DIETARY SPECIALIZATION ON HIGH PROTEIN SEEDS BY ADULT AND NESTLING SERINS

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Abstract. We examined the possible contributions of food availability and the energetic and nutritional contents of seeds on the diets of adult and juvenile Serins (*Serinus serinus*). We found that Serins are specialized granivores during the breeding season, with a single plant species (*Diplotaxis virgata*) comprising the majority of the diets' adults and offspring. Food availability did not account for this diet specialization. Rather, the high protein and energy content of this plant appears to account for this strong preference and may explain why Serins, unlike almost all other granivorous bird species, do not provision their nestlings with insects. Because Serins and many other species often breed in modern agrosystems, knowledge of feeding adaptations may be invaluable for habitat management.

*Key words: agrosystem, diet specialization, food availability, granivory, protein content,
Serinus serinus.*

Especialización Dietética en Semillas con alto Contenido Proteico por parte de Adultos y Pollos de *Serinus serinus*

Resumen. Este trabajo examina la posible contribución de la disponibilidad de alimento y del contenido energético y nutricional de las semillas en la dieta de individuos adultos y jóvenes de la especie *Serinus serinus*. Encontramos que durante la temporada de cría *S. serinus* se comporta como un granívoro especializado puesto que una sola planta (*Diplotaxis virgata*) constituye la mayor parte de la dieta de adultos y pollos. La disponibilidad de alimento no explica esta especialización trófica. Más bien, el alto contenido proteico y energético de las semillas es lo que parece explicar la fuerte preferencia de *S. serinus* por esta planta y por qué este ave, a diferencia de casi todas las especies de aves granívoras, no alimenta a sus pollos con insectos. Puesto que *S. serinus* y muchas otras especies animales a menudo se reproducen en modernos agrosistemas, el conocimiento de las adaptaciones alimenticias puede ser muy valioso en cuanto a manejo del hábitat se refiere.

INTRODUCTION

Granivorous birds generally shift to an insect diet during breeding (Wiens and Johnston 1977). The traditional explanation for this shift is that nestlings of seed-eaters require a diet supplemented with insects given the relatively low protein contents of most seeds (but see Díaz 1996) and the increased protein requirements of nestling growth (Newton 1967, Wiens and Johnston 1977). This requirement is also evident in frugivores, nectarivores and generally all noncarnivorous species, in which parents must capture invertebrates to feed chicks (Poulin et al. 1992).

Some researchers, however, have proposed that this dietary shift is an opportunistic strategy in seasonal habitats that merely reflects major temporal changes in food availability instead of changes in the nutritional requirements of birds (Wiens and Johnston 1977, Rotenberry 1980). For instance, the highly granivorous Black-faced Dioch (*Quelea quelea*) consumes seeds during the dry season while feeding primarily on insects during the rainy season as an opportunistic response to changing patterns of food availability (Ward 1965).

Many of the factors influencing diet composition and niche breadth in granivorous birds such as bill morphology and seed choice (Newton 1972, Díaz 1990, 1994), life-history traits in relation to seed distribution (Wiens and Johnston

1977), and behavioral processes like social transmission of food preferences (Newton 1972) have been considered in detail. As a result, granivorous birds have become good models for studying niche breadth and resource partitioning (Grant 1986, Price 1987). In contrast to frugivores, where the relation between diet and physiology is well known (Karasov 1990, Levey et al. 1999, Whelan et al. 2000), few studies have analyzed the energy or nutrient content of seeds in terms of feeding decisions by granivores (reviewed by Díaz 1996).

In this study we examined several potential determinants of the dietary preferences of a granivorous bird, the Serin (*Serinus serinus*, subfamily Carduelinae, family Fringillidae), breeding in extensive olive agro-ecosystems in Spain. Cardueline finches have been described as opportunistic in their choice of foods, being able to feed on a wide variety of seed species, supplemented by insects, vegetable matter, and fruits (Newton 1967, Wiens and Johnston 1977). Yet at the same time, they are considered specialized granivores, in that they are able to raise their nestlings almost exclusively on seeds (Newton 1967, Pulliainen 1972, Glück 1985, Borras et al. 2003), making them unique among avian subfamilies studied thus far. Although the seasonal dietary shift from seeds to insects has been known in cardueline finches for many years (Newton 1967, 1972), its causes and consequences remain largely unstudied (but see Díaz 1996). Here we describe the patterns of seed choices by adult Serins during the breeding season, both for themselves and for their offspring, and explore the relative contribution of two potential determinants of the diet: i) the relationship between the energy and nutrient contents of seeds, and seed choices by granivores, and ii) food availability. We also consider the conservation implications of our findings given the profound human impact on Serins habitat.

METHODS

STUDY AREA

This study was conducted in olive orchards located in Jaén province in southern Spain (37°52′N, 3°55′W), which supports the world's highest intensity of olive cultivation. Olive orchards constitute a continuous, uniform landscape of more than 400 000 ha in the province. Trees are planted in rows, keeping a fixed dis-

tance between trees of 12 m in our study plots. We selected three plantations with trees of the same age (ca. 100 years old) that differed mainly on the technique used to eliminate weeds. Within each plantation we selected one plot about 17.6 ha in size, which we refer to as A, B and C. These plots were chosen within central locations of each plantation to maximize the distances to other plantations with different weed communities, although we could not avoid the occurrence of paths with edges where weeds also occurred. The maximum distance between plots was approximately 22 km and the minimum distance was approximately 7 km.

In each of these three study plots nestling Serin diet and food availability were studied during 1990. Plot A was also studied during 1991. Additionally, during 1995 we studied the diet of Serin nestlings in another olive plantation (plot D) where food availability was not measured. The diet of adult and juvenile Serins was studied in 1995 by trapping birds in an artificial drinking trough placed in plot E, an old olive orchard plot surrounded by a large extension of olive tree plantations.

STUDY SPECIES

Serins usually inhabit agro-ecosystems (Cramp and Perrins 1994). In our study area they breed in olive orchards, placing their nests on the outer parts of the olive tree branches. The breeding season is from March to early June. Two clutches are usually laid. Incubation lasts 13 days and the nestling period is 14 days. Both sexes feed young until they become independent 9 days after leaving the nest (Cramp and Perrins 1994). Breeding success is low, approximately 68% of nests fail to fledge at least one nestling (Valera 1992). Nest losses increase rapidly as the season progresses due to the dramatic increase in the frequency of farming activities. Approximately 68% of successful nests belong to first clutches and from the end of April onwards very few nests are successful, thus preventing the sampling of nestling diets from second clutches. During the breeding season Serins feed on milky ripe seeds of weeds by foraging principally on herbs and from the ground (Cramp and Perrins 1994). Little is known about the foraging range of Serins. Steinfatt (in Cramp and Perrins 1994) reports that foraging flights rarely exceed 100 m from the nest.

The two main food plants were *Diplotaxis virgata* (Brassicaceae) and *Erodium* spp. (Geraniaceae). *D. virgata* (hereafter refered to as *Diplotaxis*), a native, annual weed common in southern Spain, reaches a height of 1.5 m and has a tree-like shape. It produces clusters of 20–50 flowers and each flower has an ovary with 30–60 ovules. Full-grown fruits (siliques) are approximately 40 mm long and seeds are about 0.8 × 0.6 mm. The two most common *Erodium* spp. (herafter refered to as *Erodium*) in our study area were *E. cicutarium* and *E. malacoides* (Geraniaceae), both of which are annuals. Stems can reach 80 cm in height. Short stems are erect but long ones are creeping with both producing clusters of up to seven flowers. Fruits have up to five seeds, that measure about 3 mm long × 1 mm wide.

DIET SAMPLING

Serin nests were found by systematically inspecting olive trees within the study plots. Nestling diet samples from plot A/1990, A/1991, B and D mainly belong to first clutches (sampling dates being from mid-March until mid-April in plots A/1990, B and D and during the first 2 weeks of April in plot A/1991). Nestling diet samples from plot C include first and second clutches (samples collected from mid-March until mid-May). Diet samples from juveniles (birds still in typical streaked brown plumage), fledglings (young birds that recently left the nest and still showed fleshy gape-flanges), and adults were obtained in plot E during the second half of the breeding season (from late April to mid-May 1995). Overall, our dataset encompasses samples obtained throughout the entire breeding season.

All juvenile and adult samples, and most nestling diet samples, were obtained by using apomorphine (Chaney and Kare 1966). Once individuals were trapped, a fresh saturated solution of apomorphine (0.04 g ml^{-1} water) was prepared and administered. Birds were held until droplets of solution placed in the eyes were absorbed and were kept in a covered container for 20 min. Regurgitation occurred within 15–20 min. Doses were adjusted to age and body size, although the effectiveness of apomorphine seems unrelated to dosage (Díaz 1989). Apomorphine was administered within 36 hr after the preparation of the solution to avoid loss of effectiveness (Díaz 1989). While sampling nestlings, we left one or two chicks in the nest to avoid desertion. Apomorphine does not have deleterious effects (Valera et al. 1997a); no nestlings died during or immediately following treatment.

Serin nestlings open their eyes when they are at least 4 days old, after which apomorphine can be administered. Apomorphine is less effective in young nestlings (<7 days old; Valera et al. 1997a) and therefore, our dataset does not represent the diet of nestlings under that age. However we obtained information from the gullet contents of 11 nestlings (ranging from 3–10 days old) in plot A/1990 that were killed by mechanical tillage (after tractors hit the olive tree branches). Similar to other emetics, apomorphine provides diet samples in which some food items are underrepresented (Valera et al. 1997a). Nevertheless there is a strong correlation between the general importance (the percent occurrence of each food item in the diet times the mean volume occupied by each item) of most food categories when comparing diet samples obtained by dissection and by the emetic ($r = 0.90$, $n = 14$ food types, $P < 0.001$, Valera et al. 1997a) and, therefore, we included data from dissected birds.

Overall, we obtained food samples from 34 nestlings in 15 nests in plot A/1990, 15 nestlings in four nests in A/1991, 16 nestlings in seven nests in plot B, 13 nestlings in six nests in plot C, and from 18 nestlings in nine nests in plot D. The diets of nestlings from the same brood were not independent and therefore we averaged the data for each nest. Additionally, samples from 15 fledglings, 10 juveniles, and 20 adult birds ($n = 9$ males and 11 females) were obtained in plot E.

ANALYSIS OF DIET SAMPLES

Samples were preserved at $-10°C$ until analyzed. Sorting and identification were performed under a dissecting microscope. Seeds were counted and measured with an ocular micrometer, and representation of each seed type was visually estimated to the nearest 5%. We distinguished five main food categories: animal, mineral, seeds, olive pulp and vegetable matter (pieces of leaves, buds, flowers, etc.). Seeds were identified against a reference collection of seeds compiled from plants. Remains of *Diplotaxis* buds could be distinguished in some samples although difficulties in their identification

very likely resulted in the undererstimation of their occurrence.

Following Rosenberg and Cooper (1990), diet data are presented in three forms: percent occurrence of each item in the diet, mean volume (expressed as a percentage of the total volume of the contents), and as a general importance index (GI). GI is the product of the two former measurements and may range from 0 to 100 000, so that the higher the value the more important the food type is in the diet (Jordano and Herrera 1981, Jordano 1988).

FOOD AVAILABILITY

The herbaceous layer of olive plantations undergoes continuous modification due to farming treatments. Different farming treatments produce different weed communities. Use of pre-emergent herbicides in autumn precludes the germination of weeds and results in a poor weed community throughout the year. In turn, spring tillage allows autumn germination of weeds and a rich community in early spring until plowing occurs (Valera 1992, Pastor et al. 1984). From then until the end of the breeding season, tillage is repeated several times and weeds are almost totally eradicated. As the season progresses, weed emergence also decreases due to the scarcity of rainfall (Valera 1992, Pastor et al. 1984).

Central areas of the space between tree rows in plot A were sprayed with pre-emergence herbicides in 1990 whereas the side areas were plowed in spring, thereby allowing growth of weeds at the beginning of that season in those lateral areas. The following year all of plot A was sprayed with pre-emergence herbicides. Plot B had been totally sprayed with pre-emergence herbicides for several years and had a poor weed community. Herbicides were not used in plot C and plowing occurred in spring.

Abundance of weeds producing edible seeds for Serins (determined from the diet samples obtained in each plot) was estimated in plots A, B, and C on the basis of sampling quadrats (625 cm^2) placed at random at two sampling strata: between the tree rows and under the canopy of olive trees. The number of individuals of each plant species in each quadrat was recorded. We used an alternative method to estimate the abundance of *Diplotaxis* and *Erodium* in plot A because the former plant species were clumped in places where herbicides were not used or where they were unsuccessful. Thus, a huge number of sampling quadrats would have been necessary to adequately estimate their occurrence and abundance. Given that these species are conspicuous plants, easy to census by visual counts, we estimated their abundance in plot A by counting all individual plants along transects of 420-m long (length of the plot) and 12-m wide (distance between adjacent lines of trees).

Because agricultural operations abruptly modify the herbaceous layer, each plot was sampled during the period when Serin diet samples were obtained. Thus, four transects were sampled in plot A during both study years and we analyzed 72 quadrats in plot A/1990, 200 in plot A/1991, 126 in plot B, and 90 in plot C.

Plot A/1990 was plowed during the diet-sampling period, so some samples were obtained when the plot had vegetation whereas later diet samples were collected when the plot had been completely plowed. This situation provided a ''natural'' experiment to study the effect of weed eradication on diet. For this purpose, our sampling effort was two transects and 36 quadrats for each period.

The abundance of each species (*Diplotaxis*, *Erodium*, and all other edible plant species pooled) was averaged for all transects and quadrats and expressed as mean number of individuals per m^2. For the natural experiment in plot A/1990 we estimated food availability in terms of number of seeds per m^2 for the two main food plants: *Diplotaxis* and *Erodium*. We collected 10 *Diplotaxis* plants and 10 *Erodium* plants before plowing occurred and 20 *Diplotaxis* plants and 20 *Erodium* plants after plowing. We counted the number of fully developed fruits and estimated the mean number of fruits per individual and the mean number of seeds per fruit. Assigning the mean number of seeds per fruit to the mean number of fruits per plant and to the mean number of plants per transect we were able to estimate food availability (seeds per m^2) of both main plant species in plot A/1990 before and after plowing.

PROTEIN AND ENERGY CONTENT OF FOOD

Milky-ripe seeds of *Diplotaxis* and *Erodium* were obtained directly from the esophageal pouches of live nestlings after being administered with the emetic or after the dissection of nestlings killed by agricultural practices. Thus, our protein and energy content data refer to the

seeds selected and consumed by the birds themselves.

About 2300 *Diplotaxis* seeds and 1900 *Erodium* seeds were collected from approximately 80 Serins. *Diplotaxis* flower buds were collected from plants from the study area and seeds and buds were analyzed for lipid, protein, and carbohydrate content. They were kept in an oven at 105°C until they reached a constant mass. The lipid content was determined by the Soxhlett procedure, using a Soxhlett Fat Extractor with ethyl ether as a solvent. After 6 hr the solution was distilled in a rotatory evaporator and the lipid residue dried and weighed. An estimate of crude protein was obtained by determining nitrogen by the micro-Kjeldahl method (Earle and Jones 1962) and multiplying the result by 6.25. Ash content was calculated by incinerating the samples at 500°C until a constant mass was achieved. The proportion of carbohydrates was calculated by subtracting the ash, protein and fat content from 100. The protein content of *Diplotaxis* and *Erodium* seeds were based on the means of two analyses while three analyses were made for flower buds.

DIPLOTAXIS VS. *ERODIUM*: TESTING SERIN PREFERENCES EXPERIMENTALLY

A diet choice experiment was designed to distinguish the relative preference for the two most common food plants. Seven adult birds were mist-netted during winter, individually banded and kept in an aviary (2 m³), at room temperature and natural photoperiod. They were fed with a mixture of commercial seeds until several days prior to the experiments when twigs of both plant species were added to the diet of the birds.

Experiments were performed during March and April 1991 in a cage measuring 2 m³ where the focal bird was transferred the day prior to the trials. Several hours before the trial the commercial seeds were removed. Some minutes before the experiment, one *Diplotaxis virgata* plant and one *Erodium cicutarium* plant were collected with roots intact, watered so that they remained stiff, planted in large pots, and placed in the experimental cage. Two trials were performed on each Serin, with each trial separated by 2 to 4 days. In all trials, buds and fruits of both plant species were available *ad libitum*.

Birds usually went to the plants rapidly and showed an initial peak of activity followed by successive periods of feeding and resting. Each bird was videotaped for 2 hr starting when the experimental plants were introduced. We recorded the total number of pecks on each food type (*Diplotaxis* fruits to obtain the seeds, *Erodium* seeds) and defined preference for a food type as the number of pecks (foraging effort). However, two possible sources of bias are associated with long recording periods: i) depletion of a food item may occur, thereby influencing the choice of the subject, and ii) the choice of the subject at a given time may be influenced by the characteristics of its' previous food source. Therefore, the time to be analyzed in each trial (or the number of contacts or pecks) is an important consideration. In this case, we recorded the number of pecks at the plant per 30 sec and analyzed the first bout of foraging until the focal individual paused (no contact with food items for 30 sec [10 of 14 trials], or a sharp decline in foraging activity after the initial peak of activity [4 trials]). Therefore, the length of time differed among trials (mean period: 6.1 ± 1.1 min, mean number of contacts: 57.9 ± 9.9, n = 14 trials for seven individuals).

ENERGETIC REWARDS OF *DIPLOTAXIS* AND *ERODIUM*

Serins manipulate the fruits of *Diplotaxis* and *Erodium* to extract individual seeds. They also feed on *Diplotaxis* buds by pecking them from the inflorescence. To calculate the energetic reward that Serins obtained from each food type and the cost-benefit ratio (time required for handling vs. energy intake per food item) we estimated the following parameters:

Number of Diplotaxis *and* Erodium *seeds per mg of dry weight.* Twenty-eight samples of a known number of milky ripe *Diplotaxis* seeds (range 186–1717 seeds) and 32 samples of milky ripe *Erodium* seeds (range 12–125 seeds) were kept in an oven at 105°C until constant mass and then weighed to within 0.0001 g. We obtained an average (± SD) of 15.6 ± 1.6 *Diplotaxis* seeds per mg and 1.4 ± 0.2 *Erodium* seeds per mg. We also weighed (after drying to constant mass) 24 *Diplotaxis* buds collected from different flower clusters and obtained a mean bud mass of 1.2 ± 0.5 mg.

Number of seeds per fruit. We collected 431 full-grown *Diplotaxis* fruits and 239 *Erodium* fruits from 20–30 individuals of each plant species from our study area during mid-March 1990 and counted the number of seeds per fruit. We

obtained a mean (± SD) of 53.5 ± 8.1 *Diplotaxis* seeds per fruit and 4.7 ± 0.6 *Erodium* seeds per fruit.

Energetic value of the main food types. Gross energy content of seeds and buds were determined from the nutrient content values (see above) using the following values: fat = 38.9 kJ g^{-1}, protein and carbohydrate = 17.2 kJ g^{-1} (Glück 1980, Díaz 1996).

Handling time. We scrutinized the videotapes and selected those cases where we could accurately measure the handling time of each food type. For *Diplotaxis* fruits we obtained 12 measurements from three individuals, and 22 measurements from four individuals for *Erodium* fruits. The small size of *Diplotaxis* buds prevented us from analyzing the handling time of single items. Therefore we chose those cases where we could accurately measure continuous feeding activity on flower clusters (six measurements from three Serins) and could count, after the completion of the experiment, the number of buds consumed. We did not observe spillage in any trial.

STATISTICAL ANALYSES

To test for differences in diet of nestlings from plot A/1990 before and after plowing we performed a mixed ANOVA with hierarchical nesting, so that "family" (nest) was nested in "plot type" (plowed or unplowed). The former factor was considered as random whereas the type of plot was fixed. The dependent variables (% volume of *Diplotaxis*, *Erodium* and "other seeds") were arcsine transformed. Diet fractions are nonindependent and their direct inclusion in statistical analyses may generate misinterpretation. Thus we used the ratio of each diet fraction to the largest fraction in each diet sample, the latter being expressed directly as a percentage of the total sample.

Parametric tests were used where data met the assumptions for normality. In some cases transformations were used to meet these requirements. A binomial test was used to test observed vs. expected frequencies. Statistical analyses were carried out with STATISTICA 6.0 (StatSoft, Inc. 2001). Unless otherwise stated, mean and standard errors are presented and we used two-tailed tests with a significance level of α = 0.05.
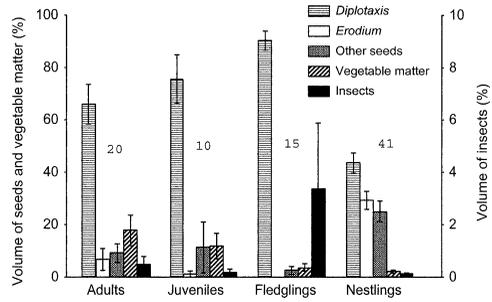
FIGURE 1.   Serin diet composition across different age-classes. The percent volume of *Diplotaxis* and *Erodium* seeds, other edible seed species, vegetable matter including olive pulp, and insects are presented as means ± SE. The number of adults, juveniles, fledglings, and nests (nestling diet composition averaged within nests) is given above each category. Note that the scale differs in both y-axes.

RESULTS

DIET SPECIALIZATION OF SERINS

Adult Serins fed predominantly on *Diplotaxis*, which comprised on average 66 ± 7.6% of the volume of diet samples and appeared in all gut contents ($n = 20$). The remainder of the diet comprised *Erodium*, other seeds, olive pulp, and vegetable matter. Vegetable matter included traces of *Diplotaxis* buds in at least 30% of individuals. Insects comprised a minute fraction (<1% in volume, Fig. 1).

The diets of male and female Serins were very similar. We did not find significant differences in the number of seed species per sample (males: 1.7 ± 0.3, females: 2.3 ± 0.5, $t_{18} = 1.0$, $P > 0.1$), the mean volume of seeds (males: 87.7 ± 7.1%, females: 76.9 ± 8.8%, $t_{18} = 0.9$, $P > 0.1$), or the mean volume of vegetable matter (males: 4.9 ± 2.5%, females: 13.1 ± 7.0%, $t_{18} = 1.0$, $P > 0.1$). Both sexes fed primarily on *Diplotaxis* (males: 75.8 ± 10.5%, females: 57.9 ± 10.6%, $t_{18} = 1.2$, $P > 0.1$), therefore, data from both sexes were pooled for subsequent analyses.

Diplotaxis was also the basis of the diet for both fledglings and juveniles to the extent that fledglings fed almost exclusively on the seeds of this species (mean volume 90.4 ± 3.6%, Fig. 1, Appendix). We could also distinguish traces of *Diplotaxis* buds in the diet of 16% of fledglings and juveniles.

Overall, parents fed nestlings mainly with *Diplotaxis* seeds (Fig. 1 and 2); the second most consumed seed being *Erodium*. *Stellaria media*
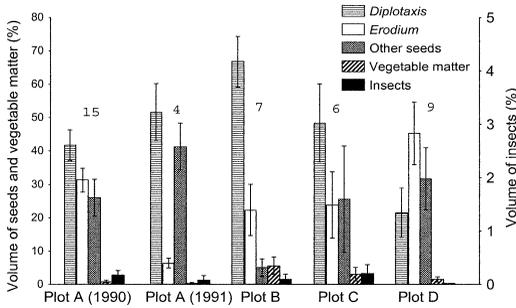
FIGURE 2.   Diet of nestling Serins in different study plots and years. The percent volume of *Diplotaxis* and *Erodium* seeds, other edible seed species, vegetable matter plus olive pulp, and insects are presented as means ± SE. Number of nests is given above bars for each study plot. Note that the scale differs in both y-axes.
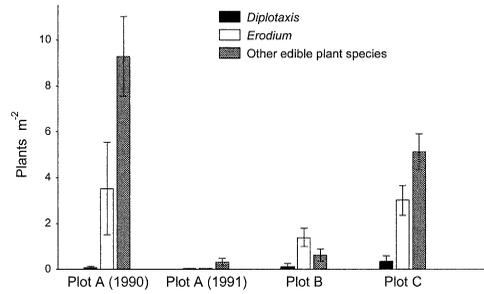
FIGURE 3.   Food availability for Serins across plots and years. Number of plants (mean ± SE) in plot A were calculated from four transects during both study years for *Diplotaxis* and *Erodium*, and 72 and 200 quadrats in 1990 and 1991, respectively, for other plant species. Plot B and C data were based on 126 and 90 quadrats, respectively. The value shown for plot A/1990 is the average of plant abundance before and after plowing (see Methods).

seeds were the third most common food item in volume. There were, however, two exceptions: in one plot *Stellaria media* was represented second highest in volume, and in another plot *Erodium* was the most preferred species, followed by *Diplotaxis*. Vegetable matter comprised a small fraction of the total diet in all cases. We could identify remains of *Diplotaxis* buds in at least 7% of nestlings. Although low in volume, olive pulp was found in the diets of nestlings in four out of five plots reaching up to approximately 5% in volume in plot B (range in this plot 0%–32%). Insects represented less than 1% in volume (Appendix). Although we were unable to sample young (<7 days old) nestlings, observation through the transparent skin of the esophageal pouches (Newton 1967, Glück 1985) of many young nestlings from different plots and years (Valera 1992) did not result in detection of noticeable amounts of insects. Dissection of three well-fed 2–3 day old nestlings killed by plows confirmed that insects have a limited role in nestling diet; in two nestlings, insects made up 1% of the total volume of food, and no insects were present in the diet sample from the third nestling.

Diplotaxis was the least abundant plant species in all four plots where food availability was measured (Fig. 3). *Erodium* was on average 14 times more common than *Diplotaxis* and a variety of seed-producing plants were more abundant than these two species in three out of four plots (Fig. 3). Tillage in plot A/1990 when diet samples were obtained modified the relative abundance of the main food plants (Fig. 4). Af-

ter plowing, the abundance of other plants in comparison to that of *Diplotaxis* was about 1.5 times higher than before plowing. Similarly, other edible plants were more than 100 times more abundant than *Erodium* in comparison to their proportion before plowing. Before plowing, seeds of *Diplotaxis* were less abundant than seeds of *Erodium* (569.8 ± 220.9 seeds m^{-2} vs. 2379.7 ± 645.3 seeds m^{-2}) and after plowing the situation changed; *Diplotaxis* seeds were more abundant than *Erodium* seeds (112.4 ± 10.9 seeds m^{-2} vs. 0.16 ± 0.01 seeds m^{-2}, respectively). Despite these alterations, we did not find any significant differences in the volume of
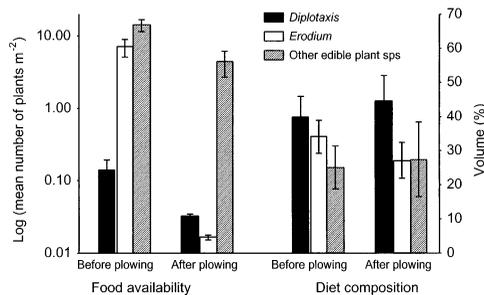
FIGURE 4.   Food availability and nestling diet for Serins before and after plowing. The volume (%) and abundance (plants per m^2) of *Diplotaxis*, *Erodium*, and other plant species are presented as means ± SE. Note that plant abundance is on a log scale. Sample sizes for food availability are based on two transects (for *Diplotaxis* and *Erodium*) and 36 quadrats for other plant species in each sampling period. Diet composition was based on nine nests before plowing and six nests after plowing.
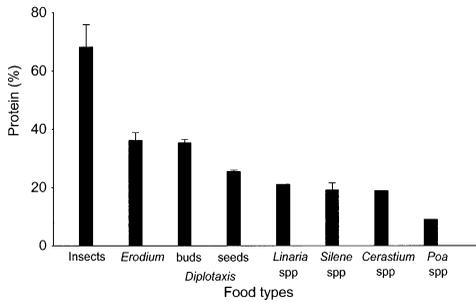
FIGURE 5. Percent protein content (mean ± SE) of *Diplotaxis* seeds and buds and of *Erodium* fruits in comparison to other food species consumed by Serins. Insect data show the mean ± range rather than standard error. Data for insects come from White (1974 in Jordano 2000) and Earle and Jones (1962) provided protein content for other plant species.

Diplotaxis (ANOVA, $F_{1,13} = 0.4$, $P > 0.1$), *Erodium* ($F_{1,13} = 1.3$, $P > 0.1$) and other seeds ($F_{1,13} = 0.1$, $P > 0.1$) in the diet of nestlings before and after plowing (Fig. 4).

HIGH PROTEIN SEEDS

Diplotaxis and *Erodium* have a high protein content relative to other less frequently consumed seed species while containing about 63% and 46% less protein, respectively, than insects (Fig. 5). *Diplotaxis* seeds have roughly 30% less protein than *Erodium* seeds but *Diplotaxis* buds, which are also consumed by Serins, contain approximately the same amount of protein as *Erodium* seeds. The third seed type in importance, *Stellaria media*, belongs to the family Caryophyllaceae, whose mean seed protein content (calculated from Earle and Jones 1962) is approximately 30% lower than that of *Diplotaxis* (Fig. 5).

DIPLOTAXIS VS. *ERODIUM*: A QUESTION OF AVAILABILITY OR PREFERENCE?

The food choice experiment suggests that Serins preferentially fed on *Diplotaxis* plants (pecks on

Diplotaxis virgata: 88.4% ± 8.9, on *Erodium cicutarim*: 11.6 ± 8.9, $n = 7$ birds). Six out of seven individuals (86%; Binomial test, $P = 0.05$) fed in both trials almost exclusively on *Diplotaxis virgata* (range of the percentage of contacts: 75%–100%). The remaining individual preferred *Erodium* in the first trial (93% of pecks), and chose *Diplotaxis* initially in the second trial (64% of pecks) but later fed on *Erodium* (36%). Within *Diplotaxis*, Serins fed almost exclusively on fruits (from which they extract the seeds) and only one individual foraged on buds (57% of pecks in one trial).

Serins need only several seconds to consume an entire bud (Table 1) that they usually eat with a single peck. The handling time of *Diplotaxis* and *Erodium* fruits was similar. After calculating the costs of handling and the benefits of energy intake, it is evident that the less profitable food plant is *Erodium* relative to both *Diplotaxis* fruits and buds (Table 1). Given that *Diplotaxis* buds have similar protein content to *Erodium* fruits (Fig. 5), *Diplotaxis* as a whole is a more nutritionally complete food plant than *Erodium*, both in terms of protein and energy.

DISCUSSION

Our findings reveal a high degree of diet specialization in a granivorous species during the breeding season. Approximately 70% of the diet of adult Serins comprised just two seed types with a single species (*Diplotaxis*) accounting for more than half the diet. Males and females had similar diet preferences and parents fed their offspring virtually the same diet as themselves. Fledglings and juveniles also mainly consumed this seed species, which comprised 90% and 75% of their diets, respectively. Despite Newton (1967) having long ago noted that Cardueline finches are able to raise offspring predominantly on a diet of seeds, the phenomenon is not widely known, except for a few finches that feed on tree

TABLE 1. Energy reward, handling time (mean ± SE) and profitability of food items for Serins.

	Food items		
	Diplotaxis bud	*Diplotaxis* fruit	*Erodium* fruit
Average size of food item (mg)	1.2	3.4	3.4
Energy reward (J mg^{-1})	16.3	20.3	17.0
Total energy per food item (J)	19.5	69.8	57.6
Handling time per item (sec)	5.5 ± 2.1	30.9 ± 3.9	31.4 ± 5.3
Net benefit (J sec^{-1})	3.5	2.3	1.8

seeds. Our results show that, in contrast to the diet shift found in many other seed-eating birds (Wiens and Johnston 1977, but see Glück 1985), neither Serin adults nor nestlings fed on insects during the breeding season.

Previous reports have described finches as opportunistic in their choice of foods (Newton 1967, Wiens and Johnston 1977, Glück 1985, Eybert and Constant 1998) being able to feed on a wide variety of food types. In contrast, we found that Serins had a limited diet and fed primarily on several species of herb seeds. To our knowledge, this degree of specialization is rare having only been reported in a few finches dependent on tree seeds, like the Citril Finch (*Serinus citrinella*, Borras et al. 2003) and crossbills (Pulliainen 1971, 1972, Benkman 1987).

Our findings are unlikely to be influenced by the timing of sampling (Moorcroft et al. 1997, Eybert and Constant 1998, Moorcroft 2000) because we sampled the diets of all age groups throughout nearly the entire breeding season. Moreover, in contrast to other studies in which flowering phenology determined seasonal diet variation (Moorcroft et al. 1997, Eybert and Constant 1998) most plant species were available during the whole sampling-breeding period (Pastor et al. 1984). This suggests that Serins were not limited in their feeding choices by plant phenology and thus specialization is unlikely to be the result of different fruiting times of food plants.

This study reveals that Serins have two levels of diet specialization: they feed on a very narrow range of seed types and are also able to feed their nestlings almost exclusively with the same seeds. What factors then produce the high degree of diet specialization found in Serins during the breeding season? Although finches are adapted to exploit unpredictable food patches and seem to easily adapt to new kinds of food types (Newton 1967, Wiens and Johnston 1977), intense farming practices can negatively impact some species through diet alteration (Donald et al. 2001). There is evidence suggesting that intense human management in olive orchards diminishes the availability of food types and impoverishes such habitat (Valera 1992, Valera et al. 1997b, 1999). Little is known about the Serin diet in other populations but in contrast to our findings of food specialization, available data suggest that Serins are food generalists (Cramp and Perrins 1994). Habitat modification and de-

pauperate plant species composition may restrict Serins' diet choice. However, faced with this situation, it seems clear that Serins prefer *Diplotaxis*, a preference that was consistent among our study plots among years (Fig. 1 and 2).

Preference for *Diplotaxis* was apparently unrelated to the availability of this plant relative to other species. Our diet data were obtained in a variety of localities and dates, suggesting that particular conditions may not greatly influence Serin preferences. Our observations of Serin preferences for *Diplotaxis* were supported by the food choice experiment.

Díaz (1996) stressed that studies on diet selection by avian granivores should take into account the chemical characteristics of seeds. Diet preferences of granivorous birds have usually been analyzed within the framework of optimal diet models that predict that birds should choose seed species that provide maximum energy intake per unit foraging time (Pyke et al. 1977, Stephen and Krebs 1986). Given a similar handling time for both *Diplotaxis* and *Erodium*, preferences for a certain species should be explained by nutrient content. In fact, we found that differences in seed chemistry make *Diplotaxis* more profitable for Serins. Therefore our findings agree with optimal diet models.

Seed chemistry can also explain why Serins do not shift to an insect diet during breeding. The traditional explanation for the shift from seeds to insects during breeding is based on the relatively low protein contents of seeds coupled with the increased protein requirements for egg production (Pinowska 1975) and for nestling growth (Newton 1967). It is thought that nestlings of granivorous birds require a diet supplemented with insects because their efficiency at digesting plant foods as compared to animal foods is initially low (Newton 1972). Díaz (1996) does not support the traditional view of protein limitation during breeding, at least for adult birds, as he found that a large proportion of seeds have far more than 16% crude protein. Our data agree with Díaz's view; our analyses show that seeds of both *Diplotaxis* and *Erodium* have a high protein content that could fulfill both adult and nestling requirements (moderate protein contents [10%–17%] enables birds to maintain their nutrient and energy balance, Díaz 1996). Although we did not systematically record nestling insect consumption during the first week after hatching, the gullet contents of sev-

eral first week nestlings suggest that Serins do not feed insects to nestlings at that time. In Canary (*Serinus canarius*) nestlings protein intake peaked between 8 and 10 days of age (Harper and Turner 2000). Thus if Serins have this same peak in protein intake, insects should have been present in diet samples if they were an important component of nesting protein, which was not the case.

In summary, Serins in our population appear to solve the problem of nestling protein requirements by specializing on two seed species with high protein content. Moreover, seed chemistry can also account for Serin preferences for *Diplotaxis* over *Erodium*. Although *Diplotaxis* seeds have lower protein content than *Erodium* seeds, Serins can obtain a second food item rich in protein from *Diplotaxis* plants (i.e., buds), which in fact appear in the diet of nestling Serins.

Understanding how ecological processes operate in human-managed habitats is an issue of growing interest given the ever-increasing proportion of habitat that is modified by humans. Serin specialization can be partly a consequence of human habitat alteration because *Diplotaxis*, as well as other weeds, is more common in olive orchards (i.e., agricultural lands) than in natural habitats. The suitability of a specific food type probably accounts for the success of Serins in olive orchards. However, other species may not be able to cope with the constraints imposed by modern agriculture (Fuller 2000, Beecher et al. 2002) or may suffer poor body condition in agrosystems (Rey and Valera 1999). Knowledge of the dietary requirements of various bird species can help to formulate a habitat management strategy. For instance, incentives to olive growers to preserve strips of weeds would result in richer bird communities, with higher densities of granivorous species (Valera et al. 1997b, 1999, Beecher et al. 2002). Future research should try to identify other factors that produce diet specialization, such as differential predation risk when feeding on different plant species, or differences among plant species in food accessibility. It would also be interesting to look for the degree of (Serin) diet specialization in environments with different degrees of human influence. In this sense, comparative studies on bird diet among natural and human-managed habitats are critical for improving our understanding of how ecological processes operate in agro-ecosystems.

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APPENDIX.   Mean volume (%), percent occurrence (PO), and general importance (GI; product of volume and occurrence divided by 100) of each item in the diet of Serins (n = 20 adults, 10 juveniles, 15 fledglings, and nestlings averaged across 41 nests). Dashes indicate that the food item was not present in the diet.

	Nestlings			Fledglings			Juveniles			Adults		
	Volume	PO	GI	Volume	PO	GI	Volume	PO	GI	Volume	PO	GI
Seed fraction												
Diplotaxis virgata	43.5	95.1	41.4	90.4	100.0	90.4	75.6	100.0	75.6	66.0	100.0	66.0
Erodium spp.	29.3	92.7	27.2	–	–	–	1.2	10.0	0.1	6.7	25.0	1.76
Cerastium glomeratum	1.2	56.1	0.7	–	–	–	0.1	10.0	0.01	0.9	10.0	0.09
Stellaria media	9.5	56.1	5.4	1.3	6.6	0.09	9.8	10.0	0.9	2.9	25.0	0.7
Cruciferae sp.	4.2	51.2	2.2	–	–	–	–	–	–	–	–	–
Poa annua	2.5	31.7	0.8	–	–	–	–	–	–	–	–	–
Senecio vulgaris	0.2	9.8	0.02	–	–	–	–	–	–	–	–	–
Chamaemelum fuscatum	2.4	24.4	0.6	–	–	–	–	–	–	–	–	–
Rapistrum rugosum	1.3	4.9	0.07	–	–	–	–	–	–	–	–	–
Biscutella sp.	2.1	19.5	0.41	–	–	–	0.4	10.0	0.04	2.6	15.0	0.4
Linaria sp.	1.0	14.6	0.1	–	–	–	0.1	10.0	0.009	2.4	15.0	0.3
Myosotis sp.	0.08	2.4	0.002	–	–	–	–	–	–	0.04	5.0	0.002
Veronica sp.	0.0	0.0	0.0	0.05	6.6	0.003	–	–	–	–	–	–
Cariofilacea sp.	0.01	2.4	0.003	1.1	20.0	0.2	0.9	10.0	0.09	–	–	–
Sinapis sp.	–	–	–	–	–	–	–	–	–	0.09	5.0	0.004
Non-seed fraction												
Vegetable matter	0.6	26.8	0.2	2.9	40.0	1.2	9.0	70.0	6.3	9.5	70.0	6.6
Olive pulp	1.5	24.4	0.4	0.8	13.3	0.1	2.8	20.0	0.5	8.3	25.0	2.1
Insects	0.1	21.9	0.03	3.4	26.7	0.9	0.2	30.0	0.06	0.5	15.0	0.07