breeding season for wood mice, the proportion of juvenile wood mice captured increased with an increase in total numbers of adult wood mice captured ($F = 18.55$, df = 1,8, $p = 0.003$) and in the number of adult male wood mice captured ($F = 10.39$, df = 1,8, $p = 0.01$; Fig. 1). In December, which is outside the breeding season, no such correlation was found between proportions of juveniles and either total numbers of adults ($F = 1.55$, df = 1,8, $p = 0.3$) or numbers of adult males ($F = 0.15$, df = 1,8, $p = 0.7$; Fig. 1).
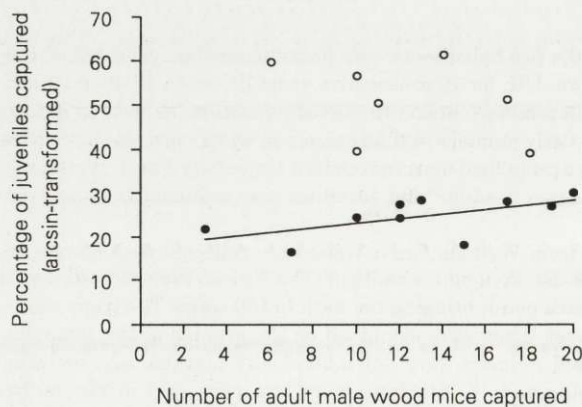

Fig. 1. The arcsin-transformed percentages of juvenile wood mice captured in Wytham Great Wood (1983–1992) in relation to numbers of adult males captured in June (filled circles, $y = 21.693 + 0.403x$, $r^2 = 0.565$, $F = 10.39$, df = 1,8, $p = 0.01$) and in December (open circles, $F = 0.15$, df = 1,7, $p = 0.7$).

The runs test revealed no sequential correlation in proportions of juveniles captured in consecutive years for either June or December ($n_1 = 5$, $n_2 = 5$, $u = 6$, $p < 0.05$, in both cases). The proportion of adult females was not correlated with densities of adult wood mice in either June ($F = 0.00$, df = 1,8, $p = 1.0$) or December ($F = 3.94$, df = 1,8, $p = 0.08$).

On the field margins the proportion of juvenile wood mice captured increased with the total numbers of adults captured ($F = 9.28$, df = 1,4, $p = 0.04$) early in the breeding season (March–June) and with numbers of adult males captured ($F = 7.601$, df = 1,4, $p = 0.04$). The proportion of adult females was not correlated with densities of adult wood mice in June ($F = 0.12$, df = 1,4, $p = 0.7$) and neither was the proportion of pregnant or lactating females ($F = 0.26$, df = 1,4, $p = 0.6$). In winter no correlation was revealed between proportions of juveniles and either total numbers of adults captured ($F = 5.88$, df = 1,3, $p = 0.09$) or numbers of adult males ($F = 4.56$, df = 1,3, $p = 0.1$). The sample size was small for December and these results can therefore be taken only as indicative of the relationship.

Discussion

This study revealed an increase in the proportion of juvenile wood mice captured in summer with numbers of adult males and with total numbers of adults captured, both on arable field margins and in mixed deciduous woodland. No such correlation was found in winter. One interpretation of this result is that juveniles disperse at low rather than at high densities, a relationship predicted by the Habitat Saturation Hypothesis rather than the Adult Aggression Hypothesis. This does not exclude the possibility that some of the juveniles captured on the grids might have been immigrants.

I shall be discussing other possible interpretations of the results, but I wish first to take another look at some of the studies, which in the past have lent support to the Adult Aggression Hypothesis. I wish to re-evaluate their findings and consider whether the Habitat Saturation Hypothesis can provide an equally satisfactory explanation.

Among the studies which are often quoted in support of the Adult Aggression Hypothesis, some are removal experiments (Flowerdew 1971), others involve behavioural encounters in cages (Flowerdew 1974, Gurnell 1977) or observations at bait stations in the wild (Garson 1975, Lambin 1988).

Flowerdew (1971) studied the effect on wood mouse densities of increased food availability and decreased density of adult males. The area in which supplementary food was supplied showed an increased density of wood mice in autumn and winter compared with a control area without food supplement, whereas the summer densities in the two areas were similar. In the first of the two years of the experiment, the area from which adult males were removed between the end

of May and the beginning of July showed an initial increase in both density and immigration of juveniles as compared with the control area. In the second year numbers did not increase significantly. This was taken as support for the hypothesis that the presence of adult males adversely affected the apparent survival of immigrants and juveniles. However, these results are consistent with the predictions of the Habitat Saturation Hypothesis, that by removing the adult males, vacant space is created causing an influx of animals searching for a home range. Being younger, they occupied less space than the mature males (Randolph 1977) and therefore immigrated in larger numbers. Unless the experiment is carried out with a control, in which the same number of females or a representative cross-section of the population are removed, and this control gives a significantly different result, the low densities of juveniles cannot reliably be attributed to the aggressive behaviour of the mature males. The hypothesis that juveniles disperse only when space is available can equally explain the observed phenomenon.

The low trappability of juveniles after they leave the natal nest (Tanton 1969, Green 1979) means that juvenile mortality is hard to determine from trapping data, and since the migrant part of the wood mouse population is also thought to be less trappable (Jensen 1975), juvenile dispersal is likely to have been underestimated in many trapping studies.

Support for the view that the slow increase in densities during the beginning of the breeding season is due to low survivorship rather than to the juveniles dispersing can be traced back to Watts (1969) quoting his doctoral thesis (1966). As Watts stated in his thesis, the evidence that the low densities were not due to dispersal was inconclusive, since there were too few results for wood mice during the first half of the breeding season to draw any conclusions regarding juvenile dispersal. Only results obtained after August were adequate and showed that no dispersal of juvenile mice took place at this time. This observation is also consistent with the more recent Habitat Saturation Hypothesis because the juveniles would be expected to disperse during the first part of the breeding season, before densities all round become too high.

Watts furthermore noted that at high densities, a relatively low proportion of fully grown females was perforate, which supports the hypothesis that the animals which are prevented from dispersing remain reproductively suppressed (Wolff et al. 1988).

Cage encounters have been used to illustrate the effect of male adults on the survival and growth of juveniles (Gurnell 1977, 1978, Wilson et al. 1993b). A juvenile confined in a cage with a strange adult male or with an adult male and adult female usually loses weight, escapes or dies (Flowerdew 1974). This does not necessarily mean that the same would happen to un-confined juveniles living within their parents' home range. In a study by Brown (1969), in which she made direct observations of wood mice in the wild in spring and summer, dominant adult males were generally avoided by other resident mice and displays of aggressive behaviour were rare. A dominant male is likely to chase off younger,

subordinate animals which tend to flee at such encounters (Gurnell 1978, Lambin 1988) but this would be expected of an animal asserting its dominance and need not result in any suffering or permanent displacement on the part of the juvenile. Furthermore, the home ranges of breeding males are known to overlap extensively with those of other males as well as with those of females (Wolton 1983, 1985, Tew 1989, Tew and Macdonald 1993).

Although the results obtained in this study can be explained by the Habitat Saturation Hypothesis, other explanations for the observed correlations could be suggested. Low food availability might lead to both low population densities and a lower proportion of breeding females which, in turn, could result in low proportions of juveniles, or it might affect the survival of the juveniles through the effect of food stress on the females ability to lactate (Campbell 1974). The woodland data was insufficiently detailed to allow a distinction to be made between breeding and non-breeding females, but the data from the field margins showed no correlation between overall adult densities and the proportion of breeding females.

We are thus left with the possibility of low proportions of juveniles being the result of poor survival due to food stress. Wood mice have in many studies been shown to have strongly density dependent population regulation over summer and autumn (Montgomery 1989b, Mallorie and Flowerdew 1994) with densities in June being inversely correlated to the rate of population growth between June and December (Mallorie and Flowerdew 1994). This suggests that low densities in June generally promotes rather than depresses juvenile survival. Even though very low juvenile densities could be a result of poor survival due to food stress during winter and spring, it cannot explain the observed increase in the proportion of juveniles over all adult densities.

The above points thus all favour the Habitat Saturation Hypothesis over the Adult Aggression Hypothesis. The latter has lately been subjected to re-evaluation on a number of grounds. In a review of population regulation in wood mice, Wilson *et al.* (1993a) evaluates evidence arising from research carried out since Watts study. Many of these studies raised doubts about Watts finding that the observed spring decline in numbers was density dependent. They quote Krebs and Boonstra (1978) who questioned the appropriateness of the statistical tests used to determine this density dependence and Montgomery (1989a) who, in a similar trapping experiment, found no evidence of such density dependence. Wilson (1992) re-examined trapping data from a woodland site (Montgomery 1989b, Montgomery *et al.* 1991) revealing a weak positive association between numbers of overwintered males and juveniles. This was interpreted as suggesting that the dispersion of juveniles and subadults was determined by similar variables to that of adult males and that male aggression was not involved in delaying or inhibiting population growth during the increase phase. The distribution of juveniles during the early and middle part of the breeding season was therefore attributed to female reproductive activity rather than to male aggression.

Both within and beyond the rodent literature, recent findings have been adding further doubts to the idea that dispersers are generally the weaker individuals in the population. In a study of deer mice *Peromyscus maniculatus* juveniles on food supplemented grids were found to disperse further than those on control grids (Teferi and Millar 1994), and in a study of imperial eagles *Aquila adalberti*, young, well fed animals were found to disperse further than less well fed individuals (Ferrer 1993). In common lizards *Lacerta vivipara*, female offspring of mothers with ectoparasites have been shown to be more philopatric than those of mothers without parasites (Sorci *et al.* 1994) and offspring of mothers which faced food shortage during pregnancy were more likely to be philopatric, while those born to well fed mothers were more likely to disperse (Massot and Clobert 1995). Voluntary dispersal, as desciber by Lidicker and Stenseth (1992) may thus be much more widespread amongst juveniles across the taxa than previously thought.

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