LONG-TERM DYNAMICS OF MEDITERRANEAN FRUGIVOROUS BIRDS AND FLESHY FRUITS: A 12-YEAR STUDY

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Abstract. The relationship between fleshy-fruited plants and their vertebrate seed dispersal agents often has been depicted as subject to important interannual variation, but no study has thus far documented such variation on a long-term basis. This paper presents the results of a 12-yr investigation on fleshy-fruited plants and avian frugivores in a Mediterranean montane locality of southeastern Spain. The main objective was to document patterns and correlates of long-term variation in the composition and abundance of fruits and birds, with particular reference to seed dispersers. During October–December (''autumn'' period) 1978–1990, abundance of ripe fruits and birds was assessed in a 4-ha plot in dense, well-preserved sclerophyllous scrub, by means of counts in permanent plots and mist-netting, respectively. Diet composition and fruit preference patterns of *Erithacus rubecula* and *Sylvia atricapilla,* the two most abundant seed dispersers, were also investigated over the same period, using fecal sample analyses. Possible consequences to the birds of annual variation in fruit supply and diet composition were investigated using data on fat deposition levels and recapture rates of mist-netted individuals.

Total fruit abundance (i.e., mean ripe fruit density of all species combined) fluctuated among years between 5.4 ± 11.1 fruits/m^2 (mean $\pm$ 1 SD; 1986) and 77.1 ± 78.0 fruits/m^2 (1989) and was positively related to the amount of rainfall in the preceding spring. Not all fruiting species bore ripe fruits every year, and among those species that did, fruit density fluctuated asynchronously and to variable degrees. Seven out of 13 species exhibited significant supra-annual periodicity in fruit abundance, with fluctuation periods ranging from 2 to 6 yr. Variation in the abundance of each of the six most abundant fruit species was unrelated to annual variation in rainfall. The autumn bird assemblage at the study site was made up of year-round resident species (54.1% of captures, all years combined) that were largely fruit predators (feeding on pulp or seeds without performing dispersal) and of autumn–winter resident species (45.5% of captures) that were largely seed dispersers. Bird abundance, all species combined, ranged between 27.1 and 61.5 captures/100 net-hours for 1987 and 1986, respectively. Depending on year, seed dispersers made up 25.6–75.4% of the total captures, and fruit predators made up 20.9–69.7%. The relative importance of nonfrugivores was always negligible (1.1–9.9%). No correlation existed across years between total fruit abundance and the capture rates of all bird species combined, seed dispersers, or fruit predators. Annual variation in the abundance of seed dispersers was positively related to November mean maximum temperature. At the individual species level, *S. atricapilla* capture rates were correlated with the abundance of the fruits of *Phillyrea latifolia,* a species exhibiting extreme annual fluctuations.

Annual variation in the importance of fruits in the diet of *S. atricapilla* and *E. rubecula* was not significantly related to changes in fruit abundance. Composition of the fruit diet of these species fluctuated markedly among years, and there was little agreement between composition of the diet and of the fruit supply. Certain fruit species were significantly preferred, and others avoided, by both *S. atricapilla* and *E. rubecula.* Ranking of interspecific fruit preferences remained consistent among years and was related to differences in carbohydrate and lipid content of fruit pulp. Fat deposition levels of *S. atricapilla* and *E. rubecula* did not vary among years and were not significantly related to fruit abundance, percentage of fruit volume in the diet, or contribution of lipid-rich fruits to the diet. Return rates of individuals of these species to the study locality in successive wintering periods were very low, and not significantly related to diet composition or fruit abundance. Prevalence of abiotic over biotic determinants of annual variations, extensive decoupling of the long-term temporal dynamics of fruits and dispersers, and the remarkable ''indifference'' of frugivores to variations in the fruit supply all point to the non-equilibrial nature of this assemblage of fleshy-fruited plants and their avian dispersers.

Key words: annual variation; avian frugivory; Erithacus rubecula; *fat deposition; food composition; fruit abundance; fruit choice; long-term patterns; Mediterranean habitats; overwintering birds; Spain;* Sylvia atricapilla.

*The "balance of nature" does not exist and per-
haps never has existed.*

—Elton (1930:16)

INTRODUCTION

Temporal variation in biotic and abiotic parameters
is a cosmically induced, quintessential feature of earth-
ly ecological systems (Preston 1969). This variation
takes place at various hierarchically nested levels, rang-
ing from daily, through annual, up to extremely long-
term, geological time scales (Bennett 1990, Roy et al.
1996). Ecology is concerned with the whole gamut of
temporal variation scales, with paleoecologists focus-
ing on medium- to very long-term patterns and (*neo*)-
ecologists on the shorter term ones. Among the latter,
efforts devoted to the study of temporal variation have
differed considerably in time scales. Although ecolog-
ical investigations have routinely incorporated the anal-
ysis of daily, monthly, or seasonal variation in ecolog-
ical parameters, annual variation has been considered
less often, and published studies based on data from
more than a few years are comparatively scarce. Mean
duration of ecological studies considered in Weather-
head's (1986) survey ($N = 380$ publications) was typ-
ically ~2.5 yr; 66.4% of studies lasted for ≤ 2 yr, and
only 5.2% lasted for ≥ 7 yr. As the causes and potential
ecological and evolutionary consequences of temporal
variation in ecologically relevant parameters differ
qualitatively among temporal scales, it follows that pre-
vailing biases in the choice of temporal frameworks
for ecological studies may lead, at the very least, to
biased ecological knowledge and, at worst, to serious
misinterpretations and misjudgments (see, e.g., Wiens
1977, Holmes et al. 1986, Weatherhead 1986, Acker-
man and Montalvo 1990, Magnuson 1990, Swanson
and Sparks 1990, Silvertown et al. 1994, Gehring et
al. 1997).

Studies on the relationships between animal-dis-
persed, fleshy-fruited plants and their seed dispersal
agents are not an exception to the patterns just noted.
Research in this field during the last two decades has
been characterized not only by a scarcity of long-term
investigations, but also, rather ironically, by frequent
claims of substantial year-to-year variability in fruit–
frugivore relationships and indications that these eco-
logical systems are characterized by intense supra-an-
nual variation (e.g., Herrera 1984*a*, 1985*a*, Fleming
1992, Jordano 1992). The few studies of plant–verte-
brate disperser systems spanning several years have
effectively documented extensive year-to-year varia-
tions in patterns of plant–animal relationships, and in
the efficiency, success, and consequences of frugivory
and seed dispersal, brought about by fluctuations in the
phenology, abundance, and composition of the fruits,
the dispersers, or both (e.g., Herrera 1984*a*, 1988*a*,
Howe 1986, Jordano 1987, 1989, 1993, 1994, Malm-
borg and Willson 1988, Innis 1989, Willson and Whe-

lan 1993, Loiselle and Blake 1994). Given this large
variation, studies of plant–seed disperser systems
should be of relatively long duration in order to en-
hance the probability of disclosing some "invisible
present" (Magnuson 1990) and detecting infrequent,
but consequential, events (Weatherhead 1986). Fur-
thermore, given the long life-span of most fleshy-fruit-
ed plants relative to their dispersal agents (Herrera
1985*b*), long-term studies (duration ≥ 10 yr) become
essential to obtain realistic pictures of the functioning
of these mutualistic systems, to understand the causes
and consequences of their variation, and to comprehend
their evolution (Thompson 1988, Jordano 1993, 1994,
Willson and Whelan 1993).

In this paper, I present the results of a 12-yr study
on the fleshy-fruited plants and the avian frugivores in
a Mediterranean montane habitat of southeastern Spain.
To the best of my knowledge, this is the longest term
study ever conducted on a plant–disperser system. Pre-
vious shorter term studies at the same locality have
documented the major descriptive and functional as-
pects of the site's plant–bird seed dispersal system
(Herrera 1984*a*, *b*, Herrera et al. 1994). These inves-
tigations have shown that, as in other Mediterranean-
climate habitats (Herrera 1995), autumn–early winter
is the critical period for the interaction between the
majority of fleshy-fruited plants and their avian dis-
persal agents. Thus, I will focus here on the analysis
of long-term variation in fruits and birds during the
autumn–early winter period, with particular emphasis
on the consequences of, and responses to, variation in
fruit abundance and composition exhibited by the two
major seed disperser species (*Erithacus rubecula* and
Sylvia atricapilla). Focusing on these two disperser
species alone is justified because other frugivores at
the study site are numerically unimportant and/or have
fruits as only a minor component of their diets (Herrera
1984*a*, Herrera et al. 1994).

At its most basic level, this study aims (1) to doc-
ument patterns and identify correlates of long-term
variation in the composition and abundance of fruits
and birds. Further questions addressed here are related
to the long-term dynamics of the plant–disperser in-
teraction, namely (2) Do the abundances of fruits and
frugivorous birds (particularly seed dispersers) vary in
unison over the years (i.e., to what extent do fruit con-
sumers track abundance of their major food resource
in the long run)? (3) Are there some predictable, long-
term rhythms in the interaction between fruiting plants
and birds that could give rise to concomitant rhythms
in seed dispersal dynamics at the plant community lev-
el? The consequences for seed dispersers of annual
variation in fruit abundance and composition will be
studied by considering the following questions: (4)
Does composition of the fruit diet of seed dispersers
reflect changes in fruit abundance? (5) Do seed dis-
persers exhibit significant fruit preferences and, if they
do, are these preferences consistent over the years? (6)

Does variation in the composition and abundance of the fruit supply influence the body condition or migratory behavior of seed dispersers? Answers to questions 1–6 will help to address the question that provided initial impetus for this study, namely (7) What are the potential implications for plants and bird dispersers of long-term patterns of variation in their interaction?

Study Site and Dates

This investigation was conducted during October–December (henceforth called the ''autumn'' period) 1978–1990, excepting 1984. With only occasional exceptions, ripe, fleshy fruits and frugivorous birds are present in the study locality without interruption from October through March. Although the species composition of birds and fruits experiences little or no change over this 6-mo period, almost all fleshy-fruited species ripen fruits and reach peak fruit densities in October–December; avian frugivores are also most abundant and rely most heavily on fleshy fruits for food during this same period (Herrera 1984*a*, Herrera et al. 1994). This provides justification for focusing only on this fraction of the autumn–winter period to document patterns of annual variation in the interactions of birds and fruits.

The study was carried out in a locality of the Guadahornillos Valley, a well-preserved 2500-ha tract of Mediterranean-type montane forest and tall shrubland located in the Sierra de Cazorla, Jaén Province, southeastern Spain (for descriptions of the vegetation of the region, see Valle et al. 1989, Luque 1995). A 4-ha plot in dense sclerophyllous scrub (3–4.5 m tall, with some sparse ''emergent'' trees up to 15 m in height) was chosen on an east-facing slope of the valley at 1150 m elevation, near Hoyos de Muñoz. This plot is the ''Cazorla'' site of Herrera (1984*a*) and the ''Hoyos'' site of Herrera et al. (1994). Dominant woody species at the site are *Quercus ilex, Phillyrea latifolia, Viburnum tinus,* and *Arbutus unedo.* Fleshy fruit-producing, bird-dispersed species represent a prominent fraction of woody plants in terms of both cover (76.5%) and number of species (65.5%) (for quantitative descriptions of local vegetation, see Herrera 1984*a*, Yela and Herrera 1993, and Herrera et al. 1994).

Climate is of a Mediterranean type. At the nearest weather station with long-term ($N = 40$ yr) data (Vadillo-Castril, 7.5 km from the study site and the same elevation), mean annual precipitation is 1119 mm, most of which (71.4%) falls in October–March. Monthly average temperatures of the coldest (January) and hottest (July) months are 4.1°C and 21.3°C, respectively. Weather records for the 1978–1990 study period are summarized in Fig. 1. Autumn monthly mean temperatures departed little from the average, except in two unusually warm years (1981 and 1983). Annual precipitation did vary widely between years (range 560–1657 mm) and was below the long-term average in 8 out of 13 years. There was also a nearly significant trend for annual precipitation to decrease from 1978 through 1990 (regression coefficient of annual precipitation vs. year = -49.64, $N = 13$, $P = 0.054$; the P value was obtained using a randomization procedure; see *Methods: Data analysis, Statistical testing*).

Methods

Fruit abundance

Abundance of fleshy fruits (berries, drupes, and functionally analogous structures) was assessed every autumn (October–December) by exhaustively counting all ripe fruits borne on plants within 10 permanent 25-m² plots homogeneously distributed over the study site. One to three fruit counts were conducted each year. In years with more than one fruit count, average figures were used. Mean density of ripe fruits (''fruit density'' hereafter, expressed as number of fruits per square meter) was computed for each plant species in each plot, and these figures provide the raw data for the analyses. It must be noted that these estimates of fruit abundance reflect the size of standing ripe fruit crops available to birds, rather than actual fruit production in the habitat. For most years, my data were insufficient to examine patterns of within-season variation in fruit abundance; thus, each year will be characterized throughout this study by single fruit abundance figures (considering species either combined or individually). This neglect of within-season variation in fruit abundance (see, e.g., Herrera 1984*a*: Table 1) is justified by the emphasis of this study on patterns of annual variation.

Bird populations

Mist nets were used to sample bird populations. Ten mist nets (2.5 m in height, 12.5 m in length, four-shelf, 36-mm mesh) were operated on 1–3 occasions, each lasting for 2–5 d, every autumn (October–December). As with any method of sampling bird populations, mist nets are subject to some biases (e.g., Karr 1979, 1981, Pardieck and Waide 1992), yet they have been widely used to obtain bird abundance data for comparative purposes (e.g., Blake and Hoppes 1986, Levey 1988, Blake and Loiselle 1991, Loiselle and Blake 1992). I tested the reliability of mist net sampling under the particular conditions of my study site by comparing monthly mist net captures during October 1989–March 1990 with the results of concomitant bird censuses conducted there on the same dates (Herrera et al. 1994; C. M. Herrera and P. Jordano, *unpublished data*) using a circular-plot method (Reynolds et al. 1980). Monthly abundance values of individual species obtained by the two methods were closely correlated in every month ($r = 0.602$–0.976, $N = 29$ species, $P < 0.001$ in all cases), as were mean abundances for the whole October–March period ($r = 0.958$, $N = 29$ species, $P \ll 0.0001$). Some biases could still occur, however, if reliability of mist net samples were to differ among species with distinct social or foraging behaviors (Remsen
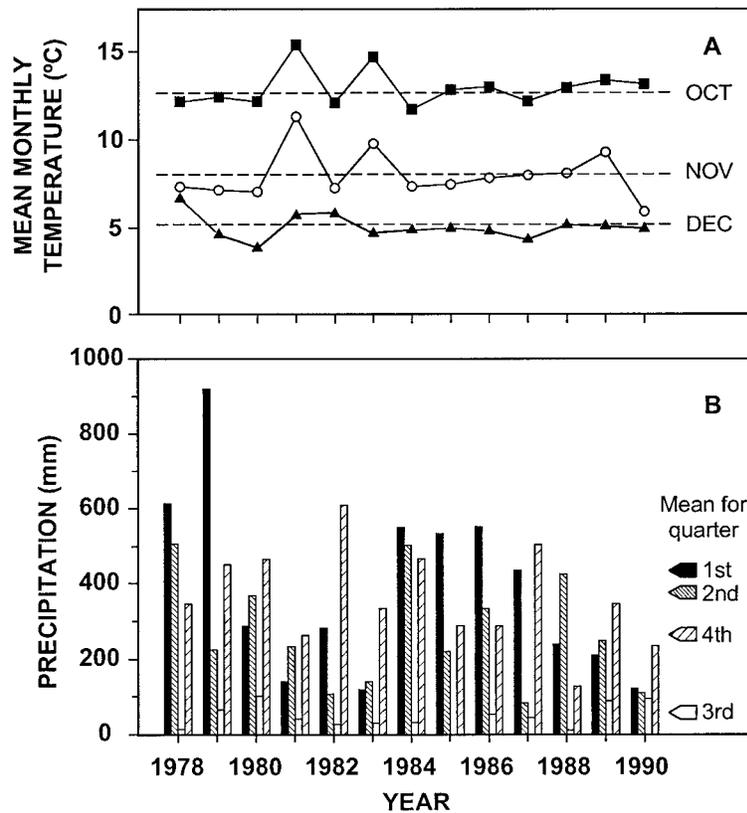
Fig. 1. Annual variation in weather conditions for the study area during the 1978–1990 study period. Meteorological data are from a weather station (Vadillo-Castril) 7.5 km from, and at the same elevation as, the Hoyos de Muñoz study site. (A) Mean monthly temperature for October, November, and December. Horizontal dashed lines indicate long-term ($N = 20$ yr) averages for these months. (B) Quarterly precipitation values. Long-term averages for each quarter (arrows) are based on $N = 40$ yr.

and Good 1996), such as seed dispersers, fruit predators, and nonfrugivores, the three frugivory classes recognized in this study. This possibility was examined, and rejected, by testing for heterogeneity among frugivory classes in the slope of the relationship between census- and mist net-determined mean species abundances ($F_{2,23} = 3.95$, $P = 0.12$; the P value was obtained using a randomization procedure; see *Methods: Data analysis, Statistical testing*). These results make me confident that, under the conditions of this study, mist net samples represent fairly reliable indicators of the size and composition of the local bird community that can be used for comparative purposes.

Nets were always placed in the same locations, which were distributed fairly homogeneously over the study site. As a rule, nets remained open from dawn to dusk on each sampling day, but I temporarily closed them during periods of heavy rain or strong winds. Record was kept of the trapping effort (net-hours) in each netting session. Over the entire 12-yr study period, nets were operated on 75 different dates and total effort was 4852 net-hours (see Appendix B for the distribution among years). Mist-netting was always conducted on the same dates as fruit counts, and net locations were

close (<200 m, for seven nets) or adjacent (for three nets) to some of the permanent plots used for fruit counts. Trapped birds were marked individually using numbered aluminum bands (or the band number was recorded if the bird had been previously banded), weighed to the nearest 0.1 g on a Pesola spring balance within 1 h of capture, and released. During 1978–1980, standard body measurements were also taken on trapped birds.

In total, 32 avian species were mist-netted during this study. For the purpose of some analyses, these were categorized as fruit predators (feeding on the pulp or seeds of fleshy fruits without performing seed dispersal), seed dispersers (ingesting whole fruits and defecating or regurgitating intact seeds), or nonfrugivores (species not eating fleshy fruits), based on information from previous investigations at the same site (Herrera 1984*a*, *b*, Herrera et al. 1994).

As noted for fruit abundance (see *Methods: fruit abundance*), bird abundance data were likewise insufficient to examine within-season patterns of abundance; thus, single abundance figures (considering species combined or individually) were used to characterize each year.

Seed dispersers: diet and body condition

The composition of the diet of *Sylvia atricapilla* and *Erithacus rubecula,* the two most abundant seed dispersers, was investigated using fecal samples obtained from mist-netted birds. The method used, and some of its potential limitations, are described in detail in Herrera (1984*a*), Jordano (1988), and Jenni et al. (1990). The relative contributions to volume made up by animal (arthropod exoskeletal remains) and plant (fleshy fruit remains other than seeds) matter were estimated visually for each fecal sample. Fleshy fruits consumed were identified to species on the basis of seed characteristics (when present) and by microscopic examination of fruit remains and comparison of fruit skin patterns (cell shape and size, presence of glands, trichomes, etc.) with a reference collection of fruit skin microphotographs. For each plant species identified in the sample, the minimum number (or fraction thereof) of fruits represented was estimated from the number of seeds and the amount of fruit pulp and skin, whichever was larger. These data were then combined with information on mean pulp mass per fruit for the different species (Appendix A) to evaluate their importance in the diet. For each bird species and year, the dietary importance of each fruit species was assessed by calculating its proportional contribution to estimated total pulp mass ingested, pooling the data from all fecal samples for that year. This method ignores possible interspecific differences in fruit digestibility and/or processing time, which may lead to biased estimates. Nevertheless, as there are no reasons to expect that the nature of these possible biases varies among years, they presumably will be inconsequential for the comparative analyses conducted in this paper.

Fat reserves play a prominent role during the wintering and migration periods of birds (Blem 1990), and may also be indicative of their health status (Merilä and Svensson 1995). As an indirect way of assessing variations in body condition, I scored trapped individuals of *S. atricapilla* and *E. rubecula* for the amount of fat deposited within the furculum of the clavicle (claviculo-coracoid fat body within the tracheal pit), using a basic scale ranging from 0 (no visible fat) to 4 (bulging lipid depot; for a description, see Herrera 1974). Each interval in this scale was subdivided into two further levels, thus leading to a 13-point scale. The amount of fat in the tracheal pit is known to be a good index of total body fat in small passerines (Blem 1990), but the reliability of fat scores as predictors of actual lipid levels is subject to between-observer variability and varies among species (Krementz and Pendleton 1990, Rogers 1991). Fat scores used in this study were unaffected by interobserver variability, as all determinations were done by me. As found in other species (e.g., Conway et al. 1994), fat scores are also reliable descriptors of total body lipids in *S. atricapilla* and *E. rubecula* (Kaiser 1992), but no data are available to compare the reliability of the method in the two species. For this reason, I will not perform any interspecific comparisons of fat scores.

Data analysis

Statistical testing.—Whenever sample sizes were relatively small or the statistical distribution of the test statistic under consideration was unknown, statistical significance was assessed using either bootstrap or randomization resampling methods (Noreen 1989, Manly 1991; review in Crowley 1992). These instances are denoted in the text by doubly subscripted P values, with the first subscript indicating the resampling method used (b for bootstrap, r for randomization) and the second the number of repetitions (e.g, $P_{b,5000}$ denotes a P value obtained using bootstrap resampling with 5000 repetitions). I wrote all routines for randomization and bootstrapping using SAS Macro Processing Language (SAS 1990*b*) and algorithms in Noreen (1989) or Manly (1991). When bootstrap resampling was used to obtain confidence intervals or to compare means, the percentile and distribution shift methods were used.

Analyses conducted in this paper often involve significance testing of arrays of concurrent statistical tests that address a common null hypothesis (see, e.g., *Results: The bird assemblage, Correlates of variation: individual species*). The probability of obtaining some statistically significant result by chance alone is inflated in these cases; thus, the probability of committing a Type I error (i.e., rejecting the null hypothesis when, in fact, it is true) is augmented above the nominal $\alpha = 0.05$ used throughout this paper. Despite this, no attempt has been made to adjust significance levels to account for this effect, partly because of the difficulty involved in devising a consistent criterion for deciding when simultaneous-inference significance tests would be required (Rice 1989), and partly as a deliberate attempt to increase the chances of detecting biologically significant (sensu Tacha et al. 1982) relationships. The implications of adopting this liberal procedure of judging statistical significance will be considered later (see *Discussion: Statistical considerations*).

Fruit abundance.—Temporal and spatial patterns of variation in fruit abundance were tested using univariate, repeated-measures ANOVA (SAS procedure GLM). Unless otherwise indicated, all analyses in this paper were performed with the SAS statistical package (SAS 1990*a*). Fruit density (log-transformed, and classified by year, plot, and plant species) was used as the dependent variable. ''Year'' was the within-subject (repeated) factor, and ''Plant Species'' and ''Plot'' were included in the model as between-subject factors. Because the data did not meet the sphericity criterion ($\chi^2 = 482.2$, df = 65, $P \ll 0.0001$; Mauchly's criterion applied to orthogonal components), the F statistics for the within-subject factor and interactions were corrected using the Greenhouse-Geisser adjustment (Littell et al. 1991, von Ende 1993).

Annual variability in fruit abundance was evaluated using the coefficient of variation of yearly fruit density (CV = 1 SD/mean), because (1) the occurrence of zeros precluded application of the most usual statistic, 1 SD (log[N]) (e.g., Williamson 1972); and (2) using 1 SD (log[N + 1]) as an alternative would lead to unacceptable biases (McArdle et al. 1990, Crowley and Johnson 1992, McArdle and Gaston 1992). The coefficient of variation provides a reasonably approximate estimator of 1 SD (log[N]), and is an acceptable index of proportional variability that is independent of the mean (McArdle and Gaston 1995).

The existence of supra-annual rhythms in fruit abundance was tested using Legendre et al.'s (1981) method of contingency periodograms to the 1978–1990 time series (missing data for 1984 were interpolated for these analyses). This method was chosen because it is particularly appropriate for analyzing short time series such as the present one (Legendre and Vaudor 1991). Because contingency periodograms require the input of categorical data, quantitative data were first divided into discrete classes, using the optimization algorithms described by Legendre et al. (1981) and Legendre and Vaudor (1991). For each time series analyzed, the contingency statistics B_i ("common entropy," Legendre et al. 1981) was computed for periods of length i = 2–6 yr. Statistical significance of the rhythm with period i was then tested by determining the probability that its associated B_i value differed from zero (the expected value if no periodicity were to exist). A significant B_i value denotes the existence of a rhythm of period i. Computations and significance testing were done using program PERIOD (Version 2.0b) in the R statistical package (Legendre and Vaudor 1991).

Bird data.—Individuals of both overwintering and resident species were often recaptured in the same and in different years. Recaptures in different years were used to assess between-year recurrence rate in the study site and to estimate survival rates. The latter was done using program JOLLY (version 24 January 1991) and the standard Jolly-Seber method for open populations, permitting time-specific capture probability and survival probability (Karr et al. 1990, Lebreton et al. 1992, and references therein). Only six species had sufficient long-term recaptures for computing survival rates, and, even in these instances, the number of recaptures was insufficient for evaluating the fit of the data to the model chosen ("Model A" in JOLLY) or allowing analyses of survival rates in relation to individual- or period-based covariates (Lebreton et al. 1992). Mean survival rates over the 1978–1990 study period were thus estimated for these species, and were used only in interspecific comparisons.

The ordinal nature of fat classes may complicate statistical analyses of fat score data (Hailman 1965, Rogers 1991, Greenwood 1992, Scott et al. 1995). Parametric statistical methods may be legitimately applied to fat scores if, in addition to the usual requirements of normality (or at least symmetry about the mean), these are linearly related to actual body lipid content (Rogers 1991). In the absence of data on the actual lipid content of frugivores, I indirectly tested this assumption by simultaneously regressing bird live body mass against fat score, its square (to account for possible nonlinearities), and wing and tarsus length (to control for individual variation in body size). Quadratic regression coefficients for fat score were not significant ($F_{1,33}$ = 0.22, P = 0.64 for *S. atricapilla*; $F_{1,75}$ = 0.48, P = 0.49 for *E. rubecula*), whereas linear coefficients were highly significant ($F_{1,34}$ = 10.73, P = 0.002 for *S. atricapilla*; $F_{1,76}$ = 71.51, $P \ll 0.001$ for *E. rubecula*), which indicates that, after controlling for body size, body mass was linearly related to fat score in both species. This result, along with a reasonably symmetrical distribution of fat scores about the mean, provide justification for my use of conventional parametric statistical methods with fat score data.

Johnson's (1980) "rank preference index," RPI (the difference between the ranks of usage and availability), was used to investigate the existence of fruit preferences among seed dispersers. Because most fruit species tended to contribute relatively little to the fruit diet in any given year, RPI was chosen over other food selectivity indices used previously in analyses of avian frugivory (e.g., Jacobs' [1974] preference index; Loiselle and Blake 1990, Boddy 1991) because of its robustness to the inclusion or exclusion of rare food categories (Johnson 1980, Krebs 1989).

Environmental correlates.—Correlates of annual variation were sought by correlating or regressing variables describing fruit and bird abundance with several weather-related parameters. The maximum number of variables that could be simultaneously included in these analyses was limited by the number of data points (N = 12 yr); thus, I often had to rely on univariate analyses and a relatively reduced number of weather variables. These were chosen rather restrictively, based on biological considerations. Water availability commonly limits photosynthesis and plant growth in Mediterranean-climate habitats (e.g., Arianoutsou-Faraggitaki et al. 1984, Tenhunen et al. 1985), whereas autumn–winter temperatures are known to affect population sizes of small birds wintering in temperate regions (Shields and Grubb 1974, Kricher 1975, Graber and Graber 1979, Spencer 1982, Brittingham and Temple 1988). I thus examined rainfall and temperature data when looking for weather correlates of annual variation in fruit- and bird-related variables, respectively. Unless otherwise stated, all weather data used are from the Vadillo-Castril station (see *Study site*).

RESULTS

Annual variation in fruit abundance

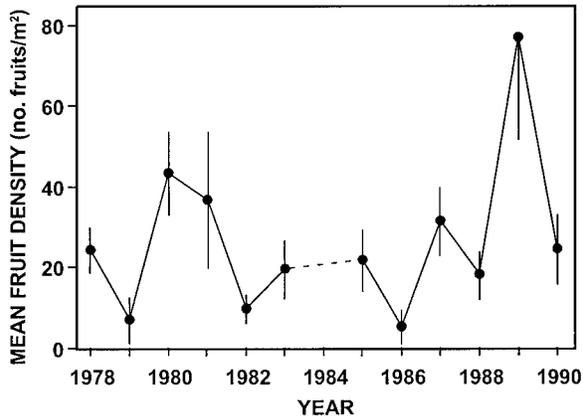*Total abundance.*—Mean ripe fruit density of all species combined ("total fruit density" hereafter) fluctu-

FIG. 2. Annual variation in abundance of fleshy fruits, for all species combined, October–December 1978–1990. Shown are ripe fruit densities (mean ± 1 SE) in 10 permanent 25-m² plots. The dashed line denotes missing data for 1984.

ated broadly and significantly ($F_{11, 1188} = 12.61$, $P \ll 0.001$; Year effect in repeated-measures ANOVA) among years (Fig. 2), ranging from 5.4 ± 11.1 fruits/m² in 1986 to 77.1 ± 78.0 fruits/m² in 1989, (mean ± 1 SD, $N = 10$ plots; this notation is used henceforth, unless otherwise stated). The Year × Plot interaction in the repeated-measured ANOVA was not significant ($F_{99, 1188} = 0.96$, $P = 0.56$), thus indicating that annual variation in fruit density was essentially a habitat-level phenomenon occurring homogeneously over the spatial scale considered in this study.

There was no increasing or decreasing trend in total fruit density over the 1978–1990 period (Fig. 2; regression coefficient of fruit density against year, $b = 1.25$, $N = 12$, $P_{r,5000} = 0.43$), and abundance of fruits in a given year was unrelated to the abundance in either the preceding or the succeeding year ($r = -0.177$, $N = 10$, $P_{r,5000} = 0.57$; correlation between total fruit density in consecutive years). Contingency periodogram analysis, however, did reveal a nearly significant trend for total fruit density to oscillate with a 3-yr periodicity (Table 1).

To look for environmental correlates of annual variation in fruit abundance, I simultaneously regressed total fruit density on four potentially influential weather variables, namely total rainfall during autumn (October–December) of the current and preceding year, the previous spring (March–June of the same year), and the preceding 12-mo period. The fitted multiple regression was statistically significant ($F_{4,7} = 6.97$, $P_{r,10000} = 0.0092$), thus denoting an overall effect of the amount of rainfall on total fruit density. Significant regression coefficients were obtained for the amount of rainfall in the preceding spring ($b = 0.128$, $P_{r,10000} = 0.020$), autumn ($b = -0.115$, $P_{r,10000} = 0.021$), and whole year ($b = -0.073$, $P_{r,10000} = 0.008$), but not for rainfall in the current autumn ($b = 0.059$, $P_{r,10000} = 0.22$).

Individual species.—Not all species bore ripe fruits

every year, and crop sizes of those that did fluctuated between years to variable degrees (Fig. 3 and Appendix A), as revealed by the broad, interspecific variation exhibited by the coefficients of variation (CV, range 51–335%; Appendix A). One extreme of the variability gradient is exemplified by *Phillyrea latifolia,* whose fruiting was essentially an ''all-or-nothing,'' very infrequent event: fruit densities were <5 fruits/m² in 10 yr (including six years without fruit production in my permanent plots), and >30 fruits/m² in two years (Fig. 3 and Appendix A). *Arbutus unedo, Rosa canina,* and *Viburnum tinus* fall on the opposite extreme, with CVs < 100% and relatively predictable, moderate-to-low fruit densities every year.

There was significant interspecific heterogeneity in between-year patterns of variation in fruit density ($F_{132, 1188} = 8.00$, $P \ll 0.0001$; Year × Species interaction in repeated-measures ANOVA). Furthermore, evidence for supra-annual periodicity in fruit abundance was found for seven out of the 13 species tested (Table 1), which exhibited fluctuation periods ranging from 2 to 6 yr. Significant fruiting rhythms ($P \leq 0.05$) were exhibited by *Pistacia lentiscus* (2-yr periodicity), *Viburnum tinus* (3-yr), *Rubus ulmifolius* (5-yr), *Smilax aspera* (5-yr), and *Daphne gnidium* (6-yr periodicity). No significant relationship was found between annual variation in the abundance of any of the six most abundant fruit species (''major'' fruit species hereafter; Fig. 3) and variation in rainfall. None of the multiple regressions between mean annual fruit density of these species and the four rainfall measurements used earlier (see *Total abundance*) was statistically significant ($P_{r,5000} > 0.10$ in all cases).

Interspecific differences in the period of supra-annual rhythms, coupled to the variable fruit densities of component species, led to dramatic fluctuations in the overall species composition of the fruit supply, which ranged from virtually monospecific (e.g., 1980, 1981, 1986, 1987) to fairly diverse (e.g., 1978, 1982, 1989)

TABLE 1. Summary of contingency periodogram analyses testing for supra-annual rhythms in fruit abundance.

	P value, by period				
Fruit species	2 yr	3 yr	4 yr	5 yr	6 yr
Daphne gnidium	0.23	0.28	0.14	0.37	**0.028**
Phillyrea latifolia	0.10	0.10	0.37	0.15	**0.056**
Pistacia lentiscus	**0.025**	0.19	0.14	0.18	**0.09**
Pistacia terebinthus	0.69	**0.050**	0.37	0.59	0.33
Rubus ulmifolius	0.23	0.87	0.33	**0.021**	0.20
Smilax aspera	0.94	0.41	0.80	**0.008**	**0.09**
Viburnum tinus	0.33	**0.042**	0.19	0.13	**0.09**
All species combined	0.56	**0.065**	0.80	0.37	**0.09**

Note: Table entries represent probabilities associated with tests of the null hypothesis that no rhythm in fruit abundance exists for a given periodicity (P values < 0.10 are shown in boldface type). All species with fruit abundance data (Appendix A) were tested, but only those yielding some significant ($P \leq 0.05$) or nearly significant ($0.05 < P < 0.10$) result are included in the table. See *Methods: Data analysis, Fruit abundance* for further details.
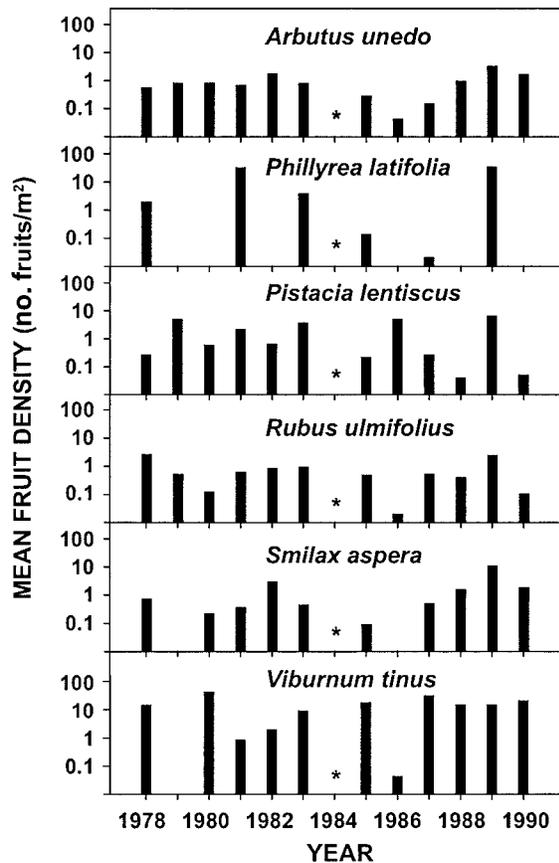
FIG. 3. Annual variation in fruit density of the most abundant fruiting species, October–December 1978–1990 (see Appendix A for data on other species). Note the logarithmic scale on the vertical axis. Asterisks denote missing data for 1984.

(Appendix A). Fruits of *V. tinus* were the most abundant in seven out of 12 years, those of *P. latifolia* and *Pistacia lentiscus* in two seasons each, and those of *S. aspera* in one season (Fig. 3). The relative contribution of the most abundant species to total fruit density was also highly variable, ranging from 28.9% (*Smilax aspera* in 1982) to 94.8% (*Viburnum tinus* in 1987) (Appendix A).

The bird assemblage

Composition.—During the autumn study period, the bird assemblage at the study site was made up largely of year-round residents (54.1% of total captures) or winter immigrants that stay there during October–March (45.5% of captures; "overwintering" species hereafter). See Appendix B for a list of bird species, information on their residence and frugivory status, and a summary of mist net captures.

Frugivory and residence status covaried nonrandomly among species ($P = 0.003$, Fisher's exact-probability test). Most resident species (91.7%) were either fruit predators or nonfrugivores, whereas most species of seed dispersers (92.9%) were nonresident. Fruit predators ($N = 12$ species) and seed dispersers ($N = 14$ species) contributed 48.5% and 46.1% of captures, respectively. The six most abundant species, accounting altogether for 75.7% of all captures ($N = 2042$, all years combined), were the overwintering seed dispersers *Erithacus rubecula* (25.4% of captures) and *Sylvia atricapilla* (14.4%), and the resident fruit predators *Parus caeruleus* (16.0%), *Aegithalos caudatus* (8.6%), *Parus cristatus* (5.7%), and *Parus major* (5.6%).

Variations in abundance.—Bird abundance, all species combined, fluctuated between 27.1 (1987) and 61.5 (1986) captures/100 net-hours (Fig. 4A). Contingency periodogram analysis did not reveal any significant supra-annual rhythm in this magnitude ($P > 0.10$, tests for 2–6 yr periods; results not shown), and there was no trend for increasing or decreasing abundance over the 1978–1990 period (regression coefficient of abundance against year, $b = -0.92$, $P_{r,5000} = 0.30$).

The proportion of captures contributed by seed disperser, fruit predatory, and nonfrugivorous species varied among years ($\chi^2 = 179.53$, df $= 22$, $P \ll 0.0001$). Seed dispersers accounted for between 25.6% (1988) and 75.4% (1981) of captures, and fruit predators for between 20.9% (1981) and 69.7% (1988). Fruit predators were the most abundant group in eight out of 12 years, whereas seed dispersers predominated in the remaining four years (Fig. 4B). This variation was caused by broad, largely asynchronous fluctuations in the abundance of the most common species of seed dispersers and fruit predators (Fig. 5). Out of a total of 15 correlations (across years) between the capture rates of the six most abundant species (Fig. 5), only those corresponding to the *P. caeruleus–P. major* ($r = 0.726$, $N = 12$ yr, $P_{r,5000} = 0.007$) and *E. rubecula–S. atricapilla* ($r = 0.647$, $N = 12$ yr, $P_{r,5000} = 0.014$) pairs were statistically significant, and thus indicative of parallel fluctuations in abundance.

Coefficients of variation of annual abundance (captures/100 net-hours) were similar for seed dispersers (45.3%), fruit predators (37.7%), and nonfrugivores (45.9%), with all species in each group combined, and the three groups did not differ in the degree of relative variability ($\chi^2 = 0.22$, df $= 2$, $P = 0.90$; Kruskal-Wallis ANOVA of proportional deviates from the mean [Sokal and Braumann 1980]). Similar results were obtained when coefficients of variation were computed separately for those species that had been captured in at least half of the study years ("major" bird species, hereafter). Coefficients of variation tended to be smaller for seed dispersers (mean 59.6 ± 9.6, range 51.4–72.9, $N = 4$ species) than for fruit predators (88.9 ± 34.1, range 48.9–145.8, $N = 11$ species), but the difference was not statistically significant ($\chi^2 = 1.70$, df $= 1$, $P = 0.19$; Kruskal-Wallis ANOVA). Nonfrugivores were not included in the analysis, because only one species in this group was captured in at least six of the study years.
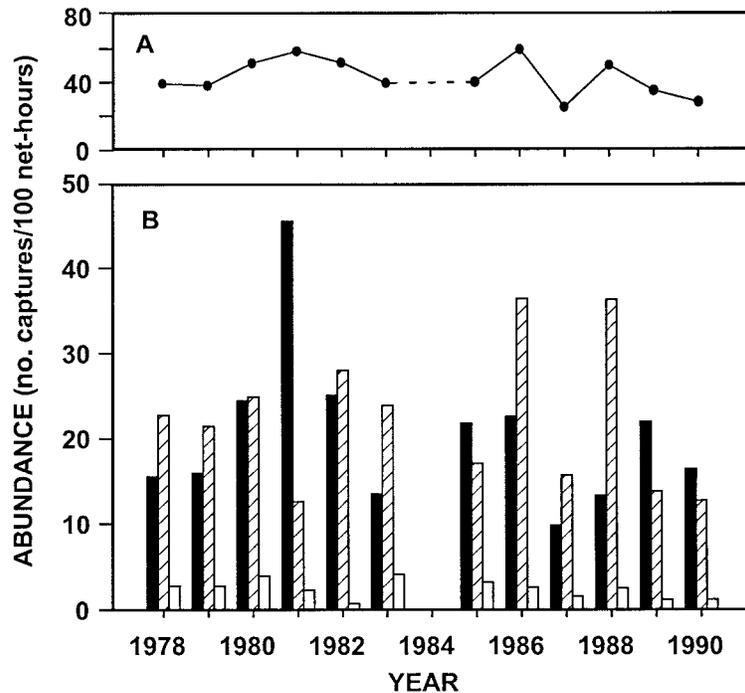
FIG. 4. Annual variation in bird abundance, October–December 1978–1990. (A) Variation in the total number of mist net captures, all species combined (the dashed line denotes missing data for 1984.) (B) Variation in the number of captures of fruit predator (hatched bars), seed disperser (solid bars), and nonfrugivorous (open bars) species. A list of species in each category and mist-netting effort in each study year are shown in Appendix B.

Correlates of variation: species groups.—Annual fluctuation in bird abundance was decoupled from changes in the size of the local fruit supply. Bird abundance was much less variable among years than was fruit abundance, as revealed by a comparison of their CVs (24.8% vs. 73.6% for birds and fruits, respectively, with all species combined in each case). Furthermore, total fruit density was not correlated across years with either the abundance of all bird species ($r = -0.243$, $N = 12$, $P_{r,5000} = 0.46$), seed disperser species ($r = 0.216$, $P_{r,5000} = 0.43$), or fruit predatory species ($r = -0.544$, $P_{r,5000} = 0.064$).

To look for the possible influence of weather on annual variation in bird populations, I correlated total bird abundance with mean monthly maximum and minimum temperatures for October, November, and December. All correlations were statistically nonsignificant ($P_{r,5000} > 0.30$), except for a marginally significant, positive relationship between total bird abundance and November mean maximum temperature ($r = 0.540$, $N = 12$, $P_{r,5000} = 0.069$). To examine this trend further, I correlated November mean maximum temperature with the abundance of fruit predators, seed dispersers, and nonfrugivores separately. The correlation involving seed dispersers reached significance ($r = 0.676$, $N = 12$, $P_{r,5000} = 0.042$), whereas the other two did not ($P > 0.70$), thus indicating that the relationship between total bird abundance and mid-autumn temperatures reflected an effect of the latter on the abundance of seed

dispersers. *E. rubecula* and *S. atricapilla,* the two most abundant dispersers, are immigrants that come to overwinter in southern Spain from central and midwestern Europe (Cramp 1988, 1992); hence, their abundance at my study site could have been influenced by weather conditions at their region of origin in early autumn. To test this possibility, I correlated the combined abundance of these two species with the October maximum and minimum mean temperatures in Bonn, Germany (49° 52′ N, 7° 9′ E). The correlation with mean minimum temperatures was not significant ($r = -0.301$, $N = 12$, $P_{r,5000} = 0.37$), whereas that with mean maximum temperatures was negative and marginally significant ($r = -0.547$, $N = 12$, $P_{r,5000} = 0.068$).

Correlates of variation: individual species.—I correlated (across years) the abundance of every major bird species ($N = 16$) with the abundance of all fruit species combined and of every major fruit species ($N = 6$). Out of 112 correlation coefficients obtained (mean -0.069 ± 0.287, 2.5–97.5% quantiles = -0.542–0.544), the one for the relationship between *Phillyrea latifolia* and *Sylvia atricapilla* ($r = 0.751$) stood out as a distinct outlier and was the only correlation reaching statistical significance ($P_{r,5000} = 0.0074$). Fruiting of *P. latifolia* was markedly bimodal (see *Results: Annual variation in fruit abundance: Individual species*), and this positive relationship denotes an increased abundance of *S. atricapilla* in the two
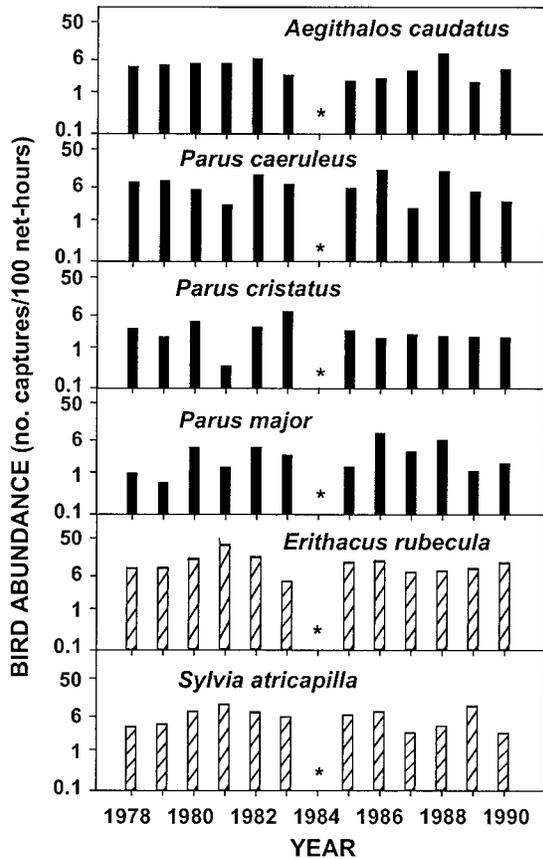
FIG. 5. Annual variation in capture rates of the six most abundant bird species (see Appendix B for data on other species). Resident fruit predators are coded with filled bars, and overwintering seed dispersers are indicated by hatched bars. Note the logarithmic scale on the vertical axis. Asterisks denote missing data for 1984.

massive fruiting events of that species (1981 and 1989; Fig. 6).

Responses of individual bird species to annual variations in temperature were also examined by computing correlations between the abundance of every major bird species and the mean monthly maximum and minimum temperatures for October, November, and December (N = 96 coefficients; mean -0.025 ± 0.300, 2.5–97.5% quantiles = -0.587–0.567). Coefficients with the largest absolute values were those involving the positive relationships between November mean maximum temperature and the abundance of both *S. atricapilla* ($r = 0.655$, $P_{r,5000} = 0.016$) and *E. rubecula* ($r = 0.605$, $P_{r,5000} = 0.073$), and the negative relationship between the abundance of *Phylloscopus collybita* (a scarce, overwintering fruit predator captured in only six years; Appendix B) and the October ($r = -0.662$, $P_{r,5000} = 0.018$) and November ($r = -0.639$, $P_{r,5000} = 0.027$) mean minimum temperatures. In these three immigrant species, at least, mean abundance during the autumn period was directly related to the mildness of November temperatures.

Frugivory of major seed dispersers

Degree of frugivory.—*Sylvia atricapilla* and *Erithacus rubecula* ingested fleshy fruits with similarly high frequencies, but the fruit fraction was more diverse and proportionally more important in the diet of the former species. Fruit remains were present in 100% of fecal samples from *S. atricapilla* ($N = 287$) and in 97.7% of samples from *E. rubecula* ($N = 479$). On average, 2.54 ± 1.04 fruit species were present in individual samples from *S. atricapilla,* as compared to 2.02 ± 0.95 fruit species in those from *E. rubecula* (Fig. 7; $\chi^2 = 41.9$, df = 1, $P \ll 0.0001$; Kruskal-Wallis ANOVA). Fruits contributed $92.1 \pm 13.2\%$ of fecal sample volume in *S. atricapilla,* and only $65.8 \pm 31.7\%$ in *E. rubecula* (Fig. 7; $\chi^2 = 236.4$, df = 1, $P \ll 0.0001$).

The frequency of occurrence of fruits in fecal samples did not vary (*S. atricapilla,* 100% in every year), or varied only slightly (*E. rubecula,* 100% in every year except 1978 [98.2%], 1985 [93.3%], and 1990 [85.4%]), among years. The percentage of volume contributed by fruits to the diet did vary significantly
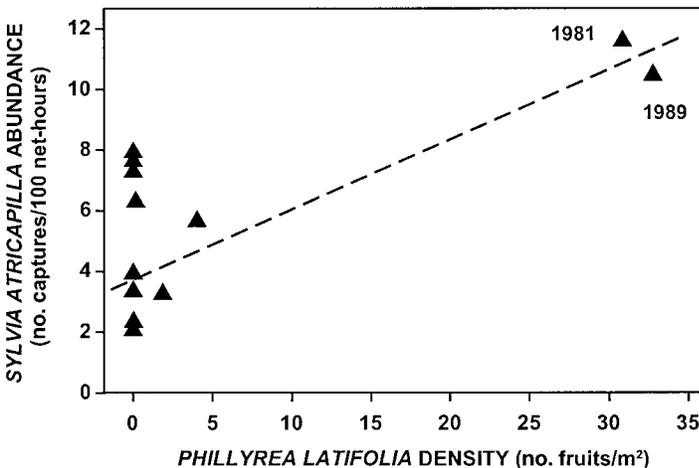

FIG. 6. Annual changes in the abundance of *Sylvia atricapilla* were related to variation in the density of *Phillyrea latifolia* fruits. Data points corresponding to the two years of massive fruiting are identified in the graph (see *Results: Annual variation in fruit abundance, Individual species*). The dashed line is a robust regression ($Y = 3.692 + 0.233X$; $R^2 = 0.856$, $F_{1,7} = 41.46$, $P = 0.0003$), fitted using the least median of squares method (Rousseeuw and Leroy 1987).
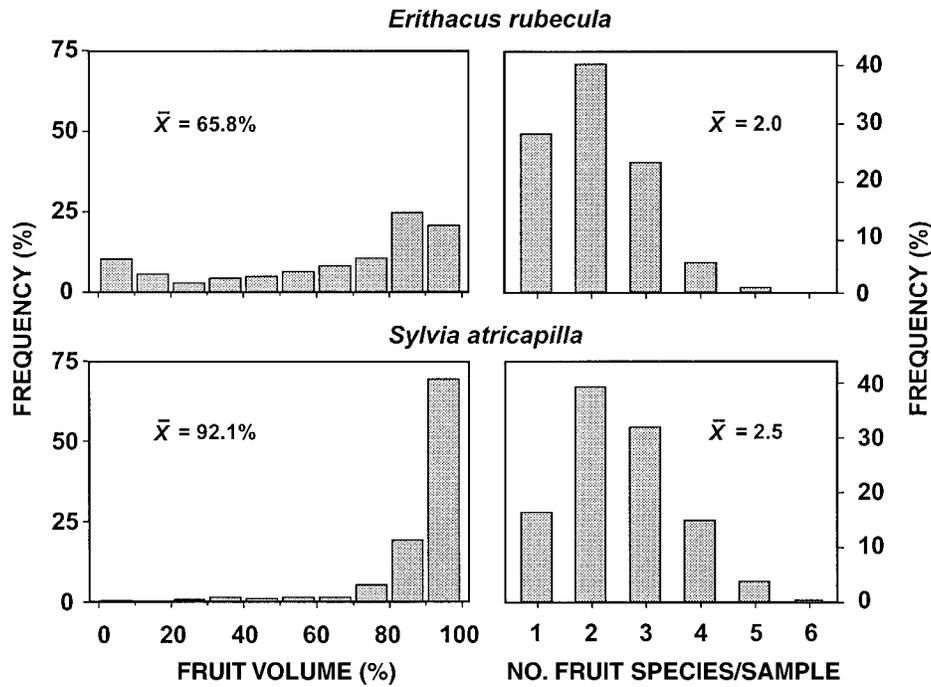
FIG. 7.   Frequency distributions of the relative importance (percentage volume) of fruit remains (left column) and number of fruit species per sample (right column) in fecal samples of *Erithacus rubecula* ($N = 479$) and *Sylvia atricapilla* ($N = 287$), October–December 1978–1990 (all years combined).

among years in both *S. atricapilla* ($\chi^2 = 42.6$, df $= 11$, $P < 0.0001$; Kruskal-Wallis ANOVA) and *E. rubecula* ($\chi^2 = 165.0$, df $= 11$, $P \ll 0.0001$), but the range of annual variation was considerably narrower in the former species (Fig. 8). In *S. atricapilla,* mean percentage of fruit volume in samples ranged between 79.0 $\pm$ 22.9% (1979) and 95.8 $\pm$ 10.6% (1989); in *E. rubecula,* it varied between 22.1 $\pm$ 26.5% (1990) and 91.4 $\pm$ 9.6 (1986) (Fig. 8). In both species, annual variation in

FIG. 8.   Annual variation in the importance of fleshy fruits in the diet of *Sylvia atricapilla* and *Erithacus rubecula* (mean percentage volume of fruit remains in fecal sample). Vertical bars extend over 2 SE of the mean. The dashed line denotes missing data for 1984. See Tables 2 and 3 for sample sizes.

mean percentage of fruit volume per sample was not correlated with variations in fruit abundance (considering either all fruit species combined or each of the six major species separately [*Arbutus unedo, Phillyrea latifolia, Pistacia lentiscus, Rubus ulmifolius, Smilax aspera, Viburnum tinus*]; $P_{r,5000} > 0.15$ in all cases). Likewise, no significant correlation was found between mean percentage of fruit volume per sample and mean monthly maximum and minimum temperatures of October–December ($P_{r,5000} > 0.10$ in all cases).

Diet composition.—On average, the fruit diet of both *S. atricapilla* and *E. rubecula* was dominated by only a few species. Fruits of *Arbutus unedo* and *Pistacia lentiscus* accounted, collectively, for an average of 64.4% and 70.2% of estimated pulp mass ingested by *S. atricapilla* and *E. rubecula,* respectively (Tables 2 and 3). Fruits of *Phillyrea latifolia* contributed a further 17.8% to the fruit diet of *S. atricapilla,* and those of *Viburnum tinus* another 15.5% to the fruit diet of *E. rubecula.*

In particular years, however, fruit food composition often departed noticeably from average values (Tables 2 and 3). The two frugivores had relatively diverse diets in certain years (e.g., 1982, 1983, 1985, and 1989 for *S. atricapilla*; 1983, 1985, and 1987 for *E. rubecula*), but in most years, they relied on the fruits of one species that contributed >50% of the estimated pulp mass ingested. This "dominant" fruit species changed between years. The diet of *S. atricapilla* was dominated by *A. unedo* in 1978, 1980, 1987, 1988, and 1990, by
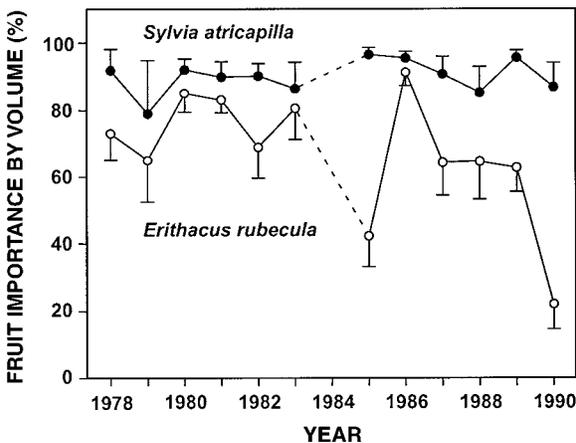
TABLE 2. Composition of the fruit fraction of the diet of *Sylvia atricapilla* at the study site, October–December 1978–1990 (see Fig. 8 for information on the overall importance of fruits in the diet). Entries represent estimates of the percentage contribution of each fruit species to the total dry mass of fruit pulp ingested (see *Methods: Diet of seed dispersers* for details). In each column, the most important species (accounting altogether for ≥50% dry pulp mass) are shown in boldface type.

Fruit species	Percentage of total dry mass of fruit pulp ingested, by year												
	1978 (25)	1979 (7)	1980 (16)	1981 (35)	1982 (13)	1983 (25)	1985 (22)	1986 (12)	1987 (10)	1988 (14)	1989 (98)	1990 (10)	Average
Arbutus unedo	**52.5**	**43.0**	**75.0**	10.5	**22.6**	18.2	**16.8**	11.2	**81.1**	**73.6**	6.2	**87.8**	**41.5**
Daphne gnidium			0.7			0.7	1.2		0.7		0.5		0.3
Juniperus oxycedrus		6.4									0.2		0.6
Lonicera implexa	5.0				12.6		5.0		2.9	6.9	2.0		2.9
Phillyrea angustifolia	1.0	0.7					0.5		0.5		0.2		0.2
Phillyrea latifolia	28.9	5.8		**65.8**		44.3	21.2		1.5	1.5	42.5	1.8	17.8
Pistacia lentiscus	5.0	39.6	9.2	16.5	30.4	28.9	8.6	**87.7**	5.4	3.2	38.6	1.3	**22.9**
Pistacia terebinthus	0.4	3.9			0.2	1.0	8.1				2.3		1.3
Rubia peregrina	1.6	0.5	4.3	0.1		0.3	0.4			0.1	0.8		0.7
Rubus ulmifolius	0.7		1.3	7.0	21.8	2.7	**27.7**			2.2	1.5		5.4
Smilax aspera	1.7		2.8	0.1	7.9	1.9	3.0	1.0	4.1	3.2	4.1	1.4	2.6
Sorbus torminalis					4.5		0.6					5.4	0.9
Viburnum tinus	3.2		6.7			1.9	6.4	0.2	3.9	6.5	1.1		2.5

Notes: N is the number of fecal samples examined, indicated in parentheses for each year. Blank cells indicate that the fruit species was not recorded in feces that year. Species appearing in single fecal samples (*Crataegus monogyna, Ficus carica,* and *Hedera helix*) have been omitted from the table.

P. latifolia in 1981, and by *P. lentiscus* in 1986. The diet of *E. rubecula,* in contrast, was dominated by *A. unedo* in 1978, 1979, 1988, and 1990, and by *P. lentiscus* in 1981, 1982, 1986, and 1989. This frugivore also fed extensively (>35% of the pulp mass ingested) on the fruits of *V. tinus* in 1980 and 1987.

Diet composition and fruit availability.—In most years, the diet composition of the two frugivores reflected poorly the overall composition of the local fruit supply, as judged from the prevalence of nonsignificant correlations between percentage abundance and percentage contribution to the diet of the different fruit species (Table 4). Rank correlations between percentage abundance and percentage contribution to the diet

were statistically significant only in one year for *S. atricapilla,* and in four years for *E. rubecula* (Table 4).

Fruit preferences

The poor agreement between the percentage composition of the diet of frugivores and of the fruit supply available in the habitat suggests the existence of food preferences. Johnson's (1980) rank preference index (RPI, hereafter) was computed for each frugivore, year, and fruit species as the difference between the ranks of usage (percentage of pulp mass contributed to the fruit diet) and abundance (percentage of pulp mass contributed to the local fruit supply).

Average patterns.—Annual RPI values were aver-

TABLE 3. Composition of the fruit fraction of the diet of *Erithacus rubecula* at the study site, October–December 1978–1990 (see Fig. 8 for information on the overall importance of fruits in the diet). Entries represent estimates of the percentage contribution of each fruit species to the total dry mass of fruit pulp ingested (see *Methods: Diet of seed dispersers* for details). In each column, the most important species (accounting altogether for ≥50% dry pulp mass) are shown in boldface type.

Fruit species	Percentage of total dry mass of fruit pulp ingested, by year												
	1978 (56)	1979 (16)	1980 (29)	1981 (91)	1982 (27)	1983 (17)	1985 (45)	1986 (22)	1987 (27)	1988 (27)	1989 (74)	1990 (48)	Average
Arbutus unedo	**65.4**	**66.8**	**48.3**	11.8	8.2	**33.0**	23.9	11.5	23.5	**63.3**	4.1	**51.6**	**34.3**
Daphne gnidium	0.2												0.01
Juniperus oxycedrus												1.2	0.1
Lonicera implexa	0.1										0.1		0.02
Phillyrea latifolia	7.2			26.5		10.3	0.2		0.2	3.0	28.4	1.7	6.5
Pistacia lentiscus	6.8	32.2	13.3	**52.9**	**77.5**	37.2	32.9	**87.0**	30.0	7.2	**53.4**	0.4	**35.9**
Pistacia terebinthus											0.1	0.1	0.02
Rubia peregrina	0.1	0.4	1.0						0.5		1.0	0.2	0.3
Rubus ulmifolius	2.2			0.7	11.0	19.0	**34.8**			9.5	5.6	0.6	7.0
Smilax aspera	0.3		0.1		2.7		0.5		1.3		0.2		0.4
Viburnum tinus	17.6	0.6	**37.3**	8.1	0.6	0.5	7.7	1.5	**44.6**	17.0	6.4	43.9	15.5

Notes: N is the number of fecal samples examined, indicated in parentheses for each year. Blank cells indicate that the fruit species was not recorded in feces that year. Species appearing in single fecal samples (*Hedera helix* and *Sorbus torminalis*) have been omitted from the table.

TABLE 4. Spearman rank correlation coefficients (r_S) between relative abundance in the habitat and relative importance in the diet of *S. atricapilla* and *E. rubecula* of the different fruit species.

Year	*Sylvia atricapilla*		*Erithacus rubecula*	
	r_S	$P_{r,5000}$	r_S	$P_{r,5000}$
1978	0.434	0.157	0.570	0.061
1979	0.329	0.288	0.186	0.542
1980	0.376	0.216	0.444	0.142
1981	0.527	0.085	0.547	0.075
1982	−0.180	0.561	0.083	0.789
1983	**0.709**	0.011	**0.604**	0.036
1985	0.127	0.707	0.240	0.455
1986	−0.121	0.704	0.048	0.888
1987	0.355	0.245	**0.737**	0.005
1988	0.297	0.345	0.369	0.243
1989	0.437	0.152	**0.681**	0.019
1990	0.286	0.373	**0.649**	0.025

Notes: Abundance in the habitat and contribution to the diet were both expressed as percentage of total pulp mass. $P_{r,5000}$ values indicate the statistical significance of the correlation, obtained by randomization and 5000 repetitions. Statistically significant correlations ($P \le 0.05$) are shown in boldface type. $N = 12$ fruit species in all correlations.

aged across years for each fruit species. I considered that, on average, a given fruit species had been significantly preferred or avoided during the study period if zero (the expected value in the absence of preference) fell outside the 95% CI of its mean RPI (obtained from bootstrap resampling with 5000 repetitions).

S. atricapilla and *E. rubecula* significantly preferred certain fruit species over others (Fig. 9). The ranking of preferences was remarkably similar for the two frugivores, and their mean RPI values for the different fruit species were closely correlated ($r = 0.843$, $N = 12$ species, $P_{r,5000} = 0.0006$). Both frugivores highly preferred *Pistacia lentiscus* and *Lonicera implexa* fruits, and avoided those of *Daphne gnidium, Juniperus oxycedrus,* and *Rubia peregrina*. Relatively minor discrepancies between the two frugivores involved the avoidance of *Viburnum tinus* fruits by *S. atricapilla,* and the preference of *E. rubecula* for fruits of *Rubus ulmifolius* (Fig. 9).

The possible dependence of fruit preferences on fruit characteristics related to size (fruit length, diameter, and fresh and dry mass) and nutritional composition of the pulp (water, protein, lipid, soluble carbohydrate, fiber, and ash content), was examined using multiple regression and general linear models. In these analyses, mean RPI was used as the dependent variable and fruit data were taken from Herrera (1987: Tables A1–A2). Due to the small number of fruit species involved ($N = 12$), inclusion of too many independent variables in a single model led to unacceptable reductions in the degrees of freedom of the error term. To avoid this effect, I successively ran different multiple regression models with different subsets of independent variables. When a reduced set of potentially influential fruit variables was identified, general linear models were run that also included interaction terms, until a relatively
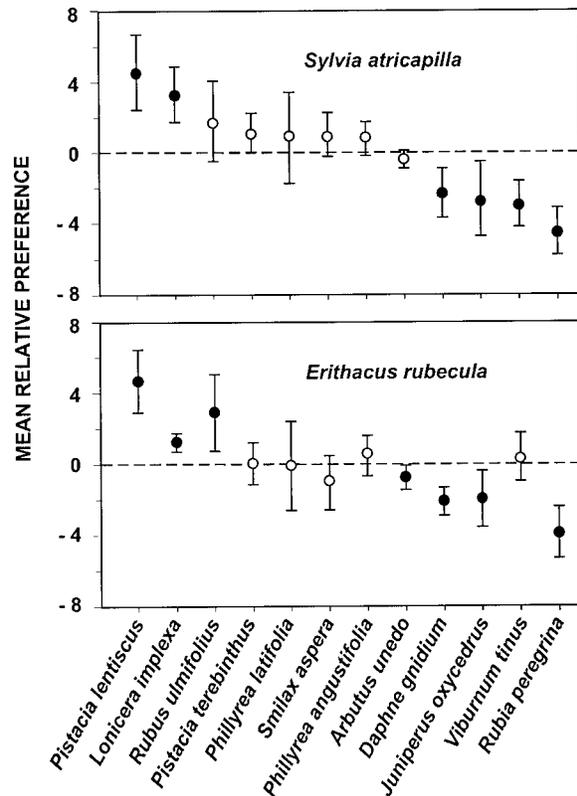

FIG. 9. Mean relative preference of *Sylvia atricapilla* and *Erithacus rubecula* for the fruits of different plants. Relative preference for a given fruit species was obtained in each year as the difference between the ranks of usage (percentage of pulp mass contributed to the fruit diet) and availability (percentage of pulp mass contributed to the local fruit supply), and species means were then obtained for the 12-yr study period. Vertical segments represent the 95% CI of means (obtained by bootstrapping with 5000 repetitions). Means departing significantly from zero (the expected value in absence of preference, denoted by horizontal dashed lines) are shown as solid symbols.

simple model explaining a significant proportion of variance in mean RPI was obtained.

The most parsimonious model explaining differences in fruit preferences had lipid and soluble-carbohydrate contents of the pulp, and their interaction, as independent variables (Table 5). The model explained 76.3% and 60.1% of the variance in mean RPI for *S. atricapilla* and *E. rubecula,* respectively. Both frugivores significantly preferred fruit species whose pulp had either a high lipid or a high soluble-carbohydrate content. The significant negative interaction between lipids and soluble carbohydrates (Table 5) indicates that the preference for one of these components was negatively affected by the abundance of the other; fruit species having pulps with moderate levels of both lipids and carbohydrates tended to be the least preferred.

Annual variation.—The preceding section has focused on "average" patterns of fruit preferences over the 12-yr study period. From the viewpoint of the dy-

TABLE 5. Summary of general linear models testing for the effects of lipid and soluble-carbohydrate content of fruit pulp (as percentage of dry mass, arcsine-transformed) on mean fruit preferences by *Sylvia atricapilla* and *Erithacus rubecula* over the 12-yr study period (Fig. 9).

Effect	b	t	$P_{r,5000}$
Sylvia atricapilla			
Lipids (L)	5.67	4.93	0.001
Soluble carbohydrates (SC)	1.74	4.04	0.007
L × SC	−3.97	4.20	0.002
Erithacus rubecula			
Lipids (L)	4.87	3.26	0.014
Soluble carbohydrates (SC)	1.14	2.04	0.068
L × SC	−3.53	2.88	0.025

Notes: Abbreviations are: *b,* standardized regression coefficient; *t,* Student's *t,*; $P_{r,5000}$, significance of regression coefficient, obtained by randomization and 5000 repetitions. Models are based on $N = 12$ fruit species.

namics of the interaction between frugivorous birds and their food plants, however, it is important to examine the extent to which these long-term preferences are replicated in particular years. In this section, I will thus examine whether (1) the two species of frugivores also exhibit significant fruit preferences in individual years; (2) some fruit species that are not preferred in the long-term are preferred in certain years; and (3) there is significant consistency over the years in the ranking of fruit preferences. Questions (1) and (2) are addressed by comparing yearly RPI estimates with zero using the 95% CI of RPI (obtained by bootstrap resampling of fecal samples with 5000 repetitions). Question (3) is addressed by testing the statistical significance of Kendall's coefficient of concordance (Siegel 1956) for the year × fruit species, RPI matrix.

Both *S. atricapilla* and *E. rubecula* exhibited significant fruit preferences, either positive or negative, when different years were considered separately (Fig. 10). Although there was some annual variation in the degree of preference for individual fruit species, most of these long-term average preferences, documented in the preceding section, tended to be replicated in individual years. In most years, for example, significant, positive preferences existed for *Pistacia lentiscus* and *Lonicera implexa* fruits, and negative ones for fruits of *Daphne gnidium, Juniperus oxycedrus,* and *Rubia peregrina.* For some species, however, the absence of significant, long-term average preferences (e.g., *Phillyrea angustifolia, Smilax aspera*) should be attributed to annual variation in preference patterns, because these spe-

cies were positively preferred in some years and negatively in others. Despite these minor variations around the long-term average trends, there was a highly significant interannual concordance in rank preferences for both *S. atricapilla* (Kendall's $W = 0.428$, $\chi^2 = 56.48$, df $= 11$, $P \ll 0.001$) and *E. rubecula* ($W = 0.376$, $\chi^2 = 49.63$, df $= 11$, $P \ll 0.001$); hence, average preference for the 12-yr study period may be considered representative of the species' fruit selection patterns.

Consequences for frugivores

In this section, I test the possibility that annual variation in composition and abundance of the fruit supply and in composition of the diet of frugivores may translate into annual differences in average body condition and patterns of site fidelity and/or survival.

Visible fat deposition.—As is commonly found among overwintering passerines that are subject only to "daily winter fattening" (Biebach 1996), the vast majority of *S. atricapilla* and *E. rubecula* individuals exhibited moderate-to-low deposits of visible fat during this study. Fat score averages are 1.47 ± 0.75 and 1.46 ± 0.87 for *S. atricapilla* and *E. rubecula,* respectively, all years combined (roughly corresponding to a furcular region half-filled with visible fat). The percentage of individuals with fat scores ≤ 2 was 81.0% in *S. atricapilla* ($N = 294$) and 76.0% in *E. rubecula* ($N = 517$).

Patterns of variation in fat scores were studied by fitting general linear models to data from individual birds. Independent variables included year, time of capture, their interaction, average minimum temperature of the three days preceding capture, and percentage of fruit volume in the fecal sample. Underlying this analysis is the biological assumption that the fat deposition level and fecal sample composition recorded for an individual bird are temporally concomitant, and related to roughly the same, short-term time span (in the order of a few hours) immediately preceding its capture. As in other small passerines overwintering in temperate areas (Newton 1969, Lehikoinen 1987, Rogers and Rogers 1990), fat deposits of *S. atricapilla* and *E. rubecula* overwintering in Mediterranean habitats vary on a daily basis, increasing from dawn to dusk (Ioalé and Benvenuti 1982, Cuadrado et al. 1989, and results shown later in this section). This agrees with the notion of daily winter fattening (Biebach 1996) and effectively points to short-term, daily fluctuations of fat stores that

$\rightarrow$

FIG. 10. Annual variation in the degree of preference of *Sylvia atricapilla* (squares, solid line) and *Erithacus rubecula* (circles, dashed line) for the fruits of different plant species. For each frugivore, year, and fruit species, relative preference was computed as the difference between the ranks of usage (percentage of pulp mass contributed to the fruit fraction of the diet) and availability (percentage of pulp mass contributed to the local fruit supply). Values departing significantly from zero (the expected value if there is no preference, indicated by the horizontal dashed line) are indicative of either positive (>0) or negative (<0) preference and are denoted by solid symbols. Significance of preference values was tested using a bootstrap procedure (see *Results: Fruit preferences* for further details).

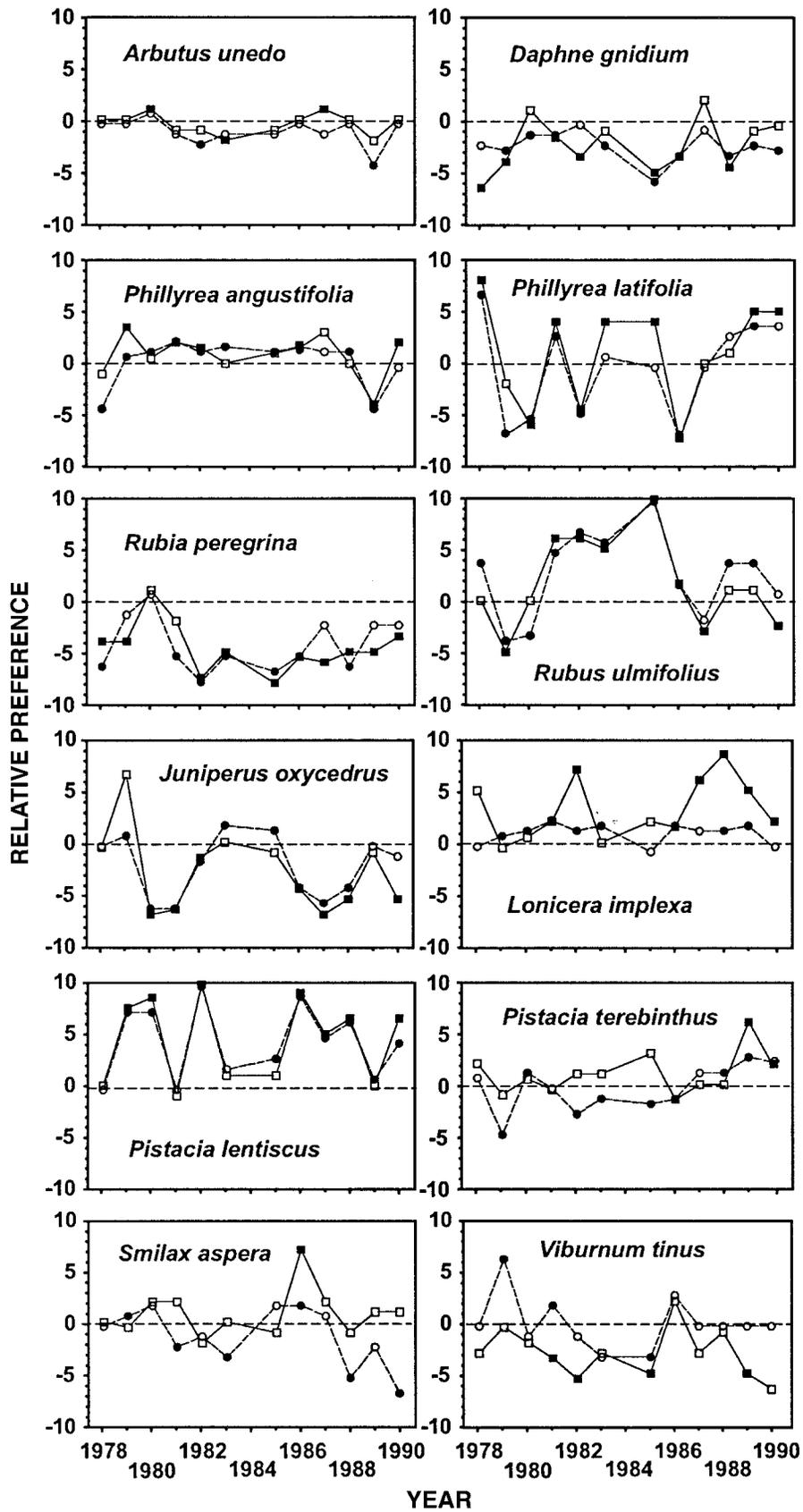LONG-TERM DYNAMICS OF BIRDS AND FRUITS

TABLE 6. Summary of general linear models testing for the effects of year, time of day, ambient temperature, and extent of frugivory on individual variation in visible fat deposition scores of *Sylvia atricapilla* and *Erithacus rubecula.*

Effect	df	MS	F	P
Sylvia atricapilla†				
Year (Y)	11	0.4369	0.95	0.49
Time of day (T)	1	3.9512	8.58	0.004
Y × T	11	0.5203	1.13	0.34
Temperature‡	1	5.1425	11.17	0.001
Percentage fruit in diet	1	1.2309	2.67	0.10
Error	261	0.4604		
Erithacus rubecula†				
Year (Y)	11	0.6314	0.94	0.50
Time of day (T)	1	5.8185	8.64	0.003
Y × T	11	0.6552	0.97	0.47
Temperature‡	1	11.7360	17.42	≪0.001
Percentage fruit in diet	1	0.0027	0.01	0.95
Error	453	0.6737		

† Overall significance of the models: *S. atricapilla,* $F_{25,261}$ = 3.37, R^2 = 0.244, $P \ll 0.0001$; *E. rubecula,* $F_{25,453}$ = 2.66, R^2 = 0.128, $P \ll 0.001$.

‡ Mean minimum temperature of the three days preceding capture.

could be influenced by diet composition. For this reason, too, time of capture of individual birds (range 0645–1745 Greenwich Mean Time) was also included among independent variables of the model.

For both *S. atricapilla* and *E. rubecula,* fat deposition levels did not vary significantly among years and were independent of the extent of frugivory exhibited by individual birds, as there were no significant effects on the fat score of year or percentage of fruit volume in the diet (Table 6). The only significant effects found were time of capture and mean minimum temperature of the 3 d preceding capture. After accounting for the other effects in the model, fat scores were negatively related to minimum temperatures during the preceding days in both *S. atricapilla* and *E. rubecula.* Fat scores increased steadily from dawn to dusk in the two species (results not shown), and the pattern of daily variation remained consistent among years (nonsignificant effect of the Time × Year interaction; Table 6). Fat scores of

S. atricapilla individuals captured within 2 h of sunrise averaged 1.24 ± 0.88 ($N = 43$), whereas individuals captured in the 2 h preceding sunset averaged 2.06 ± 0.57 ($N = 34$). Corresponding figures for *E. rubecula* were 1.43 ± 0.98 ($N = 77$) and 1.71 ± 0.80 ($N = 92$), respectively.

The fruit species eaten by *S. atricapilla* and *E. rubecula* differ widely in the lipid content of fruit pulp, and some of them have very lipid-rich fruits (e.g., *Pistacia lentiscus, P. terebinthus, Viburnum tinus*; Herrera 1987). Thus, I examined the possibility that the species composition of the fruit diet of individual birds could have some short-term effect on their visible fat deposition scores. I fitted general linear models that included the presence/absence of the different fruit species among the independent variables (assuming, as earlier in this section, a high turnover rate for lipid deposits). No evidence was found of any significant short-term effect of the composition of the fruit diet on levels of fat deposition; presentation of these results has been omitted.

Recurrence at the site.—Long-term recapture data for *S. atricapilla, E. rubecula,* and four resident species are summarized in Table 7. Individuals of *S. atricapilla* and *E. rubecula* returned rather infrequently to the site in succeeding years. Only 4.3% of individuals of *S. atricapilla* and 5.2% of individuals of *E. rubecula* were recaptured at least once in subsequent years (recapture rates of the two species did not differ significantly; $P = 0.72$, Fisher's exact-probability test). As would be expected, these recapture rates are considerably lower than those obtained for year-round resident species (range 10.1–44.1%; Table 7). This difference must be attributed to differential recurrence rates in the site, rather than to differences in survival, because annual survival rates were remarkably similar for all species (Table 7).

The percentage of birds recaptured at least once in subsequent years varied significantly with year of capture in *S. atricapilla* (range 0–25%), but not in *E. rubecula* ($P = 0.002$ and $P = 0.40$, respectively; Fisher's

TABLE 7. Recurrence in the study site and estimated survival rate of the most abundant species, based on recaptures of individual birds (October–December 1978–1990).

Bird species	No. individuals captured	No. individuals, by interval to recapture†					Total recaptured after ≥ 1 yr		Mean annual survival rate‡
		1 yr	2 yr	3 yr	4 yr	5 yr	N	%	
Overwintering (Seed dispersers)									
Sylvia atricapilla	256	7	2	1	1	0	11	4.3	0.468
Erithacus rubecula	440	11	6	6	0	0	23	5.2	0.385
Residents (Nonfrugivores and fruit predators)									
Aegithalos caudatus	123	24	7	3	1	0	35	28.5	0.503
Certhia brachydactyla	45	9	4	2	1	0	16	35.6	0.438
Parus cristatus	59	11	7	4	2	2	26	44.1	0.457
Parus major	99	6	2	1	1	0	10	10.1	0.463

† Recaptures during the same study year have not been considered.

‡ Estimated probability that an individual alive in the autumn of year i survives to the autumn of year $i + 1$, computed using the standard Jolly-Seber capture–recapture method for open populations (see *Methods: Data analysis* for details).

exact-probability tests). In *S. atricapilla,* annual variation in recapture rate was not significantly related to variation in fruit abundance, whether considering all species combined ($r = -0.192$, $N = 11$, $P_{r,5000} = 0.58$), or each of the six major fruit species separately ($P_{r,5000} > 0.20$ in all cases), and with variation in mean maximum ($r = -0.483$, $N = 11$, $P_{r,5000} = 0.15$) and minimum ($r = -0.260$, $N = 11$, $P_{r,5000} = 0.43$) temperature for the October–December period.

For *S. atricapilla,* there was a barely significant, negative correlation across years between recapture rate and mean percentage of volume of fruits in the diet ($r = -0.613$, $N = 11$, $P_{r,5000} = 0.045$), suggesting that individuals of this species tended to return to the site less often after years when they had been more extensively frugivorous. I tested this possibility using data for individual birds. Each bird was classified as either recaptured or not recaptured in subsequent years, and this qualitative variable was then regressed on the percentage of fruit volume in its fecal sample, using logistic regression (captures from all years combined). This analysis did not show any effect of the extent of frugivory on the probability of subsequent recapture ($\chi^2 = 0.686$, df $= 1$, $P = 0.41$). The same logistic regression approach was also used to test for the possible effects of consumption of each major fruit species (scored as presence–absence in fecal samples) on the probability of subsequent long-term recapture of individual birds. No evidence was found supporting such an effect for any fruit species, and presentation of these results is omitted.

DISCUSSION

Statistical considerations

A 12-yr data set is a large sample in comparison with most ecological studies, but it is a small one whenever statistical analyses require the use of years as sampling units. For hypothesis testing, the most consequential disadvantage of small sample size is an increase in Type II error (β; the probability of failing to reject a false null hypothesis) and, consequently, a reduction in statistical power ($=1 - \beta$; the probability of rejecting the null hypothesis when it is indeed false; Sokal and Rohlf 1981). Some important results of the present study are based on negative evidence, because statistical analyses often failed to reject one or another version of the generic null hypothesis of long-term independence between birds and fruits. Thus, an assessment of statistical power is needed before positive conclusions can be drawn from these results (Toft and Shea 1983, Peterman 1990). In other words, what is the probability that negative results found here reflect an actual long-term decoupling between birds and fruits, rather than merely reflecting Type II error caused by low statistical power? To save space, I will address this question by examining only the case of the relationship between bird and fruit abundance. Similar reasoning

and equivalent conclusions may be extended to other negative results of this study involving sets of simultaneous statistical tests and sharing the same biological null hypothesis.

Consider the extensive failure to reject the null hypotheses of no relationship between annual variation in fruit abundance (considering major species individually or all combined) and fluctuations in bird abundance (considering species individually or combined into separate frugivory classes). Collectively, these analyses involved testing >100 correlation coefficients for significance, all of which addressed the common *biological* null hypothesis that the abundances of fruits and fruit-eating birds are uncorrelated across years. For $N = 12$ yr and nominal $\alpha = 0.05$, the smallest effect that could be detected in *each individual* correlation analysis with a statistical power of 95%, with $\beta = 0.05$ (''comparative detectable effect size,'' CDES; Rotenberry and Wiens 1985), corresponds to $R^2 = 0.51$ (computed using program GPOWER; Faul and Erdfelder 1992). For the case under consideration, however, this fairly large effect size represents only an upper limit to the true CDES, because, for individual tests, the true $\alpha > 0.05$, since no adjustments were made for increased Type I error derived from multiplicity of tests (see *Methods: Data analysis, statistical testing*). When adjusted α values were obtained using computer simulations (using a modification of Rice's [1989: Appendix] method) for the cases of 3, 10, 20, and 30 simultaneous correlation tests, estimated CDES values (for $N = 12$ and $\beta = 0.05$) became $R^2 = 0.39$, 0.22, 0.11, and 0.05, respectively, thus considerably lower than the single-test figure. This means that we can be 95% confident that, in multiple-test situations in which no significant correlation coefficients between bird and fruit abundance were found, the proportion of total variation accounted for by the ''true'' relationship between the two magnitudes being correlated does not exceed R^2 values in the range 0.05–0.39 (depending on the number of simultaneous tests being conducted). In conclusion, there is little support to argue that persistent failure to detect a supra-annual relationship between bird and fruit abundance is just the consequence of Type II error caused by low statistical power. With a 95% probability level, the existence of a close or even moderately close long-term covariation between the abundance of fruits and fruit-eating birds can safely be ruled out.

In addition to the factors operating in the case of multiple tests, some increase in statistical power, and parallel reduction in CDES, is also expected in all instances in which statistical significance was tested by means of randomization methods with a large number of repetitions. Randomization tests have more power than classical parametric tests when data are from non-standard distributions (Manly 1991), and their power increases with the number of repetitions (Noreen 1989).

The magnitude of these effects, however, cannot be evaluated.

Variation in fruit abundance

Fleshy fruits traditionally have been considered as a resource whose abundance is subject to strong spatio-temporal patterning (Fogden 1972, Karr 1976, Herrera 1985a, Levey 1988, Fleming 1992, Jordano 1992). In contrast to spatial variation, which has been studied in detail at a variety of scales (Herrera 1985a, Blake and Hoppes 1986, Levey 1988, Jordano 1992), temporal patterns remain poorly known except for those occurring at the within-year, seasonal scale (Thompson and Willson 1979, Hilty 1980, Herrera 1984a, Levey 1988, Blake and Loiselle 1991, and many others). The present study seems to be the first to have documented long-term abundance patterns of fleshy fruits at the plant community level (see also Herrera 1988b).

Abundance and composition of fleshy fruits fluctuated dramatically among years in the Mediterranean montane habitat studied. For all species combined, there was a 10-fold variation between extreme years, and even broader variation was exhibited by certain species (e.g., Phillyrea latifolia, Viburnum tinus). For most species studied here, the CV of annual fruit abundance falls in the range reported by Kelly (1994: Fig. 2) for polycarpic plants. On average, however, mean CV of species studied here (158.8 ± 85.4, $N = 13$ species; Appendix A) is greater than that calculated for a set of fleshy-fruited species from temperate, mediterranean, and tropical habitats (CV = 102.7 ± 43.9, $N = 13$ species ($F_{1,24} = 4.45$, $P_{r,5000} = 0.044$). CVs were calculated from data or graphs in studies encompassing ≥4 yr (Davies 1976, Laine 1978, Vander Kloet and Cabilio 1984, Howe 1986, Ågren 1988, Herrera 1988a, Norton and Kelly 1988, Schupp 1990, Jordano 1993; P. Jordano and P. Rey, unpublished data).

Long-term variation in fruit composition and abundance found in this study does not reflect successional changes in the composition of the vegetation, as found by Loiselle and Blake (1994) in some tropical habitats. Although some old disturbances and small, midsuccessional patches occurred at my study site, succession seemed to proceed there at extraordinarily slow rates. Virtually no discernible changes took place during 1978–1990 in the height, vertical structure, or relative cover of woody plant species at the study site (C. M. Herrera, unpublished data). In addition, monotonic declines or increases in fruit abundance over the years were not observed for any species, as would have been expected from the steady changes in abundance of individual species typically associated with successional changes.

For most species studied here, observed annual variation in fruit abundance most likely reflects variations in both the resources available for, and the resources allocated to, fruit production. Water availability commonly limits photosynthesis and plant growth in Med-iterranean-climate habitats (e.g., Arianoutsou-Faraggitaki et al. 1984, Tenhunen et al. 1985). The significant overall effect of the amount of rainfall on total fruit abundance found here, and particularly the positive relationship between fruit abundance and rainfall in the preceding spring (when flowering and early fruit growth takes place; Herrera 1984a), supports a role of resource availability in determining year-to-year variation in fruit abundance at the plant community level. Previous studies in Mediterranean, tropical, and arid habitats (Davies 1976, Foster 1982, Jordano 1987, Chiarucci et al. 1993) have similarly suggested water limitations of fleshy-fruit production.

Moreover, the significant supra-annual rhythmicity in fruit abundance exhibited by several species is consistent with a ''resource accumulation'' hypothesis (Kelly 1994), i.e., plants have to build up sufficient reserves before an abundant fruiting episode. At least seven of the species considered in this study exhibit significant 2–6 yr periodicity in fruit abundance. To my knowledge, these results, along with Vander Kloet and Cabilio's recent (1996) report of biennial berry production in Vaccinium corymbosum, are the only quantitative demonstrations to date of significant periodicity in fruit abundance of fleshy-fruited species. The scarcity of reports of periodicity in the reproduction of fleshy-fruited plants contrasts with the frequency with which the phenomenon has been suggested or documented for dry-fruited species (Janzen 1976, Silvertown 1980, Kelly 1994). This most likely reflects the virtual absence of long-term data for fleshy-fruited taxa, rather than a real difference between the two groups of species. It must also be stressed that, if long-period rhythms (periods ≥ 4 yr) in fruit abundance occur commonly in nature, then studies <8 yr in duration would miss an important proportion of supra-annual rhythms even if they were subjected to contingency periodogram analysis, because this method requires series that are at least twice the length of the period for rhythms to be detected (Legendre et al. 1981, Legendre and Vaudor 1991).

Variation in bird abundance

It has been suggested that the extent of temporal variation in bird populations is related to the nature of food resources and, in particular, that the abundance of frugivores fluctuates more widely among years than that of other trophic groups (Karr 1976, Martin and Karr 1986). The present study does not provide support for this idea (see also Loiselle and Blake 1992), because species of strong frugivores (seed dispersers), occasional frugivores (fruit predators), and nonfrugivores did not differ in population variability, considering either individual species or all species in each group combined. In fact, the mean coefficient of variation for species of seed dispersers (which were extensively frugivorous) was smaller than that for fruit predators (for which fruits played only a minor role in the diet; Her-

rera 1984*a*, Herrera et al. 1994). Mean variability of bird species considered in this study ($cv = 79 \pm 32\%$, $N = 16$ species recorded in ≥ 6 yr) is virtually identical to that found in other long-term studies of birds from tropical ($cv = 88 \pm 60\%$, $N = 10$ species and 6 study years; computations on digitized data from Loiselle and Blake [1992: Fig. 5]) and temperate forests ($cv = 76 \pm 56\%$, $N = 26$ species occurring on at least eight of the 16 study years; Holmes et al. 1986).

Annual variation in the local abundance of frugivorous birds customarily has been interpreted as a response to fluctuations in the abundance of fleshy fruits (e.g., Tyrväinen 1970, 1975, Faaborg et al. 1984, Suárez and Muñoz-Cobo 1984, Martin and Karr 1986). However, relatively few investigations have tested this possibility using quantitative data for both bird and fruit abundance, and even these studies have been based on information from only a few years (e.g., Jordano 1985, 1993, Rey 1995, Kinnaird et al. 1996). At my study site, broad, annual fluctuations in fruit abundance did not seem to have any major effect on the local abundance of either seed dispersers or fruit predators. The only evidence of a response to the fluctuating fruit supply was the significant increase in *Sylvia atricapilla* abundance that took place during the two massive fruiting events of *Phillyrea latifolia*. (I failed to detect this relationship in the data for the period 1978–1987, which encompassed a single fruiting event [Herrera 1988*b*].) In years of massive fruiting, individuals of *S. atricapilla* depended almost exclusively (1981) or extensively (1989) on *P. latifolia* fruits for food (Table 2), which points to the existence of a numerical response of birds to the increased abundance of these fruits. Even in this case, however, the response of the frugivore was rather weak; extraordinary increases in abundance of the food resource brought about only modest increases in abundance of the consumer (Fig. 6). It thus seems safe to conclude that the abundance of frugivores at my study site depended largely on factors other than local fruit availability. Severity of autumn weather did seem to play an important role, as supported by the positive relationships found between mildness of November temperatures and the abundance of species of overwintering frugivores. The marginally significant relationship existing between midwestern European weather in early autumn and the local abundance of *S. atricapilla* and *Erithacus rubecula* further suggests a role of abiotic factors in determining the size of local populations of frugivores. (Recapture in western Germany during the breeding season of one *S. atricapilla* marked in autumn at my study site supports the biological connection implied here between weather conditions in midwestern Europe and population density at my study site; C. M. Herrera, *unpublished data*.)

Decoupling between annual variation in the abundance of fruits and of overwintering frugivores found in this study contrasts with the positive relationship

previously suggested for other southern Spanish, Mediterranean, lowland localities (Jordano 1985, Rodríguez de los Santos et al. 1986, Cuadrado et al. 1995). Three mutually non-exclusive explanations may be advanced to account for these contrasting results. First, previous investigations in lowland habitats perhaps do not reflect actual patterns of variation adequately. For *S. atricapilla*, for example, Cuadrado et al. (1995: 70) assert that ''a strong correlation [exists] between local availability of fleshy fruits and the density [of this species],'' yet, studies cited in support of their claim either lacked quantitative data or were based on observations from only a few sites or years. Secondly, lowland studies were conducted in relatively small ''islands'' of natural vegetation immersed in a ''sea'' of extensively man-modified habitats lacking wild species producing fleshy fruit (Jordano 1985, Rodríguez de los Santos et al. 1986). The extremely patchy nature of fruit resources in the lowlands thus contrasts sharply with the situation in my study region, a continuous extension of >3000 ha of well-preserved Mediterranean forests and scrublands. Hence, contrasting patterns of habitat use and responses to resource variation by frugivorous birds should be expected (Santos and Tellería 1994, Alcántara et al. 1997). Thirdly, it is possible that the abundance of frugivores in autumn–winter is actually determined by fruit abundance in the warmer, and thus climatically less adverse, lowlands, whereas the role of abiotic factors prevails in the climatically more unfavorable montane habitat studied here.

Diet of frugivores

This study has confirmed, on a long-term basis, the extensive frugivory by *Erithacus rubecula* and, particularly, *Sylvia atricapilla* during autumn–winter in Mediterranean habitats (review in Herrera 1995). With 100% of examined feces containing fruit remains and 92.1% of the diet volume made up by fruits (grand mean for all fecal samples), the extent of frugivory of *S. atricapilla* during autumn–winter at my study site (see also Jordano and Herrera 1981, Jordano 1988, Stoate and Moreby 1995) equals or exceeds that reported for some ''specialized'' (sensu Snow 1981) frugivorous birds for which quantitative data on diet composition have been published (e.g., species of Bombycillidae, Pipridae, and Trogonidae; Marini 1992, Remsen et al. 1993, Witmer 1996). Despite broad, annual fluctuation in the size and composition of the fruit supply, the degree of frugivory of *S. atricapilla* changed remarkably little over the years, which contrasts with the variable importance of fruits in the diet of the less extensively frugivorous *E. rubecula*. Similar differences between these two species were found by Jordano (1988, 1989) in a lowland Mediterranean locality. In neither *E. rubecula* nor *S. atricapilla*, however, was annual variation in degree of frugivory significantly related to variation in fruit abundance or weather (temperature) conditions. At least in the case

of *E. rubecula,* fluctuations in the extent of frugivory could perhaps reflect annual changes in insect abundance (Jordano 1989); no data are available to test this possibility, however.

A consequential result of this study is the documentation of marked annual variation in composition of the fruit diet of *E. rubecula* and *S. atricapilla,* involving drastic changes in the identity of the species that predominated in the diet. It is not possible to evaluate the generality of this result, because the vast majority of investigations on frugivore diets either have been conducted in single years or, if encompassing several seasons, report the results of all years combined. Results from the few short-term (duration = 2–4 yr) studies available, however, tend to suggest that annual fluctuations in fruit diet composition of the kind reported here are not exceptional. Malmborg and Willson (1988), in a study of 11 species of frugivorous birds in a North American temperate habitat, found marked annual changes in the principal fruits in the diet of most species. Analogous results have been reported by Jordano (1989) for *E. rubecula* in a southwestern Spanish locality, and by Loiselle and Blake (1990, 1994) for tropical frugivores in second-growth and forest habitats. If future long-term studies confirm the generality of these patterns, then the important corollary would follow that the ecological and evolutionary inferences and generalizations so frequently drawn from short-term studies of frugivore diets will most often be year-dependent. Therefore, extreme caution should be exercised when hypotheses are formulated and/or tested using such data. To illustrate the risks involved in making inferences from short-term dietary studies, consider the presumed distinction between frugivores ''specializing'' on carbohydrate- vs. carbohydrate- and lipid-rich fruit species, recently postulated for temperate frugivorous birds on the basis of single-season (Fuentes 1994) or combined long-term studies (Witmer 1996). My long-term data demonstrate that, depending on the particular year of study, single-year investigations on the diet of *S. atricapilla* would have classed this species as either an indisputable carbohydrate-rich fruit feeder (had investigations been conducted in 1980, 1981, 1987, 1988, or 1990, when the diet was dominated by either *Arbutus unedo* or *Phillyrea latifolia*), or as an unequivocal lipid-rich fruit feeder (had studies been done in 1979, 1986, or 1989; diet dominated by *Pistacia lentiscus*).

Annual variation in the composition of the fruit diet of *E. rubecula* and *S. atricapilla* presumably reflected the response of these species to changes in the abundance and composition of the fruit supply, but diet and fruit supply composition were not related in any simple way. In most years, there were no significant correlations between the rank order of individual fruit species in the diet and in the local fruit supply. This contrasts with the findings of Loiselle and Blake (1994) for a tropical frugivorous bird assemblage. Considering only the most common plant species, these authors found that changes in the combined use of a given fruit species by several species of frugivorous birds paralleled annual changes in the abundance of that fruit species. In the present study, the supra-annual ''decoupling'' between fruit supply composition and usage by *S. atricapilla* and *E. rubecula* is partly a consequence of their distinct fruit preferences.

Fruit preferences

Aviary studies have generally shown that avian frugivores exhibit fine-tuned fruit preferences based on differences in size, color, accessibility, position, and chemical composition of the pulp (e.g., Levey 1987, Avery et al. 1993, 1995, Whelan and Willson 1994, Willson 1994, and references therein). Field investigations have also documented fruit preferences by frugivorous birds, but their results generally have been more ambiguous (e.g., Borowicz and Stephenson 1985, Johnson et al. 1985, McPherson 1987, Jordano 1988, Boddy 1991, and references therein), and comparative field and laboratory studies on the same bird and fruit species have sometimes revealed contrasting results (McPherson 1988, Whelan and Willson 1994). This has led to the notion that diet choice in the field depends importantly upon contextual circumstances and temporal or spatial contingencies, thus rendering consistent selection by frugivores on fruiting traits unlikely (Whelan and Willson 1994).

In contrast with this notion, the present study has shown that *Sylvia atricapilla* and *Erithacus rubecula* did exhibit significant fruit choice, that the two frugivores had virtually the same ranking of fruit preferences, and that preference patterns remained consistent across years, in spite of changes in composition and abundance of the fruit supply. Fruit preferences were best explained by interspecific differences in the nutritional composition of fruit pulp, specifically lipid and carbohydrate content, *and* their interaction. The two frugivores preferred species that either had very high lipid (*Pistacia lentiscus*) or very high nonstructural carbohydrate (*Lonicera implexa, Rubus ulmifolius*) content, and tended to avoid species with a more equitable mixture of these two nutritional components (e.g., *Rubia peregrina, Daphne gnidium, Juniperus oxycedrus*). Previous studies have often reported negative or inconsistent evidence for a role of lipid and/or carbohydrate content in food choice by frugivorous birds (Borowicz and Stephenson 1985, Johnson et al. 1985, Borowicz 1988, Whelan and Willson 1994; but see Stiles 1993, Fuentes 1994). A neglect of the interaction between nutrients may, in some instances, explain these results. In the present study, the effects of lipid and carbohydrates on fruit preference by *S. atricapilla* and *E. rubecula* became statistically significant when, and only when, these two variables *and* their interaction were simultaneously included as independent variables in the model.

Recent studies have emphasized the importance of digestive characteristics as determinants of fruit choice by frugivorous birds, and preference patterns documented in this study may also be interpreted in these terms. Frugivorous birds appear to be process-rate limited (i.e., their rate of ingestion is limited by the rate at which their guts can process food; Levey and Grajal 1991, Levey and Duke 1992), and food retention time in the digestive tract is an essential element of their digestive strategies. Compared to birds feeding on other diets, frugivorous birds are characterized by relatively short food retention times (Herrera 1984*b*, Worthington 1989, Karasov and Levey 1990, Levey and Karasov 1992, 1994). Among frugivores, lipid-rich diets are associated with longer processing times than carbohydrate-rich ones, presumably because of the different mechanisms involved in the digestion and absorption of lipids and carbohydrates (Bosque and Parra 1992, Place and Stiles 1992, Afik and Karasov 1995). Digestion and absorption of dietary lipids is a complex process involving emulsification and hydrolysis, whereas nonstructural carbohydrates are assimilated directly (hexoses) or after a simple hydrolysis (Place and Stiles 1992, and references therein). Efficient processing of lipids and carbohydrates thus requires antagonistic adjustments of food-processing time (Afik and Karasov 1995). I suggest that the preferences of *S. atricapilla* and *E. rubecula* for either lipid-rich or carbohydrate-rich species, and their rejection of fruits with a mixture of the two nutrients, reflect the contrasting physiological mechanisms required for the digestion and assimilation of these two nutrients and the opposite demands that they place on the digestive modulation system (for an analogous interpretation of the possible dichotomy between carbohydrate- vs. lipid-feeding species of frugivorous birds, see Fuentes 1994 and Witmer 1996).

Consequences for birds and plants

Broad differences in abundance and nutritional characteristics (particularly lipid content) of fruit species led me to consider the possibility that annual fluctuations in diet composition could induce changes in body condition and/or short-term migratory behavior of major seed dispersers. No evidence was found, however, in support of this hypothesis. Time of day and mean minimum temperature during the days immediately preceding capture were the only variables significantly related to fat deposition scores in both *Sylvia atricapilla* and *Erithacus rubecula* (see Ioalé and Benvenuti [1982] and Cuadrado et al. [1989] for further data on daily variation in fat deposition in these species). After statistically controlling for the effects of these variables, there was no annual variation in fat deposition scores and no effect of the percentage of fruit volume in the diet. These findings contrast with previous reports of positive relationships between body mass and the extent of frugivory for overwintering *S. atricapilla*

(Jordano 1988) and *E. rubecula* (Debussche and Isenmann 1985). These studies, however, did not simultaneously account for the potential effects of time of day and temperature on body mass; hence, their results could have been affected by spurious correlations between these variables and the extent of frugivory. Fat deposition patterns revealed in this study are relevant to recent models on optimal energy storage in wintering birds (Lima 1986, Rogers 1987, Gosler 1996). These models assume that there are costs incurred by carrying fat, and that fat storage reflects a trade-off between these costs and the benefits derived from insurance against starvation. Fat reserve levels should vary inversely with temperature and resource abundance, and the rate of diurnal fattening should be less steep when food is more abundant. These predictions have received empirical support (Rogers 1987, Gosler 1996), but my results for *S. atricapilla* and *E. rubecula* support them only in part. Despite important annual changes in abundance of fruit resources, neither fat deposition levels nor daily fattening rates (nonsignificant Time × Year interaction, Table 6) of these species varied significantly among years. In contrast, an inverse relationship between fat deposition and temperature did exist, similar to that found in many other overwintering passerines (reviews in Blem 1990, Biebach 1996), further emphasizing the importance of abiotic factors for these frugivores at my study locality.

Annual variation in fruit availability and extent of frugivory did not induce any detectable response among *S. atricapilla* and *E. rubecula* individuals in terms of migratory behavior in subsequent winter seasons. Recapture rates did not differ among years in *E. rubecula,* and variation observed in *S. atricapilla* was unrelated to changes in either fruit abundance or importance of fruits in the diet in the year of first capture. The low long-term recapture rates of these species at the study site (4.3% and 5.2%) were comparable to those found in other Mediterranean wintering localities (Lövei 1989, Cuadrado 1992). These low recapture rates most likely reflect infrequent returns to the study locality in consecutive winters rather than low survival, as survival estimates for these species were similar to those for resident species (which had much higher long-term recapture rates). These results are consistent with previous interpretations (Cuadrado et al. 1995, Herrera 1995) that individuals of these species tend to return in consecutive winters to the same general area, rather than exactly to the same locality. *S. atricapilla* individuals marked at my study site were recaptured up to 150 km away in subsequent winters (C. M. Herrera, *unpublished data*).

Some of the patterns documented in this study presumably have important consequences for the plants, via their effects on fruit removal and seed dispersal success. First, because the relative numerical importance of seed dispersers (mutualists) and fruit predators (nonmutualists) fluctuated among years, concomitant

changes are to be expected in the proportion of fruit crops taken by each group (Jordano 1994). Secondly, some evidence indicates that, at least in some species, decoupling of fruit and seed-disperser abundances leads to disperser satiation and reduced fruit crop removal rates in years of high fruit abundance. In *Viburnum tinus,* for example, fruit removal by the end of the October–March period was 100% in two years of very low fruit production (1979, 1981), but was much lower in two years when fruits were superabundant (22 ± 14% and 51 ± 26% of ripe fruit crops, $N = 17$ plants, for 1978 and 1980, respectively; C. M. Herrera, *unpublished data*). Similar satiation effects have been documented by Herrera et al. (1994) for *Phillyrea latifolia* during years of massive fruiting at the study site, and by Jordano (1987) for *Olea europaea* in a lowland locality. Thirdly, variations in the abundance of seed dispersers, and in the species composition of their fruit diet, probably translated into annual fluctuations in the number and composition of the seeds dispersed and of the eventual number of seedlings recruited. This prediction is supported by results of censuses of *Viburnum tinus* and *Phillyrea latifolia* seedlings in permanent quadrats during 1981–1983, which revealed significant annual variation in the density of 1st-year seedlings of these species (C. M. Herrera, *unpublished data*). Fourthly, the significant consistency in the ranking of interspecific fruit preferences exhibited by the two major seed dispersers, regardless of the size and composition of the fruit supply, demonstrates that, in the long run, seeds of preferred fruit species will have a greater probability of dispersal than those of unpreferred ones. If, as evidenced for *Phillyrea latifolia* (Herrera et al. 1994, Jordano and Herrera 1995), recruitment is generally limited by seed dispersal at the study site, then long-term consistency in the sign and magnitude of fruit preferences provides support to the view that frugivores may, in the long run, influence the specific composition of the local plant community (Herrera 1995).

In summary, there seems to be a major asymmetry in the plant–bird system studied here: dispersal success of plants seems more closely tied to birds than the latter are to fruit composition and abundance (see also Herrera 1984*a*). Body condition and fruit preference patterns of major seed dispersers did not change among years, and their abundance and diet composition did change, but independently of variations in the fruit supply. In contrast, variations in the latter were presumably influential on fruit removal and seed dispersal success of the plants.

CONCLUSION: BIRD–PLANT INTERACTIONS AND THE NON-EQUILIBRIAL REALM

The relationship between major seed dispersers and fleshy-fruited plants at the study locality exhibits most of the elements that have been proposed as indicative of non-equilibrial conditions in ecological systems (Wiens 1984, DeAngelis and Waterhouse 1987), namely important temporal fluctuations, predominance of abiotic over biotic driving factors, and virtually complete decoupling of the temporal dynamics of the plant and bird species most closely involved in the interaction. As a further non-equilibrial element, previous investigations on the same plant–bird system have documented loose patterns of mutual interdependence among species of plants and avian seed dispersers (Herrera 1984*a*). Rather surprisingly, non-equilibrial views of ecological systems have not been applied explicitly to plant–bird dispersal systems, even though recent investigations increasingly suggest that prevailingly non-equilibrial conditions are probably the rule, rather than the exception, in bird communities (e.g., Wiens 1989, Blake et al. 1994, MacNally 1996) and bird–plant seed dispersal systems (Willson and Whelan 1993, Herrera et al. 1994, Jordano 1994). Acceptance of the non-equilibrial nature of the interaction between fleshy-fruited plants and their avian dispersal agents has both practical and conceptual implications. On the practical side, it highlights the need for long-term studies of plant–disperser interactions, as previously stressed by other authors (Jordano 1993, 1994, Willson and Whelan 1993). Annual changes in important descriptive and functional aspects of the plant–disperser interaction may be of such magnitude that short-term investigations will often provide, at best, only uninformative ''snapshots'' of a dynamic system and, at worst, seriously distorted or plainly erroneous pictures (consider, e.g., the arbitrariness involved in assigning *S. atricapilla* to either the carbohydrate- or lipid-feeder category, mentioned earlier). On the conceptual side, non-equilibrial relationships between plants and dispersal agents will lead to temporal inconsistencies in selection pressures associated with the interaction, which will generally operate against mutual adaptations of interacting species (e.g., Herrera 1988*c*, Horvitz and Schemske 1990, Jordano 1993, 1994). Perhaps more importantly, annual variability in fruit production and diet composition of dispersers will presumably translate into strong stochasticity of the demographic consequences of seed dispersal (and, thus, unpredictability from the plants' viewpoint), particularly in the number and species composition of seedlings recruited in the habitat. These as yet unexplored phenomena may influence the local persistence of plant populations, and they could help to explain, for example, the high species diversity of bird-dispersed plants that characterizes Mediterranean undisturbed habitats (Herrera 1995).

After flourishing in the 1980s, the study of the evolutionary ecology of seed dispersal by animals currently faces ''an uncertain development phase'' (Leighton 1995), perhaps as a consequence of the progressive fading of the concept of coevolution as the field's guiding paradigm (Wheelwright 1991). The Achilles' heel of that paradigm was precisely its unjustified reliance on equilibrial assumptions, such as notions of temporal

constancy, strong biotic interdependence, fine-tuning, and reciprocity (Herrera 1985*b*, 1986). I would therefore expect that an explicit consideration of plant–disperser systems as non-equilibrial, and use of the corresponding conceptual tools (DeAngelis and Waterhouse 1987), will stimulate new research directions in this field.

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APPENDIX A

Abundance in the habitat, food value of fruits, and annual variation in abundance of ripe fruits, of fleshy-fruit-producing species at the study site, October–December 1978–1990.

Plant species	Cover (%)†	Fruit pulp mass (mg)‡	Mean ripe fruit density (no. fruits/m²)§					
			1978	1979	1980	1981	1982	1983
Arbutus unedo	15.9	1072.3	0.51	0.78	0.78	0.62	1.69	0.76
Daphne gnidium	1.3	9.5	2.30	0.10	0.22	0.67	1.47	0.81
Juniperus oxycedrus	1.6	180.1	0.04	0	0.23	0.49	0.02	0
Lonicera implexa	0.9	36.7	0.33	0	0	0	0	0
Phillyrea angustifolia	1.1	13.0	0.94	0	0	0	0	0
Phillyrea latifolia	19.1	41.6	1.86	0	0	**30.82**	0	3.88
Pistacia lentiscus	2.3	29.0	0.26	**4.93**	0.58	2.17	0.62	3.67
Pistacia terebinthus	1.6	39.4	0	0.54	0	0.06	0.15	0.10
Rosa canina	0.8	189.1	0.34	0.08	0.13	0.13	0.12	0.18
Rubia peregrina	2.1	12.3	0.76	0.14	0.65	0.10	0.13	0.04
Rubus ulmifolius	7.7	131.2	2.59	0.51	0.12	0.59	0.83	0.96
Smilax aspera	4.0	25.1	0.69	0	0.21	0.34	**2.82**	0.43
Viburnum tinus	18.5	36.4	**13.69**	0	**40.54**	0.81	1.91	**8.74**
All species combined			24.31	7.08	43.46	36.80	9.76	19.58
Contribution of the most abundant species (%)			56.3	69.6	93.3	83.8	28.9	44.7

APPENDIX A. Extended.

Species	Mean ripe fruit density (no. fruits/m²)§						CV¶ (%)
	1985	1986	1987	1988	1989	1990	
Arbutus unedo	0.29	0.04	0.14	0.90	3.01	1.58	89.3
Daphne gnidium	1.09	0.18	0.01	0.78	0.19	0.15	103.6
Juniperus oxycedrus	0	0.01	0.11	0.06	0	0.48	152.5
Lonicera implexa	0.01	0	0	0	0	0	335.4
Phillyrea angustifolia	0	0	0	0	7.00	0	304.4
Phillyrea latifolia	0.15	0	0.02	0	**32.75**	0	210.8
Pistacia lentiscus	0.21	**4.93**	0.27	0.04	6.64	0.05	117.2
Pistacia terebinthus	0.05	0.03	0	0	0	0	198.0
Rosa canina	0.19	0.10	0.06	0.28	0.12	0.22	51.4
Rubia peregrina	0	0	0.03	0.21	0.33	0.19	115.9
Rubus ulmifolius	0.58	0.02	0.52	0.38	2.53	0.10	106.6
Smilax aspera	0.09	0	0.48	1.47	10.39	1.77	186.8
Viburnum tinus	**19.15**	0.04	**29.87**	**14.12**	14.12	**20.05**	93.0
All species combined	21.81	5.35	31.51	18.24	77.08	24.59	73.6
Contribution of the most abundant species (%)	87.8	92.1	94.8	77.4	42.5	81.5	

† Percent vegetative cover at the study site (from Herrera 1984*a,* and *unpublished data*).
‡ Mean pulp dry mass per fruit; data from Herrera (1987).
§ Fruit density estimates represent average densities in 10 permanent 25-m² plots. In each year, the density figure of the most abundant species is shown in boldface.
¶ Coefficient of variation.

APPENDIX B

Summary of bird captures in the course of this study, October–December 1978–1990. *N,* the number of net-hours (trapping effort) per year, is indicated in parentheses in the column headings.

Species	Status†	Mean body mass (g)‡	1978 (762)	1979 (183)	1980 (205)	1981 (310)	1982 (175)	1983 (436)	1985 (380)	1986 (195)	1987 (428)	1988 (405)	1989 (943)	1990 (433)
Fruit predators														
Aegithalos caudatus	R	6.7	31	8	10	15	11	11	7	4	14	34	16	15
Carduelis chloris	OW	24.0	2	1	3	1	0	1	0	0	0	0	6	2
Coccothraustes coccothraustes	OW	46.5	0	1	0	1	2	0	3	1	0	1	3	0
Fringilla coelebs	(R) + OW	21.4	12	2	6	4	1	4	3	3	4	6	13	11
Parus ater	R	8.6	5	1	0	1	1	11	2	5	4	4	11	0
Parus caeruleus	R	10.0	62	16	11	7	21	31	22	31	8	61	45	12
Parus cristatus	R	10.7	20	3	8	1	5	30	9	3	8	7	16	7
Parus major	R	17.6	7	1	8	4	7	11	5	17	13	24	10	7
Phyllocopus collybita	OW	7.1	5	1	1	0	0	0	3	2	0	1	0	0
Prunella modularis	OW	19.8	2	1	1	0	0	1	0	3	2	0	1	0
Pyrrhula pyrrhula	OW	19.0	2	0	0	0	0	0	1	0	0	0	0	0
Regulus ignicapillus	R	5.0	25	4	3	5	1	4	10	2	14	9	9	1
Nonfrugivores														
Carduelis spinus	OW	12.5	0	0	0	0	0	0	0	0	0	9	0	0
Certhia brachydactyla	R	8.4	14	5	4	7	1	11	8	4	5	1	8	5
Dendrocopos major	R	77.1	1	0	0	0	0	5	1	0	0	0	2	0
Emberiza cia	R	22.8	3	0	3	0	0	1	1	1	0	0	0	0
Sitta europaea	R	19.7	1	0	1	0	0	1	1	0	2	0	0	0
Troglodytes troglodytes	R	8.0	2	0	0	0	0	0	1	0	0	0	1	0
Seed dispersers														
Erithacus rubecula	(R) + OW	16.1	66	16	30	100	28	18	45	25	30	30	80	50
Ficedula hypoleuca	FM	14.0	0	0	0	0	1	0	0	0	0	0	0	0
Garrulus glandarius	R	159.3	4	0	0	0	0	0	1	1	0	1	0	0
Luscinia megarhynchos	FM	21.6	0	0	0	0	0	1	0	0	0	0	0	0
Muscicapa striata	FM	14.4	0	0	0	0	0	0	0	0	0	0	1	0
Phoenicurus ochruros	OW	16.2	0	0	0	1	0	0	0	0	0	0	0	0
Phoenicurus phoenicurus	FM	13.6	0	0	0	0	0	3	0	0	0	0	0	0
Sylvia atricapilla	(R) + OW	17.3	25	7	16	36	13	25	24	15	10	14	99	10
Sylvia borin	FM	18.1	0	0	0	0	0	0	0	0	0	0	1	0
Sylvia melanocephala	(R) + OW	11.4	7	3	2	3	2	7	2	2	1	2	6	1
Sylvia undata	OW	9.0	1	0	0	0	0	0	0	0	0	0	0	0
Turdus merula	(R) + OW	86.4	15	2	2	1	0	3	9	1	1	6	12	10
Turdus philomelos	OW	66.3	0	1	0	0	0	2	2	0	0	1	6	0
Turdus iliacus	OW	60.5	0	0	0	0	0	0	0	0	0	0	2	0

† FM, fall migrant; OW, overwintering; R, year-round resident. A few species had both resident and overwintering populations in the study locality. In these cases, overwintering individuals were always far more abundant than resident ones; for the purpose of analyses, these species have been included in the OW category.

‡ Based on data from birds mist-netted in the study site and other nearby localities.