

Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp.

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Fruit consumption was assessed in six species of *Sylvia* warblers and compared to variation in external morphology and digestive system. Variation in the use of fruit was determined primarily by external morphology (body-size, gape-width and hindlimb characteristics). Variation in digestive traits (intestine-length, gizzard and liver-weight) did not account for a significant fraction of variation in frugivory across species. Relative to other non-frugivorous Muscicapidae, *Sylvia* spp. exhibit digestive adaptations specific to fruit processing; however, variation in external morphology constrains the degree of dependence on fruit within the genus.

A variety of structural modifications in the feeding apparatus or digestive tract of frugivorous birds has been described (Forbes 1880, Magnan 1912, Wetmore 1914, Wood 1924, Cadow 1933, Walsberg 1975). These have been interpreted as elaborate evolutionary by-products of a sustained dependence on fruit food. Probably as relevant as these bizarre traits are to these strongly frugivorous birds, other functional, more subtle, adaptations have been reported when examining morphological and behavioural aspects of frugivory in a variety of tropical (Jenkins 1969, Moermond & Denslow 1985, Santana & Milligan 1984, Wheelwright 1985) and temperate frugivores (Berthold 1976a, b, Pulliainen *et al.* 1981, Herrera 1984b).

Both morphology and behaviour set limits to the degree of frugivory because they affect the cost-benefit balance associated with foraging for mixed diets in partial frugivores. Variation in fruit use by frugivorous birds is strongly associated with morphological and behavioural constraints (Moermond & Denslow 1983, 1985) originating from adaptations for use of alternative resources. Thus, heavy use of fruits is often related to pre-adaptations originated from specific modes of insect capture and handling (Herrera 1984b, Fitzpatrick 1980, see also Moermond 1983).

This paper examines morphological correlates of fruit use by warbler species within the genus *Sylvia*. As stressed by several authors (Leisler 1980, Lederer 1984, Leisler & Winkler 1985), restriction of the analysis to closely related taxa emphasizes variation which is independent of parallel, phylogenetic variation in other traits. Particular emphasis is paid to between-species variation in external morphology and digestive anatomy as well as variation among plant species in fruit characteristics associated with consumption by *Sylvia*.

Methods

Field work was conducted at 'Hato Ratón', a property located at the northeast border of the Doñana National Park, just on the northern natural limit of the Guadalquivir Marismas, 3 km south of Villamanrique de la Condesa (Sevilla).

The study period extended from early 1981 throughout April 1983, encompass-

ing three consecutive fruiting seasons. Additional data on certain species were taken during 1984 and 1985 in the nearby places of 'El Viso' (see Herrera 1984a) and 'Reserva Biológica de Doñana', mostly to complete data for certain autumn-passage migrants.

The main study site is a medium to high (2.5–5.0 m) dense sclerophyllous shrubland growing on sandy soils at 13 m elevation. Vegetation is dominated by tall shrubs and treelets of *Pistacia lentiscus* (Anacardiaceae), *Olea europaea* var. *silvestris* (Oleaceae), *Phillyrea angustifolia* (Oleaceae) and *Rhamnus lycioides* (Rhamnaceae). The shrubland is characteristic in having a great cover and diversity of plants producing fleshy fruits (72.2%, $n=21$ species), but is dominated by *P. lentiscus* (33.4% cover).

Rainfall in the area averages 538.9 mm per year, with a dry season lasting from mid-April to mid-September. Average temperature is 18 °C, with ranges of 25.5 and 10.8 °C as average maximum and minimum temperatures; not more than 0.5% of the days in a year have ambient temperatures below 0 °C. Detailed descriptions of the site and climate can be found in Jordano (1984a, 1985); see also Rivas-Martínez *et al.* (1980) for information on the vegetation of the Doñana area.

Bird populations

Weekly counts were carried out along a permanent, 1-km-length transect following the procedure of Emlen (1971) (see also Verner 1985). Density estimates, as well as records of presence in the area, were derived from these counts. A total of 6–10 nets was operated weekly, 2 days per week, to complement the monitoring of the bird populations; the nets were opened from dawn to dusk and checked at hourly intervals. An additional objective of mist-net operation was to obtain faecal samples and bird measurements.

Diet analysis

Information on food composition was gathered exclusively by analyses of faecal samples (see Ralph *et al.* 1985). These were obtained directly either from cloth bags where the birds were kept individually after capture, or by flushing a dilute sodium-chloride solution through the gut (Moody 1970, Jordano & Herrera 1981).

The relative importance of animal prey (mostly arthropods) and vegetable remains (mostly fruits but also flowers in some species) in faeces was assessed by estimating visually the percent volume occupied by each fraction (to the nearest 10%). Both seeds and pulp remains were identified, the latter by microscopic inspection of the pericarp tissue (Jordano & Herrera 1981). Quantification of seeds alone underestimates both the number of fruits and fruit species in individual faecal samples of frugivorous birds, probably as a result of differential residence time of pulp and seeds in the gut, with seeds being defaecated or regurgitated more rapidly (Johnson *et al.* 1985). However, all the *Sylvia* species considered here regularly defaecate seeds and regurgitation is exceptional. All the measures of gut passage time (GPT, see below) were obtained during autumn–winter, when the species considered are actively consuming fruits.

An analogous procedure was employed to obtain estimates of food passage time through the digestive tract. A small amount of an aqueous suspension of barium sulphate, coloured with an innocuous stain, was introduced in the gizzard with the aid of an orally inserted catheter connected to a syringe. Birds were kept in individual cloth bags and the time between administration and first appearance of stained faeces was recorded. This method is described in Herrera (1984b) and enables estimation of

interspecific variation in gut passage time (GPT); the advantages and shortcoming of the procedure are discussed there.

External measurements were obtained from netted specimens by standard procedures (Svensson 1970).

Digestive system

Specimens for dissection came from several areas from southern Spain and were mostly obtained from hunters, road kills, or accidents during mist-netting. The measurements obtained included: gizzard (with food removed) and liver weights (wet), and intestine length, from gizzard to cloaca (see Schieck & Millar 1985 for similar procedures).

Results

The birds

A total of seven *Sylvia* species has been recorded in the study area. They show variable residence times and the group is characterized by its non-resident status. Monthly average densities for the two year-round residents, namely Sardinian Warbler *Sylvia melanocephala* and Dartford Warbler *S. undata*, were 17.0 ± 6.1 and 2.0 ± 1.4 individuals per 10 ha, respectively (Jordano 1985), both populations remaining relatively stable throughout the year.

The Blackcap *S. atricapilla* is the only wintering species among the non-residents, spending about nine months in the area from September to May (average residence period, 7.0 months). This species showed extensive between-year variation in abundance, with maxima of 28.7 individuals per 10 ha (October) in the 1981–82 season and 169.0 individuals per 10 ha (January) in the 1982–83 season.

The transient species (Garden Warbler *S. borin*, Common Whitethroat *S. communis* and Subalpine Warbler *S. cantillans*) were especially abundant during the autumn passage, from late July to mid-November; these species typically reached peak densities during September (7.0 and 22.4; 3.4 and 2.7; 7.3 and 4.7 individuals per 10 ha, respectively, for the 1981 and 1982 seasons). The average residence period for these three species during autumn passage was 2.4, 1.5, and 1.7 months, respectively. Residence periods were much shorter for the spring passage (1.4, 0.9, and 1.5 months, respectively). Finally, the Orphean Warbler *S. hortensis* was recorded only for a brief period during autumn migration in the two years, being extremely scarce in the area; this species has been excluded from the analyses below due to the small sample size obtained.

Composition of the fruit diet

Appendix 1 summarizes the diet (fruit fraction) of the species considered. The main point is the generalized reliance on *Pistacia lentiscus* fruits for all the species; this aside, consumption of the remaining fruits is strongly associated with the relative importance of the vegetable fraction in the diet (see below). The variation in the relative importance of the different fruits is related to the residence status of each species in the area and the matching of their stay with the ripening period of the different plant species. Thus, the passage of trans-Saharan migrants matches the ripening period of the late-summer species, with *P. angustifolia*, *R. lycioides*, *R. ulmifolius*, and *T. communis* being extensively consumed by Garden, Subalpine and

Table 1. Fruit consumption-related variables for *Sylvia* warblers in southwestern Spain

	Frugivory ¹ index	Gut passage time (min) ($\bar{x} \pm$ s.d.)	FPR ² (mm/min)	Fruit species in diet <i>n</i>	Fruit species/sample ($\bar{x} \pm$ s.d.) <i>n</i>
<i>Sylvia atricapilla</i>	85.0	34.4 ± 21.9 (120)	4.6	14	1.93 ± 0.93
<i>Sylvia borin</i>	92.4	44.6 ± 14.8 (15)	3.5	12	2.43 ± 1.11
<i>Sylvia cantillans</i>	61.8	30.1 ± 13.7 (9)	4.1	6	1.79 ± 0.86
<i>Sylvia communis</i>	64.4	40.8 ± 17.8 (6)	3.4	5	1.70 ± 0.82
<i>Sylvia melanocephala</i>	68.6	32.3 ± 16.5 (72)	4.2	12	1.71 ± 0.89
<i>Sylvia undata</i>	19.2	—	—	2	1.33 ± 0.52

Notes: ¹ Frugivory index is the product of the average frequency of appearance of fruit remains in faecal samples and the average percent volume of this material.

² Food passage rate (FPR): intestine length divided by gut passage time.

Common Whitethroat. In contrast, the wintering Blackcap and the resident Sardinian show higher consumption of autumn- and winter-ripening fruits (*O. europaea* var. *sylvestris*, *A. acutifolius*, *M. communis*), the consumption index for the late summer species (except *P. angustifolia*) being less than 1.0.

A continuum of variation exists in the relative importance of the fruit diet (Table 1). Animal prey ranges between 7.6 and 61.7% volume (cf. Appendix 1); as the relative importance of insects increases in the diet, both the quantity and diversity of

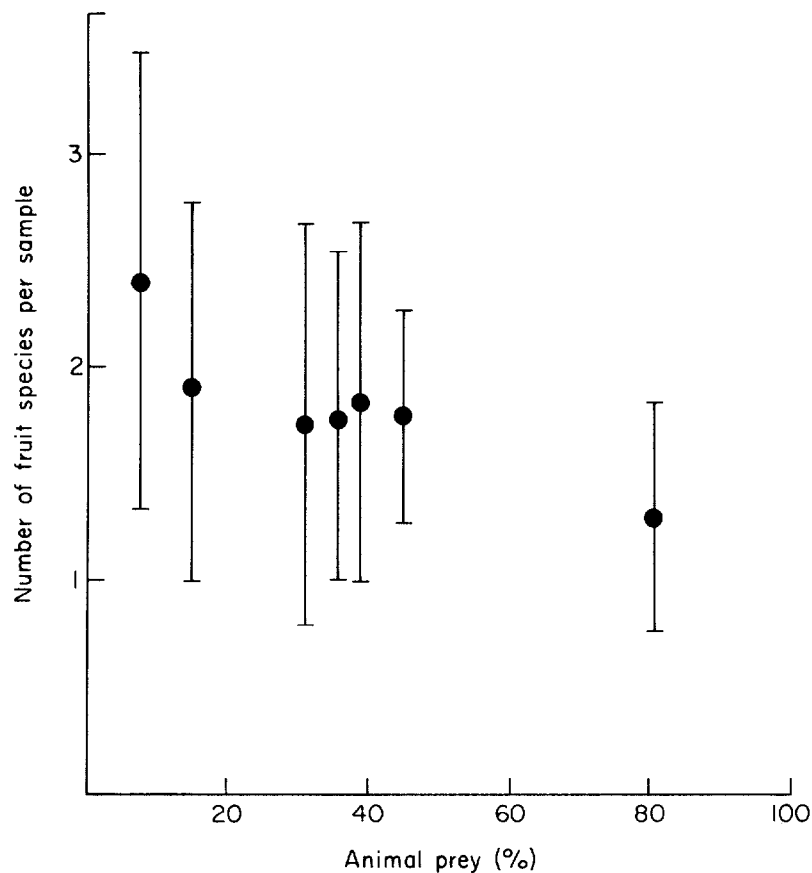


Figure 1. Relationship between the percentage of animal prey in the diet (by volume) and the average number of fruit species in individual faecal samples of *Sylvia* warblers. Segments indicate $\bar{x} \pm 1$ s.d. for each warbler species.

fruits decreases. Only two fruit species were consumed by the Dartford Warbler, the most insectivorous species, but a minimum of 14 were recorded for the Blackcap.

The diversity of the fruit fraction in individual faecal samples was correlated inversely with increasing insectivory across the warbler species (Fig. 1) ($r_{s7} = -0.829$, $P < 0.05$), suggesting that fruits and insects are used as alternative food resources for obtaining the basic nutrients. Thus, individual faecal samples of Dartford Warblers typically include only one fruit species while those of Blackcap may contain up to seven species. Since food processing times for these warblers are extremely short (see below), this implies that the more frugivorous species actually take a very diverse fruit diet even during short feeding bouts.

The overall consumption of each fruit species by the *Sylvia* assemblage was calculated by summing, across plant species, the number of fruits included in the faecal samples analysed for each bird species. Variables characterizing each fruit species were obtained from Herrera (1984a) and Jordano (1984a). These included abundance in the area, fruit diameter, relative yield of pulp with respect to fresh-weight of fruit, and nutrient content (lipids, protein, non-structural carbohydrates and ash, as % dry mass of pulp). These variables were included as independent variables in a multiple regression analysis taking overall consumption by *Sylvia* as the dependent variable. They explain a significant fraction of variation in consumption ($R^2 = 0.8446$, $F_{7,8} = 7.25$, $P = 0.007$) (Table 2). However, only two fruit traits directly determine fruit use by the warbler assemblage.

Fruit diameter explains 40.3% of the variance in consumption levels; the negative sign of the partial regression coefficient ($r_{14} = -0.787$, $P < 0.01$) indicates that as fruit size increases, overall consumption decreases, this being specially marked for fruits with cross width above 7.5 mm (only the Blackcap and Garden Warbler have gapes wider than this). Thus, the relative consumption for species with fruit diameter below 7.0 mm tends to be higher than consumption of fruits wider than 7.0 mm ($U_{15} = 41$, $P = 0.07$, Mann-Whitney U-test). The only additional variable contributing to variance in consumption (although only marginally,

Table 2. Results of multiple correlation analysis between fruit attributes and overall consumption of plant species utilized by *Sylvia* spp.

Variable	R^2	R_{part}	Coefficient	Probability
Fruit diameter	0.403	-0.787	-3.275	$P < 0.01$
Fruit production	0.287	0.719	0.280	$P = 0.08$
Ash	0.089	-0.546	-3.484	n.s.
Protein	0.063	0.535	0.160	n.s.
Relative yield ¹	—	0.092	0.369	n.s.
Nonstructural ¹ carbohydrates	—	-0.097	0.020	n.s.
Intercept	—	—	2.962	—

Notes: $R^2 = 0.8446$, $F_{7,8} = 7.25$, $P = 0.007$ for the whole set of variables.

¹: these variables failed to enter a stepwise, multiple correlation analysis (associated F -to-enter ≤ 4.00) and have only marginal contribution to R^2 .

Fruit production (no. ripe fruits/ha) and diameter were log-transformed prior to analysis; angular transformation was employed with the remaining variables.

$P < 0.08$, Table 1) is fruit production; plant species showing greater fruit production experience a higher overall consumption by the *Sylvia* warblers.

Additional variables, especially those relating to nutrient content, are not directly related to consumption and have only marginal contributions to R^2 . The set of nutrient content variables, considered separately, fails to account for a significant fraction of variance in the dependent variable ($R^2 = 0.474$, $F_{7,8} = 2.25$, $P = 0.14$).

Morphological correlates of frugivory

A summary of relevant variables of external morphology and digestive system is included in Appendix 2. An analysis of multiple correlation of these morphological variables on the frugivory index (see Table 1) is precluded by the low number of cases (warbler species) relative to the number of variables to be included (see e.g., Johnson 1981). Therefore, non-parametric correlations were calculated for single morphological traits and the frugivory index (Table 3). In addition to those variables of external morphology and digestive anatomy (Appendix 2), the 'composite' variables defined by Leisler & Winkler (1985) by means of principal component analysis (PCA) were included. These authors characterized *Sylvia* morphology on the basis of three principal components extracted from PCA of the feeding apparatus, the hindlimb characters, and the forelimb characters. The first component of each analysis characterized *Sylvia* morphology according to the following traits: (1) bill-shape and length of the rectal bristles; (2) foot-size and pelvis-width, and (3) wing-roundness and wing-loading. The six *Sylvia* species were ranked according to their position on the corresponding component (see Figs 3, 4, and 5 in Leisler & Winkler 1985) and these rankings were correlated with the frugivory index (see Table 3).

There are three categories of frugivory, ranging from the strongly insectivorous, small-bodied, Dartford Warbler to the larger, frugivorous, Blackcap and Garden Warbler; an intermediate group includes the three medium-sized species (Common Whitethroat, Subalpine Warbler and Sardinian Warbler). The frugivory index is therefore strongly associated with body-weight (Table 3, Fig. 2). Therefore, the original variables were scaled by body-weight prior to analysis in order to emphasize shape effects. Aside from this effect of body-weight the only external variables

Table 3. Spearman rank correlations between variables related to fruit use and morphology for warbler species (genus *Sylvia*)

	Body-weight	Gape-width	Bill shape ¹	Hindlimb ²	Forelimb ³	Gizzard-weight ⁴	Intestine length ⁴	Liver-weight ⁴
Frugivory index	0.8986*	0.9276**	n.s.	0.8571*	n.s.	n.s.	n.s.	n.s.
Number of fruit species/sample	0.8117*	n.s.	-0.7143*	0.9286**	n.s.	n.s.	n.s.	n.s.

Notes: Probabilities * $P < 0.05$; ** $P < 0.01$; $n = 6$ species.

Variables coded 1–3 correspond to morphological trends as defined by principal components of bill, hindlimb and forelimb characters. The six *Sylvia* species were ranked according to their positions on the corresponding component and these rankings were correlated with the frugivory index and the number of fruit species per sample (see text and Leisler & Winkler 1985).

¹ bill shape: more slender bills, shorter bristles.

² hindlimb: smaller feet, broader pelvis, decreasing clinging ability.

³ forelimb: less pointed wing, higher wing loading.

⁴ these variables were scaled with respect to body-weight prior to analysis (see Methods).

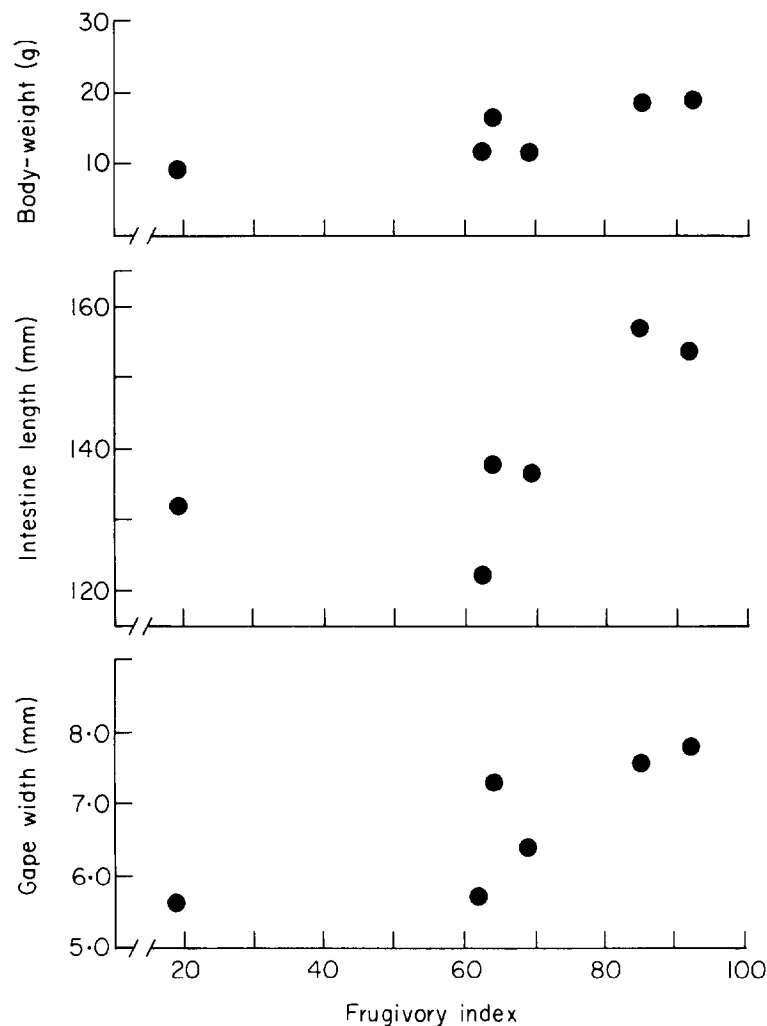


Figure 2. Plots of the frugivory index (product of average frequency of occurrence and average percent volume of fruit material in faecal samples) and morphological variables for six *Sylvia* species. For the three relations, $r_s > 0.820$, $P < 0.05$.

having significant correlations (across species) with the frugivory index were bill-shape, gape-width, and hindlimb (Table 3). Among variables of the digestive system, not one had a significant correlation.

Gape-width strongly limits the size and variety of fruits included in the diet (Fig. 3). The average fruit size consumed (calculated on the basis of the cross-width of each fruit species ingested weighted by its relative consumption) is strongly correlated with gape-width ($r_{s6} = 0.886$, $P < 0.05$). A wider gape determines the inclusion in the diet of a wider range of fruit sizes and a greater reliance on fruit food (Fig. 2). Also, gape-width increases with bill-width at the base and this may explain the negative correlation between the bill shape gradient and the number of fruit species/sample (Table 3). Thus, species with more slender bills, associated with increasing insectivory, experience severe constraints where handling fruits prior to ingestion.

Hindlimb morphology is related functionally to pedal locomotion. High scores in this component were interpreted by Leisler & Winkler (1985) as associated with increased perching ability. Accordingly (see Table 3), species such as Blackcap and Garden Warbler, showing extensive frugivory, score high in this trait; on the other hand, the Dartford and Subalpine Warblers, typical inhabitants of scrub with low bushes, show relatively larger feet with increased clinging ability. Thus, even among

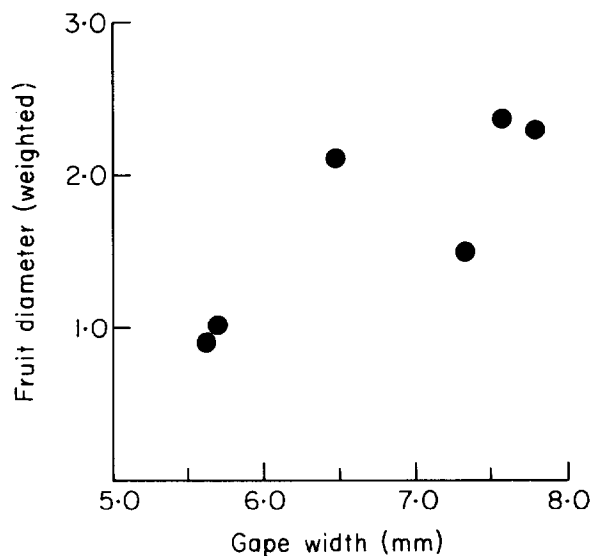


Figure 3. Relationship between gape-width and weighted average fruit diameter in the diet of *Sylvia* warblers. For each bird species, fruit diameter of each plant species in the diet was weighted by its relative consumption in order to calculate the weighted average fruit diameter.

a typical perching genus such as *Sylvia* (Leisler 1980), slight variations in hindlimb morphology may influence frugivory by restricting the accessibility to fruits.

Discussion

Correlates of frugivory

Variation in fruit use by *Sylvia* spp. was closely associated with character variation in external morphology, especially body-weight, bill-shape, and hindlimb. Variation in characteristics of the digestive system failed to relate to the observed gradient in frugivory. Table 4 summarizes the main trends related to frugivory in *Sylvia*.

The marked variation in dependence on fruit for food is determined primarily by external morphology. The evolution of structural modifications of the digestive tract, such as extreme degeneration of the gizzard or shortening of the intestine, might be constrained by the need of processing varied food types of differing digestibilities (McLelland 1979, Herrera 1984b). Information presently available shows that *Sylvia* warblers experience extreme seasonal shifts from strongly frugivorous to totally insectivorous diets (Berthold 1976a, Brensing 1977, Bibby 1979, Jordano & Herrera 1981, Debussche & Isenmann 1983), and these types of constraints may, therefore, operate. However, *Sylvia* GPT's ($\bar{x} = 36.4$ min) are much shorter than GPT in the non-frugivorous Muscicapidae (*Phylloscopus* spp., Firecrest *Regulus ignicapillus*) ($\bar{x} = 49.6$ min) (see Herrera 1984b, Jordano 1984a). Additionally, relative intestine size is larger in *Sylvia* ($\bar{x} = 58.0$ v. 48.7, respectively), but the genus shows a more rapid rate of food processing ($\bar{x} = 3.96$ v. 1.87 mm/min, respectively) (Fig. 4). These trends support the contention of Herrera (1984b) that shorter GPT are an adaptive evolutionary response to fruit-feeding in frugivorous Muscicapidae. Moreover, *Sylvia* spp. exhibit higher rates of food passage through a relatively larger digestive tract: not only are retention times shorter, but the volume of food processed per unit time is greater than in non-frugivorous Muscicapidae. While these traits appear as adaptations to digest a watery, fibreless, low-nutritive food such as fruit pulp (Milton 1981, Sibly 1981), external morphology might constrain the degree of dependence on fruit within the genus.

Table 4. *The main characteristics of Sylvia spp. associated to three basic diet categories*¹

	Frugivorous	Omnivorous	Insectivorous
(1) Breeding range	Central and North Europe	Mediterranean	Mediterranean
(2) Wintering range	Central and North Africa, South Europe	Central and North Africa, circum- Mediterranean	Circum-Mediterranean
(3) Breeding habitat	Tall forest	Tall scrub	Low scrub
(4) Body size	Large (> 15 g)	Medium (10–15 g)	Small (< 10 g)
(5) Bill shape	Robust, wide at base gape > 7.0 mm	Pointed, wide at base gape 6–7 mm	Long, pointed slightly curved gape ≤ 6 mm
(6) Wing	Long, pointed	Intermediate	Short, rounded
(7) Hindlimb	Wide pelvis, relatively small feet	Intermediate	Narrow pelvis, large feet
(8) Species	<i>atricapilla</i> <i>borin</i> <i>nisoria</i> <i>communis</i> <i>hortensis</i>	<i>melanocephala</i> <i>cantillans</i> <i>conspicillata</i> <i>curruca</i>	<i>undata</i> <i>sarda</i>

Note: ¹ Frugivorous: fruits representing ≥ 70% of diet volume; omnivorous, 50–70%; insectivorous, ≤ 25%.

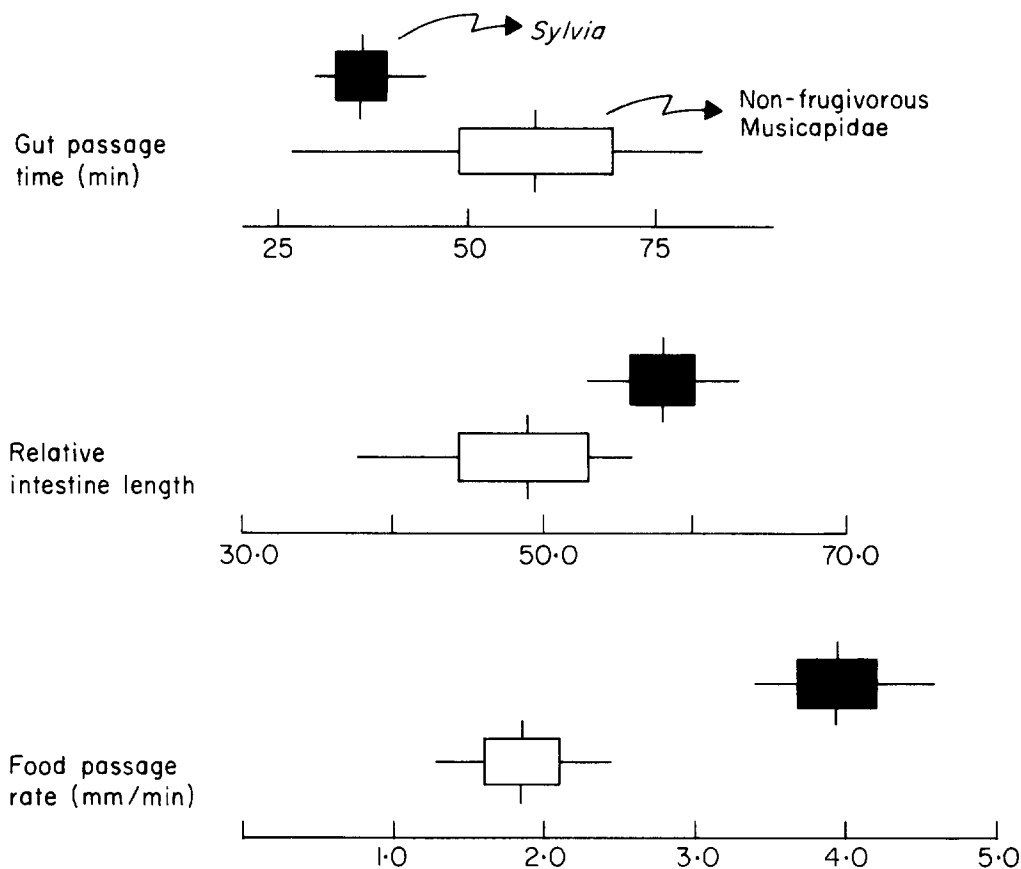


Figure 4. Comparison of food-processing variables in *Sylvia* spp. (see Table 1 and Appendix 2) and non-frugivorous Muscicapidae (*Phylloscopus bonelli*, *P. collybita*, *P. trochilus*, *Regulus ignicapillus*, *Muscicapa striata*, and *Hippolais polyglotta*; data from Herrera 1984b and C.M. Herrera & P. Jordano (unpublished information)). Bars indicate mean, standard error and range. Intestine length was scaled to cube root of body-weight.

Fruits are consumed by every *Sylvia* species examined here, but it is evident from the analysis that extensive reliance on fruit food has been developed only in the particular subset of heavier species (see Table 4). These are characterized by: (1) relatively short, wide at base and robust bills, allowing the inclusion of a wide range of fruits in the diet; (2) a combination of hindlimb characters which provide increased ability to perch and reach fruits; and (3) long wings with high aspect-ratio (also related to migratory distance), allowing both direct and hover flight. Very similar trends have been observed among a variety of tropical taxa (Coerebidae, Snow & Snow 1971; Tyrannidae, Fitzpatrick 1980; Thraupidae, Moermond & Denslow 1985) and have been related to increased frugivory. Correlates of frugivory (Table 4) parallel those found by other authors (Cody & Walter 1976, Leisler 1980, Leisler & Winkler 1985) between character variation, habitat utilization and migration. Frugivory appears well established among the larger-sized species (Barred Warbler *S. nisoria*, Garden Warbler, Blackcap, Common Whitethroat and Orphean Warbler) which are long-distance migrants with wintering grounds centred south of the Sahara (e.g., between 10°N and 10°S latitude) and breeding in a variety of boreal and central European habitats (Moreau 1972, Harrison 1982). Mixed diets with an important animal component are the rule among the smaller species (Sardinian, Subalpine, Dartford and probably also Spectacled *S. conspicillata* and Marmora's *S. sarda* Warblers) with wintering ranges centred between 35 and 10°N latitude (Cody & Walter 1976, Harrison 1982) and breeding centred in scrubland vegetation of the Mediterranean Basin. Fruit consumption in *Sylvia* thus appears as a secondary 'adaptation' in the genus, closely related to the radiation in habitat use and foraging behaviour and probably to the evolution of the characteristic 'leap-frog' migration pattern (see Erard & Yeatman 1966, Berthold 1973, Klein *et al.* 1973). While the ability to exploit fruits appears as a characteristic of the genus closely related to the evolution of functional digestive traits, species-specific morphologies have limited the degree of dependence on fruit food and resulted in the observed gradient of frugivory within the genus.

Fruit traits and consumption by *Sylvia*

Only two variables, fruit size and fruit availability, accounted for a significant fraction of variance in consumption level for a total of 16 plant species. It is worth emphasizing that neither nutrient content nor fruit design variables accounted for a significant fraction of this variation. Thus, the analysis revealed the relevant size-determination of frugivory among *Sylvia* warblers. Wheelwright (1985) also reports a strong size-limitation to frugivory among a diverse set of neotropical birds. However, Johnson *et al.* (1985) failed to find consistent correlates between both nutrient content and fruit size on consumption by several North American passerines. Note that size constraints are probably less limiting for their set of medium-sized birds (averaging 41.6 g body weight) than for *Sylvia* spp. with average body weight of 14.5 g (see also Wheelwright *et al.* 1984). The assemblage of avian seed dispersers in Mediterranean shrubland is dominated by these small birds, as compared to north-temperate and tropical assemblages (Herrera 1984a, Jordano 1984a).

Other things being equal, decreasing fruit size makes ingestion possible for an increasing fraction of the seed dispersers potentially available. This is so because gape-width strongly limits the maximum diameter of fruit that can be profitably handled and swallowed by a frugivore. Thus, fruit-size alone determines to a great extent the number of frugivorous bird species using the fruits (Moermond & Denslow 1985, Wheelwright 1985) but other fruit traits are clearly involved. Gape

limitations of this kind have obvious consequences for seed dispersal because they imply size selectivity by the frugivores. Direct effects include variation in fruit removal rates for conspecific plants differing in fruit size (Howe & Vande Kerckhove 1980, Wheelwright 1985), dispersal of different-sized conspecific fruits by different sets of dispersers (Jordano 1984b) or shifts in the behaviour of legitimate dispersers from swallowing whole fruits to pecking pulp and discarding seeds (Howe & Vande Kerckhove 1981).

Size effects on frugivore foraging should limit primarily the level of dependence on fruit food. If only a small fraction of the fruit species available can be used, sustained frugivory is difficult to achieve. The main limitation arises from the fact that totally or highly frugivorous diets must be diverse: no single fruit species provides the basic combination of nutrients required for sustained activity. In particular, fruits are extremely poor in protein, and show imbalanced combinations of minerals (Foster 1978, Herrera 1981, Moermond & Denslow 1985, Johnson *et al.* 1985). If frugivores are stenophagic on fruit species ingested they must supplement the diet with other items (e.g., insects, nectar) in order to supply adequate amounts of certain nutrients. The strong negative correlation between insect consumption and number of fruit species per sample found in *Sylvia* spp. supports this view.

The smaller-sized *Sylvia* usually concentrate on one or two abundant fruiting species (e.g., *P. lentiscus*, *R. lycioides*, *P. angustifolia*) which are also the 'majors' in the diets of the highly frugivorous Blackcap and Garden Warbler. 'Minor' fruit species, appearing consistently in low proportions in individual samples of these two warblers, are totally absent in the more omnivorous warblers which instead take animal prey. The fact that 'minor' fruits show higher proportions of protein and minerals than the 'major' species (which typically are higher in lipids or carbohydrates, Herrera 1984a) suggests that they may be included in the diet to supply these basic nutrients.

The more insectivorous species should select relatively abundant fruits which minimize searching costs and maximize ingestion rates during the feeding bouts between insect captures. Both sets of omnivorous and frugivorous species can supply their basic energy demand with fruits. The nitrogen and trace-element needs, however, might be actually obtained from different resources, animal prey and 'minor' fruit species, respectively. Together with fruit size, abundance is therefore a key component of fruit choice in these warbler species.

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Appendix

Table 1. Composition of the fruit diet of *Sylvia* species. *n*: number of faecal samples examined and the number containing fruit remains (in parenthesis). *FA*: frequency of appearance of each plant species, % volume: percent volume contributed to the fruit diet, averaged over the faecal samples containing that species (therefore not adding to 100%); *CI*: consumption index, the product of *FA* by % volume. The relative importance of animal prey in the diet is given as $\bar{x} \pm 1$ s.d. of % volume of animal matter in faecal samples. Note that *CI* and animal matter do not add to 100% since *CI* is actually a composite variable of the frequency of appearance of each fruit species and its average volume contribution when present

	Atricapilla		Borin		Communis		Melanocephala		Cantillans		Undata	
	FA %	CI	FA %	CI	FA %	CI	FA %	CI	FA %	CI	FA %	CI
<i>Pistacia lentiscus</i>	93.6	61.10	84.9	42.75	54.6	44.77	77.9	49.37	66.7	40.20	50.0	36.33
<i>Olea europaea</i> ¹	31.5	13.98	2.0	0.71	—	—	5.6	0.55	—	—	—	—
<i>Asparagus acutifolius</i>	3.5	0.64	—	—	—	—	3.1	0.15	—	—	—	—
<i>Rubus ulmifolius</i>	1.6	0.42	19.6	6.80	27.3	4.10	16.9	2.34	14.3	6.68	—	—
<i>Smilax aspera</i>	4.6	0.52	7.8	1.10	—	—	2.6	0.27	—	—	—	—
<i>Phillyrea angustifolia</i>	6.4	2.16	44.4	15.39	18.2	66.8	12.8	2.72	19.0	7.70	—	—
<i>Lonicera periclymenum</i>	0.2	0.16	1.3	0.16	—	—	1.5	0.04	—	—	—	—
<i>Rhamnus lycioides</i>	3.2	0.77	41.8	16.22	34.6	22.8	30.3	12.70	38.1	5.3	—	—
<i>Daphne gnidium</i>	8.6	2.38	19.0	5.10	18.2	9.3	4.6	1.25	19.0	8.27	—	—
<i>Crataegus monogyna</i>	1.3	0.03	—	—	—	—	—	—	—	—	—	—
<i>Myrtus communis</i>	4.6	0.67	—	—	—	—	2.6	0.16	4.8	0.01	16.7	2.02
<i>Rubia peregina</i>	3.0	0.43	11.1	1.93	—	—	—	—	—	—	—	—
<i>Osyris alba</i>	0.5	0.04	2.0	0.01	—	—	0.5	0.05	—	—	—	—
<i>Pyrus bourgaeana</i>	0.5	0.15	—	—	—	—	—	—	—	—	—	—
<i>Tamus communis</i>	—	—	1.3	0.13	—	—	1.0	0.02	—	—	—	—
<i>Asparagus aphyllus</i>	—	—	1.3	0.06	—	—	—	—	—	—	—	—
Unidentified species	0.4	0.08	0.7	0.04	—	—	—	—	—	—	—	—
<i>n</i>	636 (634)		153 (153)		11 (10)		195 (181)		21 (19)		12 (6)	
Animal prey	13.9 ± 20.4		7.6 ± 8.9		29.1 ± 30.7		26.1 ± 31.2		31.7 ± 34.8		61.7 ± 44.1	

Note: ¹ var. *sylvestris*.

Appendix

Table 2. Variables of external morphology and digestive system for *Sylvia* species in mediterranean shrubland from southwestern Spain. See methods for details. Weights are given in g and linear measurements in mm. Figures for internal organs are \bar{x} and s.d. (sample size)

	Wing	Tail	Tarsus	Culmen ¹	Culmen width	Culmen height	Gape width	Body weight	Gizzard weight	Intestine length	Liver weight
<i>Sylvia atricapilla</i>	72.7	60.4	20.8	15.5	4.6	3.5	7.6	18.5	0.5677 0.1105 (40)	156.7 19.4 (40)	0.7420 0.2350 (40)
<i>Sylvia borin</i>	76.9	55.2	20.2	15.5	4.7	3.7	7.8	19.0	0.4159 0.0542 (9)	154.4 10.2 (9)	0.8398 0.2689 (9)
<i>Sylvia cantillans</i>	58.0	54.4	18.3	12.9	3.5	2.8	5.6	11.5	0.2455 0.0341 (6)	122.0 5.7 (6)	0.5038 0.0666 (6)
<i>Sylvia communis</i>	71.0	62.0	21.3	14.9	4.3	3.5	7.3	17.4	0.3887 0.0212 (4)	137.5 7.6 (4)	0.7710 0.0954 (4)
<i>Sylvia melanocephala</i>	59.1	61.0	19.8	14.7	3.6	3.2	6.4	11.5	0.4962 0.1215 (27)	136.8 19.7 (16)	0.4712 0.1029 (22)
<i>Sylvia undata</i>	52.8	63.2	18.8	13.4	3.2	2.7	5.6	9.1	0.3243 0.0671 (11)	131.6 14.6 (7)	0.4356 0.1124 (11)

Note: ¹ to cranium.