

Philip E. Hulme

## Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands

Received: 19 August 1996 / Accepted: 25 January 1997

**Abstract** The post-dispersal fate of seeds and fruit (diaspores) of three vertebrate-dispersed trees, *Crataegus monogyna*, *Prunus mahaleb* and *Taxus baccata*, was studied in the Andalusian highlands, south-eastern Spain. Exclosures were used to quantify separately the impact of vertebrates and invertebrates on seed removal in relation to diaspore density and microhabitat. The three plant species showed marked differences in the percentage of diaspores removed, ranging from only 5% for *C. monogyna* to 87% for *T. baccata*. Although chaffinches (*Fringilla coelebs*) fed on diaspores, rodents (*Apodemus sylvaticus*) were the main vertebrate removers of seed and fruit. Two species of ant (*Cataglyphis velox* and *Aphaenogaster iberica*) were the only invertebrates observed to remove diaspores. However, the impact of ants was strongly seasonal and they only removed *P. mahaleb* fruit to any significant extent. While removal of seed by rodents was equivalent to predation, ants were responsible for secondary dispersal. However, their role was limited to infrequent, small-scale redistribution of fruit in the vicinity of parent trees. Rodents and ants differed in their use of different microhabitats. Rodents foraged mostly beneath trees and low shrubs and avoided open areas while the reverse was true of ants. Thus, patterns of post-dispersal seed removal will be contingent on the relative abundance and distribution of ants and rodents. Studies which neglect to quantify separately the impacts of these two guilds of seed removers may fail to elucidate the mechanisms underlying patterns of post-dispersal seed removal. The coincidence of both increased seed deposition by the main avian dispersers (*Turdus* spp.) and increased seed predation with increasing vegetation height suggested that selection pressures other than post-dispersal seed predation

shape the spatial pattern of seed dispersal. Rather than providing a means of escaping post-dispersal seed predators, dispersal appears to direct seeds to microhabitats most suitable for seedling survival. Nevertheless, the reliance of most vertebrate-dispersed trees on regeneration by seed and the absence of persistent soil seed banks imply that post-dispersal seed predators may exert a strong influence on the demography of the plants whose seeds they consume. Even where microsites are limited, the coincidence of the most suitable microhabitats for seedling establishment with those where seed predation is highest provide a means by which selective seed predators can influence community composition.

**Key words** Ants · Density-dependence · Rodents · Seed dispersal · Seedling recruitment

### Introduction

Although frugivores and the fruit they consume have been the subject of intensive ecological research, the role of seed dispersal in plant demography remains poorly understood (Estrada and Fleming 1986; Fleming and Estrada 1993; Herrera 1995). Most experiments examining the post-dispersal fate of seeds have identified high, but spatially variable, rates of seed predation as characteristic of many vertebrate-dispersed plants (Hulme 1993). The demographic consequences of seed dispersal have therefore often been interpreted as a means of escaping post-dispersal seed predation (Venable and Brown 1993). Seed dispersal may reduce rates of seed predation if seeds are scattered at a density insufficient to elicit a response from seed predators or if seeds are deposited in “safe sites” where seed predators are relatively scarce (Howe 1986; Willson 1992). In the simplest case, safe sites may only be a function of the distance from the parent (Janzen 1970; Clark and Clark 1984; Terborgh et al. 1993), or alternatively they may be particular habitats or microhabitats (Webb and Willson 1985; Schupp 1988; Kollmann 1995). However, the

generality of these patterns has been questioned by studies which have failed to detect consistent trends in seed survival with respect to seed density (Notman et al. 1996; Gryj and Dominguez 1996), distance from parent (Burkey 1994; Notman et al. 1996) or microhabitat (Willson and Whelan 1990; Whelan et al. 1991). This has led a number of authors to suggest that selection acting through spatial and temporal patterns of seed predation may not have a strong effect on the patterns of seed dispersal (Willson and Whelan 1990; Whelan et al. 1991).

However, such a conclusion may be premature, since few studies have simultaneously examined the effects of density, distance and microhabitat in relation to actual seed shadows, nor have they quantified the impact of different post-dispersal seed predators. Once dispersed, seeds are further moved or destroyed by a variety of animals, but particularly by mammals and insects (Howe 1986; Willson 1992; Hulme 1993). Nevertheless, only a few studies have attempted to assess the relative importance of these different animals on seed survival (Perry and Fleming 1980; Abbot and van Heurck 1985; Whelan et al. 1991; Hulme 1992; Terborgh et al. 1993). Separation of the impact of vertebrates and invertebrates on seed survival is particularly important since these animals are likely to differ in both the temporal and spatial scales of their effects, their functional responses and preferences for different plant species, as well as the consequences of their foraging (predation or secondary dispersal). Studies which ignore these differences may misrepresent factors thought to be important in plant demography.

The objective of this study was to examine the post-dispersal fate of seeds and fruit of vertebrate-dispersed trees in order to assess the possible impact of post-dispersal seed predators on the demography of vertebrate dispersed plants. In particular it aimed to:

1. Use selective exclosures to separately quantify the impact of vertebrates and invertebrates on the post-dispersal fate of seeds and fruit (diaspores) of vertebrate dispersed plants.
2. Examine whether fallen fruit and seeds are harvested at different rates by animals and if their ultimate fate (predation or secondary dispersal) differs. Although fallen fruit are generally only found beneath or near the parent they may constitute as much as 20% of the total offspring (Herrera and Jordano 1981; Manzur and Courtney 1984).
3. Determine whether diaspore removal is density-dependent.
4. Compare diaspore fate beneath tree canopies and other microhabitats, including open sites, in order to identify whether seed survival is a function of distance from the parent or of the microhabitat where seeds are deposited.
5. Assess the generality of these findings by examining a range of vertebrate dispersed species which differ in their phenology and fruit/seed characteristics.

## Materials and methods

### Study site

The study was carried out in the Andalusian highlands during 1990 in the Reserva de Navahonda-Guadahornillos (Parque Natural de las Sierras de Cazorla, Segura y las Villas, Jaen Province, south-eastern Spain; see Valle et al. 1989 for a description of the area). The study area is part of a limestone outcrop located within a fenced ungulate exclosure ( $\approx 10$  ha) in Nava de las Correhuelas (1615 m above sea level). The vegetation is dominated by fleshy-fruited trees and shrubs including *Berberis hispanica*, *Crataegus monogyna*, *Daphne laureola*, *Prunus mahaleb*, and *Rosa canina* which occur on deep soils while *Juniperus communis*, *J. phoenicia* and *Taxus baccata* occur on adjacent rocky slopes (plant species nomenclature follows Tutin et al. 1964–1980). The site experiences a mediterranean montane climate typified by summer drought and autumn/winter precipitation, which at these altitudes often falls as snow (see Hulme 1992 and Jordano 1994 for further details of the site).

### Plant species

This study reports the results of the post-dispersal fate of fruit and seeds of *Crataegus monogyna*, *Prunus mahaleb* and *Taxus baccata*. Choice of species was based on the following criteria:

1. In order to compare directly the effect of the presence of fruit pulp on rates of diaspore removal only species with single-seeded fruit were selected. In addition to the three species chosen, only one other species with single-seeded fruit was relatively abundant in Nava de las Correhuelas, *Daphne laureola*, and patterns of post-dispersal diaspore removal for this species are reported elsewhere (Hulme 1992).
2. Comparison of published data reveals marked differences between the three species in the design and nutritional components of their fruits and seeds (Table 1; Barnea et al. 1993). Drupes of *C. monogyna* have a relatively high seed burden (18%) and consist of a large seed within an energy-poor, fibrous pulp which contains a variety of toxic secondary compounds including cyanogenic glycosides, flavonoids and saponins. In contrast, the arillate fruit of *T. baccata* have a much lower seed burden (9%) and contain a toxic seed partially enclosed by an energy-rich, watery aril which is relatively free of toxic secondary compounds. The drupes of *P. mahaleb*, are the smallest fruit chosen, yet have the highest seed burden (21%) and the nutritional content of the pulp falls between that of *C. monogyna* and *T. baccata*.
3. The interactions of all three species with their particular avian frugivore assemblages have been intensively studied in both the Andalusian highlands and elsewhere in Europe e.g. *P. mahaleb* (Herrera and Jordano 1981; Guitian et al. 1992; Jordano 1994); *C. monogyna* (Snow and Snow 1988; Manzur and Courtney 1984; Guitian and Fuentes 1992); *T. baccata* (Snow and Snow 1988; Barnea et al. 1993; Hulme 1996b). Although the three species exhibit different fruiting phenologies and fruit characteristics they all rely to a large extent on thrushes (*Turdus* spp.) for effective seed dispersal.

### Post-dispersal removal experiments

Each experimental unit comprised three exclosure treatments, placed within 1 m of each other, which were used to identify and quantify the sources of diaspore removal:

1. Open treatment: diaspores were presented on an upturned Petri dish lid, fixed (by a central nail) flush with the ground surface and were available to birds, mammals and invertebrates.
2. Invertebrate treatment: diaspores were also presented on an upturned Petri dish lid, fixed (by a central nail) flush with the

**Table 1** Design and nutritional characteristics of the three species of vertebrate-dispersed trees. Data are drawn from Herrera (1987) with the exception of the energy content which was calculated following Snow and Snow (1988)

Species	Fruit design components						
	Dimensions (mm)			Mass of components (mg)			Water (%)
	Colour	Length	Diameter	Fresh fruit	Seed	Dry pulp	
<i>Crataegus monogyna</i>	red	12.1	9.3	675.4	123.7	171.0	56.4
<i>Prunus mahaleb</i>	black	8.0	8.3	378.0	79.5	48.4	63.8
<i>Taxus baccata</i>	red	10.9	10.3	764.0	69.9	158.7	66.3

Species	Fruit nutritional components						
	Composition of dry fruit pulp (%)				Energy (kcal/g)		
	Lipids	Protein	Fibre	NSC	Ash	Dry pulp	Whole fruit
<i>Crataegus monogyna</i>	2.3	2.5	20.5	72.4	4.3	3.24	0.68
<i>Prunus mahaleb</i>	3.2	2.8	5.7	83.4	6.3	3.78	0.48
<i>Taxus baccata</i>	0.2	2.3	2.6	93.5	1.4	3.88	0.72

ground surface but within a 1 cm wire mesh cage (15 cm × 15 cm × 20 cm) and were therefore available to invertebrates only.

- Rodent treatment: to enable access to diaspores by rodents but not invertebrates, a ring of acetate sheeting was firmly glued to the rim of a Petri dish such that it formed a 1-cm overhang with both the inside and outside of the dish. Tanglefoot, an insoluble sticky agent, was applied to the exterior of the Petri dish while the inside of the Petri dish was painted with a Teflon emulsion (Fluon). The function of the Tanglefoot was to deter ants from attempting to enter the dish, while Fluon made the inside of the dish too slick for ants to climb and thus prevented the escape of any ants that might have managed to enter the dish. Preliminary experiments revealed this mechanism to be successful at preventing removal of diaspores by ants but not rodents. To ensure only rodents had access to the diaspores, birds were excluded from the dish by placing it in a 3-cm-mesh wire cage (15 cm × 15 cm × 20 cm).

Each experimental unit of three enclosure treatments was replicated five times in each of five representative microhabitats in the site. For *T. baccata* and *P. mahaleb* these were: (1) open herbaceous vegetation; (2) within rock crevices; (3) under low shrubs (*B. hispanica* or *J. communis*); (4) beneath *P. mahaleb* canopy; and (5) beneath *T. baccata* canopy. For *C. monogyna*, the microhabitats were the same but for microhabitat (4) where the diaspores were placed beneath a canopy of *C. monogyna* instead of one of *P. mahaleb*.

For each experimental unit one of four diaspore manipulations, either ten seeds, ten fruit, a single seed or a single fruit, was placed in each treatment and left for three days, after which time any remaining diaspores were recorded. Diaspore remains were then removed and replaced by a different, randomly chosen manipulation, such that in the course of the study every experimental unit received all four diaspore manipulations. Great care was taken to ensure fruit were not damaged prior to presentation in the field and that seeds were thoroughly cleaned of pulp. The experiments were undertaken during the natural period of seed dispersal of each species: *P. mahaleb* (1–13 August), *T. baccata* (9–21 October) and *C. monogyna* (10–22 November).

#### Distribution and abundance of invertebrates and rodents

A capture-mark-recapture study of the small mammal populations in each site ran concurrently with the diaspore removal experiments. From July 1990 onwards, 50 Longworth live-traps were distributed over the site in order to sample rodents in all representative microhabitats. Over 4 consecutive nights each month rodents were caught, individually marked and released. Trapping immediately preceded or followed the diaspore removal experi-

ments. Pitfall traps (plastic coffee cups) were sunk, flush with the soil surface in the vicinity of each experimental unit. The traps were half-filled with a mixture of water and detergent and were run each month over the same period as the small-mammal trapping. After 4 consecutive days the pitfall traps were removed and their contents identified.

#### Data analysis

For each plant species, a factorial analysis of variance (ANOVA) was undertaken on the proportion of diaspores removed (arcsine square root transformed) in relation to the following main effects – enclosure, diaspore (seed or fruit), density and microhabitat. Bartlett's test was used to test for homogeneity of variances and where treatment effects were significant, individual means were compared using Tukey's honestly significant difference (Sokal and Rohlf 1995).

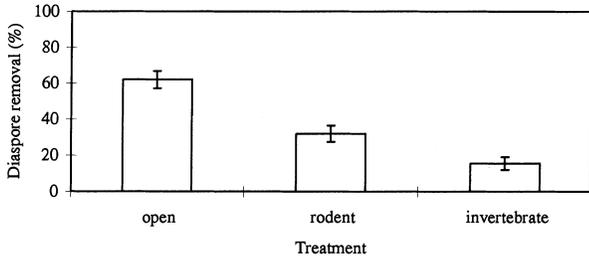
## Results

The three plant species showed marked differences in the percentage of diaspores removed, ranging from an almost negligible 5% for *C. monogyna* to 87% for *T. baccata* (Fig. 1). Statistically significant differences were found between enclosure treatments for *P. mahaleb* and *T. baccata* but differences were borderline for *C. monogyna* (Table 2). Nevertheless the trend was similar for all three species with removal rates decreasing in the following order: open > rodent only > invertebrate only treatment (Fig. 1).

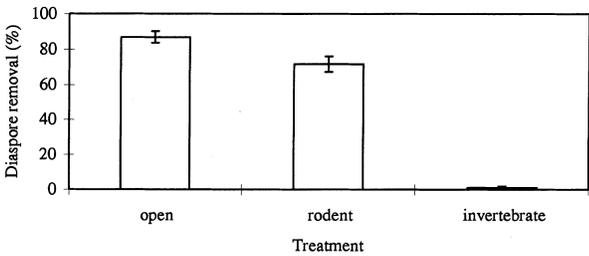
Rodents (principally *Apodemus sylvaticus* L.) were abundant throughout the study period (Fig. 2). They were the main post-dispersal removers of diaspores of both *P. mahaleb* and *T. baccata*, but had only a minor impact on *C. monogyna*. The only invertebrates seen foraging on diaspores were three species of ant. *Pheidole pallidula* (Nyl.) fed primarily on fruit pulp in situ and rarely removed diaspores whereas *Cataglyphis velox* (Sants.) and *Aphaenogaster iberica* (Em.) were responsible for diaspore removal. However, ants only removed diaspores of *P. mahaleb* to any significant extent. The

limited impact of invertebrates on *T. baccata* and *C. monogyna* coincided with the scarcity of ants from

a) *Prunus mahaleb*



b) *Taxus baccata*



c) *Crataegus monogyna*

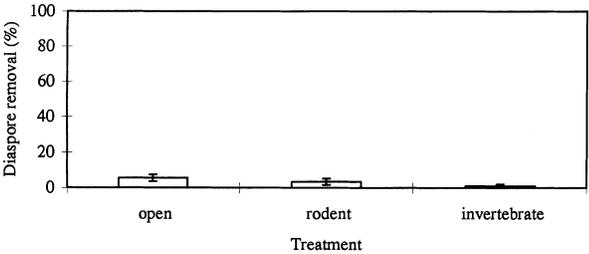


Fig. 1a–c Mean rates of diaspore removal in the three exclusion treatments for *Prunus mahaleb*, *Taxus baccata* and *Crataegus monogyna*. Error bars represent 1 SE either side of the mean

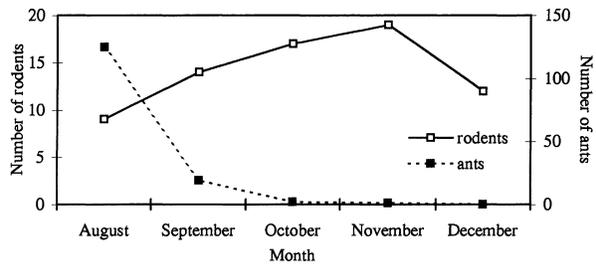


Fig. 2 The abundance of the main removal agents of diaspores during the experimental period. Rodent abundance represents the total number of *Apodemus sylvaticus* individuals caught each month. Ant abundance relates to the total number of *Aphaenogaster iberica* and *Cataglyphis velox* individuals (workers and queens) found in pitfall traps each month

October onwards (Fig. 2). Although the majority of diaspore losses from the open treatment could be attributed to the combined effects of invertebrates and rodents, for both *P. mahaleb* and *T. baccata* approximately 14% of diaspores were additionally removed (Fig. 1). This additional loss was, in part, attributable to birds (in particular *Fringilla coelebs* L.). In the rodent treatment, removal of diaspores at the higher density was significantly correlated with that in the corresponding open treatment for both *P. mahaleb* (Spearman rank correlation for seeds  $r_s = 0.63$ ,  $df = 23$ ,  $P < 0.001$ ; for fruit  $r_s = 0.54$ ,  $df = 23$ ,  $P < 0.01$ ) and *T. baccata* (for seeds  $r_s = 0.80$ ,  $df = 23$ ,  $P < 0.001$ ; for fruit  $r_s = 0.70$ ,  $df = 23$ ,  $P < 0.001$ ). This suggests that although birds, rodents and invertebrates all had access to the open treatment, for these plant species most diaspore removal was due to rodents.

Irrespective of whether vertebrates or invertebrates were responsible, a significantly greater proportion of intact fruit than seeds was removed for both *P. mahaleb* (53.3% vs. 19.5%, Table 2) and *C. monogyna* (6.2% vs.

Table 2 Summary of factorial analyses of variance examining the significance of exclusion treatment, diaspore type, diaspore density and microhabitat on the proportion of diaspores removed (arcsine square root transformed) for each of three vertebrate dispersed tree species. The table presents the degrees of freedom ( $df$ ), mean square ( $MS$ ) and  $F$  value

	$df$	<i>Prunus mahaleb</i>			<i>Taxus baccata</i>			<i>Crataegus monogyna</i>		
		MS	F	P	MS	F	P	MS	F	P
Exclusion (ex)	2	13.442	38.293	***	51.361	211.515	***	0.178	2.963	
Diaspore (di)	1	20.799	59.249	***	1.028	4.234	*	0.677	11.286	**
Density (de)	1	0.219	0.624		0.480	1.976		0.007	0.118	
Microhabitat (mi)	4	1.161	3.306	*	1.250	5.148	**	0.052	0.869	
Ex × di	2	1.103	3.143	*	0.472	1.945		0.120	1.994	
Ex × de	2	1.482	4.221	*	0.187	0.768		0.143	2.384	
Ex × mi	8	0.850	2.422	*	0.355	1.463		0.077	1.283	
Di × de	1	0.043	0.123		0.083	0.343		0.070	1.174	
Di × mi	4	0.574	1.634		0.193	0.794		0.075	1.245	
De × mi	4	0.305	0.868		0.171	0.703		0.122	2.041	
Ex × di × de	2	0.624	1.776		0.047	0.193		0.134	2.237	
Ex × di × mi	8	0.213	0.607		0.134	0.552		0.086	1.426	
Ex × de × mi	8	0.247	0.704		0.072	0.297		0.037	0.613	
Di × de × mi	4	0.440	1.253		0.198	0.816		0.080	1.333	
Ex × di × de × mi	8	0.190	0.542		0.109	0.448		0.041	0.691	
Residual	240	0.351			0.243			0.060		
Total	299									

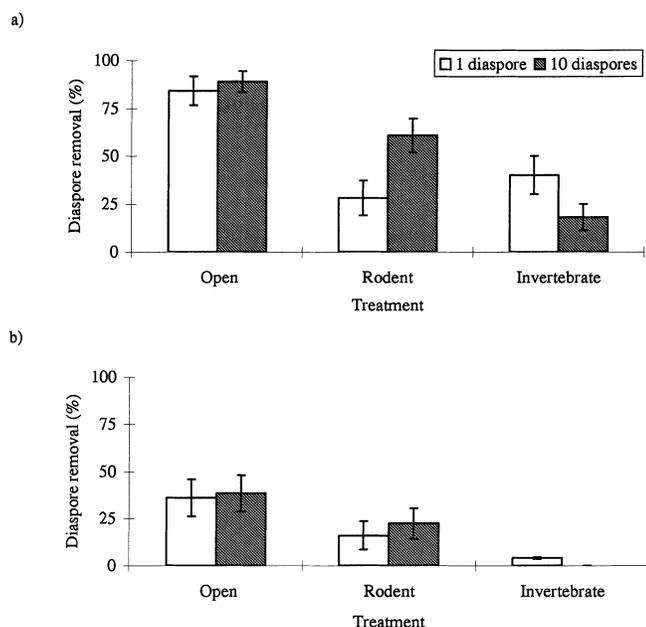
\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$

0.4%, Table 2). This difference was particularly marked for ants, which removed 29.0% of intact *P. mahaleb* fruit but only 2.0% of seeds (Fig. 3). In contrast, irrespective of treatment, a greater proportion of *T. baccata* seed than intact fruit was removed (56.8% vs. 49.5%, Table 2). Indeed, on a number of occasions, when

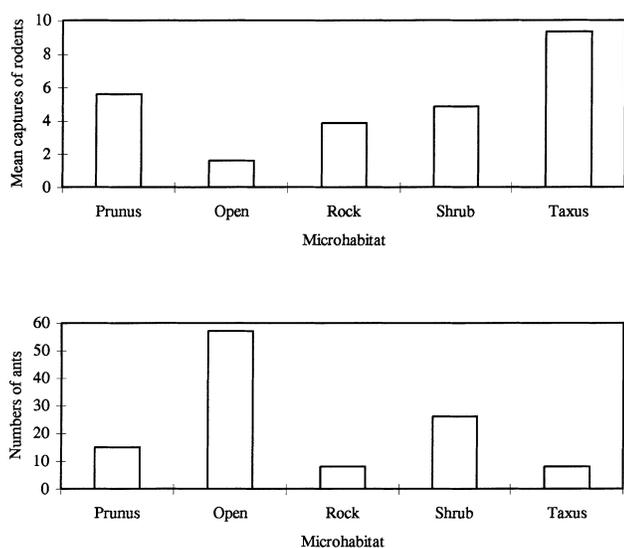
feeding on *T. baccata* fruit rodents would remove the seeds and leave the empty arils behind.

Data for *P. mahaleb* revealed that ants and rodents responded differently to an increase in diaspore density (Fig. 3). Rodents responded to an increase in diaspore density by removing in total twice as many diaspores, whereas removal by ants was reduced by over 50%. For both ants and rodents, the density effect was stronger for fruit than seeds. By increasing diaspore density rodents located fruit more frequently, whereas ants located fruit equally well at either density but only removed half of the fruit at the higher density. No effect of diaspore density on the proportion of fruit or seeds removed was found for either *T. baccata* or *C. monogyna* (Table 2).

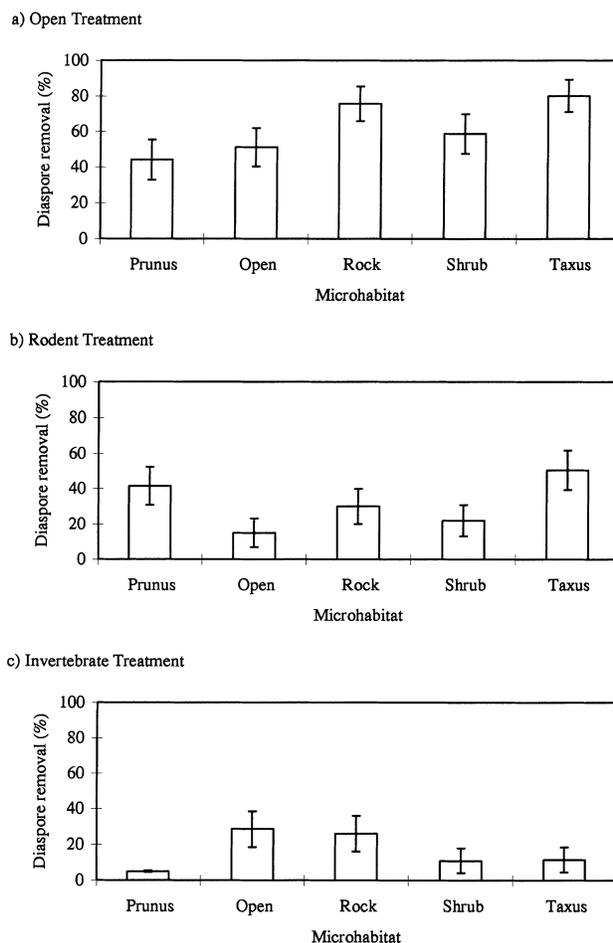
Diaspore removal was a function of microhabitat for both *P. mahaleb* and *T. baccata* (Table 2). Rodents and ants differed in their use of different microhabitats (Fig. 4). Rodents mostly foraged beneath *P. mahaleb*, low shrubs and *T. baccata* and avoided open areas whereas the reverse was true of ants. These different microhabitat affinities were reflected in the pattern of



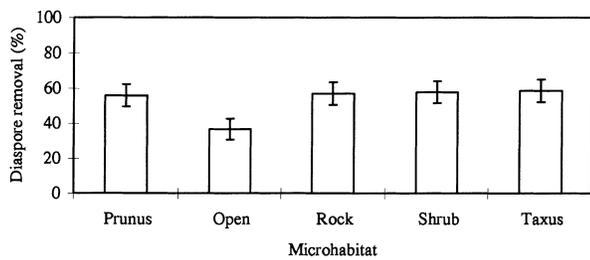
**Fig. 3a,b** The effect of diaspore density on the proportion of **a** *Prunus mahaleb* fruit and **b** seeds removed from each of the three enclosure treatments. Error bars represent 1 SE either side of the mean



**Fig. 4** The abundance of rodents and ants within different microhabitats during the study period. Rodent abundance represents the mean number of *Apodemus sylvaticus* individuals caught in each microhabitat while ant abundance relates to the total number of *Aphaenogaster iberica* and *Cataglyphis velox* individuals (workers and queens) found in pitfall traps in each microhabitat



**Fig. 5a-c** Microhabitat variation in mean rates of removal of *Prunus mahaleb* diaspores from each enclosure treatment. Error bars represent 1 SE either side of the mean



**Fig. 6** Overall microhabitat variation in mean rates of removal of *Taxus baccata* diaspores. Error bars represent 1 SE either side of the mean

diaspore removal between different microhabitats for *P. mahaleb* (Fig. 5). The complementary nature of ant and rodent foraging reduced the microhabitat variation in diaspore removal in the open treatment (Fig. 5). Microhabitat variation in the removal of *T. baccata* diaspores primarily reflected the activity of rodents and was similar to that found in the rodent treatment for *P. mahaleb* (Fig. 6).

## Discussion

The post-dispersal seed fate of vertebrate-dispersed plants in the Andalusian highlands revealed a number of parallels with both temperate and tropical ecosystems (Hulme 1993). Rodents were the principal removers of seeds and fruit, but the magnitude of their impact was a function of the plant species. Species variation in removal was not a simple function of the physical or chemical characteristics of the seed and fruit (Table 1). Whereas the combination of a hard lignified endocarp and a flavonoid-rich pulp probably explains the low removal of *C. monogyna* diaspores, rodent removal was highest for the smaller, toxic seeds of *T. baccata* but not their energy-rich aril. The greater removal of *P. mahaleb* fruit than seeds may not reflect the nutritive quality of the pulp but may be because fruits present a stronger olfactory cue to rodents. This was the case for *Daphne laureola*, where even though the fruit pulp is highly toxic to mammals, rodents removed fruit more often than seeds (Hulme 1992). This may explain why rodents responded positively to an increase in fruit but not seed density for *P. mahaleb* and *D. laureola* (Hulme 1992). The absence of any significant density effects on seed removal is consistent with density-dependence being a function of seed size and rarely found for seeds larger than 10 mg (Hulme 1993, 1994). Microhabitat variation resulted from rodents foraging more frequently where vegetation cover was dense (Hulme 1993). The pattern of microhabitat variation in rodent removal was not only similar in August (*P. mahaleb*) and October (*T. baccata*) but also in June (*D. laureola*, Hulme 1992) and thus appeared to be relatively constant over time. Furthermore, microhabitat variation in rodent seed removal was similar to that found for *T. baccata* in four

temperate woodlands (Hulme 1996b). This suggests that open microhabitats may be customarily free from rodent post-dispersal seed predators.

Ants only appeared to be important in the post-dispersal fate of *P. mahaleb* and were responsible for removing almost 30% of fruit. The thermophilic nature of the ant species responsible for diaspore removal in the Nava de las Correhuelas (*Aphaenogaster iberica* and *Cataglyphis velox*) limits their spatial and temporal variation to relatively open microhabitats between April and September (Fig. 1; P. Hulme, personal observation). Therefore variation between the three plant species in fruit removal by ants probably reflects changes in the abundance of ants, rather than preferences for particular fruit characteristics. For example in June, when ants are most abundant, they remove almost 60% of *D. laureola* diaspores (Hulme 1992). At lower altitudes, these ants may remain active until November (Cerda et al. 1988, 1988) and are known to remove large numbers of fruit in autumn (Traveset 1994). The impact of ants on seed distributions in the Mediterranean appears greater than that found for temperate ecosystems but less than that reported for tropical ecosystems (Hulme 1993) which is consistent with the existence of a latitudinal gradient in ant predation (Jeanne 1979).

Ants and rodents differed considerably in their patterns of seed removal. Seed removal by rodents occurred most frequently where vegetation cover was highest and was intense beneath parent plants whereas ants favoured open sites and rarely foraged beneath parent plants. Similar results were found for diaspores of *D. laureola* in the same site (Hulme 1992). Thus, patterns of post-dispersal seed removal will be contingent on the relative abundance and distribution of ants and rodents. Studies which neglect to quantify separately the impacts of these two guilds of seed removers may fail to elucidate the mechanisms underlying patterns of post-dispersal seed removal.

The ecological consequences of seed removal by ants and rodents requires a knowledge of the fate of diaspores once removed. *Apodemus sylvaticus* is primarily granivorous (Hansson 1985) and remains of seed and fruit characteristic of rodent predation were often found within the rodent and open treatments. Removal of seed by rodents was equivalent to predation since most seeds were either consumed locally or placed in deep larder-holds from which successful establishment is unlikely (Montgomery and Gurnell 1985). As in all other species of the genus, *C. velox* collects mainly corpses of insects and other arthropods whereas *A. iberica*, belongs to a more omnivorous genus (Cerda et al. 1988, 1989). Both their strong preference for *P. mahaleb* fruit over cleaned seeds and the presence of intact seeds in their middens suggest that removal was equivalent to secondary dispersal. Both species of ant moved diaspores only a short distance (mean = 2.55 m,  $\sigma_{n-1} = 1.48$ ,  $n = 30$ ) from where they were encountered to the ants nest sites, which were in rocky/open microhabitats. The preference shown by ants for intact fruit rather than seeds suggests

their role at this site is limited to infrequent, small-scale redistribution of fruit in the vicinity of parent trees.

Although rates of seed predation by rodents were relatively high beneath the canopies of *T. baccata* and *P. mahaleb*, only dispersal to open microhabitats would significantly reduce rates of seed predation. This implies that microhabitat is a better gauge of predation intensity than simply distance from the canopy. The demographic implications of post-dispersal seed predation by rodents must be made with reference to the seed shadows of the plant species concerned. Thrushes (*Turdus merula* and *T. viscivorus*) disperse the majority of seed of all three plant species and deposit seeds heterogeneously in the study area, favouring shrub microhabitats while avoiding open areas (Herrera and Jordano 1981; Herrera 1984; Schupp 1993; P. Hulme, unpublished work). Thus, for these species, avian seed dispersal does not appear to be an effective means of escaping post-dispersal seed predators. Combined with the low levels of seed predation found for *C. monogyna* in all microhabitats, these findings suggest that selection pressures other than post-dispersal seed predation shape the spatial pattern of seed dispersal.

Shrubs act as nurse plants facilitating seedling survival through provision of shade and/or protection from browsing vertebrate herbivores and appear essential for successful regeneration of *T. baccata* (Hulme 1996b) and *P. mahaleb* (Schupp 1995). The coincidence of high rates of seed predation in shrub microhabitats suggest seed predators may exert a considerable influence on the regeneration of these species. This may be particularly true of these vertebrate-dispersed trees due to their dependence on regeneration by seed and the absence of persistent soil seed banks (Hulme 1996a). Indirect support for this is found in the relative abundance of *C. monogyna*, *P. mahaleb* and *T. baccata* at the study site which mirrors the extent to which they suffer from post-dispersal seed predation.

**Acknowledgements** The study was undertaken while the author held a Royal Society Postdoctoral Fellowship funded by the Science and Engineering Research Council (UK) as part of its NATO plan. I am grateful to the Agencia de Medio Ambiente, Junta de Andalucía for authorization to conduct research in Cazorla and for financial support from DGICYT grant PB87-0452 to C.M. Herrera. I would like to thank Xavier Espadaler for identifying the ant species and Carlos Herrera for stimulating my interest in plant-animal interactions.

## References

- Abbot I, Heurck P van (1985) Comparison of insects and vertebrates as removers of seed and fruit in a Western Australian forest. *Aust J Ecol* 10:165–168
- Barnea A, Harborne JB, Pannell C (1993) What parts of fleshy fruits contain secondary compounds toxic to birds and why? *Biochem Syst Ecol* 21:421–429
- Burkey TV (1994) Tropical tree species-diversity – a test of the Janzen-Connell model. *Oecologia* 97:533–540
- Cerda X, Bosch J, Alsina A, Retana J (1988). Dietary spectrum and activity patterns of *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Annu Soc Entomol Fr* 24:69–75
- Cerda X, Retana J, Bosch J, Alsina A (1989) Daily foraging activity and food collection of the thermophilic ant *Cataglyphis cursor* (Hymenoptera:Formicidae). *Vie Milieu* 39:207–212
- Clark DA, Clark DB (1984) Spacing dynamics of a tropical rain-forest tree: evaluation of the Janzen-Connell hypothesis. *Am Nat* 124:769–788
- Estrada A, Fleming TH (1986) Frugivores and seed dispersal. Junk, Dordrecht
- Fleming TH, Estrada A (1993) Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer, Dordrecht
- Gryj EO, Dominguez CA (1996) Fruit removal and postdispersal survivorship in the tropical dry forest shrub *Erythroxylum havanense* – ecological and evolutionary implications. *Oecologia* 108:368–374
- Guitian J, Fuentes M (1992) Reproductive biology of *Crataegus monogyna* in northwestern Spain. *Acta Oecol* 13:3–11
- Guitian J, Fuentes M, Bermejo T, Lopez B (1992) Spatial variation in the interactions between *Prunus mahaleb* and frugivorous birds. *Oikos* 63:125–130
- Hansson L (1985) The food of bank voles, woodmice and yellow-necked mice. *Symp Zool Soc Lond* 55:141–168
- Herrera CM (1984) Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* 63:386–393
- Herrera CM (1987) Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecol Monogr* 57:305–331
- Herrera CM (1995) Plant-vertebrate seed dispersal systems in the Mediterranean – ecological, evolutionary, and historical determinants. *Annu Rev Ecol Syst* 26:705–727
- Herrera CM, Jordano P (1981) *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecol Monogr* 51:203–218
- Howe HF (1986) Seed dispersal by fruit eating birds and mammals. In: Murray DR (ed) *Seed dispersal*. Academic Press, Sydney, pp 123–189
- Hulme PE (1992) The ecology of a temperate plant in a mediterranean environment: post-dispersal seed predation of *Daphne laureola*. In: Thanos CA (ed) *Plant-animal interactions in mediterranean type ecosystems*. Athens University Press, Athens, pp 281–286
- Hulme PE (1993) Post-dispersal seed predation by small mammals. *Symp Zool Soc Lond* 65:269–287
- Hulme PE (1994) Rodent post-dispersal seed predation in grassland: magnitude and sources of variation. *J Ecol* 82:645–652
- Hulme PE (1996a) Herbivory, plant regeneration and species coexistence. *J Ecol* 84:609–616
- Hulme PE (1996b) Natural regeneration of yew (*Taxus baccata* L): microsite, seed or herbivore limitation? *J Ecol* 84:853–861
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jeanne, RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224
- Jordano P (1994) Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb* – patterns and consequences. *Oikos* 71:479–491
- Kollmann J (1995) Regeneration window for fleshy fruited plants during scrub development on abandoned grassland. *Ecoscience* 2:213–222
- Manzur MI, Courtney SP (1984) Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. *Oikos* 43:265–270
- Montgomery WI, Gurnell J (1985) The behaviour of *Apodemus*. *Symp Zool Soc Lond* 55:89–115
- Notman E, Gorchoff DL, Cornejo F (1996) Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species. *Oecologia* 106:221–227
- Perry AE, Fleming TH (1980) Ant and rodent predation on small animal-dispersed seeds in a dry tropical forest. *Brenesia* 17:11–22

- Schupp EW (1988) Seed and early seedling predation in the forest understory and in the tree fall gaps. *Oikos* 51:71–78
- Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108:15–29
- Schupp EW (1995) Seed seedling conflicts, habitat choice and patterns of plant recruitment. *Am J Bot* 82:399–409
- Snow B, Snow D (1988) *Birds and berries*. Poyser, London
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Terborgh J, Losos E, Riley MP, Bolaños Riley M (1993) Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. *Vegetatio* 107/108:375–386
- Traveset A (1994) Cumulative effects on the reproductive output of *Pistacia terebinthus* (Anacardiaceae). *Oikos* 71:152–162
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1964–1980) *Flora Europaea*, volumes 1–5. Cambridge University Press, Cambridge
- Valle F, Gomez F, Mota JF, Diaz C (1989) Parque Natural de Cazorla, Segura y Las Villas. Guía botánico-ecológica. Rueda, Madrid
- Venable DL, Brown JS (1993) The population dynamic functions of seed dispersal. *Vegetatio* 107/108:31–55
- Webb SL, Willson MF (1985) Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67:150–153
- Whelan CJ, Willson MF, Tuma CA, Souza Pinto I (1991) Spatial and temporal patterns of postdispersal seed predation. *Can J Bot* 69:428–436
- Willson MF (1992) The ecology of seed dispersal. In: Fenner M (ed) *Seeds. The ecology of regeneration in plant communities*. CAB International, Wallingford, pp 61–85
- Willson MF, Whelan CJ (1990) Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. *Oikos* 57:191–198