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5 DETERMINANTS OF SEED DISPERSER EFFECTIVENESS: THE QUANTITY

6 COMPONENT AND PATTERNS OF SEED RAIN FOR PRUNUS MAHALEB

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25 Running head: DISPERSER EFFECTIVENESS: QUANTITY

1   Abstract.— In this paper we analyze the seed dispersal stage of the <u>Prunus</u> <u>mahaleb</u>-

2   frugivorous bird interaction from fruit removal through seed delivery within the context of

3   disperser effectiveness. The effectiveness of a frugivorous species as a seed disperser is the

4   contribution it makes to plant fitness. Effectiveness depends on the quantity of seed dispersed

5   and the quality of dispersal provided each seed. For the main frugivores, we studied

6   abundance, visitation rate and feeding behavior, the major variables influencing the quantity

7   component of effectiveness, and the post-foraging microhabitat use and resultant seed

8   shadows which set the stage for postdispersal factors that will influence the quality component

9   of effectiveness.

10   Legitimate seed dispersers (SD) swallowed fruits whole and defecated or regurgitated

11   intact seeds; pulp consumers (PC) pecked fruits to obtain pulp and dropped seeds to the

12   ground, but some species occasionally dispersed seeds (PCSD species). Overall numbers of

13   fruits removed (i.e., handled) by avian frugivores were similar in the two study years;

14   however, the estimated percentage of seeds dispersed differed significantly, with lower

15   relative dispersal success in the year with greater relative abundance of PC species. Similar

16   numbers of seeds were dispersed in the two years despite a near four-fold difference in

17   number of fruits produced. Fruit crop size explained >80% variance in the number of seeds

18   dispersed/tree.

19   A total of 38 species of birds were recorded during censuses, with frugivores

20   representing 68.8 % of them; the relative representation of SD, PC, and PCSD species was

21   42.2, 17.2, and 9.4 %, respectively. There were no significant trends in overall frugivore

22   abundance between the two study years, but 10 of 16 SD species tended to be more abundant

23   in 1989 and 4 of 6 PC species tended to be less abundant, resulting in a greater relative and

24   absolute representation of SD species among frugivores in 1989, the year with greater relative

25   seed dispersal success. Individual trees showed extensive variation in visitation rates ranging

26   from 0.3 to 41.6 visits/10 h in any year. The main visitors were the SD species <u>Phoenicurus</u>

27   <u>ochruros</u>, 10.8 visits/10h; <u>Turdus</u> <u>viscivorus</u>, 9.2 visits/10h; <u>Erithacus</u> <u>rubecula</u>, 3.5 visits/10h;

1 and <u>Sylvia</u> <u>communis</u>, 2.6 visits/10h and the PC species <u>Fringilla</u> <u>coelebs</u>, 16.7 visits/10h and

2 <u>Parus</u> <u>ater</u>, 4.7 visits/10h.

3   Species with large quantity components of effectiveness typically had either high visit

4 or high feeding rates, combined with high probability of dispersing a handled seed. Variation

5 among species in fruit handling behavior, however, was the main factor influencing variation

6 in the quantity component. Visit rate in turn was influenced largely by local abundance. No

7 single frugivore trait, however, can adequately estimate the quantity component of disperser

8 effectiveness. A 'gulper'/'masher' dichotomy helps explain differences in fruit handling

9 among major frugivore types and shows many correlates with other aspects of frugivore

10 activity that ultimately influence the quantity component.

11   Most species showed marked preferences for microhabitats with plant cover, especially

12 <u>P. mahaleb</u>, mid-height shrubs, and <u>Pinus</u> (86.1 % of the departure flights) and avoided open

13 microhabitats. Most flights were over short distances (77.5 % to perches located within 30 m).

14 Among the main frugivores, 40.3 % of the exit flights were to perches >15 m away from the

15 feeding tree, but only 18.5 % of these flights were to perches >15 m from any <u>P. mahaleb</u>.

16 Covered microhabitats received significantly more seeds (39.3 ± 5.0 seeds dispersed/m^2, 1988;

17 31.7 ± 5.9 seeds dispersed/m^2, 1989) than open microhabitats (2.8 ± 0.7 seeds dispersed/m^2,

18 1988; 1.8 ± 0.4 seeds dispersed/m^2, 1989).

19   The potential contribution of each bird species to the seed rain in each microhabitat

20 was estimated from the number of visits recorded, the mean number of seeds dispersed/visit,

21 and the proportion of exit flights to each microhabitat. Microhabitats differed strongly in the

22 proportions of seeds delivered by the main frugivores, and bird species also differed in the

23 proportions of seeds delivered to a given microhabitat. The seed rain to covered microhabitats

24 was delivered by a more heterogeneous assortment of species than the seed rain to open sites.

25 The resulting seed shadow was a complex result of the interaction between movement patterns

26 of a suite of bird species differing in both the quantity of seed dispersed and microhabitat

27 preferences, and the landscape distribution of these microhabitat patches. This seed shadow

1 was extremely non-random due to both a strong overall preference by most of the birds for the

2 relatively scarce covered microhabitats, and to species-specific preferences for particular types

3 of covered microhabitats. Different microhabitat types not only received variable amounts of

4 dispersed seed, but also differed in the number and identity of disperser species contributing to

5 that seed rain.

6

7 Key words: avian frugivory; frugivory; fruit removal fruit size; Mediterranean scrubland;

8 mutualism; plant demography; seed dispersal; seed rain; Spain; Sylvia; Turdus.

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10 Key phrases.— Seed dispersal by birds: correlates of plant fecundity and fruit traits;

11 Demographic consequences of plant-bird interactions; Habitat selection by frugivorous birds:

12 implications for seed rain patterns; Variation in feeding rates and fruit handling by frugivorous

13 birds: implications for fruit removal.

1 <u>Introduction</u>
2

3   The effectiveness of frugivores as seed dispersal agents of their food plants depends on

4 both the quantity of dispersal, or the amount of seed dispersed, and the quality of dispersal, or

5 the probability seeds are deposited unharmed in sites with high prospects for establishment.

6 Ultimately, disperser effectiveness is the contribution a disperser makes to plant fitness,

7 ideally measured as the number of reproductive adults recruited through the activity of a

8 dispersal agent (Schupp 1993), and both quantity and quality components of frugivore

9 behavior influence it in measurable ways (Herrera and Jordano 1981). Even with the immense

10 amount of information on seed dispersal by frugivorous animals obtained during the last 20

11 years, we still lack a clear picture of how effects of frugivore activity translate into

12 demographic and evolutionary consequences for the plants (Howe 1990, Jordano 1992,

13 Herrera <u>et al</u>. 1994, Schupp 1995, Schupp and Fuentes 1995). A central objective of this paper,

14 and a first step in this direction, is to document the immediate consequences of frugivore

15 activity for plant recruitment, specifically to assess quantitatively the landscape pattern of seed

16 delivery by individual frugivore species. The quantity component of disperser effectiveness

17 provides a unifying theme for addressing this objective.

18   The net result of frugivore activity is fruit removal, which may or may not result in

19 seed dispersal away from the parent. Fruit removal in this study is equated with fruit handling,

20 and includes any successful or unsuccessful (e.g., fruit is too large to swallow) attempt by a

21 frugivore to consume fruit pulp, whether or not the fruit is detached from the peduncle.

22 Removal generally leads to successful seed dispersal if done by legitimate seed dispersers, or

23 seed loss if done by pulp/seed consumers that damage seeds or drop them beneath the parent

24 canopy. Whether fruit removal leads to successful seed dispersal (away from the parent) thus

25 depends largely on frugivore feeding behavior, fruit processing, and post-feeding movements.

26 Immediate influences on seed fate depend on whether or not seeds are damaged during

27 mandibulation and digestion (Levey 1987, Corlett and Lucas 1990), and whether or not seeds

1   are dropped beneath the parent canopy (Howe and Vande Kerckhove 1981, Wheelwright

2   1991). Lasting influences on seed and seedling survivorship depend on the types of microsites

3   where seeds are delivered. As the movement patterns of frugivores are frequently non-random

4   relative to available microhabitats, and microhabitats frequently differ substantially in abiotic

5   (e.g., light levels, water availability, soil texture) and biotic (e.g., competition, seed predator

6   and herbivore pressure) conditions, differences in post-removal behavior of frugivores should

7   have deferred effects on the recruitment of new plants (Schupp 1993, Schupp 1995). Whether

8   or not frugivore activity results in successful recruitment thus depends on fruit processing,

9   disperser movement and microhabitat use, and biotic and abiotic influences on survivorship of

10   seeds, seedlings and saplings. Categorization and quantification of these aspects and outcomes

11   of frugivore foraging is thus a prerequisite for assessing disperser effectiveness.

12   Two stages can therefore be envisioned with respect to the consequences of the

13   interactions between frugivores and their food plants. First, the dispersal stage encompasses

14   the visit to the fruiting tree and the post-feeding sequence of activities resulting in seed

15   delivery (frugivore-generated seed rain). This stage is directly influenced by frugivore activity.

16   Second, the post-dispersal stage includes the sequential phases of seed stay in the soil,

17   germination, early seedling establishment, and seedling and sapling growth and survival

18   (regeneration). Fate at this stage is also influenced by initial frugivore activity, but indirectly;

19   that is, fate is a delayed consequence of the pattern of seed fall generated by frugivore activity.

20   The complete sequence of steps in this process has seldom been considered for any species

21   (but see, Howe et al. 1985, Reid 1989, Howe 1993, Murphy et al. 1993, Herrera et al. 1994,

22   Jordano and Herrera 1995, Schupp 1995, Wenny and Levey 1998). Even for the well

23   documented seed dispersal stage, we lack a clear understanding of how its components

24   (visitation rate, visit length, feeding rate, fruit handling and seed processing) influence the

25   quantity component of effectiveness- the amount of seeds dispersed by a given frugivore

26   species (Schupp 1993). An integrative approach to seed dispersal that fully investigates both

27   dispersal and post-dispersal stages of the interaction from the perspective of disperser

1   effectiveness is a powerful approach for developing an understanding of the ecological and

2   evolutionary consequences of plant-frugivore mutualisms.

3   Although the concept of disperser effectiveness was developed as a framework for

4   evaluating contributions of individual disperser species to plant fitness, it can be viewed from

5   a variety of perspectives (Schupp 1993). In particular, a thorough investigation of the quantity

6   component of seed dispersal should consider not only the quantity of seed dispersed by

7   individual frugivore species, but also the quantity of seeds dispersed from individual trees.

8   The absolute numbers of of seeds removed by frugivores (removal success) and disperesed

9   away from the parent's canopy by legitimate dispersers (dispersal success) are ultimately

10   limited by the number of ripe fruits produced by a plant. Recent studies have suggested that

11   frugivore activity might limit fruit removal and seed dispersal (Davidar and Morton 1986,

12   Herrera 1988, Jordano 1989, Carr 1992, Herrera et al. 1994, Laska and Stiles 1994), so that

13   actual dispersal success is frequently less than this maximum. If, for example, visitation by

14   fruit and seed predators is frequent, or visitation by legitimate seed dispersers is infrequent

15   relative to fruit crop size, individual plants may disperse only a fraction of the seeds produced.

16   Thus, plants differ not only in the absolute number of seeds removed and dispersed, but also in

17   the proportion of the seed crop removed (relative removal success) and dispersed (relative

18   dispersal success). Both absolute and relative measures are relevant for understanding seed

19   dispersal systems. To the extent that seed dispersal is beneficial, absolute dispersal success can

20   be viewed as a correlate of parental plant fitness. In contrast, independent of absolute dispersal

21   success, relative dispersal success can be considered a measure of the extentr to which a plant

22   attains its potential fitness.

23   Both absolute and relative dispersal success depend on a number of factors "intrinsic"

24   (plant size, fruit set, fruit crop size, fruit size, pulp/seed ratio) and "extrinsic" (neighborhood

25   of conspecifics, surrounding habitat structure, availability of other fruit, etc.) to the plant.

26   Understanding the influences of these "intrinsic" (e.g., the pre-dispersal flower and fruit loss

1   that limits fruit production, Jordano 1989) and "extrinsic" (e.g., influence of surrounding

2   vegetation on visitation, Herrera and Jordano 1981, Traveset 1994) factors on both absolute

3   and relative dispersal success is thus central to understanding of the role of frugivores as

4   determinants of dispersal success. For example, variation among-trees in the total number of

5   seeds dispersed could be simply due to differences in crop size, or, if legitimate seed

6   dispersers preferentially visit certain trees, to differences in in relative dispersal success

7   (Davidar and Morton 1986, Jordano 1989, Carr 1992, Herrera et al. 1994).

8   In this study we quantify the seed dispersal stage of the <u>Prunus</u> <u>mahaleb</u>-frugivorous

9   bird interaction from fruit removal to seed delivery. The focus is on the quantity component of

10   seed disperser effectiveness and its correlates, and on the microhabitat pattern of seed rain

11   created by individual disperser species. In order to develop a more complete quantitative

12   understanding of seed dispersal, we also consider the quantity of seed dispersed by individual

13   trees and the intrinsic and extrinsic factors influencing it. Deferred consequences of seed

14   dispersal for seed survival and germination and seedling and sapling establishment will be

15   presented in subsequent papers. The primary specific issues addressed here are: 1) do

16   frugivore species differ predictably in visitation patterns, number of fruits consumed,

17   probability of dispersing a handled seed and number of seeds dispersed per visit? 2) how do

18   these variables covary across species in this assemblage? 3) how do these variables affect the

19   quantity component of <u>P.</u> <u>mahaleb</u> seed dispersal by individual species? 4) are differences

20   among dispersers consistent between years? 5) do dispersers in this assemblage differ

21   predictably in the types of microsites to which they deliver seeds? and 6) do these differences

22   generate a predictable seed shadow?

23

24   <u>Methods</u>

25   <u>Definitions</u>

1   Frugivory types.— Four main types of frugivorous birds that visit P. mahaleb can be

2   distinguished based on foraging mode and immediate consequences for seed dispersal. Seed

3   dispersers (SD, hereafter) swallow the fruits whole and defecate or regurgitate intact seeds.

4   Pulp consumers (PC) peck the fruit to obtain pulp pieces either without detaching it from the

5   peduncle or, after plucking, by tearing off the pulp while the fruit is in the bill or held against a

6   perch. In both cases the seed is eventually dropped to the ground. Pulp consumer-dispersers

7   (PCSD) are PC species that in rare instances pluck the fruit and leave the tree to eat the pulp

8   on another perch, thus performing infrequent dispersal of seeds without ingestion. Finally,

9   seed predators (SP) feed on the seed contents and always damage the seeds. Additional details

10   on feeding behavior of frugivores visiting P. mahaleb can be found in Herrera and Jordano

11   (1981), Guitián et al. (1992) and Jordano (1994); see also Snow and Snow (1988).

12

13   Fruit removal and seed dispersal.— We scored a fruit as removed whenever a frugivorous bird

14   handled it. Removal actually implies plucking the fruit from its peduncle, but we also include

15   those instances when pieces of the pulp are torn off the fruit by PC species without separating

16   it from the peduncle. Such fruits rapidly desiccate and are highly unlikely to be consumed by a

17   legitimate disperser; instead, they eventually fall to the ground. Fruit removal may or may not

18   result in dispersal of the enclosed seed away from the parent's canopy. Thus, the initial fates

19   of individual ripe fruits on P. mahaleb can be categorized as: 1) "removed", when a fruit is

20   handled by a frugivorous bird, whether it is detached from the peduncle or not; 2) "ripe

21   damaged", when invertebrates damage a ripe fruit; or 3) "ripe desiccated", when fruits are not

22   removed and, eventually, the pulp desiccates and the fruit falls to the ground beneath the

23   parent. Fruit removal can result in seed dispersal away from the parent plant when removal is

24   by SD species and, on rare occasions, by PCSD species. In contrast, damage by invertebrates

25   and fruit removal by PC and PCSD species that results in the fruit immediately or eventually

26   falling beneath the parent do not lead to seed dispersal.

1   We refer to the number of fruits removed from a tree as fruit removal success.

2 Similarly, seed dispersal success is the estimated number of seeds dispersed away from the

3 tree's canopy; only a fraction of fruit removal results in seed dispersal. Relative removal or

4 dispersal success for a tree is simply the proportion of fruits removed, or seeds dispersed,

5 relative to the initial crop of ripe fruits.

6

7   <u>Study</u> <u>area</u>

8   This study was conducted during 1988-1989 in the Reserva de Navahondona-

9 Guadahornillos (Parque Natural de las Sierras de Cazorla, Segura y las Villas, Jaén province,

10 Southeastern Spain). The study area was located in Nava de las Correhuelas, a site in the

11 highlands of the park, at 1615 m elevation. The main study site extends over ca. 100 ha and

12 includes both deep cool soils and rocky, exposed slopes. Deciduous vegetation, including

13 <u>Crataegus</u> <u>monogyna</u>, <u>Prunus</u> <u>mahaleb</u>, <u>Lonicera</u> <u>arborea</u>, <u>Berberis</u> <u>hispanica</u>, <u>Daphne</u> <u>laureola</u>,

14 <u>Rosa</u> <u>canina</u> and <u>Acer</u> <u>granatense</u>, occupies the deep soils. Adjacent rocky slopes are

15 dominated by open pine forest (<u>Pinus</u> <u>nigra</u>, subsp. <u>salzmannii</u>) with <u>Juniperus</u> <u>communis</u>, <u>J.</u>

16 <u>phoenicea</u>, <u>J.</u> <u>sabina</u>, and scattered <u>Taxus</u> <u>baccata</u> (Valle et al. 1989). The climate is of

17 Mediterranean montane type. Rainfall averages 1527 mm and is concentrated in autumn-

18 winter. Only 9 % of total annual precipitation falls during June-September, the main ripening

19 season for <u>P.</u> <u>mahaleb</u> fruits. Average temperatures for coldest and hottest months are 2.9 and

20 22.5 °C. Snowfalls are frequent from November to March.

21   The study of fecundity variation, seed removal success, bird censuses and feeding

22 observations was carried out on trees growing scattered throughout this main study site.

23 Within this larger study area, we set up a 90 x 120 m intensive study plot for observational

24 work on microhabitat patterns of post-feeding bird flights and of seed rain. Although

25 restricting these observations to a small plot may limit the generality of the results, it is

26 necessary in order to adequately characterize flight and seedfall patterns relative to

27 microhabitat availability. Additional observational and experimental work associated with a

1 long-term study of post-dispersal processes (germination, seed predation, and seedling and

2 sapling survival and growth) to be reported later is also taking place in this plot.

3

4 <u>Plant</u> <u>natural</u> <u>history</u>

5 <u>Prunus</u> <u>mahaleb</u>, the Saint Lucie's or Mahoma's cherry, is a small tree (2-10 m height)

6 that grows scattered at mid-elevations (1250-1900 m) in Southeastern Spanish mountains,

7 through the Pyrenees and central and eastern Europe to Ukraine, and from Morocco through

8 Syria to west-central Asia (Webb 1968, Ceballos and Ruiz 1979). Detailed information on the

9 pollination biology has been published elsewhere (Jordano 1993b; also see Guitián 1993,

10 Guitián et al. 1993). Fruits are drupes, black when ripe, 8.0 ± 4.4 mm long and 8.3 ± 0.5 mm

11 wide (N = 20), and with a sugary, water-rich pulp (Herrera and Jordano 1981). Chemical

12 analyses of the fruit pulp reported by these authors yielded 3.2 % crude fat, 2.8 % crude

13 protein, 6.3 % ash, 5.7 % fiber, and 82.0 % soluble carbohydrates. Fruit crops of individual

14 trees usually range between 700-30 000 fruits.

15 Information on interactions of <u>P.</u> <u>mahaleb</u> with frugivorous animals that consume fruits

16 and disperse seeds has been reported by Herrera and Jordano (1981), Herrera (1989), Guitián

17 et al. (1992), and Jordano (1994). At least 28 bird species, four mammals, and one lizard have

18 been recorded feeding on the fruits at our site (P. Jordano and E.W. Schupp, pers. obs.).

19

20 <u>Trees</u>

21 We assessed fruit removal and seed dispersal in a sample of 21 trees. These were a

22 stratified sample of the trees in an initial census of 120 adult trees scattered through the main

23 study site. The trees in the sample grow in 4 large patches over ca. 10 ha area that slightly

24 overlaps the intensive study plot. The range of growing conditions in the overall site are

25 represented in this area. Crop sizes of final-sized fruits were estimated by direct counts of all

26 marked plants during the last two weeks of July in 1988 and 1989 (see Jordano 1994, 1995,

27 for a detailed account of the method). During this period fruits start to ripen, but massive fruit

removal has not yet begun. We used weekly counts of individual fruits on marked branches to estimate the standing crops and proportions of unripe, ripe, and damaged fruits, as well as pre-dispersal loss of fruits (see Jordano 1987a, Herrera 1988, Jordano 1989, Jordano 1994 for detailed description of the methods). Depending on tree size, up to 5 branches per tree were randomly selected in a stratified manner, with one branch selected at each of up to 5 positions regularly spaced around the canopy. The total number of fruits followed in marked branches were 3560 and 3780 fruits in 1988 and 1989, respectively. This repeated counts of branches was used to estimate the fraction of the fruit crop ripened, removed by frugivores, and potentially dispersed.

Fruit loss estimates (fruits considered unsuitable for frugivorous birds) for each tree were scored during the periodic branch counts as ripe desiccated (DES), ripe damaged by invertebrates (DAM; invertebrate damage to ripe fruits of P. mahaleb is extremely rare at the site and was recorded only on a few marked fruits), unripe desiccated (UNR), or pecked with pulp remains attached (PEC). The proportion of fruits removed was calculated by: [MARK-(DES + DAM + UNR)]/MARK, where MARK is the number of fruits initially marked on the tree. Any fruit not entering the DES, DAM, or UNR category by the end of the survey period was clearly missing (detached from its peduncle) and was considered removed, as were PEC fruits.

In order to estimate seed dispersal we first estimated the maximum proportion of seeds potentially dispersed from the tree (maximum potentially removed by legitimate seed dispersers) as: [MARK-(DES + DAM + UNR + PEC)]/MARK. These seed dispersal estimates from branch counts will overestimate dispersal, however, because fruits plucked from peduncles by PC species, and most of those plucked by PCSD species, are not taken away from the tree, but are dropped beneath the parent instead. Consequently, not all missing fruits have been dispersed. To correct this overestimation we proceeded as follows. Just after the 1988 fruiting season we counted fruit and seed remains on the ground, beneath the canopies of sampled trees. Between 3 and 8, 0.5 m x 0.5 m quadrats were sampled per tree depending on

1   tree size (7.5-18.5% of the canopy area), and all fruit and/or seed remains (except dispersed

2   seeds in regurgitations or faeces, that likely originate from other trees) were recorded and

3   counted. These quadrats were located at regularly-spaced locations beneath the canopy,

4   approximately midway between the trunk and the canopy edge. Fruit and seed removal by

5   rodents and/or ants is scarce during this period (P. Jordano, pers. obs.), so that repeated counts

6   of fruit and seed in unprotected ground may provide reasonably adequate estimates of seed

7   and fruit fall. The number of DES, DAM, UNR, and PEC fruits were counted in each ground

8   sample and a figure for the whole tree was estimated by extrapolating the sampled surface to

9   the area of the canopy projection. We then subtracted this figure from the total crop size to

10   obtain the estimated numbers of fruits consumed and seeds dispersed. This is analogous to

11   seed trap methods (see Jordano 1994, 1995) and was used to assess consistency in the

12   estimates of fruit loss and of seed removal derived from branch counts and to assess the

13   reliability of our estimates of the proportions of seeds leaving the trees derived from branch

14   counts.

15   As expected, PEC figures were underestimated in the branch counts (due to the fact

16   that some missing fruits here being taken by PC species that drop the partially consumed fruit

17   and seeds beneath) and the use of branch counts alone would overestimate seed dispersal

18   success. The proportion of PEC fruits estimated from ground counts was, however,

19   significantly correlated with the proportion estimated from branch counts ($R^2 = 0.801$, $\underline{P} <$

20   0.01). For individual trees in 1988, we used the PEC estimate derived from ground counts,

21   together with the DES, UNR, and DAM figures obtained from branch counts, to estimate seed

22   dispersal. For 1989 we applied the 1988 regression to the PEC values obtained from the

23   branch counts and used this estimate of the proportion of PEC loss in the calculation of seed

24   dispersal success for each tree (Jordano 1994).

25   We sampled intact ripe fruits directly from branches before extensive fruit

26   consumption had started in the area. Fruits were measured (maximum length and cross

1   diameter, to the nearest 0.05 mm, with digital calipers), and weighed to obtain masses of both

2   pulp and seed (sum= whole fruit).

3

4   <u>Birds</u>

5   <u>Censuses</u> <u>and</u> <u>feeding</u> <u>records</u>.— We censused line transects of fixed width (120 m, between

6   715-775 m length) 3 d/wk (not consecutive) during the two study seasons to determine the

7   abundance of birds (expressed as number of birds/km census) and obtain feeding records on

8   fruits (1 feeding record= consumption of 1 fruit; Snow and Snow 1988). Total sampling effort

9   was 4.3 km (<u>N</u>= 6 censuses) and 6.2 km (<u>N</u>= 8 censuses), with 560 and 673 individuals

10   censused in 1988 and 1989, respectively. The number of feeding records was 2854 for the two

11   years pooled. The dataset included those records reported by Jordano (1994) and feeding

12   records on 4 trees growing within the intensive study plot. See Jordano (1993a, 1994) for

13   details of the census methods.

14

15   <u>Feeding</u> <u>observations</u>.— We conducted direct watches at a total of 15 trees in 1988 ($N = 99.6$

16   h observation, 190.3 tree-h); and 12 trees in 1989 ($N = 82.9$ h observation, 165.0 tree-h). Tree-

17   hours were greater than total hours because more than one tree could be observed at one time

18   in some cases. Observation effort was allocated among trees so that each tree was observed on

19   multiple days and at least once during each of the following periods of the day: 0530-0800h,

20   1000-1400, and after 1600h. Most observations, however, were between 0630-1500 h GMT.

21   Observation periods lasted 1h, and all individuals visiting the tree were identified to species,

22   when possible, and the time of the visit recorded.

23   We intensively studied the behavior of birds while feeding on fruits either during the

24   direct watches or during additional observation periods. For each bird sighted, the following

25   data were recorded whenever possible: (1) total time spent at the tree, (2) number of fruits

26   handled ("removed", by our definition), (3) number of fruits swallowed, (4) number of fruits

27   dropped, (5) number of fruits touched but not detached from the peduncle, (6) number of times

the bird moved during the observation sequence (number of "moves"), (7) total time stopped

during the observation sequence, (8) number of fruits carried away from the tree in the bill,

and (9) for bird species eating only pulp, whether the pulp was pecked from the fruit without

detaching it from its peduncle or was stripped from the seed while holding it in the bill (and

the seed dropped). Birds could not always be observed for complete visits to the trees; in these

instances ("partial" visits, hereafter), the record was omitted for the computation of number of

fruits and seeds taken per visit, but was used to estimate feeding rates (e.g., fruits and

seeds/min).

Visitation rates, post-feeding flights, and the seed shadow.— We intensively studied visitation

patterns to 4 trees located in the intensive study plot to attempt to quantify the number of seeds

potentially reaching different microhabitat types by means of delivery by different frugivore

species. Thus, for this subset of the trees we simultaneously studied removal success, bird

visitation rates and feeding behavior (numbers of fruits handled, ingested, and dropped), and

the type of microhabitat where birds first perched after feeding on the fruits and leaving the

tree, as well as the distance between the tree a bird fed in and the first landing perch after

leaving the feeding tree. We used the following intervals: 0, <5 m, 5-<15 m, 15-<30 m, 30-

<50m, 50-<100m, and   100 m. When a bird stayed in the tree more than 15 min after feeding

we coded the microhabitat destination as P. mahaleb and the distance as 0 m because of the

high likelihood that the seed had been regurgitated or defecated in this time, and thus not

dispersed. We also included other sporadic observations of birds leaving trees within the plot

after consuming fruit. These incidental data were used to increase the sample size for analysis

of post-feeding behavior of individual species, not in any comparisons among species.

        To study visitation rates to each of these 4 focal trees we sampled a total of 16 tree-

days per year, with observations carried out during five periods of the day: 0530-0800 h,

0800-1000 h, 1000-1200 h, 1200-1600 h, and after 1600 h GMT. Watching periods of variable

1 duration were assigned to each interval and all four trees received a similar observation effort

2 at different times of the day. The total observation time was 107.3 h.

3   We defined 9 types of microhabitats based on both the type of soil and vegetation

4 cover: (1) "P. mahaleb", on or beneath a conspecific tree; (2) "low shrubs", including

5 Juniperus communis, Berberis hispanica, and Rhamnus spp. and juveniles < 1m height of the

6 taller shrub species; (3) "mid-height shrubs", including Crataegus monogyna, Rosa canina,

7 and Lonicera arborea; (4) "high trees", Pinus nigra subsp. salzmannii; (5) "high trees above

8 low shrubs", P. nigra with J. communis or B. hispanica undergrowth; (6) "deep soil", with

9 thick cover of herbaceous vegetation; (7) "gravelly soil", with gravel and cobble < 0.06 m^2

10 surface area and sparse herbaceous cover; (8) "stones on soil", on or within 25 cm of a larger

11 (0.06 m^2-< 0.25 m^2) generally elevated rock that is usually associated with gravelly soil; and

12 (9) "rock", boulders and rock substrate > 0.25 m^2 (generally much greater), and with fissures.

13 We were unable to adequately distinguish flights to microhabitats 4 and 5 when observing

14 birds flying a long distance. Thus, we recorded all exit flights to high trees for each species

15 and multiplied these figures by the relative proportions of 4 and 5 in the habitat to estimate

16 their relative use by each species. This is valid since it is very unlikely that the presence or

17 absence of ground-level shrubs affects tree choice by species flying to the canopies of pines.

18 We categorized types 6-9 as "open" microhabitats and types 1-5 as "covered" microhabitats.

19 The relative abundance of these microhabitat types was estimated by random point sampling

20 (N = 700 points) along 20, 120-m long parallel transects (N= 35 random points/transect)

21 running the length of the intensive study plot. Starting points of transects were randomly

22 located along one short (90 m) side of the plot with a minimum separation of 2 m between

23 adjacent transects.

24   To quantify microhabitat patterns of seedfall we sampled the 5 covered microhabitats

25 with seed traps, 0.41 x 0.41 m, 0.12 m depth, plastic trays, covered with 1.2 cm mesh wire to

26 protect fallen seeds and fruits from potential consumption by animals. Previous trials showed

27 that fallen fruits or seeds rarely bounce off the trap mesh (see Kollmann and Goetze 1997).

1   For the 4 open microhabitats we used quadrats of the same size. The sampling scheme

2   consisted of 15 replicates per microhabitat type, each with 4 traps or quadrats laid out in a

3   square with 0.5-0.75 m between adjacent traps or quadrats. Traps and quadrats were in

4   operation throughout the fruiting season (mid July- mid September, 1988 and 1989). Traps

5   were checked weekly for identification and counts of fallen fruits and seeds. Quadrats were

6   generally checked every day late in the afternoon following most seed dispersal but before

7   rodent seed predators became active. On several occasions we skipped a day but we have no

8   reason to belive this should cause serious bias in the estimates. Locations of replicates for

9   microhabitats 1-4 were selected randomly from the total available shrubs or trees; those for

10 category 5 were all those available within the plot. For open microhabitats (categories 6-9

11 above) we haphazardly selected three to four representative areas of each and

12 pseudorandomly located three to five replicates in each area by blindly tossing a stick and

13 setting the quadrats where it landed.

14   We characterized the environment surrounding each replicate (set of 4 traps or

15 quadrats) by recording the following variables: 1) type of microhabitat (as described above);

16 2) distance from the center of the cluster of 4 traps or quadrats to the nearest edge of the

17 nearest P. mahaleb >= 10.0 cm basal stem diameter (this size was chosen to represent a tree

18 large enough to have a reasonably large fruit crop; i.e., exceeding 1000 fruits); 3) basal stem

19 diameter of the nearest P. mahaleb; 4) distance to the nearest vegetation cover with thick

20 tangle of stems or branches coming low to the ground (<= 0.5 m above ground); 5) number of

21 P. mahaleb trees >= 1 m tall with at least a portion of the crown within 10 m of the center of

22 the 4 traps or quadrats; 6) basal stem diameters of these P. mahaleb trees with a portion of the

23 crown within 10 m of the traps; and 7) number of P. mahaleb fruits on trees having at least 1

24 branch within 10 m of the traps or quadrats, estimated from the linear regression of fruit crop

25 size against basal stem diameter (in cm; both variables log-transformed) for a random sample

26 of 90 trees in the study area: log (number of fruits)= 0.4546 + 2.1981 log (BSD); F = 199.2, P

27 < 0.0001, df = 2, 84, R^2 = 0.7059).

1   For each replicate and census date we tallied across all four traps or quadrats the

2   number of intact ripe fruits that had not had any pulp consumed, the number with pieces of

3   pulp attached (handled and dropped by PC species), the number of clean seeds (dispersed by

4   SD species) and the number of seeds broken open, presumably by rodents in trees. Both clean

5   seeds and seeds with pulp pieces attached or other signs of bird handling will be referred to as

6   "removed fruits", while only clean seeds (regurgitated) or those in faeces will be referred to as

7   "dispersed seeds" (see Jordano 1995 for details and definitions).

8

9   Data analyses

10   For statistical analyses we used parametric tests whenever their requirements were met.

11   Original data were subjected to log- (for linear or mass measurements) or angular

12   (percentages) transformations to normalize the data prior to parametric statistical tests. We

13   used non-parametric tests or resampling statistics (Manly 1991) whenever transformations did

14   not adequately normalize the data. In the case of very skewed distributions (e.g., crop sizes,

15   seed rain data), we report the median and 25th-75th percentiles; the mean $\pm$ 1 SE are given

16   otherwise. Specifically, we used randomization tests for paired comparisons of fruit crop size

17   data and number of seeds dispersed/tree in the two years. When randomization tests were

18   applied to multiple regression analyses, we assessed the significance from the extra sum of

19   squares accounted for by each X_j variable when the others X_{j-1} were already incorporated. We

20   used Manly's (1991; p. 96-111) test, with additional routines from Press et al. (1992) and $\underline{N}$ =

21   5000 resamplings.

22   We used survival analysis (LIFESTAT procedure; SAS Institute 1988) to test for

23   differences in visitation patterns among trees, years, and frugivore groups (see Muenchow

24   1986). Advantages of failure-time methods to assess visitation patterns include comparing the

25   shape of the distribution of failure times (time until a tree is visited by a bird), accounting

26   adequately for censored data, and being robust to deviations from normality (Fox 1993). We

27   tested the heterogeinity among groups (trees, years, etc.) by means of the Wilcoxon test (SAS

1   Institute 1988) due to its increased power relative to the log-rank test when there is censoring.

2   We recorded visit time to the nearest minute to minimize ties, which seriously reduce power

3   (Muenchow 1986, Fox 1993).

4

5   <u>Results</u>

6

7   <u>Fruiting and fruit removal</u>

8   <u>Fruiting intensity and its correlates</u>.— Flower production was similar in the two study years

9   (Table 1; see Jordano 1993b for details) ($\underline{P}$ = 0.502, randomization test for paired

10   comparisons, $\underline{N}$ = 5000 resamplings; Manly 1991). The number of full-sized fruits produced

11   by individual plants was, however, significantly ($\underline{P}$ = 0.0001, randomization test for paired

12   comparisons) greater in 1988 than in 1989, with median fruit crops of 7565 fruits and 1935

13   fruits, respectively. As reported in Jordano (1993b), the sharp decrease in fruiting intensity

14   during 1989 was due to extremely low pollination success associated with unfavorable

15   weather conditions during the flowering period (e.g., only 18.0 ± 2.4 % flowers setting fruit in

16   1989, $\underline{N}$ = 39 inflorescences, compared to 46.9 ± 3.8 %, $\underline{N}$ = 15, in 1988). However, the rank

17   order of fruit crop sizes remained relatively consistent, even with the marked between-year

18   variation in fruiting intensity (r_s = 0.457, $\underline{P}$ = 0.04, $\underline{N}$ = 21).

19   Variation in individual fecundity could therefore be caused by a variety of factors,

20   including individual size differences, intensity of flowering, and/or consistent variation in fruit

21   set. Results of a multiple regression analysis for the 1988 and 1989 data revealed significant

22   effects only for plant size (1988, ß = 27.62, $\underline{F}$ = 292.7, $\underline{P}$ = 0.001, $\underline{N}$ = 21 trees; 1989, ß =

23   110.9, $\underline{F}$ = 5.22, $\underline{P}$ = 0.04; randomization test, $\underline{N}$ = 5000 resamplings; Manly 1991) and the

24   initial number of flowers produced (only significant in 1988, ß = 0.27, $\underline{F}$ = 272.0, $\underline{P}$ = 0.002,

25   $\underline{N}$ = 21 trees) in determining fruit production.

26

1   Fruit removal and seed dispersal.— We compared fruit removal levels between years by

2   means of repeated measures ANOVA, using repeated observations on the 21 marked trees.

3   The overall number of fruits removed by avian frugivores differed only marginally between

4   the two study years ($\underline{F}$ = 3.21, $\underline{P}$ = 0.09, df = 1, 20) (Table 1). However, the estimated

5   percentage of seeds dispersed (removed by legitimate dispersers) differed significantly, with

6   lower relative dispersal success in 1988 ($\underline{F}$ = 19.52, $\underline{P}$ = 0.0003, df = 1, 20) (Table 1). This

7   difference reflects greater fruit losses to pulp and pulp-seed consumers in 1988 (24.58 $\pm$

8   3.62 %) compared to 1989 (12.77 $\pm$ 3.61 %) ($\underline{F}$ = 5.31, $\underline{P}$ = 0.02, df = 1, 20). This variation in

9   the overall effect of frugivores on fruit removal did not result in between-year differences in

10   seed dispersal: the absolute number of seeds dispersed/tree in 1988 (median= 2664 seeds) was

11   not significantly different from 1989 (1894 seeds) ($\underline{P}$ = 0.40; randomization test for paired

12   comparisons, $\underline{N}$ = 5000 resamplings), even with greater proportional removal success in this

13   year.

14   Table 2 summarizes the results of a multiple regression analysis aimed at dissecting the

15   correlates of seed dispersal success, estimated by its two components: the absolute number of

16   seeds dispersed by legitimate dispersers (absolute dispersal success) and the proportion of

17   seeds dispersed relative to the initial crop size (relative dispersal success). As expected,

18   absolute dispersal success is primarily influenced by fruit crop size, which explains >80% of

19   the variation in both years. The partial $\underline{R}^2$ accounted for by both losses due to desiccation (%

20   fruits desiccated) and consumption by pulp/seed consumers (PC, PCSD, and SP frugivores,

21   which are not legitimate seed dispersers) was small in both years. In contrast, relative dispersal

22   success was greatly influenced by losses to non-legitimate seed dispersers and desiccation,

23   accounting together for 93.9 % and 71.6 % the variation in 1988 and 1989, respectively (Table

24   2). For the two years pooled, the partial correlations between these two variables and relative

25   dispersal success were $\underline{r}$ = -0.976 and -0.137, respectively, suggesting a greater negative effect

26   of consumption by pulp/seed consumers than of desiccation in determining relative removal

27   success. The influence of fruit diameter on relative dispersal success was only marginally

1 significant in both years (Table 2). To summarize, significantly higher relative dispersal

2 success (Table 1) in the year with lower fruit production, largely caused by lower fruit

3 consumption by non-legitimate dispersers (Table 2), tended to compensate for the variation in

4 fruit crop sizes yielding similar absolute numbers of seeds dispersed from trees (Table 1).

5

6 <u>The quantity component of seed dispersal and its correlates</u>

7

8 <u>Bird abundance</u>.— A total of 38 species of birds were recorded during censuses, with

9 frugivores representing 68.8 % of them. The relative representation of SD, PC, and PCSD

10 species accounted for 42.2 %, 17.2 %, and 9.4 % of all the species recorded, respectively

11 (Appendix 1). Between-year differences in the proportions of species in these frugivory

12 groups were not significant (^{2}= 0.56, $\underline{P}$ = 0.90, df= 2). The overall frugivore abundance

13 (averaged over censuses) also did not differ significantly between the two study years (128 ±

14 33 birds/km, $\underline{N}$ = 6 censuses in 1988; 105 ± 13 birds/km, $\underline{N}$ = 8 censuses in 1989; $\underline{F}$ = 0.11,

15 $\underline{P}$ = 0.73, df = 1, 48). We explored trends in between-year changes in community and

16 functional group abundances by means of paired comparisons of both the absolute abundances

17 of frugivore species (Appendix 1) and the proportion of total individuals recorded that year

18 that were contributed by each species. There was no consistent trend for either increase or

19 decrease in the abundances of individual frugivore species (signed-rank test = -35.5,

20 $\underline{P}$ = 0.35). However, considered as a group, there was a significant increase from 1988 to 1989

21 in both the number (signed-rank test = 65.0, $\underline{P}$ < 0.0001) and proportion (signed-rank

22 test = 65.0, $\underline{P}$ < 0.0001) of SD individuals, as well as a marginally significant decrease of

23 proportion of PC (signed-rank test = 9.5, $\underline{P}$ = 0.06), with no evident trend for either numbers or

24 proportions of PCSD (signed-rank tests < -3.0, $\underline{P}$ = 0.25). <u>Erithacus</u> <u>rubecula</u> and <u>Turdus</u>

25 <u>viscivorus</u> were important SD species showing greater abundance in 1989, while the main PC

26 species, <u>Fringilla</u> <u>coelebs</u>, showed a dramatic decrease in that year (Appendix 1). To

27 summarize, there were no significant trends in overall frugivore abundance between the two

1 study years; 10 of 16 SD species tended to increase in abundance in 1989 and 4 out of 6 PC

2 species tended to decrease, resulting in a greater relative and absolute representation of SD

3 species among frugivores in 1989, the year with greater relative seed dispersal success.

4

5 Visitation.— Individual trees showed extensive variation in visitation rates (Fig. 1), ranging

6 from 0.3 to 41.6 visits/10 h (in either year). Between-tree differences in visitation, as depicted

7 by the survivorship functions for both 1988 and 1989 (Fig. 1), were highly significant

8 ($x^2 = 94.8$, $\underline{P} < 0.0001$ and $x^2 = 234.2$, $\underline{P} < 0.0001$, respectively; Wilcoxon test, SAS Institute

9 1988). Only four trees (1931, 1932, 1933, and 1939, Fig. 1) differed in visitation rate between

10 years ($x^2 > 4.5$, $\underline{P} < 0.03$). For the remaining trees, both the composition of the assemblage and

11 visitation rates were similar in the two years. Though not significantly, overall visitation rate

12 tended to decrease for most trees in 1989.

13 Birds favored similar trees in both years (trees no. 1820, 1823, 1921, 1937-1940; Fig.

14 1), while other trees (1929, 1934, 1936) consistently received few visits (Fig. 1). Visitation by

15 the four types of frugivores differed significantly among individual trees ($x^2 = 166.9$, $\underline{P} <<$

16 0.0001), but not between years ($x^2 = 0.11$, $\underline{P} = 0.94$), although the tree*year interaction was

17 significant ($x^2 = 52.41$, $\underline{P} < 0.01$) (model with tree and year as main effects; CATMOD

18 procedure, SAS Institute 1988).

19 Individual bird species differed significantly in visit rate measured as the number of

20 visits/10 h ($\underline{F} = 5.91$, $\underline{P} < 0.0001$), with no significant species*year interaction ($\underline{F} = 0.69$, $\underline{P} =$

21 0.83). Frequent visitors to the trees included both SD (P. ochruros, 10.8 visits/10h; T.

22 viscivorus, 9.2 visits/10h; E. rubecula, 3.5 visits/10h; and S. communis, 2.6 visits/10h) and PC

23 or PCSD species (F. coelebs, 16.7 visits/10h; P. ater, 4.7 visits/10h).

24

25 Feeding behavior.— Avian frugivores visiting P. mahaleb trees showed three types of feeding

26 behavior with regard to the proximate consequences for the plant (Appendix 2). Legitimate

27 seed dispersers (SD) swallow fruits whole, usually > 75% of the fruits handled (they never

1 pecked the fruits for pulp pieces), and defecate or regurgitate the seeds unharmed. Once a fruit

2 is detached, failures to swallow handled fruits are largely a consequence of small body size

3 and gape width. The smaller species typically fail to successfully detach fruits from peduncles,

4 or drop detached fruits due to handling failures (Appendix 2). Thus, among Sylvia species, the

5 percentage of fruits swallowed decreased with decreasing gape width from the larger S. borin

6 (100.0% fruits swallowed) to S. communis (95.2 %) and S. atricapilla (95.0 %) to S.

7 melanocephala (83.3 %) to S. cantillans (72.8 %), to S. conspicillata (18.2 %). These

8 differences among Sylvia species in percent fruits swallowed were significant (F= 2.70, P=

9 0.048). In contrast, congeneric species spanning smaller size differences did not differ in

10 percentage of fruits swallowed (F = 2.63, P = 0.10, Phoenicurus spp.; F = 2.33, P = 0.13,

11 Turdus spp.; Appendix 2). The percentage of fruits swallowed was positively correlated with

12 gape width across all SD species (r_s = 0.723, P = 0.03, N = 10; gape width measurements from

13 P. Jordano, unpubl. data).

14   Pulp consumers (PC) do not swallow any fruit. Rather, they peck fruits and separate

15 pieces of pulp, either from fruits not detached from the infructescences ("Pecked", Appendix

16 2) or from fruits that have been plucked and are handled in the bill or against a branch

17 ("Picked", Appendix 2). All the seeds picked by PC species are dropped beneath the parent

18 plant, and the pecked fruits almost always end up there as well (Appendix 2). Pulp consumers-

19 seed dispersers (PCSD) are PC species that occasionally swallow fruits whole (G. glandarius,

20 S. europaea), leave the tree to cache fruits in crevices of nearby branches (S. europaea, P.

21 ater), or go to another tree to eat the pulp (P. ater). Thus, all of these species occasionally

22 perform dispersal (Table 3). All the parids, S. europaea, and G. glandarius usually picked

23 fruits, held them against the perch and pulled off tiny pieces of pulp. In contrast, F. coelebs

24 and other finches frequently pecked the fruits, leaving the seeds with variable amounts of pulp

25 attached to the peduncles. Despite the occasional dispersal event, the percentage of removed

26 seeds that is actually dispersed away from the parent plant by these species was generally very

27 low (Appendix 2).

1   Feeding rates varied widely among frugivore species (Table 3, Fig. 2), ranging from

2   0.4 to 7.4 fruits/min. The number of seeds potentially dispersed per visit varied even more, as

3   a consequence of differences in visit duration, feeding rate, and percentage of fruits swallowed

4   (Appendix 2, Table 3). The larger species (C. palumbus, D. major, G. glandarius and Turdus

5   spp.) took > 5 seeds/visit on average, due to larger body size, while smaller species took only

6   ca. 3 fruits/visit on average (Table 3). Both the number of seeds removed per visit ($r = 0.922$,

7    $P < 0.01$, $N = 24$) and the number dispersed away from the tree ($r = 0.763$, $P < 0.01$) were

8   positively correlated across species with body size (both body mass and gape width). Relative

9   to both PC and PCSD species, SD species dropped significantly smaller percentages of seeds

10   per visits (Appendix 2), moved less frequently but spent less time stopped per fruit handled

11   (see Fig. 2), removed more fruits per min foraging, and swallowed and dispersed a greater

12   number of seeds per visit (Table 3, Appendix 2) ($P < 0.0001$ for all a posteriori, Scheffé

13   contrasts among frugivory types).

14   Visits were typically of short duration, < 2 min (Table 3), with feeding sequences (Fig.

15   2) including bouts of movement, while looking for fruits within the canopy, alternating with

16   pauses that include resting and/or fruit handling time. Frugivores in the SD, PCSD, and PC

17   categories differed markedly in the shape and patterns of these foraging curves, illustrating

18   contrasting patterns of fruit foraging. Most SD species (Sylvia spp., C. palumbus, Turdus spp.,

19   Fig. 2) foraged by gleaning fruits from perches, using rapid movements and very short

20   handling times. Characteristic foraging curves for these species (Fig. 2) include a steep

21   "ladder" with narrow steps. The number of fruits handled/min by gleaners (from 3.8 in S.

22   communis to 8.2 in T. merula) was well above the feeding rate of other SD species that forage

23   for fruits either by hopping from branch to branch or on the wing (E. rubecula, 2.5 fruits/min,

24   and Phoenicurus spp., 3.1 fruits/min). The foraging bouts of these species showed less

25   frequent moves (more time stopped between fruit handlings), but handling times were similar,

26   as they also swallow fruits whole. Their characteristic foraging curve (Fig. 2) is not steep, with

27   wide steps reflecting the longer stop periods among feeding bouts. The foraging curves for

1   both PCSD and PC species (<u>G. glandarius</u>, <u>S. europaea</u>, <u>P. ater</u>, and <u>F. coelebs</u>) differed

2   markedly from these patterns. They are low-slope "ladders" with narrow but high steps,

3   reflecting the greater handling time per fruit. In contrast, foraging moves among fruit

4   "captures" were extremely short as illustrated by <u>P. ater</u> (Fig. 2).

5

6   <u>Correlates of the quantity component of seed dispersal</u>-. Table 4 summarizes variables that

7   determine the quantity component of disperser effectiveness for each of the main frugivore

8   species in <u>P. mahaleb</u> seed dispersal. Species differed widely in all variables (Table 4). There

9   was a significant trend for SD species to score with larger quantity components (Kruskal-

10   Wallis test; ^{2} = 7.97, df = 2, $\underline{P}$ = 0.019). Those with large quantity component values (<u>T.</u>

11   <u>viscivorus</u>, <u>T. merula</u>, <u>Ph. ochruros</u>, <u>E. rubecula</u>, and <u>S. communis</u>) typically showed high visit

12   and/or high feeding rates, combined with a high probability of seed dispersal. <u>F. coelebs</u>,

13   however, had a relatively high quantity component despite a low probability of dispersing

14   removed seeds because it had an extremely high visit rate (Table 4).

15   To account for the relative influences of abundance, visit rate, fruits/visit, and

16   probability of dispersing handled seeds (Table 4) on the quantity component, we examined the

17   standardized coefficients for the regression of log-transformed values of the quantity

18   component on the log-transformed values of these variables. The model accounted for 82.2 %

19   of the variation in the quantity component across species ($\underline{F}$ = 21.97, $\underline{P}$ < 0.0001, df = 4, 19),

20   but only visit rate ($\underline{t}$ = 3.01, $\underline{P}$ = 0.007), fruits/visit ($\underline{t}$ = 2.67, $\underline{P}$ = 0.015), and probability of

21   dispersing handled seeds ($\underline{t}$ = 4.22, $\underline{P}$ = 0.0005) had significant effects. The high partial

22   correlation between abundance and visit rate ($\underline{r}_{part}$ = 0.7388) indicates a significant, but

23   indirect, effect of abundance on the quantity component mediated by its influence on visit rate.

24   Taken together, fruit handling variables seem to have a greater effect on the quantity

25   component than visit rate or abundance in the area, especially if comparing SD vs. PC species

26   (with zero or very low probability of dispersing a handled seed). For example, species with

27   relatively infrequent visits and low abundance in the area (<u>S. atricapilla</u> and <u>Ph. phoenicurus</u>)

1 but with high probability of dispersing handled seeds show higher quantity component values

2 than species that disperse few seeds but visit trees frequently (P. ater, F. coelebs; Table 4).

3

4 <u>Among-tree variation in visitation and seed dispersal success</u>

5 The number of seeds dispersed from trees by each bird species is the product of its visit

6 rate and the number of seeds successfully dispersed per visit. Given that individual trees

7 differed widely in the identity and visit rate of different bird species, we might expect among-

8 tree differences in seed removal to reflect this variation. Thus, the percentage of total visits by

9 SD species to individual trees ranged from 18.75 % - 92.31 % in 1988 and 23.68 % - 100.0 %

10 in 1989, with a marginal trend for the percentage of visits by SD species to be correlated

11 between years for individual trees (r_s = 0.449, $\underline{P}$ = 0.08, $\underline{N}$ = 16 trees).

12 Data for both bird visitation and seed dispersal success is available for only 11 trees.

13 To assess the relative effects of visitation by the three frugivore groups, we fit a regression

14 model including the percent of seeds dispersed as a dependent variable (estimating relative

15 seed dispersal success) and the percent of visits by SD, PCSD, and PC species for the two

16 years pooled. Among-tree variation in the proportion of visits made by the three frugivore

17 groups accounted for a significant fraction of variance in relative seed dispersal success

18 ($\underline{F}$ = 6.70, $\underline{P}$ = 0.003, df = 3, 17, R^2 = 0.542). Seed dispersal success was positively

19 significantly correlated with visitation by SD species (standardized regression coefficient, $\underline{b}$ =

20 0.882, $\underline{t}$ = 4.48, $\underline{P}$ = 0.0003), and negatively significant ly correlated with visitation by PC

21 species   ($\underline{b}$ = –0.599, $\underline{t}$ = 2.55, $\underline{P}$ = 0.021).

22

23 <u>Post-feeding exit flights</u>

24 <u>Availability of microhabitats</u>.— The frequency profile of available microhabitats characterizes

25 an open area rich in rocky substrates, with sparse, scattered patches of mid- and low shrubs

26 and pine forest edges. Open microhabitats made up 66.4 % of the sampled points (deep soil,

27 19.7 %; gravelly soil, 17.9 %; stones on soil, 8.3 %; and rock, boulders, and rock substrate,

1   20.6 %). Microhabitats with plant cover (beneath <u>Prunus</u>, 6.6 %; low shrubs, 10.4 %; mid-

2   height shrubs, 3.3 %; high trees, 10.9 %; and high trees above low shrubs, 2.4 %) represented

3   only one third of the sampled points (33.6 %).

4

5   <u>Destinations of exit flights from the feeding trees</u>.— We considered only the 7 main frugivore

6   species, for which we have adequate data on visitation records, feeding rates, and flight

7   observations; they included <u>E. rubecula</u>, <u>Ph. ochruros</u>, <u>S. cantillans</u>, <u>S. communis</u>, <u>S. europaea</u>,

8   <u>T. merula</u>, and <u>T. viscivorus</u>. Taken together, these 7 species accounted for 81.8 % of all seeds

9   dispersed, as estimated from visit records, mean number of fruits handled per visit, and

10   probability of dispersing a handled seed. A total of 86.1 % of the departure flights recorded

11   were to microhabitats with plant cover. Taken individually, microhabitat use by these

12   representative species of the frugivore assemblage differed significantly from the expectation

13   based on availability (^{2}> 15.7, df = 1, <u>P</u> < 0.0001, for all possible comparisons). Open

14   microhabitats were used much less frequently than expected, while microhabitats with plant

15   cover, especially <u>P. mahaleb</u>, mid-shrubs, and <u>Pinus</u> were strongly preferred (see Fig. 3;

16   ^{2}= 21.1, df = 1, <u>P</u> < 0.0001, for the contrast of "open" <u>versus</u> "covered" microhabitats;

17   CATMOD procedure, SAS Institute 1988).

18   We used the analysis of frequencies in the species x microhabitat contingency table to

19   assess preference patterns in the post-feeding exit flights of each species (i.e., cell

20   combinations that exhibit large residuals, differing significantly from expected value).

21   Individual bird species showed distinct tendencies to use particular microhabitat types (Fig. 3;

22   ^{2}= 231.2, df = 7, <u>P</u> <.0001). Examination of residual cell frequencies for the log-linear model

23   incorporating species and microhabitat effects (Fig. 3) reveals that most species flew to

24   microhabitats with plant cover more often than expected while avoiding open microhabitats.

25   An exception was <u>Ph. ochruros</u>, which disproportionately flew to and perched on rocks. The

26   significant, overall, preference for <u>Pinus</u> was due to very large numbers of <u>T. viscivorus</u> flying

27   to pines; despite the overall pattern, most species avoided <u>Pinus</u> and frequently flew to low or

1   mid-shrubs or other P. mahaleb tree (Fig. 3). As a consequence, microhabitat types differed

2   significantly in the relative frequencies with which bird species used them; i.e., the identity

3   and relative frequency of bird species flying to different microhabitats differed significantly

4   (^{2}= 61.3, df = 8, P <.0001).

5

6   Flight distances.— Bird species included in Fig. 3 also differed significantly in distances

7   flown to the first perch after leaving the feeding trees (^{2}= 197.8, df = 12, P <.0001). Most

8   flights were of short distance (77.5 % to perches located within 30 m). Only the two Turdus

9   species flew longer distances with some frequency (60.2 % of the flights by T. viscivorus and

10   4.3 % by T. merula to distances > 30 m). The remaining species usually perched within 15 m

11   of the feeding tree (> 50 % of the flights recorded).

12   Similarly, bird species included in Fig. 3 differed significantly in the distance from the

13   first perch used after feeding and the nearest P. mahaleb tree whether or not it was the feeding

14   tree (^{2}= 159.7, df = 12, P <.0001). For all species except the two Turdus, most exit flights

15   (>92.0 %) were to perches within 15 m of a P. mahaleb tree. Thus, whether or not the first

16   perch used after feeding on fruits was a P. mahaleb tree, and independent of distance flown,

17   most birds feeding on Prunus tended to perch close to Prunus trees. Turdus viscivorus,

18   however, rarely flew to perches < 5 m from a P. mahaleb tree (1.9 % of the flights), and

19   generally flew to perches >15 m away from the nearest Prunus tree. Some exit flights by Ph.

20   ochruros (7.5 %), S. communis (4.5 %), and T. merula (4.3 %) were also to perches >15 m

21   away from the nearest Prunus. Pooling data for all bird species (those included in Fig. 3),

22   40.3 % of the exit flights were to perches >15 m away from the feeding tree, but only 18.5 %

23   of these flights were to perches >15 m from any P. mahaleb.

24

25   Seed rain

26   Correlates of spatial variation in seed rain.— The overall number of seeds dispersed/m^2 was

27   similar in 1988 and 1989 (23.1 ± 3.4 seeds dispersed/m^2, 1988; 18.4 ± 3.3 seeds dispersed/m^2,

1   1989; $\underline{F}$ = 1.93, $\underline{P}$ = 0.1660, df = 1, 252). Microhabitats differed significantly in seed rain

2   density (Fig. 4) ($\underline{F}$ = 34.65, $\underline{P}$ < 0.0001, df = 8, 252) and there were differences in seed rain

3   between years for particular microhabitats ($\underline{F}$ = 2.31, $\underline{P}$ = 0.021, df = 8, 252, for the

4   microhabitat * year interaction; see Fig. 4). Covered microhabitats received significantly more

5   seeds (39.3 ± 5.0 seeds dispersed/m^2, 1988; 31.7 ± 5.9 seeds dispersed/m^2, 1989) than open

6   microhabitats (2.8 ± 0.7 seeds dispersed/m^2, 1988; 1.8 ± 0.4 seeds dispersed/m^2, 1989) ($\underline{F}$

7   > 30.0, $\underline{P}$ < 0.0001, df = 1, 134, for the contrasts between the two groups of microhabitats in

8   the comparisons for 1988 and 1989). In 1988, both the <u>Prunus</u> and high-trees (<u>Pinus</u>)

9   microhabitats showed significantly greater seed rain than any other microhabitat in the two

10 years. In 1989, <u>Prunus</u> received the greatest seed rain, followed by mid-height shrubs and high

11 trees (<u>Pinus</u>) microhabitats (Fig. 4).

12   We analyzed the correlates of seed rain intensity in each replicate group of traps or

13 quadrats by means of a linear model incorporating the effects of microhabitat type and

14 quantitative habitat variables including the distance to, and basal stem diameter of, the nearest

15 <u>Prunus</u> (NEARPRU and BSD, respectively), distance to nearest cover of shrubs with branches

16 < 50 cm above ground (DISTCOV), number of <u>Prunus</u> trees with at least one branch within a

17 10-m radius (NUMPRU), and estimated fruit crop size of these nearby trees (CROPNEIG).

18 For both years, the fitted model explained a significant proportion of variation in seed rain ($\underline{R}^2$

19 = 0.7320, $\underline{F}$ = 25.42, $\underline{P}$ < 0.0001, df = 13, 121, 1988; $\underline{R}^2$ = 0.6953, F = 21.24, P < 0.0001, df =

20 13, 121, 1989; Table 5). The type of microhabitat was the best predictor of seed rain density at

21 a particular patch, with a significant effect in both years (F   22.3, P < 0.0001, df = 8, 126;

22 Table 5). Among the quantitative habitat variables characterizing the neighborhood of each

23 trap replicate, only NEARPRU (F   5.0, P < 0.026, df = 1, 133) and BSD (F   6.2, P < 0.01,

24 df = 1, 133) had significant effects in either year. The distance effect was evident only in 1989,

25 with seed rain density decreasing with increasing distance from <u>Prunus</u> trees. In both 1988 and

26 1989, there was a positive correlation between the BSD of the nearest <u>Prunus</u> tree and seed

27 rain density at a particular patch (Table 5).

1   The significance of distance to the nearest <u>Prunus</u>, and the size of the nearest <u>Prunus</u>

2   could be artifacts of including the data from traps beneath <u>Prunus</u>, since NEARPRU = 0 m for

3   this microhabitat type by definition. Thus, a 'distance' effect could be due simply to <u>Prunus</u>

4   microhabitats having a distance equal to 0 and a greater seed rain density than any other

5   microhabitat (Fig. 4). Consequently, we also fit a multiple regression model incorporating

6   only the quantitative habitat variables (NEARPRU, BSD, DISTCOV, NUMPRU, and

7   CROPNEIG), separately for 1988 and 1989, and excluding the data from traps beneath <u>Prunus</u>

8   trees (Table 5, column <u>ß</u>). The models were still significant but explained a much lower

9   fraction of variance in seed rain than the one including the effect of microhabitat type (R^2 =

10   0.1006, 1988; R^2 = 0.1558, 1989). For both years the model had only DISTCOV with

11   significant effects, and BSD, NUMPRU and CROPNEIG with insignificant effects (Table 5).

12   The seed rain falling in a particular trap or quadrat replicate set decreased with increasing

13   distance either to nearest shrub cover or to nearest <u>Prunus</u> in both years.

14   To summarize, the seed rain received by a given patch was strongly associated with the

15   microhabitat type of the patch and increased in the neigborhood of <u>Prunus</u> trees and understory

16   cover, but was unrelated to fruit production or size of <u>Prunus</u> trees in the vicinity of the patch.

17

18   <u>Contribution of frugivore species to the seed rain in microhabitats</u>.— The potential

19   contribution of each of the 7 main bird species to the seed rain in each microhabitat was

20   estimated from the number of visits recorded, the mean number of seeds dispersed from a

21   tree/visit, and the proportion of exit flights to each microhabitat. We first calculated the

22   contribution of each frugivore species to the total seed rain. We pooled the data from the two

23   study years, and multiplied the number of visits recorded for each species by the mean number

24   of seeds dispersed/visit. The number of seeds delivered to each microhabitat was obtained, for

25   each species, by multiplying these total numbers of seeds by the proportion of flights to each

26   microhabitat. The number of seeds delivered to microhabitat i by bird species j relative to the

1   total number of seeds delivered to i by all 7 species yields the proportional contribution of

2   species j to the seed rain in i.

3   Microhabitats differed strongly in the proportions of seeds contributed by the main

4   frugivores (CATMOD procedure, SAS Institute 1988; ^{2}= 2644.1, $\underline{P}$ < 0.0001, Fig. 5), and

5   bird species also differed in the proportions of seeds contributed to a given microhabitat (^{2}=

6   5048.7, $\underline{P}$ << 0.0001, Fig. 5). In particular, "open" and "covered" microhabitats differed

7   significantly in the proportional contribution to their seed rain by the different bird species.

8   The seed rain to covered microhabitats was delivered by a more heterogeneous assortment of

9   species than the seed rain to open sites (Fig. 5). For example, seeds dispersed to "stones on

10   soil", "rock", or "gravelly soil" sites were dispersed mainly by redstarts (Ph. ochruros), while

11   no single species contributed more than 45% of the seed rain to "mid-height shrubs", "low

12   shrubs", or "Prunus" microhabitats.

13   We examined the significance of the patterns depicted in Fig. 5 by fitting a log-linear

14   model (CATMOD procedure, SAS Institute 1988) incorporating the microhabitat and species

15   effects. The significance of the residuals from this model can be used to identify those

16   disperser * microhabitat combinations that depart from the seed rain expected on the basis of

17   the relative abundances of both microhabitat types and birds. Most species dispersed fewer

18   seeds than expected to the deep soil and gravelly soil substrates lacking woody vegetation

19   cover; only Ph. ochruros showed residuals consistently positive and significant in these

20   microhabitats (^{2} 20.0, $\underline{P}$ < 0.007). The remaining species either did not use these

21   microhabitats (Fig. 5) or did so much less frequently than expected (e.g., T. viscivorus on

22   rocks, ^{2}= 109.1, $\underline{P}$ < 0.0001). Most species, with the exception of T. viscivorus, dispersed no

23   or few seeds to the pine forest microhabitats ("high trees (Pinus)" and "high trees (Pinus) plus

24   low-shrubs" combined) and showed significant negative residuals.

25

26   Discussion

1   A simple, heuristic, definition of effectiveness is the contribution dispersers make to

2 plant fitness (Schupp 1993), and depends on both the quantity of seeds dispersed (quantity

3 component) and the probability a dispersed seed will recruit a new reproductive adult (quality

4 component). Our results concern the quantity component and the multiple factors that

5 influence it.

6   As can effectiveness itself, the quantity component can be considered from the

7 perspectives of both the dispersal agents and the dispersed plants, and at a variety of scales

8 from individuals to communities. We emphasize variation among bird species (or occasionally

9 functional groups) in the quantity of seeds they dispersed, but we also consider variation

10 among indiviudual trees in the quantity of seeds they <u>had</u> dispersed. Further, we address the

11 patterns of seed rain created by dispersers. By combining these perspectives, we believe we

12 have developed a thorough understanding of seed dispersal and the myriad factors influencing

13 dispersal from fruit production through the microhabitat pattern of seeds on the ground.

14   Ultimately, the quantity component of disperser effectiveness is limited by fruit crop

15 size; potential maximum effectiveness would be achieved whenever dispersers successfully

16 deliver all the seeds produced, although maximal fitness returns can eventually occur under

17 submaximal disperser effectiveness (e.g., all available "safe sites" are saturated). Thus, from a

18 plant's perspective, both the absolute number of seeds dispersed and the proportion dispersed

19 relative to the fruit crop produced would be important components of success in the interaction

20 with frugivores. We first examine the correlates of fruit removal success in the <u>P. mahaleb</u>

21 population and assess the potential of frugivore activity to limit seed dispersal for individual

22 trees. We then discuss factors that determine variation among frugivores in both the quantity

23 component of effectiveness and variation in the seed shadows that each species generate. A

24 detailed examination of the quality component of seed dispersal in <u>P. mahaleb</u> will be

25 presented elsewhere.

26

1   <u>Fruiting, fruit removal, and seed dispersal success</u>

2   With similar levels of flowering intensity in the two years, a 2.6-fold decrease in fruit

3   set in 1989 resulted in a near 4-fold decrease in ripe fruits available for frugivores, suggesting

4   an added negative effect of increased abortion of unripe fruit in that year. Similar effects of

5   pre-dispersal losses on fruit availability for frugivores have been documented previously for

6   other Mediterranean tree and shrub species (Jordano 1987a, 1989). Our limited 2-yr data for <u>P.</u>

7   <u>mahaleb</u> suggest that the absolute number of flowers produced did not limit the size of the

8   fruit crop in 1988, when all trees had a large proportion of flowers setting fruit; but under

9   conditions impairing fruit set (e.g., bad weather resulting in low, generalized, fruit set level),

10 among-tree variation in fruit crop size is best explained by variation in flowering intensity.

11   Our regression analysis of seed dispersal success revealed a dramatic impact of

12 variation in fruit crop size on among-tree variation in the absolute number of seeds dispersed.

13 This major influence of plant fecundity alone has been reported previously for many species

14 (Davidar and Morton 1986, Herrera 1991, Carr 1992, Sallabanks 1992, Laska and Stiles 1994)

15 and suggests that among-individual differences in rate processes (such as the fraction of

16 flowers pollinated or fraction of ripe seeds dispersed) rarely compensate for differences in

17 absolute numbers (Herrera 1988, 1991, Jordano 1987a); i.e., more fecund plants might

18 disperse a greater absolute number of propagules even if, for example, they have low relative

19 seed dispersal success. In the particular case of <u>P. mahaleb</u>, where some fruits are removed by

20 pulp consumer species, differences in seed dispersal success may also result from annual

21 variation in visitation frequency by pulp consumers relative to legitimate seed dispersers

22 (Herrera <u>et al</u>. 1994, Jordano 1994). We were able to account for the negative effect of

23 visitation by non-legitimate frugivores (PC and PCSD species) on absolute seed dispersal and

24 demonstrate that among-tree differences in visitation rate by these frugivores explained a

25 small, but significant, fraction of the variance in seed dispersal.

1   Changes in particular frugivore groups at the study site have been documented

2   previously (Jordano 1994) and the reasons behind such inter-annual changes are not clear.

3   Most species feeding on P. mahaleb fruits breed in the area, and both adults and first-year

4   juveniles of the main consumers (Phoenicurus spp., Turdus spp., F. coelebs, and Parus spp.)

5   were observed at the trees during the post-reproductive period coincident with P. mahaleb fruit

6   ripening (late July- late August). Thus, yearly changes in abundance of these species could be

7   attributable to variations in the size of the breeding population and breeding success (see

8   Obeso 1987 for further discussion). Local breeding populations of F. coelebs, the main species

9   contributing to the observed changes among PC frugivores, vary greatly among years (Obeso

10   1987, Asensio and Carrascal 1990). Variation in the composition of the frugivore assemblage

11   between years thus shows an important effect on population-level seed dispersal success, with

12   greater average relative seed dispersal success in the year with less abundant PC and PCSD

13   species.

14   Summarizing the main trends, despite a large difference in the initial fruit crop size

15   (Table 1) at the population level, lower fruit loss to non-disperser species in 1989 (greater

16   dispersal success in this year) resulted in similar absolute number of seeds dispersed per tree

17   in the two study years and similar seed fall density. Increased consumption by legitimate seed

18   dispersers thus somewhat compensated the low fruit availability in that year. At the individual

19   tree level, variation in frugivore activity, in particular among-tree variation in visitation by PC

20   and PCSD species, best explained among-tree variation in the fraction of the fruit crop that

21   was successfully dispersed (see longer-term data in Jordano 1994); however, among-tree

22   variation in the absolute number of seeds dispersed was more strongly dependent on the initial

23   number of ripe fruits produced.

24

25   Dissecting the quantity component of effectiveness

1   No factor influencing the quantity component of effectiveness (Table 4) can

2 adequately estimate it alone (Schupp 1993). All need to be assessed when evaluating the

3 effectiveness of different frugivore species.

4 <u>Visitation</u>.— The strongest correlate of visitation rate by a frugivore species is its abundance

5 in the area, and our results indicate that, for frugivores that consume <u>P. mahaleb</u> fruits, census

6 records are crude predictors of visitation frequency at the trees. The overall picture for the

7 frugivore assemblage of <u>P. mahaleb</u> is of high reliability in terms of species composition and

8 relative abundance. First, there was no significant species*year interaction in the ANOVA

9 analysis of between-year variation in frugivore abundances; second, the composition of bird

10 assemblages visiting individual trees varied among trees, but was consistent between the two

11 study years. Most likely this high reliability of the frugivores is related to the fact that birds

12 visiting <u>P. mahaleb</u> are largely locally breeding species. Long-term census data at this site

13 (Jordano, 1994, and pers. observ.) reveal a high among-year consistency in the composition of

14 the local avifauna. Although annual variations certainly exist, as shown by shifts in the

15 abundances of major groups of frugivores (see <u>Results: Bird abundance</u>), the relative

16 magnitude of variation is much lower than reported for frugivore assemblages composed

17 chiefly of migratory or non-breeding birds (Herrera 1984, Jordano 1985, Jordano 1993a,

18 Herrera 1998).

19 <u>Variation among frugivore species</u>.— Between-year changes in the abundance and feeding

20 records of the most frequent SD visitors to the trees (<u>P. ochruros</u>, <u>T. viscivorus</u>, <u>E. rubecula</u>,

21 and <u>S. communis</u>) were small, but species differed significantly in visitation rate. These

22 species, together with <u>T. merula</u> and, among PC species, <u>P. ater</u> and <u>F. coelebs</u>, are locally

23 dominant at mid- and high-elevation sites within the general study area just after the breeding

24 season, when ripe <u>P. mahaleb</u> fruits are available (Obeso 1987, P. Jordano pers. obs.). The

1   largest between-year variations in abundance were recorded for the PC species <u>P. ater</u> and <u>F.</u>

2   <u>coelebs</u>, as was also reported previously for lower elevation sites (Obeso 1987).

3   <u>Consequences for the trees of variation in visit rate by different frugivore groups</u>.— Between-

4   year changes in the composition of the frugivore assemblage had an effect on overall fruit

5   removal rates in the two years, but effects of among-tree differences in composition were far

6   more dramatic. Visits by SD species ranged from 19 to 92% of the total visits by frugivores to

7   individual trees, and this variation had a large effect on potential seed dispersal success. More

8   importantly, these individual differences tended to be consistent between years, suggesting an

9   important long-term impact on dispersal success of individual trees if some trees consistently

10   receive visits by SD species while others are consistently visited by PC species. Differences

11   among individual plants in the composition of the frugivore assemblages have only rarely

12   been reported previously (Herrera and Jordano 1981, Traveset 1994) and their consequences

13   have never been addressed in detail. In the present study, we found that among-tree variation

14   in the proportion of visits by the three frugivore groups accounted for 54% of the variation in

15   relative seed dispersal success, and that the positive effect on seed dispersal success of

16   visitation by SD species was greater than the negative effect of visitation by PC species,

17   probably because of the greater feeding rates of SD species. By focusing on individual tree

18   variation, our results demonstrate not only that some trees consistently received very few

19   visits by frugivores while others were visited frequently, but also that different trees

20   consistently received visits by distinct combinations of SD, PC, and PCSD groups.

21   <u>Fruit foraging and fruit handling</u>.— Together with visitation frequency, fruit handling

22   behavior, especially feeding rate, is the major correlate of the quantitative importance a given

23   frugivore has for a plant species. Frugivores visiting fruiting plants typically differ widely in

24   feeding rates (e.g., McDiarmid et al. 1977, Howe and Vande Kerkchove 1981, Jordano 1983,

25   Snow and Snow 1988; see Schupp 1993 for review) but it remains to be seen if a high feeding

1   rate can eventually compensate for a lower visitation rate. At least for <u>P. mahaleb</u>, variation in

2   feeding rate did not compensate for variation in visitation rate. Rare visitors with high feeding

3   rates (e.g., <u>Columba palumbus</u>) had a lower quantity component than more frequent visitors

4   with slow feeding rates (e.g., <u>Fringilla coelebs</u>) (also see Sun et al. 1997). In general, the total

5   quantity of seeds dispersed correlates better across species with number of visits than with

6   number of seeds dispersed/visit (Schupp 1993, for a review), and our results support this

7   generalization.

8   What aspects of foraging best explain variation in seeds dispersed/visit? For a given

9   visitation rate, frugivores feeding on <u>P. mahaleb</u> fit neatly into three distinct types of fruit

10 handling behavior that affect the probability that a handled seed will be dispersed away from

11 the plant. First, PC species just peck pulp pieces and drop seeds beneath parent canopies, thus

12 dispersing no seeds (with the exception of <u>F. coelebs</u>, which in extremely infrequent occasions

13 takes a fruit in the bill and leaves the tree) . Second, PCSD species are very similar to PC

14 species except they carry fruits away from the parent on occasion and in the process disperse a

15 small fraction of the seeds handled; in this group, only <u>S. europaea</u> disperses more than 14%

16 of handled seeds. Finally, SD species swallow fruits whole and thus generally disperse most

17 handled seeds, although species vary greatly in the probability of dispersing a handled seed

18 (0.182-1.000). This variation among SD species in the probability of dispersing a handled seed

19 is largely attributable to size differences, especially gape width, and resulting variation in fruit

20 handling success. This is evident among the <u>Sylvia</u> warblers, where the mean percentage of

21 fruits dropped during feeding bouts was negatively correlated across species with mean gape

22 width (see also Jordano 1987b).

23   But despite these differences, resulting variation in probablity of dispersing a seed

24 handled among SD species was much smaller (>0.80 for all species the two smaller <u>Sylvia</u>

25 warblers, Table 4) than the differences between SD and PC-PCSD species (the latter showed <

26 0.40 probablity of dispersing a handled seed). These broad differences among frugivore

1 categories most likely reflect the large differences in feeding modes among 'gulpers' and

2 'mashers' (Foster 1987, Levey 1987), the two major feeding types among frugivorous birds

3 (Jordano 1992). Finches and tits feeding on P. mahaleb fruit exhibit a similar feeding pattern

4 to typical 'mashers' like neotropical tanagers and finches, with relatively long fruit handling

5 times and low overall feeding rate (Trainer and Will 1984, Levey 1986, Foster 1987, Levey

6 1987). All SD species show a characteristic 'gulper' behavior, with the overall feeding rate

7 more directly limited by the type of foraging maneuver used to pluck the fruits. Birds taking

8 fruits while perched on branches, like warblers, had high feeding rates with extremely short

9 handling times, short stopping times, and rapid movements in search of fruits. In contrast,

10 birds taking fruits on the wing, like the robin and redstarts, have slower feeding rates linked to

11 long 'stopping' times between successive fruit 'captures'. The 'gulper'/'masher' dichotomy

12 helps to explain major differences in fruit handling among major frugivore types and shows

13 many correlates with other aspects of frugivore activity that ultimately influence effectiveness.

14 However, differences among species within the same category (e.g., among SD species) is

15 best explained by variation in foraging maneuvers (e.g., gleaning fruits from branches vs.

16 taking the fruits on the wing), especially if differences in body size are accounted for.

17

18   <u>Patterns of seed delivery and the seed shadow</u>

19   A given seed disperser species has a characteristic seed delivery pattern which depends

20 on the total amount of seed dispersed (its relative contribution to the total final seed rain

21 reaching the ground) and the spatial distribution of this contributed seed rain. This distribution

22 obviously has a distance component, which most analyses of animal-mediated seed dispersal

23 emphasize (Willson 1993). Perhaps more important in many systems, however, is the

24 distribution of seeds across the distinct patch types making up the landscape. It is well

25 documented that, in general, frugivore activity results in extremely heterogeneous seed

26 shadows (Debussche et al. 1982, McDonnell and Stiles 1983, Hoppes 1987, Hoppes 1988,

27 Izhaki et al. 1991, Debussche and Isenmann 1994, Kollmann and Pirl 1995, Kollmann and

1   Schneider 1996, Loiselle et al. 1996). Most studies, however, have emphasized the description

2   of the final seed shadow generated by the whole array of dispersers (Debussche et al. 1985,

3   Holthuijzen and Sharik 1985, Alvarez-Buylla and Martínez-Ramos 1990, Clergeau 1991,

4   Martínez-Ramos and Soto 1993, Chávez-Ramírez and Slack 1994, Debussche and Isenmann

5   1994, Sargent 1995, Kollmann and Schneider 1996) or concentrated on particular species

6   (Howe and Primack 1975, Murray 1988, Mack 1995, Sun et al. 1997). Few have attempted a

7   comparative analysis of the main frugivores that disperse a plant (Reid 1987, Katusic-

8   Malmborg and Willson 1988, Reid 1989, Schupp 1993, Graham et al. 1995, Larson 1996) or

9   addressed explicitly the problem of quantifying disperser effectiveness. Every frugivore

10   species has a species-specific pattern of seed delivery that, to the extent microhabitat patches

11   differ in suitability for plant recruitment, will largely control variation in the quality of

12   dispersal.

13   <u>Direct effects on seedfall intensity</u>.— Ultimately, among-year variation in density of dispersed

14   seed (no. seeds m^{-2}) can be caused by variation in the number of fruits produced by the plants,

15   by variation in the abundance of frugivores, by changes in seed dispersal success or by a

16   combination of these three factors. Our study demonstrates that increased abundance of

17   legitimate seed dispersers resulted in a generalized increase in the <u>fraction</u> of the seed crop

18   successfully dispersed away from individual trees. Despite a dramatic decrease in fruit

19   availability in 1989 (Table 1), seed rain density, estimated by seed trap and quadrat data, was

20   similar in 1988 and 1989 (means of 23.1 and 18.5 seeds m^{-2}, respectively). The greater relative

21   seed dispersal success in 1989, that resulted from a lower abundance of PC species and a

22   greater abundance of SD species, somewhat compensated for the reduction in fruiting

23   intensity. Documenting both absolute and relative fruit removal and the fraction of it that

24   results in seed dispersal is thus necessary to adequately assess the potential of frugivores to

25   limit plant recruitment.

1 The seed shadow: patterns of differential delivery to microhabitats.— Variation among

2 microhabitat types in the number of dispersed seeds m^{-2} largely reflected variation in the

3 relative frequency of flights received by each particular microhabitat. The resulting seed

4 shadow was therefore a complex result of the interaction between the movement patterns of a

5 suite of bird species differing in microhabitat preferences and the specific landscape

6 distribution of these microhabitat patches. Previous studies have pointed out the relevance of

7 fruiting conspecifics (Herrera and Jordano 1981, Denslow 1987, Hoppes 1987, Hoppes 1988,

8 Murray 1988, Sargent 1990, Izhaki et al. 1991, Sallabanks 1993) in influencing the post-

9 foraging movements of frugivores. We emphasize that beyond the "fruiting environment"

10 surrounding a plant, the overall assortment of physiognomically distinct patches in the

11 surrounding landscape influences the post-foraging movements of frugivores, the landscape

12 pattern of seedfall, and ultimately the quality of dispersal performed by each frugivore

13 species.

14 From a plant's perspective, a seed shadow is an array of survival probabilities for the

15 seeds produced in a reproductive event. For animal-dispersed species this array is directly

16 determined, assuming no secondary dispersal, by the activity patterns of frugivores. The

17 continuous array of survival probabilities is generated by the interaction of microhabitat

18 preferences of the frugivores while foraging with the suitabilities of these microhabitat

19 patches for germination, seedling emergence and establishment, and survival and growth to

20 adulthood. Critical characteristics of the seed shadow generated by a particular frugivore

21 species are the total amount of seed dispersed, the distribution of these seeds among patches

22 that differ in suitability for establishment, and the distribution of distances from maternal

23 plants. By combining detailed observations of habitat use by the birds with extensive sampling

24 of seed rain density we were able to assess these components of the P. mahaleb seed shadow.

25 Distance effects are important in seed dispersal not only because they influence aspects

26 like the colonizing ability (Willson 1993), but because survival and growth of propagules

1 (seeds or seedlings) frequently depend on distance to conspecifics and/or density effects

2 (Clark and Clark 1984, Howe et al. 1985, Webb and Willson 1985, Schupp 1988, Fleming and

3 Williams 1990, Willson and Whelan 1990, Willson 1992). For P. mahaleb, density of

4 dispersed seed increased in the vicinity of Prunus trees, although it was unrelated to tree size

5 or fruit crop size, at least within the range of tree sizes considered (> 10 cm dbh, large enough

6 to exceed 1000 fruits). The distance effect was due to the fact that most exit flights were to

7 short distances (< 15 m, and in most cases, < 5 m). The strong preferences of bird species for

8 particular microhabitats was, however, the major cause of the highly spatially-heterogeneous

9 seed shadow. In particular, microhabitats with woody cover, representing only about 33 % of

10 the total cover, received nearly 86 % of total exit flights and 96 % of total seed rain. Combined

11 with the significant distance effect, this suggests a seed shadow concentrated beneath woody

12 vegetation in the neigborhood of adult Prunus trees. This seems to be a general pattern in

13 Mediterranean and Central European forest and scrubland, where similar patterns have been

14 reported previously (Debussche et al. 1985, Izhaki et al. 1991, Herrera et al. 1994, Kollmann

15 and Pirl 1995, Kollmann and Schneider 1996, Verdú 1996, Kollmann and Poschlod 1997). It

16 is noteworthy, however, that the activity, flight, and seed delivery patterns of the two main P.

17 mahaleb seed dispersers, T. viscivorus and Ph. ochruros, depart markedly from this dominant

18 pattern. The former frequently fly long distances after feeding while the latter intensively use

19 rock outcrops.

20   Our results suggest that in many cases it is important to consider not only dispersal

21 distance, but also the resulting distance from dispersed seeds to nearest conspecific trees.

22 Although dispersal distances influence genetic structure of the population, distance to a

23 conspecific is likely a better determinant of seed and seedling fate. In this study, birds tended

24 to perch close to another Prunus, irrespective of distance flown, a tendency related to bird

25 preference for covered microhabitats and the frequent presence of Prunus trees in these types

26 of patches. Mack (1995) has also addressed this important distinction. In our study system it is

1 clear that different <u>Prunus</u> trees not only differ in seed dispersal success, but also in their role

2 in attracting the seedfall from other conspecifics.

3   Differences among microhabitat types in the density of dispersed seeds were large, as

4 expected based on previously documented responses of avian frugivores to habitat

5 heterogeneity (Bairlein 1981, Herrera and Jordano 1981, Willson <u>et al</u>. 1982, Martin and Karr

6 1986, Katusic-Malmborg and Willson 1988, Blake and Loiselle 1991, Izhaki <u>et al</u>. 1991,

7 Loiselle and Blake 1993, Kollmann and Pirl 1995). Our study is one of the few to demonstrate

8 that not only do frugivorous birds use particular microhabitat types far more or less frequently

9 than expected based on their relative availability (e.g., Herrera and Jordano 1981), but also

10 that different species use different combinations of microhabitat types (see also Izhaki <u>et al</u>.

11 1991). Therefore, the bird-generated seed shadow for <u>P. mahaleb</u> is extremely non-random,

12 due to both a strong overall preference by most of the birds for the relatively scarce covered

13 microhabitats, and to species-specific preferences for particular types of covered

14 microhabitats. Different microhabitat types not only received variable amounts of dispersed

15 seed, but also differed in the number and identity of disperser species contributing to that seed

16 rain. Consequently, year-to-year and site-to-site differences in the avian frugivore community

17 will lead to potentially large differences not only in the number of seeds dispersed, but also in

18 the microhabitat distribution of the seed shadow. If microhabitats differ in the suitability to

19 <u>Prunus</u> recruitment, different disperser assemblages may have very different effects on plant

20 recruitment independent of the quantity of seed dipsersed.

21   Differential habitat use by avian frugivores during the post-foraging movements has

22 been reported previously (Herrera and Jordano 1981, Willson <u>et al</u>. 1982, Hoppes 1987,

23 Katusic-Malmborg and Willson 1988, Izhaki <u>et al</u>. 1991, Wenny and Levey 1998), although it

24 has been related generally to distinct dichotomous habitat types (understory vs. canopy, gap

25 vs. forested habitat, etc.). No broad generalizations can be made as to the effect of woody

26 plant cover on density of dispersed seed, as the type of habitat preference is extremely site

1 (bird species) specific. Thus, covered sites received greater P. mahaleb seed input than open

2 places, yet Hoppes (1987) reported the lowest seedfall in forest interior (also see Katusic-

3 Malmborg and Willson 1988). Moreover, some species with a relatively broad range of

4 microhabitat use in this study (e.g., blackbirds) have been reported to use a narrower range of

5 microhabitats in other Mediterranean shrublands (Izhaki et al. 1991). At least for

6 Mediterranean high-elevation sites (and probably for mountain xeric habitats with an

7 important component of open ground), an important distinction among the frugivorous birds is

8 between those that forage in relatively dense shrubby cover (e.g., Sylvia, T. merula, Parus

9 spp.) and those that also forage frequently in open sites like rocky places and grassy ground

10 (Phoenicurus spp., T. viscivorus).

11   An additional marked difference between covered and open microhabitats is that they

12 differed greatly in the number of disperser species that contributed to the seed rain. Covered

13 patches received seed delivered by 7-11 bird species, while the seeds arriving in open patches

14 were contributed by only 1-2 species (Phoenicurus spp. and T. viscivorus). Even within

15 covered or open microhabitats differences in which species deliver seeds were marked. Pine

16 sites, for example, were chiefly selected by T. viscivorus and only rarely received flights by

17 other dispersers. It is worth noting that the two pine-covered microhabitats concentrated a

18 sizeable fraction of the P. mahaleb seed shadow despite being avoided by most dispersers

19 because T. viscivorus, disperse far more seeds than any other species in the frugivore

20 assemblage. The situation for the rock microhabitat is similar, with Phoenicurus spp.

21 contributing most of the dispersed seed.

22   A strong potential for genetic or other (e.g., competitive) consequences due to this

23 heterogeneous pattern of seed delivery can be envisioned (see, e.g., Loiselle et al. 1995,

24 Alvarez-Buylla et al. 1996, Bruederle et al. 1998). For example, if neighborhood effects (e.g.,

25 effects of distance to potential parent trees) are controlled for, we may expect greater genetic

26 heterogeneity among the seed propagules in a microhabitat where the seedfall is contributed

1   by a greater number (both individuals and species) of avian frugivores (we are advancing

2   preliminary genetic analyses in this direction; P. Jordano, pers. obs.). A successful

3   combination of careful observations of habitat use by the birds, demographic methods to

4   characterize the seed and seedling shadows, and molecular techniques is thus required to

5   understand these far-reaching consequences of frugivore activity for seed dispersal.

6

7   Implications and perspectives

8   The main differences among frugivore species that visit and disperse a plant are the

9   frequency of visitation, the rate of fruit handling and ingestion, and the species-specific flight

10   patterns and post-foraging patterns of habitat use. However, even detailed knowledge of these

11   characteristics is insufficient to adequately assess disperser effectiveness. Quality components

12   are strongly dependent on differences among patches in seed survival, germination, and

13   seedling survival and growth. The potential thus exists for the sequence of concatenated

14   postdispersal events (Herrera et al. 1994, Jordano and Herrera 1995, Schupp 1995, Schupp and

15   Fuentes 1995) to erase any initial differences imposed by variations in the quantity component

16   of effectiveness.

17   Nonetheless, a thorough analysis of the quantity component of disperser effectiveness

18   is a critical first step in understanding the intricacies of any dispersal system. In this study, the

19   quantity component suggests a clear initial difference in importance for dispersal among the

20   major frugivore functional groups, SD, PCSD, and PC. Because these are rather broad

21   categories of frugivory types (i.e., the "gulper-masher" continuum), we may generalize that an

22   initial categorization of species in a frugivore assemblage may best be achieved by only

23   quantifying aspects of fruit removal and handling and of visitation. For example, in our system

24   SD species were consistently more efficient than PCSD species, but even an inefficient PCSD

25   species with a high frequency of visitation might show a greater quantitative effectiveness

26   than a scarce SD visitor. An important conclusion of this study is that due to behavioral

1 differences, considerable variation in the quantity component also exists within the apparently

2 homogeneous group of legitimate seed dispersers (SD). The quantity component of dispersal,

3 then, is determined by feeding and fruit handling behaviors, which are largely species-specific

4 characteristics, and by visitation rate, which is partly a species-specific trait and partly a

5 function of species abundance.

6 Although an analysis of the quantity component is a critical and valuable first step

7 towards understanding disperser effectiveness, assuming that effectiveness can be measured

8 by quantity alone can mislead more than inform (Schupp 1993). Just as a high visitation rate

9 may compensate for low dispersal efficiency. Even small differences in quality of seed

10 deposition might compensate for an initial quantitative difference among SD species. In this

11 study, the large differences among species in microhabitat patterns of seed dispersal my

12 present such a case. Previous detailed studies, either implicitly or explicitly analyzing both

13 quantitative and qualitative components of seed dispersal systems have dealt with parasitc

14 mistletoes (Reid 1989, Martínez del Río et al. 1995, Larson 1996, Martínez del Río et al.

15 1996). Given that highly directed dispersal is required for successful mistletoe establishment,

16 subtle differences in quality of treatment by the disperser have impacts on seedling

17 establishment (Murphy et al. 1993). Although not specifically aimed at assessing disperser

18 effectiveness, studies of non-parasitic trees and shrubs with more complex dispersal systems

19 (Howe et al. 1985, Schupp et al. 1989, Howe 1990, Chávez-Ramírez and Slack 1994, Guitián

20 et al. 1994, Herrera et al. 1994, Jordano and Herrera 1995, Martínez-Ramos and Alvarez-

21 Buylla 1995, Wenny and Levey 1998; see review in Schupp 1993), suggest that microhabitat-

22 specific suitabilities for seed germination, survival, and seedling emergence and establishment

23 are so large that differences among frugivores in the quality of deposition might generally

24 have critical consequences for the final pattern of recruitment.

25

26

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Appendix 1. Relative abundances and feeding records of frugivorous birds visiting <u>Prunus mahaleb</u> trees in the two study years.

Species	Frugivory type*	1988		1989	
		Abundance†	Records‡	Abundance†	Records‡
<u>Columba palumbus</u>	SD	0.2 ± 0.2 (0.2)	2 (0.1)	0.7 ± 0.5 (0.6)	5 (0.6)
<u>Corvus corone</u>	SD	0	0	1.3 ± 0.5 (1.2)	3 (0.3)
<u>Dendrocopos major</u>	SD	0	4 (0.2)	4.0 ± 0.3 (0.2)	0
<u>Erithacus rubecula</u>	SD	5.5 ± 1.2 (4.3)	140 (7.2)	6.6 ± 0.9 (5.9)	64 (7.0)
<u>Ficedula hypoleuca</u>	SD	0.2 ± 0.2 (0.2)	0	0.2 ± 0.2 (0.1)	0
<u>Muscicapa striata</u>	SD	0	0	0.2 ± 0.2 (0.1)	0
<u>Phoenicurus ochruros</u>	SD	24.3 ± 7.2 (19.3)	417 (21.5)	21.3 ± 2 (19.9)	192 (21.0)
<u>Phoenicurus phoenicurus</u>	SD	1.7 ± 0.9 (1.2)	18 (0.9)	5.3 ± 0.6 (4.9)	52 (5.7)
<u>Sylvia atricapilla</u>	SD	2.0 ± 0.7 (1.6)	19 (1.0)	1.2 ± 0.5 (1.3)	15 (1.6)
<u>Sylvia borin</u>	SD	0	6 (0.3)	0.4 ± 0.2 (0.3)	3 (0.3)
<u>Sylvia cantillans</u>	SD	1.2 ± 0.5 (0.9)	27 (1.4)	0.6 ± 0.3 (0.6)	33 (3.6)
<u>Sylvia communis</u>	SD	7.0 ± 1.8 (5.5)	85 (4.4)	8.4 ± 1.6 (8.0)	65 (7.1)
<u>Sylvia conspicillata</u>	SD	0.2 ± 0.2 (0.2)	2 (0.1)	0	0
<u>Sylvia melanocephala</u>	SD	1.1 ± 0.4 (0.9)	8 (0.4)	1.4 ± 0.5 (1.2)	9 (1.0)
<u>Turdus merula</u>	SD	11.2 ± 3 (8.4)	150 (7.7)	9.0 ± 1.6 (8.2)	79 (8.7)
<u>Turdus viscivorus</u>	SD	10.4 ± 3 (8.0)	380 (19.6)	14.6 ± 5.3 (13.8)	105 (11.5)
<u>Garrulus glandarius</u>	PCSD	0.8 ± 0.7 (0.5)	31 (1.6)	3.6 ± 0.8 (3.4)	37 (4.1)
<u>Parus ater</u>	PCSD	6.5 ± 1.1 (4.6)	119 (6.1)	5.2 ± 0.9 (6.2)	94 (10.3)
<u>Sitta europaea</u>	PCSD	1.1 ± 0.6 (0.7)	14 (0.7)	1.4 ± 0.4 (1.2)	14 (1.5)
<u>Fringilla coelebs</u>	PC	37.8 ± 9.7 (30.2)	477 (24.6)	10.9 ± 2.8 (11.0)	71 (7.8)
<u>Parus caeruleus</u>	PC	1.1 ± 0.6 (0.9)	27 (1.4)	2.0 ± 0.4 (1.8)	60 (6.6)
<u>Parus cristatus</u>	PC	0.6 ± 0.4 (0.5)	11 (0.6)	0.5 ± 0.3 (0.5)	4 (0.4)
<u>Parus major</u>	PC	0.9 ± 0.6 (0.7)	4 (0.2)	0.5 ± 0.3 (0.5)	6 (0.7)
<u>Serinus citrinella</u>	PC	0.5 ± 0.5 (0.4)	0	0.3 ± 0.3 (0.3)	1 (0.1)
<u>Serinus serinus</u>	PC	0	0	0.2 ± 0.2 (0.1)	1 (0.1)

* SD, seed disperser; PC, pulp consumer; PCSD, pulp consumer–seed disperser.

† Number of birds censused/km; mean ± 1 se, and percentage of total birds censused.

‡ Number of feeding records, and percentage of to the annual total for all species combined.

Appendix 2. Fate of fruits and seeds consumed by frugivorous birds visiting Prunus mahaleb trees. Data from 1988 and 1989 combined.

Species	N	Fruit and seed handling *				Fruit picking †		Seed delivery ¶	
		Swallowed	Carried	Failed	Dropped	Pecked	Picked	Away	Beneath
Columba palumbus	7	100.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Dendrocopos major	4	95.8±4.2	0.0	4.2±4.2	0.0	0.0	0.0	95.8±4.2	0.0
Erithacus rubecula	13	100.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Fringilla coelebs	51	0.0	0.4±0.4	0.0	0.0	45.5±6.3	53.7±6.2	0.4±0.4	99.2±0.8
Garrulus glandarius	32	6.8±4.2	7.0±4.4	0.3±0.3	0.3±0.3	0.0	85.9±5.9	13.9±5.8	86.1±5.8
Parus ater	18	0.0	14.4±7.7	8.3±6.1	0.0	9.4±6.1	76.2±8.9	14.4±7.7	85.6±7.7
Parus caeruleus	12	0.0	0.0	0.0	0.0	16.7±11.2	83.3±11.2	0.0	100.0
Parus major	5	0.0	0.0	0.0	0.0	0.0	100.0	0.0	100.0
Phoenicurus ochruros	45	88.9±3.7	0.0	15.6±4.3	6.7±2.7	0.0	0.0	88.9±3.7	6.7±2.7
Phoenicurus phoenicurus	12	97.2±2.8	0.0	5.6±3.7	2.8±2.8	0.0	0.0	97.2±2.8	2.8±2.8
Sitta europaea	6	4.2±4.2	55.6±20.5	0.0	0.0	0.0	40.3±18.6	59.7±18.6	40.3±18.6
Sylvia cantillans	9	72.8±11.0	0.0	27.2±11.0	27.2±11.0	0.0	0.0	72.8±11.0	27.2±11.0
Sylvia communis	36	84.8±3.8	0.0	15.2±3.8	15.2±3.8	0.0	0.0	84.8±3.8	15.2±3.8
Sylvia melanocephala	3	83.3±16.7	0.0	16.7±16.7	16.7±16.7	0.0	0.0	83.3±16.7	16.7±16.7
Turdus merula	15	92.9±3.8	3.3±3.3	5.5±2.3	1.9±1.3	0.0	0.0	96.2±2.2	1.9±1.3
Turdus viscivorus	56	99.9±0.1	0.0	0.1±0.1	0.1±0.1	0.0	0.0	99.9±0.1	0.1±0.1

Entries are percentages, Mean ± 1 se, of the fruits 'touched' during visits.

* Percentage of fruits swallowed, carried away from the tree in the bill, failed to detach from peduncles, and dropped.

† Method of fruit handling by non-legitimate seed dispersers (legitimate dispersers pluck all fruits). Pecking, biting pulp pieces without detaching the fruits from peduncles. Picking, pluck fruits and drop them after tearing off pulp pieces.

¶ Percentages of seeds estimated to leave the tree after feeding bouts, or fall beneath the tree.

1

1

2

3 <u>Table</u> 1. Fruiting intensity and estimated number and percentages of fruit removed and seed

4 dispersed for <u>Prunus</u> <u>mahaleb</u> trees in two study years.

5 _____

	Year	
	1988	1989
Number of flowers[*]	18048 [1548-57768]	15166 [1721-149000]
Number of fruits[*]	7565 [3275-9992]	1935 [1150-3707]
Number of fruits removed[*§]	4657 [2228-7092]	2396 [1023-3433]
% fruits removed[†§]	74.97 ± 2.45	80.59 ± 2.56
Number of seeds dispersed from tree[*¶]	2664 [1791-6237]	1894 [790-2850]
% seeds dispersed[†¶]	50.39 ± 5.17	67.82 ± 3.71

21 $\underline{N}$ = 21 trees.

22 [*] Median [25-75 % quantiles] $\underline{N}$ = 21 trees.

23 [†] Mean ± 1 SE ($\underline{N}$ = 21).

24 [§] Refers to overall fruit consumption and removal by legitimate (SD) and non-legitimate

25 (PC, PCSD and SP) seed dispersers.

26 [¶] Refers to fruit consumption and removal by legitimate (SD) seed dispersers only.

Table 2. Variance in two components of seed dispersal success, the absolute number of seeds dispersed away from the canopy and the percentage relative to initial fruit crop size, of Prunus mahaleb trees explained by number of fruits produced, fruit loss due to desiccation and consumption by non-legitimate seed dispersers (PC, PCSD, and SP frugivores that eat fruit but do not disperse seeds), and fruit size.

Seed dispersal component	Fruit crop size	% fruits desiccated	% fruits consumed by non-legitimate seed dispersers	Fruit diameter
1988 - Increase in R^2				
Number of seeds dispersed from tree	82.4**	1.6 NS	13.1*	0.5 NS
% seeds dispersed	0.7 NS	10.9*	83.0**	1.1 NS
1989 - Increase in R^2				
Number of seeds dispersed from tree	95.3**	1.2 NS	2.0 NS	0.8 NS
% seeds dispersed	1.3 NS	36.5*	35.1**	4.2 NS

Figures are the percent variance in the two components of seed dispersal success explained by the four independent variables in a multiple-regression analysis, and its significance, estimated by randomization ($\underline{N}$ = 5000 resamplings; Manly 1991, p. 96).

** $\underline{P}$ = 0.001; * $\underline{P}$ < 0.05; NS non-significant, 0.05 < $\underline{P}$ < 0.1. Significance values for the extra sum of squares accounted for by each variable with the remaining variables already in the model.

1

Table 4. Summary of main variables associated with the quantity component of Prunus mahaleb seed dispersal by frugivorous birds.

Species	Frugivory type	Abundance[*]	Diet[¹]	Visit rate[²]	No. fruits handled per visit	Probability dispersing a handled seed	Quantity component
Columba palumbus	SD	0.45	·	0.01	22.4	1.000	0.20
Dendrocopos major	SD	2.00	·	0.25	5.0	1.000	1.12
Erithacus rubecula	SD	6.05	····	3.50	1.9	1.000	6.99
Ficedula hypoleuca	SD	0.20	·	+	1.0	1.000	0.05
Muscicapa striata	SD	0.10	·	+	1.0	1.000	0.05
Phoenicurus ochruros	SD	22.80	····	10.85	1.8	0.872	17.45
Phoenicurus phoenicurus	SD	3.50	····	1.47	2.4	0.964	3.31
Sylvia atricapilla	SD	1.60	···	0.64	…	0.950	1.70
Sylvia borin	SD	0.20	··	0.11	4.0	1.000	0.45
Sylvia cantillans	SD	0.90	···	0.67	2.9	0.536	1.01
Sylvia communis	SD	7.70	····	2.63	2.8	0.814	6.06
Sylvia conspicillata	SD	0.10	··	+	…	0.182	0.03
Sylvia melanocephala	SD	1.25	··	+	1.5	0.750	0.05
Turdus merula	SD	10.10	···	2.82	6.5	0.979	17.65
Turdus viscivorus	SD	12.50	···	9.23	9.7	0.998	83.19
Garrulus glandarius	PCSD	2.20	··	1.76	6.9	0.139	1.32
Parus ater	PCSD	5.85	···	4.67	1.9	0.111	1.04
Sitta europaea	PCSD	1.25	·	0.48	2.5	0.400	0.48
Fringilla coelebs	PC	24.30	··	16.72	3.4	0.060	3.30
Parus caeruleus	PC	1.55	·	2.51	2.1	0.000	0.00
Parus cristatus	PC	0.55	·	0.24	2.0	0.000	0.00
Parus major	PC	0.70	·	0.65	2.0	0.000	0.00
Serinus citrinella	PC	0.40	·	+	6.5	0.000	0.00
Serinus serinus	PC	0.10	·	+	3.0	0.000	0.00

[*] Average number of birds censused/km, 1988 and 1989 data pooled.

[¹] Relative degree of reliance of P. mahaleb fruit for food (scored from extensive reliance, ····, to sporadic consumption, · (Obeso 1987a,

1987b; P. Jordano, unpubl. observ.).

[²] Average number of visits/10 h, 1988 and 1989 data pooled; +, <0.01 visits/10 h.

[³] Average proportion of the seeds handled per visit that are removed from the parent tree.

Table 5. Effects of habitat characteristics surrounding the seed traps on seed rain density of
Prunus mahaleb (number of seeds m^{-2}, log-transformed) in 1988 and 1989. For each year,
results are given for the general linear model (GLM, F values and significance) incorporating
the effect of microhabitat type and five quantitative variables describing the habitat
surrounding each replicate set of traps, as well as those from a multiple regression (MR;
randomization test) analysis of the quantitative variables (parameter estimate, ß and
significance). The traps located beneath Prunus were excluded from the multiple regression
analysis (distance to nearest Prunus = 0 m, by definition).

		1988		1989	
	df	GLM	MR (ß[†])	GLM	MR (ß[†])
Microhabitat type	8	31.92*	...	22.25*	...
Distance to nearest Prunus	1	2.38 [NS]	-0.047 [NS]	7.21*	-0.059**
BSD of nearest Prunus	1	8.88*	0.003 [NS]	6.50*	0.002 [NS]
Distance to nearest shrub vegetation cover	1	1.27 [NS]	-0.064 *	0.35 [NS]	-0.057 *
Number of Prunus trees within 10 m	1	0.02 [NS]	-0.026 [NS]	2.28 [NS]	-0.042 [NS]
Fruit crop size of Prunus trees within 10 m	1	0.12 [NS]	0.18E-5 [NS]	0.05 [NS]	0.72E-6 [NS]

†, coefficient estimate (ß), and significance value, obtained by randomization, for the extra
sums of squares accounted for by each variable with the remaining variables already in the
model (Manly 1991). * P < 0.01; [NS], not significant.

1   FIGURE LEGENDS

2

3   Figure 1. Product-limit estimates of the survivorship functions describing visitation by

4   frugivorous birds to individual <u>Prunus</u> <u>mahaleb</u> trees in 1988 (A) and 1989 (B). Individual

5   trees are labeled with numerals. The curves depict, for each tree, the decaying probability

6   that a tree will remain unvisited (steeper curves illustrate trees with more visitation).

7   Plotted on the abcissa is the time elapsed since the start of an observation period.

8

9   Figure 2. Feeding rates of main bird species visiting <u>Prunus</u> <u>mahaleb</u> trees. Foraging rates

10   are illustrated as "saw-tooth" curves for each species-specific feeding behavior. The usual

11   feeding sequence includes a series of short bouts separating successive ingestion of fruits.

12   The horizontal projection of each bout ("tooth") is the total time invested per fruit. The

13   horizontal part of the step depicts the time stopped after each fruit ingestion; the ascending

14   portion of the step depicts the time involved in searching and/or handling the fruit. The

15   average feeding rate (in fruits ingested/unit time) is depicted by the slope of the straight

16   line. See Cody (1974, pages 39-41) for further description of this type of graph.

17

18   Figure 3. Residuals of a contingency-table analysis including bird species and microhabitat

19   type. Individual bars depict residual frequencies and their significance, indicating

20   microhabitats favored (positive significant residuals) or avoided (negative significant

21   residuals) by each bird species. Combinations of species and microhabitats without bars

22   indicate lack of use of that particular microhabitat by the bird species. * <u>P</u> < 0.05; ** <u>P</u> <

23   0.01; *** <u>P</u> < 0.0001.

24

25   Figure 4. Box plots of estimated viable <u>Prunus</u> <u>mahaleb</u> seed fall to different microhabitat

26   types in 1988 and 1989. Horizontal lines show the medians, vertical boxes span the first

27   and third quartile range, vertical lines span the 10th - 90th percentile range and crosses

1 depict extreme values. $\underline{N}$ = 135 seed traps or sampling quadrats/year. Median seed fall was

2 6 seeds · m^{-2} (0 - 28 seeds · m^{-2}; 25%-75% quantiles, 1988) and 3 seeds · m^{-2} (0 - 16 seeds ·

3 m^{-2}, 1989).

4

5 Figure 5. Estimated proportion of seed fall to each microhabitat type contributed by the

6 main frugivore species visiting Prunus mahaleb trees. Bars depict the relative contribution

7 of each species to the total seed rain (contributed by all 7 species) in a particular

8 microhabitat. Estimates derived from visitation records, number of fruits handled per visit,

9 and probability of dispersing a handled seed indicate that these 7 species contributed 81.8

10 % of all the seed rain in the two study years.
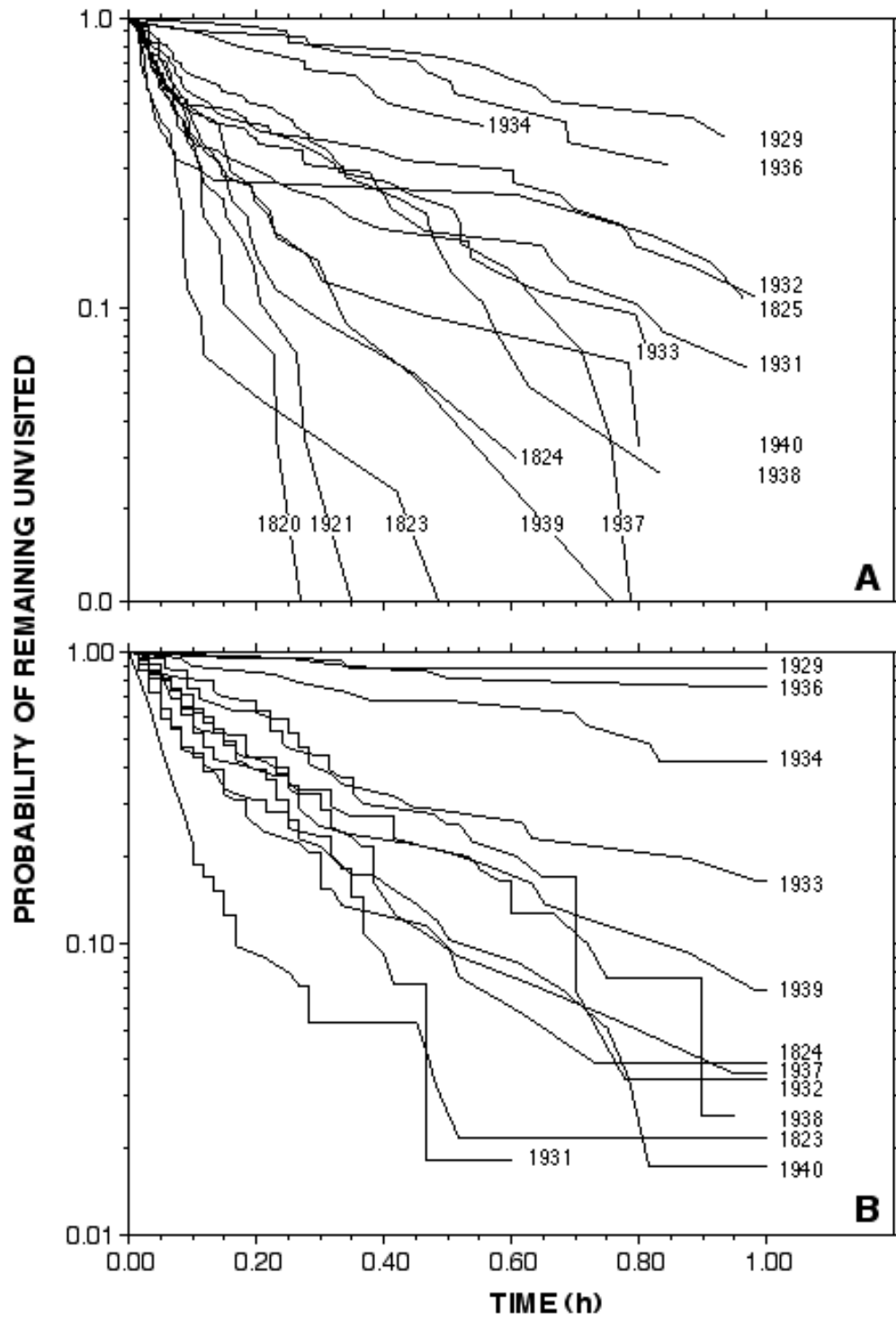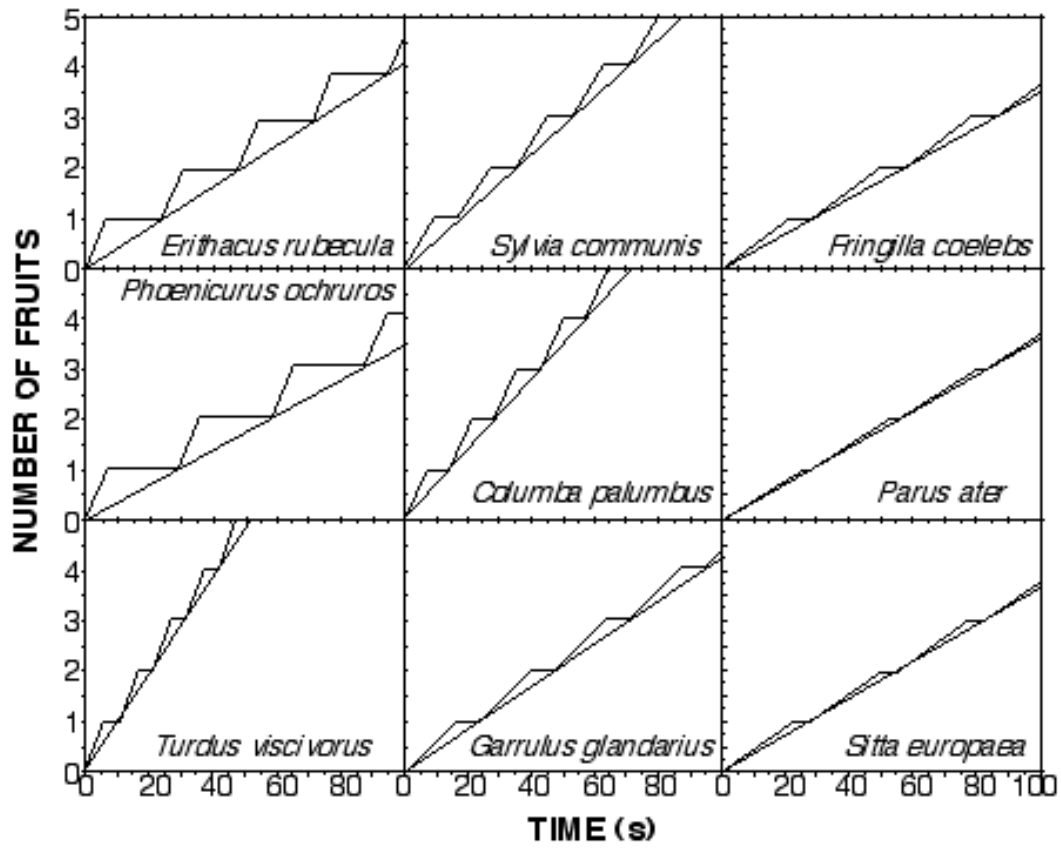
Figure 1
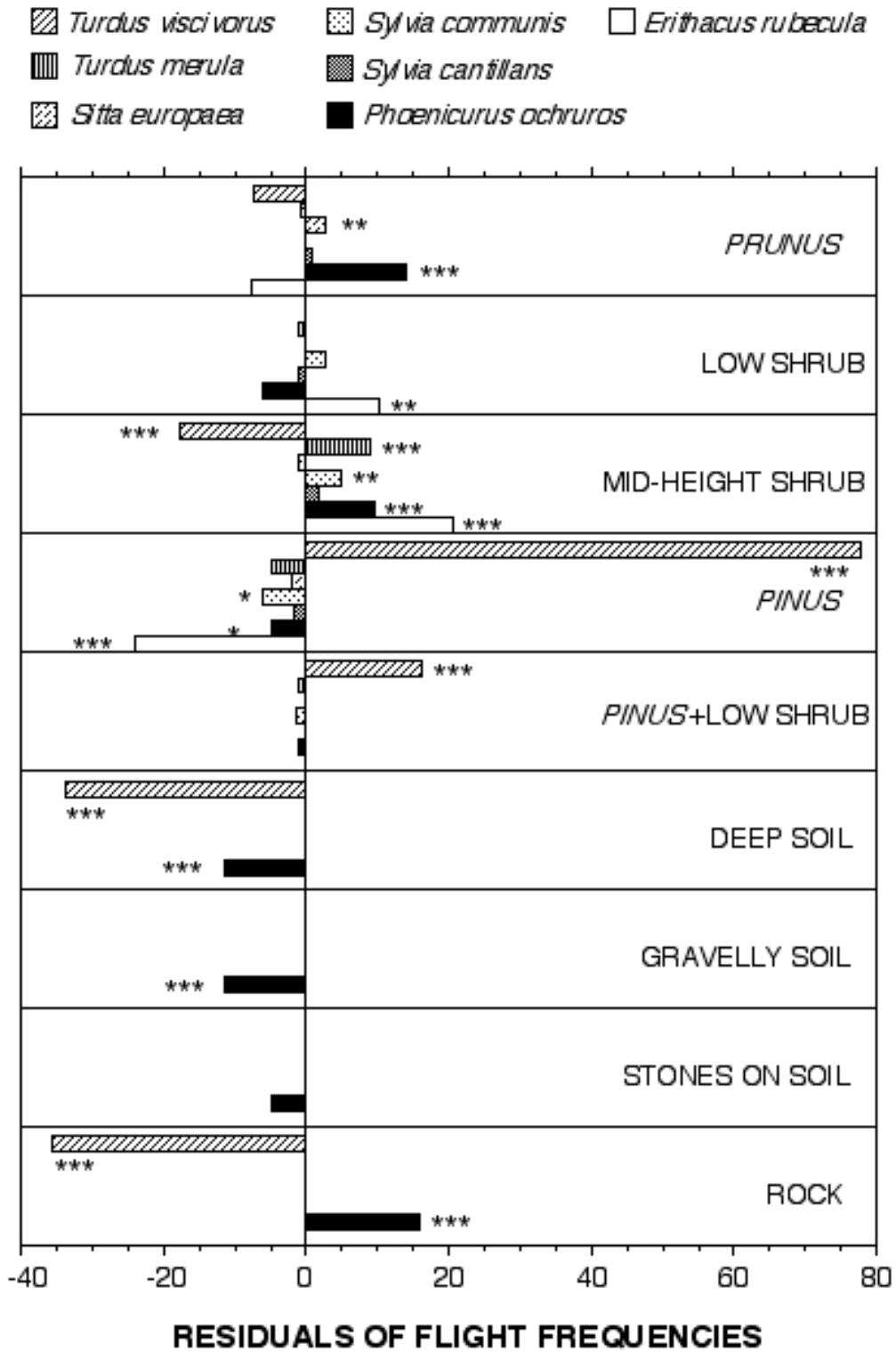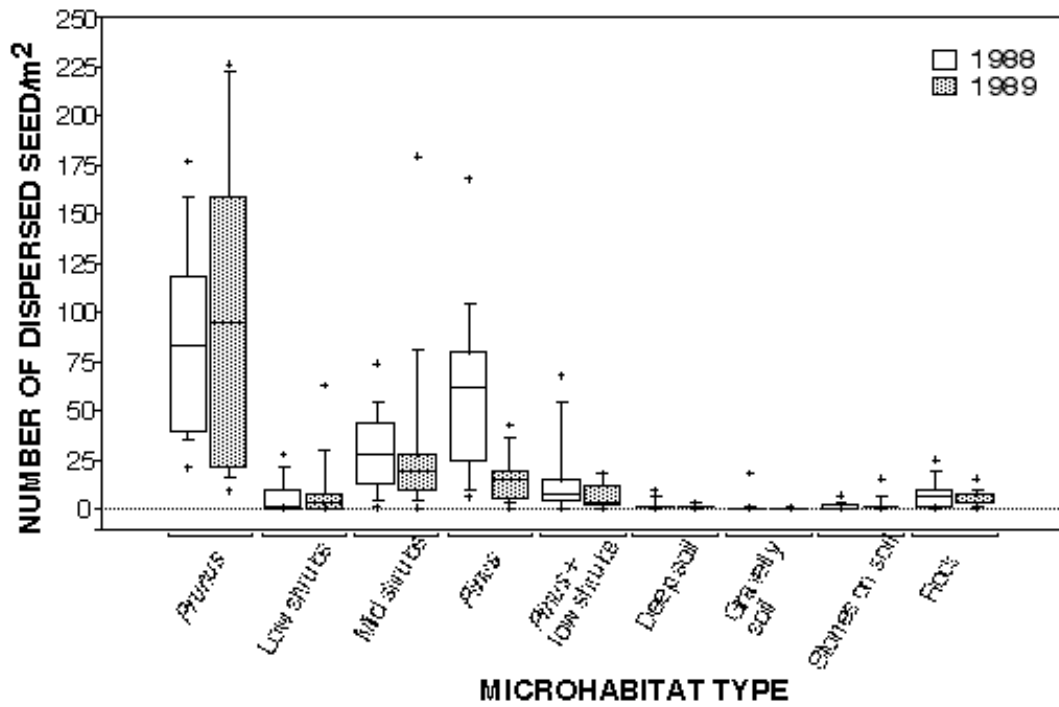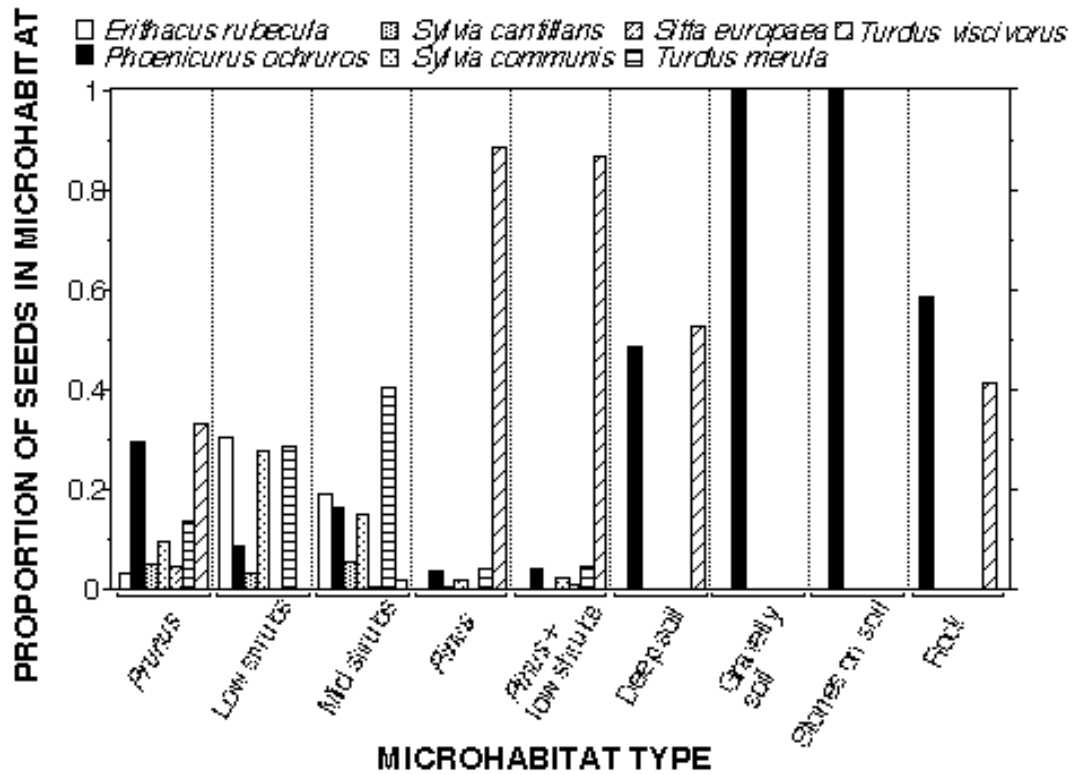Jordano and Schupp

Figure 2
Jordano and Schupp

1

Figure 3
Jordano and Schupp

Figure 4
Jordano and Schupp

1

Figure 5
Jordano and Schupp