DIET, FRUIT CHOICE AND VARIATION IN BODY CONDITION OF FRUGIVOROUS WARBLERS IN MEDITERRANEAN SCRUBLAND

PEDRO JORDANO

Estación Biológica de Doñana, Apdo. 1056, E-41013, Sevilla, Spain

CONTENTS

1. INTRODUCTION

Most dispersal mutualisms between animals and plants depend on the inclusion of plant propagules (seeds, pollen) as a part of the animal food, and result from the animal feeding on the plant (Janzen 1985). A major constraint on the evolution of a tight mutuatistic relationship between animals that gather food and plants that provide this food is that no single plant part produces an adequately balanced set of nutrients for the consumer and, as a consequence, the animal must build up a diverse diet in terms of both plant species and plant parts. The consequences of these nutritional constraints for the animals involved have been repeatedly documented (*e.g.* Belowski 1978, Westoby 1978, Bergeron & Jodoin 1984, Karasov 1985), and involve, as a generalization, the need to build up a diverse diet including 'minor' components that might be difficult to obtain. This has consequences for the patterns of habitat use, time budget, digestive physiology or body condition.

Frugivorous birds feeding on fleshy fruits experience nutritional constraints quite similar to those

of herbivores feeding on vegetative plant parts (Foster 1978, Moermond & Denslow 1985). The fruit pulp is extremely scarce in protein and, if the amount present is adequate, it is usually imbalanced with other fractions, such as lipids or carbohydrates, resulting an inadequate food even when ingestion rate is not limiting (Foster 1978, Robbins 1983). The need to obtain minor nutrients (minerals, vitamins) and the presence of secondary plant metabolites, acting as digestion inhibitors or poisons, might impose deviations from the predictions derived from energetic models by creating partial preferences (Westoby 1978). Shortage of specific nutrients may result in individual preferences for particular meals, *i.e.*, combinations of food items that better supply the nutritional needs (Rozin & Kalat 1971, Clark 1980). In addition, the seed(s) acts as an indigestible ballast decreasing the profitability of the nutrients within the fruit (Herrera 1981, Levey 1986). Therefore, a short retention time of the ingesta is the most commonly reported characteristic of frugivores. It can be seen as an adaptation to deal with digestive bottlenecks, arising when the caloric demand is fulfilled but the nitrogen or mineral need is not supplemented because food processing is limiting (Sibly 1981).

In this paper I examine in detail the patterns of diet composition in two warbler species, the Blackcap *Sylvia atricapilla* and the Garden Warbler *S. borin*. Both species are insectivorous during the nesting period but can feed the nestlings sporadically with fleshy fruits (Berthold 1976b, Simms 1985). Both warbler species show annual periodicities in food preferences, with spontaneous changes in the amounts of animal and vegetable food ingested. For the Blackcap, an endogenous rhythm of preference for fruit develops in connection with the migratory restlessness, preceding migration, but the fruit diet must be supplemented, as determined for captive birds, with animal food (Berthold 1976a, p. 141). The extreme protein de-

ficiency of the fruit pulp seems to be the major determinant of this nutritional insufficiency but the generalized presence of secondary compounds in the pulp of ripe fruits may also affect the patterns of fruit choice and the degree of dependence on fruit food that can be developed (Herrera 1981). Previous studies of these species in Mediterranean shrublands (Herrera 1984a, 1985a, Jordano 1981, 1987, Jordano & Herrera 1981, Rodríguez et al. 1986, Gardiazábal 1986) indicate that they are strongly frugivorous during the migration and wintering periods. Here, I relate variations in fruit choice at the population level to seasonal and annual variations in the fruit supply and examine the relation between dietary patterns and body condition of the birds. I document intra-population variation in fruit use in the populations studied, the consumption of particular combinations of fruit species (meals) differing in nutronal reward to the birds, and the correlates of these trends for the body condition of the individuals, specially body mass variations and fat accumulation.

2. METHODS

2.1. STUDY SITE

Individuals of the two warbler species were regularly netted during 1981-83 in Hato Ratón, a locality close to Villamanrique de la Condesa, Sevilla province, southern Spain. Ten mist-nets, operated weekly, were located in tall sclerophylous shrubland on sandy soils dominated by Pistacia lentiscus (Anacardiaceae) and Olea europaea var. sylvestris (Oleaceae). At least 21 species of fleshy-fruited shrubs and treelets have been recorded in the area and together they represent 72% of the vegetation cover. Average annual temperature and rainfall at the study site are 18.1 °C and 539 mm, respectively (for detailed descriptions see Jordano 1984, 1985). I made weekly counts of birds along a line transect following the procedures of Emlen (1971) and obtained absolute densities for the two species in the area (Jordano 1985).

2.2. THE FRUIT SUPPLY

Seasonal and between-year variations in the fruit supply were monitored by counting the fruits of every plant species present in fifteen, 1.5 × 15 m plots. Fruit production was thus assessed when fruits were unripe and of final size, prior to the ripening and consumption. Phenological variations were monitored by weekly counts of fruits on tagged branches. Sample sizes varied between species but for most of them I made periodic censuses on a minimum of 1500 fruits (usually > 3000 fruits) on ten plants per species (see Jordano 1984 for details). The fraction of the total fruit crop that was ripe in a given time interval was derived from the counts and, together with the estimates of fruit abundance from plot counts, was used to determine variations in the supply of ripe fruits available to birds. Arthropod availability was sampled by means of sticky traps placed on the ground and suspended from shrub branches (see Jordano 1984, 1985 for additional details).

Data on nutrient content of the pulp and fruit characteristics were obtained from Herrera (1984a, 1987, pers. comm.) and Jordano (1984). Nitrogen content of Ulex minor (Roth.) (Leguminosae) flowers was estimated by micro-Kjeldahl extraction from 9 replicates.

2.3. DIET ANALYSES

Birds captured in mist-nets were kept individually in cloth bags and later measured, weighed to the nearest 0.1 g, ringed and released. The amount of fat in the tracheal pit was scored visually on a 0–4 scale (ranging from no fat visible to bulging). All the bird measurements were made by the author.

Diet samples were obtained either by recovering faeces from the bags or by flushing the digestive tract with 1% sodium chloride water solution (Jordano & Herrera 1981). The observation of birds kept in captivity after this procedure was completed, confirmed that almost all the digestive contents were recovered in the diet sample, including both gizzard and intestinal material (pers. obs.). In addition, processing large number of birds usually delayed the flushing procedure for a given individual 20 min to 1 h after its capture, a time enough to evacuate most gastro-intestinal contents in the bag (see Herrera 1984b, Jordano 1987).

Samples obtained by any of these two methods, or both, were collected on filter paper, dried at ambient temperature and stored for later analysis. A total of 787 samples of the two species were examined. The relative volume of animal and vegetable matter in the sample was visually estimated to the nearest 5%, prior to microscopical examination. I consider here in detail only the plant fraction of the diet (fleshy fruits) and variations of the relative amount of animal prey. The animal fraction of the diet has been described elsewhere for these species (e.g. Jordano 1981, Herrera 1985a, Gardiazábal 1986).

All plant food was identified to species either from the seeds or the fruit skins. This was accomplished by examining the complete samples under a microscope (× 100) and comparing cell shapes, sizes and other traits of the epicarp tissue (presence of stomata, trichomes, etc.) with a reference collection of photomicrographs. Since seeds are processed by the birds faster than pulp (Levey 1986), a serious bias would have been introduced in the analysis had the fruit species been identified by relying only on the seeds present. The whole diet sample was examined, usually by inspecting one or two slides for each sample; use of a sliding stage ensured a complete but unduplicated scanning of the material. The relative volume of the non-seed vegetable fraction made up by each species present was determined visually by estimating the minimum number of fruits of each species present, either from the number of seeds recorded or by estimating the amount of fruit skin remains.

Fruit species appearing in > 10% of the samples, from any given year or bird species, and contributing > 30% of the fruit material, will be referred to, throughout the paper, as 'major'. 'Minor' fruit species are defined as those appearing < 10% in the samples and contributing < 30% volume.

3. RESULTS

3.1. FRUIT SUPPLY AND COMPOSITION OF THE DIET

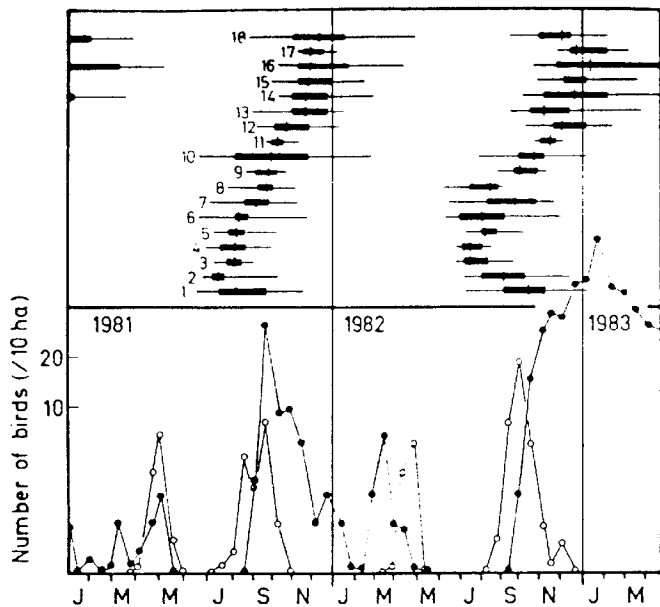The two warbler species are migratory birds

Fig. 1. Phenological sequences of ripe fruit availability for the plant species in the study area. Lines indicate the length of the fruiting period; the thick bar encompasses the period when > 50% of the fruits are ripe and the vertical line marks the date of peak availability. The lower half of the figure shows the seasonal variation of warbler abundance. Dots: Blackcap; open circles: Garden Warbler. Identifications of fruit species: 1, *Daphne gnidium*; 2, *Phillyrea angustifolia*; 3, *Tamus communis*; 4, *Lonicera periclymenum*; 5, *Rubus ulmifolius*; 6. *Rhamnus lycioides*; 7, *Osyris alba*; 8, *Bryonia dioica*; 9. *Chamaerops humilis*; 10, *Smilax aspera*; 11, *Asparagus aphyllus*; 12, *Pyrus bourgaeana*; 13. *Pistacia lentiscus*; 14, *Olea europaea* var. *sylvestris*; 15, *Myrtus communis*; 16, *Ruscus aculeatus*; 17, *Asparagus acutifolius*; 18, *Crataegus monogyna*.

whose local residence periods match the ripening periods of different plant species (Fig. 1). The peak of autumn passage for the Garden Warbler encompasses the fruiting peak of twelve (1981) and ten

species (1982) that ripen fruits before late October. The Blackcap is a fall migrant, also wintering in great numbers in the area. Its peak densities (> 50% of individuals recorded) match the ripening of eight (1981-82) and ten (1982-83) species, mostly maturing their fruits in winter. The rank of fruit species in the ripening sequence was maintained for the two consecutive fruiting seasons ($r_s = 0.933$, $P < 0.01$), this being specially evident for the winter-ripening species (Fig. 1). Fruit production was more variable, the availability of ripe fruits increasing from 376.9×10^3 fruits ha^{-1} in the 1981-82 season to 3457×10^3 fruits ha^{-1} in 1982-83 (Fig. 2, see Jordano 1985). Individual fruit species also showed marked changes in fruit production from one season to the next (see below).

Fruit food averaged above 80% of the diet for the two warbler species, although there are differences between the two study seasons (Table 1). Increased reliance on fruits in 1982 was significant only for Blackcaps and was associated with a significant decrease in fruit diet diversity, as measured by the number of fruit species found in individual samples. Such changes were not recorded for Garden Warblers (Table 1). The more diversified fruit diet of Garden Warblers as compared to Blackcaps (Table 1) was expected from the more diverse supply of fruits that is available in the area from August through October (Figs. 1, 2), relative to the winter fruit supply, dominated by a few species.

I compared the relation between the relative availability of fruit species and their relative consumption by correlating the monthly paired

Table 1. Summary of the composition of the fruit diet of Blackcaps and Garden Warblers. The number of fruit species and the per cent volume made up by fruit remains were averaged over the diet samples examined (in parenthesis). Samples from Blackcaps were collected during the two wintering seasons (September 1981-March 1982 and September 1982-February 1983); those from Garden Warblers, during the autumn migrations (August-October 1981 and 1982).

	1981-82	1982-83	Student's test
Blackcap			
Mean no. spp. per sample[1]	1.9 ± 0.9 (115)	1.4 ± 0.7 (521)	4.35**
No. fruit species consumed	13	12	
% vegetable matter[1]	80.3 ± 25.8 (115)	87.4 ± 18.7 (521)	3.44**
Garden Warbler			
Mean no. spp. per sample[1]	2.2 ± 0.2 (45)	2.5 ± 1.2 (105)	1.95^NS
No. fruit species consumed	9	11	
% vegetable matter[1]	93.2 ± 9.4 (45)	92.3 ± 8.4 (106)	0.62^NS

** $P < 0.001$; ^NS, $0.05 < P < 0.10$; [1] mean ± 1 S.D. (n)

Table 2. Fruit diet of the Blackcap and Garden Warbler in 1981 and 1982. Figures are mean percentage (by volume) of the vegetable fraction of the diet contributed by each fruit species and frequency of appearance (FA: number and percentage of diet samples with remains of each species). Minor fruit species in the diet are denoted by asterisks.

| | Sylvia atricapilla | | | | Sylvia borin | | | |
| | 1981-1982 | | 1982-1983 | | 1981 | | 1982 | |
	Mean	FA	Mean	FA	Mean	FA	Mean	FA
Pistacia lentiscus L.	76.3	98 (85.2)	70.0	462 (88.7)	60.4	32 (71.1)	55.6	99 (93.4)
Olea europaea var. sylvestris Brot.	39.2	43 (37.4)	49.0	120 (23.0)	40.1	3 (6.7)	—	—
Phillyrea angustifolia L.	22.8	2 (1.7)	36.5	71 (13.6)	8.1	6 (13.3)	39.2	61 (57.5)
Rhamnus lycioides L.	36.3	9 (7.8)	20.1	13 (2.5)	51.7	31 (68.9)	31.4	35 (33.0)
Smilax aspera L.*	11.5	20 (17.4)	14.3	9 (1.7)	13.2	6 (13.3)	16.7	7 (6.6)
Rubus ulmifolius Schott	46.1	5 (4.3)	7.3	5 (1.0)	43.2	15 (33.3)	28.3	15 (14.2)
Myrtus communis L.*	27.4	20 (17.4)	15.0	35 (6.7)	—	—	—	—
Daphne gnidium L.	15.7	9 (7.8)	32.4	47 (9.0)	31.5	3 (6.7)	27.3	26 (24.2)
Crataegus monogyna Jacq.*	2.4	7 (6.1)	5.3	1 (0.2)	—	—	—	—
Rubia peregrina L.*	5.3	1 (0.9)	15.1	21 (4.0)	—	—	17.7	18 (16.9)
Osyris alba L.*	—	—	8.4	3 (0.6)	1.7	1 (2.2)	10.2	3 (2.8)
Lonicera periclymenum L.*	80.9	1 (0.9)	—	—	10.0	1 (2.2)	15.0	1 (0.9)
Asparagus acutifolius L.*	26.9	5 (4.3)	17.5	17 (3.3)	—	—	—	—
Asparagus aphyllus L.*	—	—	—	—	—	—	5.3	2 (1.9)
Tamus communis L.*	—	—	—	—	—	—	10.1	2 (1.9)
Pyrus bourgaeana (Decne)*	26.3	4 (3.5)	—	—	—	—	—	—

the significance of these variations, I compared the ranking of each fruit species in the two years. However, to account for the strong seasonal variation in diet, I compared the rankings of fruit species separately for each month (Figs. 2, 3). For the Garden Warbler, all monthly comparisons (August through October) were non-significant (r_s < 0.643, P > 0.10, Fig. 2). The same trend occurred in Blackcaps (r_s < 0.400, P > 0.10), with the exception of the comparisons January 1981-January 1982 (r_s = 0.911, P < 0.01) and February 1981-February 1982 (r_s = 0.786, P < 0.05) (Fig. 3). These annual differences in monthly composition of fruit food might be indicative of bird responses to variations in phenology and fruit abundance observed between the two years (Fig. 1).

A major trend, common to both species, concerns variations in the consumption of the principal food, P. lentiscus (Figs. 2, 3). In 1981, a year with low availability of ripe fruits of this species, R. lycioides was not substituted as the top diet species for Garden Warblers until October, when its supply decreased below 10^3 (Fig. 2). For Blackcaps, a shift to O. europaea var. sylvestris in Jan-

uary and February 1982 marked the decrease in availability of P. lenticus by late winter (Fig. 3). In contrast, P. lentiscus was the principal fruit food in 1982 for both warblers, appearing in more than 80% of the samples (Table 2) and being the top species in the diet from August throughout January. This trend paralleled the seasonal variation in its fruit supply, dominated from September to February by this species.

In the case of Garden Warblers, consumption of two major species (R. lycioides and P. angustifolia) showed great between-year variation (Table 2), reflecting their variation in fruit production (Fig. 2). Most P. angustifolia individuals failed to set fruit in 1981, but did heavily in 1982, resulting in a 98.8% increase in fruit production. A similar trend occurred for Blackcaps with reference to P. lentiscus and O. europaea var. sylvestris (Fig. 3).

Changes in the importance of the minor fruit species in the diet of the two warblers also reflected variations in availability. This was particularly evident for T. communis, A. aphyllus and R. peregrina, that dit not fruit at all or had low fruiting in 1981 and were not consumed by Garden

for plant species with increasingly larger fruits, this effect being significant while holding all other variables constant (Table 3).

The four top species in the diet of the two warblers (*P. lentiscus*, *O. europaea* var. *sylvestris*, *P. angustifolia* and *R. lycioides*) have by far the largest fruit crops in the area (Figs. 2 and 3) but are also characterized by other traits that might explain their high consumption levels. Both *P. lentiscus* and *O. europaea* var. *sylvestris* have the highest lipid content (> 40%); and both *P. angustifolia* and *R. lycioides* have the highest concentration of soluble carbohydrates (> 91%); also, these four species have the highest value of dry pulp weight per fruit (relative yield > 21%). The remaining species appear in a small fraction of the samples or in low volume proportions. These minor species are rare and, consequently, have low availability of fruits per unit area (Figs. 2, 3); with respect to fruit characteristics, they have lipid content < 5%, soluble carbohydrates > 75% and relative yield of pulp < 15%. A result is that the net caloric value of their pulps (kcal g^{-1} dry mass of pulp) is, on average, lower than for the major

species (U = 6, P = 0.006, Mann-Whitney U-test) and the same occurs for the protein content (U = 11, P = 0.03). However, as a group, the most striking difference with the major fruit species is in mineral content (ash), 6.16% versus 2.18%, on average, respectively (U = 4.5, P = 0.004).

Several types of plant secondary metabolites have been recorded in the pulp of ripe fruits consumed by Blackcaps and Garden Warblers namely, tannins, alkaloids, resins, volatile compounds, glycosides and saponins, among others (Table 4). Of them, only alkaloids are more frequently present among minor species (75% of the species with alkaloids present; P = 0.0093, Fisher exact probability test). Tannins are frequently recorded in the major species (67%, only 37% among the minor species but the difference is not significant, P = 0.2961). These differences might also account for the fact that minor species with important concentrations of secondary metabolites in the pulp (*e.g. R. peregrina*, *O. alba*, *T. communis*, *Asparagus* spp., *S. aspera*) are consistently recorded in low quantities in the samples (Table 2).

Table 4. Major types of secondary compounds (potentially acting as digestive inhibitors or poisons) present in the pulp of ripe fruits consumed by Blackcaps and Garden Warblers in the study area. Major fruit species are those present in more than 10% of the samples examined and contributing more than 30% volume to the frugivorous diet. Minor species are those consumed more sporadically (see Table 2 and text). References: Kear (1968), Sherburne (1972), Altmann (1980), Font Quer (1981), Herrera (1981, 1982) and Sorensen (1981).

Species	Compounds	Fruit part	Category of fruit species
Pistacia lentiscus	Tannins. Terpenes and sesquiterpenes	All present in the pulp	Major
Olea europaea var. *sylvestris*	Tannins. Oleuropreine (glucosid) Citric, malic and oxalic acids	All present in the pulp	Major
Phillyrea angustifolia	Tannins	Pulp	Major
Rhamnus lycioides	Glucosids (cyanoglucosids) Anthrones. Saponins. Rhamnoxantine	Pulp and seeds	Major
Smilax aspera	Saponins. Alkaloids	Pulp	Minor
Crataegus monogyna	Flavones. Lactones	Whole fruit	Minor
Rubus ulmifolius	Tannins. Citric, lactic and oxalic acids	All present in the pulp	Major
Myrtus communis	Tannins. Terpenes. Resins and esences Malic and citric acids	All present in the pulp	Minor
Daphne gnidium	Resins. Dafnine (glucosid)	Pulp	Major
Rubia peregrina	Glucosids	Pulp	Minor
Tamus communis	Alkaloids. Pectine. Oxalate crystals	All present in the pulp	Minor
Lonicera periclymenum	Tannins	Pulp	Minor
Asparagus spp.	Asparagine (alkaloid) Glucosids. Saponins	All present in the pulp	Minor

Table 5. Major combinations of fruit species present in individual diet samples of Blackcap and Garden Warblers. For each fruit species (columns), presence in each combination is denoted by 1 and absence by 0. The percentage of samples including each combination of fruit species is shown for the two study seasons, as well as the figure expected according to a Monte Carlo simulation of random assortment of fruit species in meals (see text). Only fruit combinations present in ≥ 2% of the samples from any year are shown, sorted by increasing number of species per combination.

Abbreviations: PL = *Pistacia lentiscus*, OE = *Olea europaea* var. *sylvestris*, PA = *Phillyrea angustifolia*, SA = *Smilax aspera*, MC = *Myrtus communis*, DG = *Daphne gnidium*, RL = *Rhamnus lycioides*, RU = *Rubus ulmifolius*, OT = other species (see Table 2). + combination present in less than 2% of the samples examined (see text).

							1981		1982	
							Observed	Expected	Observed	Expected
Blackcap							n=115		n=521	
PL	OE	PA	SA	MC	DG	OT				
1	0	0	0	0	0	0	23.3	47.1	43.6	55.8
0	1	0	0	0	0	0	9.5	22.5	3.8	17.4
1	1	0	0	0	0	0	16.4	9.6	18.6	9.7
1	0	1	0	0	0	0	0.0	7.5	6.1	5.5
1	0	0	1	0	0	0	3.4	4.3	+	4.6
1	0	0	0	1	0	0	8.6	4.3	2.0	3.3
1	0	0	0	0	1	0	+	2.1	2.9	2.2
1	0	0	0	0	0	1	6.9	0.4	3.6	0.1
1	1	0	1	0	0	0	2.6	0.9	0.0	0.7
1	1	0	0	1	0	0	2.6	0.9	2.0	0.5
1	0	0	1	0	0	1	5.2	0.04	0.0	0.04
1	0	1	0	0	1	0	0.0	0.4	2.0	0.3
Garden Warbler							n=45		n=106	
PL	RL	PA	RU	SA	DG	OT				
1	0	0	0	0	0	0	11.1	36.3	17.0	41.4
0	1	0	0	0	0	0	13.3	35.6	+	27.0
1	1	0	0	0	0	0	22.2	11.6	+	11.0
1	0	1	0	0	0	0	0.0	5.5	17.0	6.1
1	0	0	0	1	0	0	6.7	2.1	0.0	4.4
1	0	0	0	0	1	0	0.0	1.7	4.7	2.6
1	0	0	0	0	0	1	4.4	1.1	+	1.2
0	1	0	1	0	0	0	8.9	2.0	+	2.7
1	1	1	0	0	0	0	+	1.8	5.7	1.4
1	1	0	1	0	0	0	6.7	0.9	+	1.1
1	0	1	1	0	0	0	0.0	0.4	3.8	0.7
1	0	1	0	0	1	0	0.0	0.4	4.7	0.3
1	0	1	0	0	0	1	+	0.2	4.7	0.2
0	1	1	1	0	0	0	6.7	0.1	0.0	0.1
1	1	1	0	0	1	0	0.0	0.1	3.8	0.01
1	1	1	0	0	0	1	0.0	0.1	5.7	0.01
1	1	0	0	1	1	0	4.4	0.1	0.0	0.01

3.3. COMBINATIONS OF FRUIT SPECIES IN THE DIET

Individual fruit species differ in their probability of being included in different meals, i.e., combinations of species in the samples (Fig. 4). Major species are usually found either as the only fruit species in the sample or, with another major, in a two-species combination. Minor species are more frequently found in samples containing 3 or 4 species, usually in low quantities and accompanying 1 or 2 majors. Table 5 summarizes the fraction of samples with each of the most frequent combinations of fruit. Minor fruit species have been pooled in the category 'others' because they are found in a small fraction of the samples, thus resulting in seven possible food categories that can be present or absent in any combination.

There are 127 possible combinations of these seven fruit species (including the others category). Note that certain combinations can not occur if
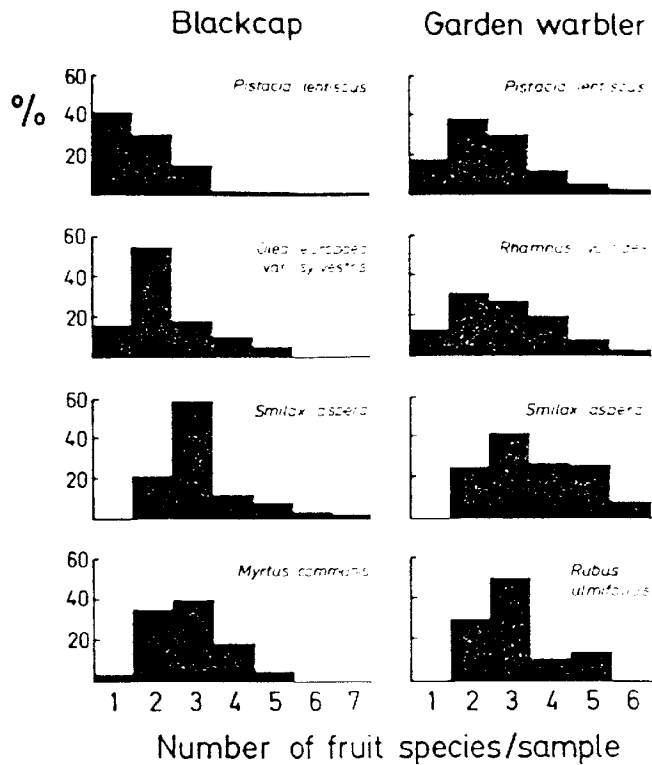
Fig. 4 Frequentie of appearance of different fruit species in diet samples containing different numbers of fruit species.

two fruit species do not match their fruiting seasons (Fig. 1). For this reason, there are 53 (41.7%) 'forbidden' combinations for Blackcaps. This is not the case for Garden Warblers, probably because of its short stay in the area (Fig. 1), and all 127 combinations are theoretically possible.

A small subset of these combinations of fruits was recorded in a relatively large fraction of the diet samples (Table 5). Only 42 combinations were recorded for Blackcaps either in 1981 or 1982 (56.8% out of the 74 possible) and for Garden Warblers I recorded 36 combinations (38.3% of the 127 possible) in either year. One-species combinations, including any of the major species, are present in nearly 25% of the samples; most of them include *P. lentiscus* and either *O. europaea* var. *sylvestris* or *R. lycioides* are the other species usually present alone. The low fruiting of any species in a given year might explain the failure to record diet samples containing them. This appears to be the cause of the low frequency of combinations including *P. angustifolia* in 1981, *S. aspera* in 1982, or, for Garden Warblers, *R. lycioides* in 1982.

A Monte Carlo simulation of fruit combinations under the hypothesis of random assortment of fruit species in meals were run for the two warbler species on the data from the two study seasons. The simulation assumed that fruit species would be included in any combination in proportion to their relative availability in each season and independently of the other species included in the meal. For each warbler species and year I averaged the simulated frequencies of each meal obtained in each of 10 runs of 1000 iterations. Expected frequencies for each of the top combinations are included in Table 5. Differences between observed and expected frequencies are highly significant in all cases ($\chi^2 \gg 50.0$, d.f. = 1, P $\ll$ 0.001), indicating that certain combinations of fruits are consumed more (or less) frequently than expected on the basis of relative availability of the species included. Particularly, one-species combinations are consumed less frequently, and multi-species combinations more frequently, than expected.

The similarity between the two years in the relative importance of the top combinations (Table 5) is not significant, both for Blackcaps (Kendall's coefficient of concordance, W = 0.711, P = 0.155) and Garden Warblers (W = 0.281, P = 0.874). There is not a significant concordance when considering all the combinations consumed (W = 0.618, P = 0.144, and W = 0.381, P = 0.842, respectively) resulting in a low between-year consistence of the structure of the fruit diet both in the types of fruit meals consumed and in the relative frequency of those consumed in the two years. Indeed, those combinations consumed are only a minor fraction of the possible meals available.

Table 6 compares the % protein, minerals, and caloric content of the meals consumed by the two warbler species in the wild (see Table 5) with the estimated yields of the same combinations without the inclusion of insect prey (*i.e.*, totally frugivorous diets). Observed meals yielded, on average, 11.39% protein, and totally frugivorous meals included only 5.34%. The simulated meals also showed very low protein: calorie ratios (0.0091 ± 0.0003), as compared with observed meals (0.02 ± 0.001, mean ± 1 S.E). Apparently, small amounts of insect prey could yield important increases in protein income to foraging birds.

Table 6. Amounts of different nutrients yielded by the observed meals consumed by Blackcaps en Garden Warblers as compared to those that would result if the birds consumed these meals without including the fraction of insect material.

Fruit combination[1]	Proportion of animal prey in meal	Observed nutrient yield of the meal[2]			Expected nutrient yield[3] (100% fruit meal)		
		Protein	kJg	Minerals	Protein	kJg	Minerals
Blackcap							
PL	0.15	0.149	29.10	0.028	0.055	30.27	0.025
PL OE	0.10	0.126	27.93	0.024	0.065	28.85	0.021
PL SA	0.09	0.111	27.63	0.036	0.055	28.22	0.034
PL MC	0.15	0.146	26.84	0.033	0.051	27.59	0.030
PL OT	0.14	0.140	25.79	0.031	0.052	26.50	0.028
PL PA	0.07	0.090	25.33	0.022	0.045	25.62	0.020
PL DG	0.07	0.108	25.08	0.030	0.064	25.37	0.029
PL/OE/SA	0.14	0.144	28.18	0.034	0.055	28.85	0.031
PL/OE/MC	0.08	0.114	26.50	0.026	0.064	26.88	0.024
PL;SA/OT	0.10	0.115	24.58	0.038	0.052	24.83	0.037
PL/PA/DG	0.11	0.119	21.98	0.024	0.049	21.77	0.021
Garden Warbler							
PL	0.13	0.137	29.27	0.028	0.055	30.27	0.025
RL	0.07	0.095	17.83	0.014	0.051	17.50	0.012
PL/SA	0.15	0.149	28.68	0.030	0.055	29.73	0.027
PL/PA	0.09	0.103	25.54	0.022	0.046	25.87	0.020
PL/RL	0.07	0.104	24.16	0.021	0.053	24.37	0.019
RL/RU	0.07	0.099	18.76	0.019	0.056	18.46	0.022
PL/RL/PA	0.08	0.099	24.33	0.021	0.048	24.45	0.019
RL/PA/RU	0.00	0.051	17.71	0.014	0.051	17.71	0.014
PL/RL/PA/OT	0.05	0.078	21.77	0.022	0.046	21.81	0.021

[1] See Table 5 for initials of fruit species. The same meal might yield different amounts of nutrients because of differences between the species in the relative amounts of animal prey or different fruits included in each combination.

[2] Nutrient yield was estimated for each meal by multiplying the relative amounts of animal prey and pulp of each fruit species (averaged for the observed diet samples of each combination) by the amounts of the specific nutrients (g per 100 g dry mass). Values for nutrient contents for animal prey were obtained from White (1974), Moermond & Denslow (1985) and Robbins (1983); those for pulp and pulp per fruit from Herrera (1984a, 1987) and Jordano (1984).

[3] Nutrient yields calculated for the same proportions of each fruit species but assuming a totally frugivorous diet (no insect material). Differences between observed and expected yields of kJ g^{-1}, protein, and minerals (t-test for paired values): $t = 10.45$, $P < 0.0001$; $t = 3.85$, $P < 0.01$ and $t = 6.09$, $P < 0.001$, respectively.

3.4. BODY CONDITION OF THE BIRDS AND ASSOCIATED VARIATION IN THE FRUGIVOROUS DIET

Variation of body mass and associated changes in fat accumulation shown by the two warbler species during their stay in the area reflect their different residence status. Individual Blackcaps showed small variations of body mass between recaptures (0.12 ± 1.39 g mean increment, n = 35 recaptures), in accordance with their status of winter residents (Fig. 5). In contrast, Garden Warbler individuals showed pronounced changes in body mass during their shorter passage period (2.6 ± 2.9 g, n = 17 recaptures, range: -2.0 to $+9.4$ g) revealing a characteristic pattern of a transient migrant (Fig. 5).

The observed changes of body mass and tracheal-pit fat scores were associated with variation in fruit consumption (as measured by averaging the % volume made up by fruits in the samples of the first capture and the recapture). For individual Blackcaps, the gains in both body mass and fat score were negatively correlated with % of fruits in the diet ($r = -0.382$, $F = 5.2$, $P = 0.027$ and $r = -0.370$, $F = 5.6$, $P = 0.022$, respectively, with angular transformation of percentages). Negative correlations were also obtained for individual Garden Warblers ($r = -0.470$, $F = 4.3$, $P = 0.054$, for variation in fat score) but the correlation with body mass variation was not significant ($r = -0.380$, $F = 2.5$, $P = 0.130$).
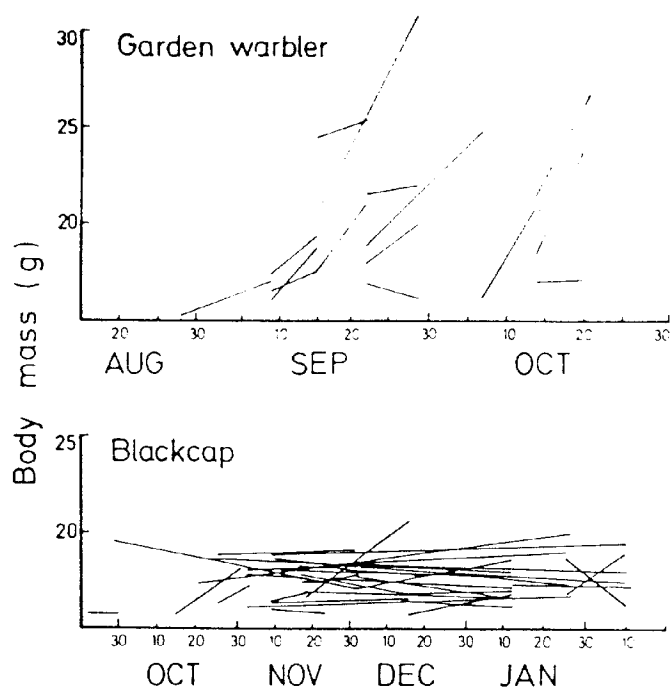
Blackcaps that showed body mass increases be-

Fig. 5. Body mass changes of individual Blackcaps and Garden Warblers by date. Data from the 1981-82 and 1982-83 seasons have been pooled. Note different scales in the abscissa corresponding to the different periods of stay in the area.

als (gains of 0.7 g for Blackcaps and 3.7 g for Garden Warblers, on average. Table 7). However, the latter maintained approximately constant body mass (average gain −0.3 g for 'frugivorous' Blackcaps) or had small increases (1.2 g. for 'frugivorous' Garden Warblers). Thus, greater reliance on fruits had a small effect, if any, on body mass variation between recaptures but birds with a diet richer in insects obtained greater increases in body mass.

In addition, fat accumulation was not independent of diet. Frugivorous diets were recorded more frequently among individuals of both species with well developed fat depots (fat score $\geq$ 3) (χ^2 = 13.88, d.f. = 1, P = 0.05, n = 336 birds, for Blackcaps; G = 3.75, 0.05 < P < 0.10, n = 75 birds, for Garden Warblers). These differences were not attributable to variations in size between the two groups of birds being compared, as indicated by the non-significant difference in wing lengths (Table 7). This suggests that insects are needed for significant body mass gains, but frugivorous diets are often shown by heavier birds without this having a significant effect on body condition, at least on the short-term basis indicated by recaptures.

These results from recaptures suggest that individuals with low body mass or small fat depot should be forced to consume more insect prey in order to achieve a large mass increase, while heavier birds would consume more fruits without this having any detrimental effect on body condition. When considering all the samples obtained for both warbler species, individuals with frugivorous diets (< 5% of diet volume made up by insects) averaged greater body mass than birds showing a greater reliance ($\geq$ 20%) on insect prey (Table 7).

tween recaptures $\geq$ 1 g had, on average, 17.8% of diet volume made up by insects; those with changes < 1 g (even showing decreases of body mass) had 5.2% of animal prey (U = 33, P < 0.001). Average % volume of insects for Garden Warblers was 11.4% and 6.3 for those with gains $\geq$ 1g and < 1g, respectively (U = 79.5, P = 0.019). Thus, relatively larger increases in body mass ($\geq$ 1g) between captures were significantly associated to diets with more insect prey. Note that individuals with 'insectivorous' diets showed greater mass changes than 'frugivorous' individu-

Table 7. Body condition of individual Blackcap and Garden Warbler differing in the relative importance of fruits in their diet.

	Insectivorous diet ($\leq$ 80% fruits)	Frugivorous diet (> 95% fruits)	Difference
Blackcap			
Body mass (g)	17.5 ± 1.4 (154)	18.1 ± 1.6 (182)	3.22**
Wing length (mm)	72.9 ± 1.9 (154)	73.2 ± 1.8 (286)	1.29 N.S.
Body mass change between recaptures (g)	0.7 ± 1.6 (16)	-0.3 ± 1.0 (19)	2.22*
Garden Warbler			
Body mass (g)	18.2 ± 2.6 (25)	19.6 ± 2.8 (49)	2.16*
Wing length (mm)	76.6 ± 1.8 (21)	76.3 ± 2.3 (41)	0.35 N.S.
Body mass change between recaptures (g)	3.7 ± 1.8 (8)	1.2 ± 2.4 (8)	2.32*

[1] Values of Student's t-test. * P < 0.05. N.S. not-significant. Figures are means ± 1 S.D. (n)

4. DISCUSSION

4.1. FRUIT CONSUMPTION: CORRELATES OF AVAILABILITY AND CHARACTERISTICS OF THE FRUITS

Blackcaps and Garden Warblers are strongly frugivorous, feeding on almost all fruit species available in the area during their residence periods. Most of the differences they show in reliance on fruit food result from their non-coincident stay in the area and the different supply of fruits that is available to them. Thus, Garden Warblers feed upon a more restricted set of fruits than Blackcaps, but in a more equitable way, as expected from the more diverse autumn fruit supply that matched its passage, relative to the winter fruit supply. The overlap between the diets of the two warbler species, as derived from the Morisita's index (Zaret & Rand 1971) was 0.47, well below the value of 0.87 obtained by Worthington (1983) for two sympatric, year-round resident manakins (Pipridae) in neotropical forest. Thus, the two warblers shared 11 out of 15 fruit species but the delay in their residence period resulted in great variation in the dependence on each plant species and low overlap in diet.

· The relative consumption of each fruit species was much the same between the two years for both the Blackcap and Garden Warbler in spite of the strong between-year variations in the fruit supply. However, the significant differences obtained when comparing the rankings of the species consumed in the same month of different years suggest that birds were adjusting their diet to the variations in phenology and fruiting intensity. Since the ripening sequence of the fruit species showed a highly similar ordering in the two study years, these differences were most likely responses to the different fruit supply encountered in the same month of the two fruiting seasons. Thus, changes in the relative representation of the fruit species in the diet were associated to the fruiting intensity of the plants and similar responses to this variation were observed in the two warbler species, relative consumption of each fruit species being closely related to relative availability in each fruiting season. Both showed a strong dependency on *P. lentiscus* and had similar responses to its variation in fruiting: Garden Warblers shifted the diet from alternative, earlier ripening species (*R. lycioides* or

P. angustifolia) as their supply decreased; Blackcaps, increased consumption of late-ripening species (*e.g. O. europaea* var. *sylvestris*) as the supply of *P. lentiscus* decreased. Changes in the fruit supply of the minor species had also a great effect on their relative importance in the diets. Both the timing of these shifts and the species involved were strongly dependent upon fruit availability, monthly variation in composition of the fruit diet 'tracking' the availability of the different fruit species. Similarly, consumption of different fruits by Blackcaps and Robins *Erithacus rubecula* at mid-elevation shrublands in southern Spain closely tracks the supra-annual variation in fruiting intensity of *Viburnum tinus* (L.), *Phillyrea latifolia* (L.) and *P. lentiscus* (Herrera pers. com., see Rodríguez *et al.* 1986).

Regression analyses showed that fruit availability is a major determinant of fruit choice in these warblers, consumption of individual fruit species being positively correlated with their availability. In addition to this non-nutritional trait of the plants, both warbler species selected high-lipid fruits and the significant partial regression coefficients suggest that, holding other traits constant, pulps with high energy value might be preferred. The relative mass of pulp per fruit and the mineral content appeared as additional variables affecting fruit selection by the Blackcap. Finally, both warbler species showed negative responses to fruit size only in the second year when the fruit supply was exceptionally high, suggesting that consumption of larger fruits, more difficult and costly to handle and ingest than smaller fruits, might be favoured if smaller fruits are in short supply and/or fruit availability is limiting.

Previous studies on diet selection found that fruit availability, measured either as density of fruiting trees, fruit crop size, ripe fruit availability of any combination of them, was the main variable affecting fruit consumption by frugivorous birds (*e.g.* Worthington 1982, 1983, Jordano 1984, Wheelwright *et al.* 1984) and other frugivorous vertebrates (Terborgh 1983, Fleming 1986, Janson *et al.* 1986, Sourd & Gauthier-Hion 1986). Frugivores should have a high encounter rate with an abundant fruit species and easily use it as a major dietary component. Other fruits, vegetative parts of plants or insect prey would be included to supplement other nutrients. Laboratory test of feed-

ing preferences and fruit choice should take in acount that non-nutrional traits and factors extrinsic to the fruit as a food item may have a major effect on diet selection by frugivores.

Fruit size has been pointed out as affecting consumption of fruits both in inter- (Herrera 1984a, Jordano 1984, Wheelwright et al. 1984. Wheelwright 1985) and intra-specific comparisons (Howe & Vande Kerckhove 1980, Wheelwright 1985, Piper 1986), increasing fruit size limiting the array of frugivore species feeding on fruits, decreasing the profitability of fruits by increasing handling costs, or decreasing the percentage of seeds removed from plants by dispersers. My results, even with the limitation of only two years of data, also suggest that the selection pressures on fruit size by frugivorous birds might vary from year to year because variations in the fruit supply might enhance or damp selectivity by the foraging birds.

I suggest that non-nutritional fruit traits directly affect the foraging mode of frugivores in the wild, selection of other nutritional traits of the fruits being dependent on the degree of reliance on fruit for food and the consequent choice between other fruits or alternative foods for the obtainment of specific nutrients. Variation in the number of fruit species consumed by *Sylvia* warblers was inversely correlated with percentage of animal prey in the diet (Jordano 1987). Only strongly frugivorous birds should include minor (rare) fruit species to supply other needs aside the basic energy demand. The dietary patterns reported here for frugivorous warblers in the wild are consistent with these hypotheses, but carefully designed cage experiments are needed to obtain conclusive evidence.

4.2. FRUGIVORY IN RELATION TO BODY CONDITION

Major fruit species in the diet of both the Blackcap and Garden Warbler in any of the two study years shared three basic traits: they were abundant in the area, had high relative amounts of pulp per fruit, and the pulp was either rich in lipids (winter fruits) or soluble carbohydrates (summer-autumn fruits). Presumably both warbler species supplied their energy demands by feeding on these abundant, highly rewarding fruits. However, the dietary pattern observed involves the selection of meals including a large fraction of one or two major species and small quantities of up to four or five,

but mostly only one, minor fruit species. The fact that only a small subset of all the possible combinations of fruit species appeared in the diet suggests that warblers were selecting meals rather than simply individual fruit species while foraging (see Clark 1980, for a similar finding in black rats).

The fact that the pulps of minor fruit species are far more richer in minerals than those of the majors, suggests that they contribute to balance the frugivorous diet by supplying micro-nutrients or trace elements that are deficitary in the major fruit species. Minor fruit species were included in diverse meals, rarely as the only component of the diet sample. Worthington (1983) and Sourd & Gauthier-Hion (1986) found that rare species, minoritary in the diet, supplied higher concentrations of specific nutrients (lipids, protein, potassium, manganese, etc.) than the major species. Thus, strongly frugivorous birds like the Blackcap and Garden Warbler should eat these fruits when encountered, since a frugivorous diet must be diverse in order to supply a balanced set of nutrients (Herrera 1984a, Moermond & Denslow 1985). The greater incidence of secondary compounds, predominantly alkaloids, in their pulps should account for the fact that they are usually consumed in low quantities, fruit toxicity being a potential limitation for a sustained reliance on these species by a frugivore. I suggest that the increased detoxifying abilities documented for frugivorous birds relative to insectivorous or granivorous species (Seuter 1970, Eriksson & Nummi 1982) enable them to efficiently use these minor fruit species and build up diverse fruit diets.

Complete reliance on fruit food for maintenance was not observed, either for the Blackcap or the Garden Warbler, both supplementing it with variable amounts of insect prey. Both the accumulation of fat and the gain of body mass between recaptures of ringed birds were negatively correlated with the quantity of fruits in their diets. Thus, the rapid increases in these variables for 'insectivorous' individuals contrasted with slight decreases or variations observed in the body condition of 'frugivores'. These results are quite similar to those reported by Feare & McGinnity (1986) with captive Starlings *Sturnus vulgaris*: body mass increased with increasing proportion of invertebrate food in the diet (see also Berthold 1976a). On the other hand, Catterall (1985) showed that frug-

ivorous Silvereyes *Zosterops lateralis* were unable to balance their energy budgets on a diet of insects alone, presumably because of the increased foraging costs entailed. Energy-rich but protein-poor food such as fruits is therefore adequate for the obtention of the daily energy requirement but inadequate to supply the nitrogen needs for long-term maintenance. Bairlein (1985) demonstrated that captive Garden Warblers show increased food intake and efficiency of fat and carbohydrate utilization (but not protein) during fattening, rather than by a short supply of lipid-rich fruits. My results also indicate that birds in the wild might be limited by their protein demands during fattening. Birds with low fat reserves, either because a recent arrival at the stopover site (Garden Warbler) or adverse climate condition in winter nights (Blackcap) might also show impaired protein reserves in muscle (Jones 1980) thus imposing a higher protein demand.

Protein deficiency has been pointed out repeatedly as the main limiting factor of the fruit pulp as food (Berthold 1976a, Foster 1978, Robbins 1983, Moermond & Denslow 1985). Should the diets of these partially frugivorous warblers be deficitary in protein were they totally frugivorous? The simulation of nutrient yields in total frugivorous diets showed that frugivorous warblers should obtain significantly reduced amounts of protein and minerals per meal and significantly higher energy rewards. Thus, even the inclusion of minor amounts of insect prey increased dramatically the protein yield of the meals. Observed meals yielded, on average (dry mass basis), 11.39% protein, a figure above the 4-8% pointed out as necessary for maintenance (see Berthold 1976a), but totally frugivorous meals included only 5.34%. Moreover, the simulated meals showed extremely low protein: calorie ratios as compared to values reported as adequate for maintenance (Moermond & Denslow 1985 and references therein). These results, together with the finding that Blackcaps included sizeable amounts of *U. minor* flowers in the second year, paralleling a decrease in arthropod abundance, additionally support the view that the birds were constrained by the protein need. Thus, consumption of flowers could yield enough protein to supplement the decreased arthropod abundance and this might explain their inclusion in the diet, strongly associated to pure *P. lentiscus* meals.

Reliance on abundant fruit species highly profitable in terms of both pulp- and energy-reward per fruit seems to be the basic diet pattern that accounts for sustained frugivory in these warblers; their ability to obtain efficiently other nutrients from a variety of scarce fruit species explains their low dependence on alternative insect prey.

4.3. CONSEQUENCES FOR THE DISPERSAL OF THE SEEDS

Frugivorous warblers in the wild showed diverse fruit diets assembled by a non-random process of fruit choice and arthropod consumption. This resulted in meals differing greatly in species composition and nutrient yield. This paper has examined the consequences of these variations for the warblers themselves, but the plants might also be affected through the differential seed dispersal performed by these frugivores.

Warblers consumed fruit species in relation to their relative availability in a given fruiting season. However, seeds of minoritary species were dispersed in greater proportion than expected by their relative availability, always within 'packages' dominated by any major species. Therefore, birds assembled predictable combinations of fruits in their diets, on the basis of relative availability, nutrient content of the pulp, and fruit size. This adds new evidence and perspective to earlier findings of several authors suggesting that frugivore foraging is not random with respect to the location of the plants or to habitat structure, resulting in non-random seed deposition patterns (*e.g.* Fleming & Heithaus 1981, McDonell & Stiles 1983, Herrera 1984c, Stiles & White 1986, see review in Herrera 1985b).

Plants do not interact with dispersal agents as single entities in space or time. Sets of plant species, with the constraint of phenological coupling, present fruit displays that result in predictable patterns of consumption by frugivorous warblers. The results presented here are limited to the analysis of dietary variation among the seed dispersers, the resulting patterns of seed deposition and seedling emergence and establishment being not examined. However, I consider the above results as additional support to the hypothesis of plant guilds, conceived as integrated sets of species that differentially interact with consumers via their common configuration of abundance. nutrients,

secondary metabolites, etc. (Atsatt & O'Dowd 1976, Rathcke 1983, Herrera 1985b). Selective patterns of consumers, therefore, not only have consequences for the consumers themselves, as stressed in this paper. If certain plant species are functionally interdependent for their dispersal, this may contribute in the long-term to a reconfiguration of the plant assemblages.

5. ACKNOWLEDGEMENTS

6. SUMMARY

The frugivorous diets of Blackcaps and Garden Warblers in Mediterranean shrubland, determined by faecal analysis, are described. Variation in fruit consumption is related to the fruit supply and the relation with body mass and fat accumulation is examined. The overall diet was highly similar in the two study years but the rankings of the fruit species consumed in the same month of different years differed, suggesting that birds were adjusting the diet to variations in phenology and fruiting intensity. Regression analysis showed that fruit availability was the main factor correlated with fruit consumption. Both warbler species selected fruits with high energy-value and showed negative responses to fruit size only in the year when fruit supply was exceptionally high. Both species selected a small subset of the possible combinations of fruits (meals), including a large fraction of one or two major fruit species and small amounts of several minor species or insects. Meals of several fruit species were consumed more frequently than expected under the hypothesis of random and independent assortment of component fruits. Minor fruit species were consumed more frequently than expected from their relative availability. Pulp of minor fruits was significantly higher in minerals than the pulp of majors, that characteristically showed a higher energy content. Alkaloids were more frequently present in minor species. Both the accumulation of fat and body mass gain between recaptures of ringed birds were negatively correlated with the amount of fruit in their diet. A simulation of the diet under the premise of a total reliance on fruit food showed that warblers eating only fruits should obtain significantly reduced amounts of protein and minerals but increased energy income. Inclusion of minor amounts of insect prey dramatically increased the protein yield of the meals and this may be necessary to increase body mass and fattening. The implications of these patterns of dietary variation and fruit choice on plant seed dispersal are discussed.

7. REFERENCES

Altman, H. 1980. Plantas y animales venenosos de Europa. Omega, Barcelona.

Atsatt P. R. & D. J. O'Dowd. 1976. Plant defense guilds. Science 193: 24-29.

Bairlein, F. 1985. Efficiency of food utilization during fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin*. Oecologia (Berlin) 68: 118-125.

Belowski, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theor. Popul. Biol. 14: 105-134.

Bergeron, J. M. & L. Jodoin. 1984. Impact de 12 plantes communes de milieu ouvert sur les variations de poids corporel et de poids d'organes internes du campagnol des champs (*Microtus pennsylvanicus*). Can. J. Zool. 62: 50-57.

Berthold, P. 1976a. The control and significance of animal and vegetable nutrition in omnivorous songbirds. Ardea 64: 140-154.

Berthold, P. 1976b. Uber den Einfluß der Nestlingsnahrung auf die Jugendentwicklung, insbesondere auf das Flügelwachstum, bei der Mönchsgrasmücke (*Sylvia atricapilla*). Vogelwarte 28: 257-263.

Caterall, C. P. 1985. Winter energy deficits and the importance of fruit versus insects in a tropical island bird population. Aust. J. Ecol. 10: 265-279.

Clark, D. A. 1980. Age- and sex-dependent foraging strategies of a small mammalian omnivore. J. Anim. Ecol. 49: 549-563.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88: 323-242.

Eriksson, K. & H. Nummi. 1982. Alcohol accumulation from ingested berries and alcohol metabolism in passerine birds. Ornis Fenn. 60: 2-9.

Feare, C. J. & N. McGinnity. 1986. The relative importance of invertebrates and barley in the diet of Starlings *Sturnus vulgaris*. Bird Study 33: 164-167.

Fleming, T. H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In: Estrada, A. & T. H. Fleming (eds.). Frugivores and seed dispersal. Junk, Dordrecht.

Fleming, T. H. & E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropical Suppl. 13: 45-53.

Font Quer, P. 1981. Plantas medicinales. Editorial Labor, Barcelona, 6th ed.

Foster, M. S. 1978. Total frugivory in tropical passerines: a reappraisal. Tropical Ecol. 19: 131-154.

Gardiazábal, A. 1986. Jahreszeitliches Auftreten, Gewichte und Ernährungsökologie von Garten- und Mönchsgrasmücke (*Sylvia borin, Sylvia atricapilla*) im Rast- und Überwinterungsgebiet 'Coto Doñana'. Südwestspanien. Univ. Köln.

Herrera, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? Amer. Nat. 118: 896-907.

Herrera, C. M. 1982. Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. Amer. Nat. 120: 218-241.

Herrera, C. M. 1984a. A study of avian frugivores, bird-dispersed plants and their interaction in Mediterranean shrublands. Ecol. Monogr. 54: 1-23.

Herrera, C. M. 1984b. Adaptation to frugivory in Mediteranean avian seed dispersers. Ecology 65: 609-617.

Herrera, C. M. 1984c. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. Oecologia (Berlin) 63: 386-393.

Herrera, C. M. 1985a. Aposematic insects as six-legged fruits: incidental short-circuiting of their defense by frugivorous birds. Amer. Nat. 126: 286-293.

Herrera, C. M. 1985b. Habitat-consumer interactions in frugivorous birds In: Cody, M. L. (ed.). Habitat selection in birds. Academic Press, New York.

Herrera, C. M. 1987. Vertebrate-dispersed plants of the Iberian Penninsula: a study of fruit characteristics. Ecol. Monogr. 57: 305-331.

Howe, H. F. & G. A. Vande Kerckhove. 1980. Nutmeg dispersal by tropical birds. Science 210: 925-927.

Janson, C. H., E. W. Stiles & D. W. White. 1986. Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. In: Estrada, A. & T. H. Fleming (eds.). Frugivores and seed dispersal. Junk, Dordrecht.

Janzen, D. H. 1985. The natural history of mutualisms. In: Boucher, D. H. (ed.). The biology of mutualism. Ecology and evolution. Croom Helm, London.

Jones, M. M. 1980. Nocturnal loss of muscle protein from House Sparrows (*Passer domesticus*). J. Zool. Lond. 192: 33-39.

Jordano, P. 1981. Alimentación y relaciones tróficas entre los Passeriformes en paso otoñal por una localidad de Andalucía central. Doñana Acta Vert. 8: 103-124.

Jordano, P. 1984. Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana. Ph. D. thesis, Univ. Sevilla.

Jordano, P. 1985. El ciclo anual de los paseriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. Ardeola 32: 69-94.

Jordano, P. 1987. Frugivory, external morphology and digestive system in Mediterranean sylviid warblers (*Sylvia* spp.) Ibis 129: 175-189.

Jordano, P. & C. M. Herrera. 1981. The frugivorous diet of Blackcap populations *Sylvia atricapilla* wintering in southern Spain. Ibis 123: 502-507.

Karasov, W. H. 1985. Nutrient constraints in the feeding ecology of an omnivore in a seasonal environment. Oecologia (Berlin) 66: 280-290.

Kear, J. 1968. Plant poisons in the diet of wild birds. Bull. Brit. Orn. Club 88: 98-102.

Levey, D. J. 1986. Methods of seed processing by birds and seed deposition patterns. In: Estrada, A. & T. H. Fleming (eds.). Frugivores and seed dispersal. Junk, Dordrecht.

McDonell, M. J. & E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird dispersed plant species. Oecologia (Berlin) 56: 109-116.

Milton, K. & F. R. Dintzis. 1981. Nitrogen-to-protein conversion factors for tropical plant samples. Biotropica 13: 177-181.

Moermond, T. C. & J. S. Denslow. 1985. Neotropical frugi-

vores: the influence of nutrition, behavior and morphology on fruit choice. In: Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely & F. G. Buckley (eds.). Neotropical ornithology. Amer. Orn. Union Monog. No. 36.

Piper, J. K. 1986. Seasonality of fruit characters and seed removal by birds. Oikos 46: 303-310.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. In: Real, L. (ed.). Pollination biology. Academic Press, New York.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York.

Rodríguez, M., M. Cuadrado & S. Arjona. 1986. Variation in the abundance of Blackcaps (*Sylvia atricapilla*) wintering in an olive (*Olea europaea*) orchard in southern Spain. Bird Study 33: 81-86.

Rozin, P. & J. W. Kalat. 1971. Specific hungers and poison avoidance as adaptive specializations of learning. Psychol. Rev. 78: 459-486.

Seuter, F. 1970. Ist eine endozoische Verbeitung der Tollkirsche durch Amsel und Star möglich? Zool. Jahr. Physiol. 75: 342-359.

Sherburne, J. A. 1972. Effects of seasonal changes in the abundance and chemistry of the fleshy fruits of northern woody shrubs on patterns of exploitation by frugivorous birds. Ph. D. Dis., Cornell Univ.

Silby, R. M. 1981. Strategies of digestion and defecation. In: Townsend, C. R. & P. Calow (eds.). Physiological ecology: an evolutionary approach to resource use. Blackwell Scientific Publications, London.

Simms, E. 1985. British warblers. Collins, London.

Sorensen, A. E. 1981. Interactions between birds and fruit in a temperate woodland. Oecologia (Berlin) 50: 242-249.

Sourd, C. & A. Gauthier-Hion. 1986. Fruit selection by a tropical forest guenon. J. Anim. Ecol. 55: 235-244.

Stiles, E. W. & D. W. White. 1986. Seed deposition patterns: influence of season, nutrients, and vegetation structure. In: Estrada, A. & T. H. Fleming (eds.). Frugivores and seed dispersal. Junk, Dordrecht.

Terborgh, J. 1983. Five New World primates. A study in comparative ecology. Princeton Univ. Press.

Westoby, M. 1978. What are the biological bases of varied diets? Amer. Nat. 112: 627-631.

Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds: Ecology 66: 808-818.

Wheelwright, N. T., W. A. Haber, K. G. Murray & G. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica 16: 173-192.

White, S. C. 1974. Ecological aspects of growth and nutrition in tropical fruit-eating birds. Ph. D. Diss., Univ. Pensylvania.

Worthington, A. 1982. Population sizes and breeding rhythms of two species of manakins in relation to food supply. In: Leigh Jr., E. G., A. S. Rand & D. M. Windsor (eds.). The ecology of a tropical forest. Seasonal rhythms and long-term changes. Smithsonian Inst. Press, Washington.

Worthington, A. 1983. How rare plants attract fruit dispersers: the role of nutritional rewards. Bull. Ecol. Soc. Amer. 64: 53.

Zaret, T. M. & S. A. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

8. SAMENVATTING

Door middel van faecale analyse kon het vruchten-dieet van Zwartkop en Tuinfluiter in een Mediterrane struikvegetatie worden bepaald. Verschillen in de consumptie van vruchten is gerelateerd aan het aanbod van vruchten en het verband met lichaamsmassa en vet-accumulatie is onderzocht. Over het algemeen was het dieet in de twee studiejaren in hoge mate gelijksoortig alhoewel de rangvolgorde van de soorten vruchten die gegeten werden in dezelfde maand maar in de verschillende jaren niet dezelfde was. Dit suggereert dat de vogels hun dieet aanpasten aan variaties in de fenologie en in de mate van vruchtzetting. Door middel van een regressie analyse kon worden getoond dat de beschikbaarheid van vruchten de belangrijkste factor was die correleerde met het eten ervan. Beide soorten vogels selecteerden vruchten met een hoge energieinhoud en slechts in het jaar dat het aanbod van vruchten uitzonderlijk hoog was, vertoonden beide soorten een negatieve relatie tussen het aandeel van soorten vruchten in het dieet en de grootte van die vruchten. De beide vogelsoorten selecteerden slechts een kleine subset van alle mogelijke combinaties van vruchtesoorten; deze subsets bestonden voor een groot deel uit een of twee belangrijke soorten vruchten en voor een klein deel uit verscheidene minder belangrijke soorten of insekten.

Maaltijden bestaande uit verscheidene soorten vruchten kwamen vaker voor dan verwacht op basis van de hypothese dat er willekeurig zou worden gefoerageerd. Minder belangrijke soorten vruchten werden vaker gegeten dan werd verwacht op basis van het relatieve voorkomen van die soorten. Het vruchtvlees van die soorten vertoonde een hogere concentratie aan mineralen dan dat van de belangrijke soorten vruchten, maar dat van de laatste groep had een hogere energie-inhoud. Alkaloïden waren vaker aanwezig in de minder belangrijke soorten vruchten. Zowel de vetaccumulatie als de toename in lichaamsmassa tussen de momenten van vangst en terugvangst van geringde individuele vogels waren negatief gecorreleerd met de hoeveelheid vruchten in het dieet. Een simulatie van het dieet onder aanname dat de vogels totaal afhankelijk waren van een vruchtendieet, toonde aan dat dit als consequentie had voor de vogels een verminderde opname van eiwitten en mineralen maar een verhoging van de energie-opname. De toevoeging van slechts geringe hoeveelheden insekten aan dat dieet zorgde voor een dramatische toename van de eiwit opbrengst van de maaltijden, en wellicht is dat juist nodig voor een toename in lichaamsgewicht en voor het opvetten. De gevolgen van de patronen van dieetvariatie en keuze aan vruchten worden bediscussieerd in samenhang met de verspreiding van plantezaden. — H.P.

A sight-record of a White-bellied Storm Petrel *Fregetta grallaria* in the western Palearctic

In August and September 1986 the last of seven Dutch scientific expeditions to the West African coast took place (CANCAP VII). During the outward voyage of the research vessel H.M.S. Tydeman to the Cape Verde Islands, which took ten days, continuous bird observations were carried out for almost ten hours every day. Apart from the commonly occurring species which can be seen on this route, a White-bellied Storm Petrel *Fregetta grallaria* was seen on 17th August, north of the Cape Verde Islands (23°48′ N, 22°01′ W).

Accompanying two Madeiran Storm Petrels *Oceanodroma castro*, an unusual, strikingly black-and-white coloured storm petrel draw the attention. The lower breast, flanks and ventral parts were pure white, in contrast to the completely blackish head, upper breast and dorsal parts. The rump was white, contrasting with the dark back and tail feathers. The underwings were white in the centre with broad dark margins on the fore wing, and the black flight feathers formed a contrasting trailing edge. A light patch on the upperwing was caused by the clearly white-fringed wing-coverts. During its zig-zagging flight the bird progressed steadily, pushing the water aside with its long legs, swinging from one side to the other, allowing a very good view of the dorsal and ventral parts. Thus it was possible to notice the total absence of black feathers on the belly between the legs. During several minutes the storm petrel, which was observed under excellent light conditions, flew along with our ship at a distance of only 30 m. This bird certainly belonged to a species of the genus *Fregetta*, for it missed the diagnostic facial pattern and the grey-brown wing coverts of the White-faced Storm Petrel *Pelagodroma marina*.

Identification of the two *Fregetta* species is not always easy, due to the fact that some White-bellied Storm Petrels have black-tipped feathers on the abdomen. On the other hand Black-bellied Storm Petrels *F. tropica* sometimes show black feathers on the belly with an extremely white edge, which could induce an observer to think he was seeing a white belly. This may cause misidentification (Harrison 1985, Bourne 1962). The bird of 17th August had a clearcut black breast band, a completely white belly, and also showed more contrast on the upperwing than the Black-bellied Storm Petrel. In the latter species this contrast is hard to be seen in the field (pers. obs.).

Besides this record, only two records of birds of the genus *Fregetta* are known from the northern hemisphere in the Atlantic Ocean. Bourne (1962) mentions the unusual catch of not less than seven White-bellied Storm Petrels on board a ship in the harbour of St. Marks, Florida. The only specimen that was collected seems to have disappeared. Bourne classified these birds as *F. tropica*, which cannot be verified anymore. The second record can be found in the recent reports in British Birds 73 (1980); this pertains to an undocumented sight-record of a White-bellied Storm Petrel passing by Seascale (Cumbria) on 23rd October 1979.

The White-bellied Storm Petrel breeds in the southern hemisphere and is known to occur in the northern hemisphere only in the Arabian Sea (Bailey 1968). In the Atlantic Ocean the northern most known breeding places are on Tristan da Cunha. Its wintering range in the Atlantic Ocean, according to Harrison (1985), extends to the equator. The record mentioned in this article indicates that White-bellied Storm Petrels at least occasionally reach the coast of Northwest Africa.

REFERENCES

Anon. 1979. Recent Reports. Brit. Birds 73: 51.
Bailey, R. S. 1968. The pelagic distribution of seabirds in the western Indian Ocean. Ibis 110: 493-519.
Palmer, R.S. 1962. Handbook of North American Birds, Volume I. Yale Univ. Press, New Haven London.
Harrison, P. 1985. Seabirds: an identification guide. Croom Helm, Beckenham.

B. J. M. Haase,
Willem Kuyperstraat 68, 2584 XX Scheveningen, The Netherlands