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Seed selection by the trumpeter finch, *Bucanetes githagineus*. What currency does this arid-land species value?

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We tested the hypothesis that in harsh environments seed contents, specifically water, and handling time will determine food preferences in an arid bird species, the trumpeter finch. Rape (69.9%) and canary (23.9%) were the most commonly consumed seeds. Mean handling time differed among the tested seed types. There existed a non-linear inverse relationship between mean handling time of different seeds and their selectiveness by individuals. Data estimated from five hypothetical diets and their respective nutritional intakes indicate that this arid land passerine selects a balanced diet optimizing energy and total water intake (energy and water gain per unit of time), rather than a diet that maximizes just energy intake. For birds inhabiting arid and semiarid habitats, food selection should be highly adaptive as selected food items must maximize energy intake rate, but also must contain or produce adequate water to satisfy metabolic requirements.

Introduction

Behavioural and morphological adaptations, as well as availability of seeds, have been described as the fundamental factors influencing diet composition in granivorous birds. Many interspecific studies have documented strong correlations between bird or beak size and seed size (e.g., Newton 1972, Grant 1986, Díaz 1994). These relationships are based on the association between the size and structure of bird bills and the speed at which different sized seeds are processed (Newton 1972, Pulliam 1985, Grant 1986, Smith 1987, Benkman & Pulliam 1988, Díaz 1990, 1994). Correlations between seed preferences and content of energy (Glück 1985, Shuman *et al*. 1990), fat (Kear 1962, Sprenkle & Blem 1984, Greig-Smith & Willson 1985), protein (Kear 1962, Valera *et al*. 2005), and carbohydrates (Kelrick *et al*. 1986) have also been found. These correlations have been presented as evidence for food preferences based on the nutritional characteristics of seeds. Stronger correlations are found when both nutrient composition and seed size are considered together to explain seed preferences by different granivorous bird species (Díaz 1996). However, harsh conditions may modify seed preferences. For example, a decrease in temperature modifies seed preferences toward increasing efficiency (larger seeds, seeds containing more calories, or seeds providing the highest rate of energy intake are selected; Myton & Ficken 1967, Willson & Harmeson 1973).

Optimality models of food selection assume that individuals are capable of assessing food value. Energy intake rate is a currency that plays a role in food selection, being used in most models (Stephen & Krebs 1986). Thus, it has been demonstrated that granivorous birds prefer to feed on seeds with shorter handling times to maximize energy intake rate (Willson 1971, Hrabar & Perrin 2002). For birds inhabiting arid regions, however, other currencies such as water intake rate might also play a role in the food selection process.

Arid and semiarid habitats experience high temperatures, low relative humidity, and scant rainfall (Lázaro *et al*. 2001). Food and water limitations are of great importance, and birds inhabiting these harsh environments have coping adaptations (Louw & Seely 1982). Most of these adaptations are behavioural: searching for food at dawn and night, flying to water early in the morning or late in the evening, or minimizing activity during the hottest parts of the day (for a review *see* Davies 1982). Other adaptations are physiological: minimizing cutaneous water loss and oxygen consumption (Williams & Tieleman 2005). It has also been shown that some species are able to obtain water from their diet by increasing the amount of insects eaten (Williams & DuPlessis 1996).

The trumpeter finch (*Bucanetes githagineus*) is a fringillid inhabiting desert and semi-desert regions, from Sahara across North Africa to Middle East, Morocco and recently South of Spain (Cramp & Perrins 1994, Carrillo *et al*. 2007). Its main food includes seeds, seedlings, and buds of the families Cruciferae, Gramineae, and Solanaceae (Cramp & Perrins 1994). This animal will fly long distances to obtain water (Cramp & Perrins 1994). The aim of this paper is to examine seed preferences in the trumpeter finch through a multi-choice seed experiment. We tested the hypothesis that in this arid land species, seed contents and handling time will determine food preferences. Because nutrient composition of seeds affect water intake (Bartholomew 1972), we expect this finch species to feed preferably on seeds with lower handling times to maximize energy intake rate, but also seeds with higher water production yields.

Methods

Study species

Thirteen adult trumpeter finches (seven females and six males) were mist-netted and individually colour-banded at the beginning of September 2005 at Tabernas (Almería province, 37°00´N, 2°33´W), one week before the experiments were performed. The birds' exact age could not be reliably determined (Svensson 1992), although all of them were older than one calendar year. Adult birds were not moulting at this time of the year (Svensson 1992, Cramp & Perrins 1994).

Experiments were carried out in September 2005 in outdoors aviaries at Parque de Rescate de Fauna Sahariana (a facility of the Consejo Superior de Investigaciones Científicas, nearby Almería city). Before running the experiments, birds were separated according to their gender in two 2 × 2 × 2 m maintenance aviaries with an *ad libitum* diet of a mixture of seeds (*see* below) and water with vitamins. This enabled them to familiarize with different seeds used in the experiments. After this acclimatization period, each bird was released into an experimental aviary (2 × 2 × 2 m) where they were deprived of food, but not of water, for 16 hours before the trials. We used this starvation period according to a preliminary study performed for estimating the optimal time for birds to be highly motivated to feed. The experimental aviaries were cleaned thoroughly before the experiment, to ensure that no other seeds were present.

Because of their presumed relationships with feeding behaviour (Newton 1972, Grant 1986, Van der Meij & Bout 2000, Todd *et al*. 2003), the bills of all individuals (length up to the skull, maximum depth, and maximum width; Table 1) were measured with digital calliper to the nearest 0.01 mm. Seed selection in finches is also related to body size (Díaz 1994). Accordingly, we measured body mass as an appropriate estimate of the body size. Prior to the experiments body mass was recorded with a digital balance to the nearest 0.5 g (Table 1). It could be argued that other measures, such as e.g. keel length, are better estimates of structural body size (for a review *see* Senar & Pascual 1997). In our experimental population body mass and keel length were highly correlated ($R = 0.63$, $p = 0.01$), and results obtained in further analyses with either body mass or with keel length were highly consistent. We assumed all individuals were in good condition throughout the experiments as their body masses (range: 17.0–20.7, mean ± SD = 19.13 ± 1.2, n = 13) did not fall below those observed in the field (own field data; range: 16.9–25.1, mean ± SD = 20.8 ± 1.4, n = 300). All experiments were completed by the end of September and birds were subsequently released where they were captured. Their body masses when released fell within the range observed in the field.

Experimental seeds

Six commercial seed types were used in the trials (Table 2): rape (*Brassica rapa*), millet (*Panicum miliaceum*), canary (*Phalaris canariensis*), linseed (*Linum usitatissimum*), oat (*Avena sativa*), and husked sunflower (*Helianthus annuus*). These commercial seeds were chosen because of their availability and different nutrient composition, shape, and size. Values of nutritional content variables (free water, protein, fat, carbohydrates and energy; Fig. 1) were obtained from the literature (Willson 1971). Because water is also a byproduct of metabolism of fats, proteins, and carbohydrates, we calculated the metabolic water of seed types by using the values of Barne and Levy (1998): fat 1.07 ml g^{-1}, protein 0.396 ml g^{-1} and carbohydrates 0.556 ml g^{-1}.

Two kinds of seed mixtures were used: (i) a maintenance mixture, composed of a homogeneous combination of equal volumes of the six seed types. It was used in the maintenance rooms. This procedure allowed birds to learn how to handle the seeds (Kear 1962) while minimizing the risk of developing a seed preference based on their differential abundances (Díaz 1990, 1994, Endler 1991). (ii) An experimental mixture used to determine seed preferences, which was a mixture of fixed numerical seeds composition established according to the criteria of Díaz (1990): (a) each species should occupy approximately the same surface when set on a plain base (4 cm^2), in order to avoid biases due to the differential abundance of each seed type; and (b) none of the seed types should be completely consumed by the bird during the feeding trial. This was intended to eliminate the possibility of overestimating the ingestion of secondarily preferred seeds.

Table 1. Mean ± SD for characters obtained for all the trumpeter finches used in the experiments.

Sex	Body mass (g)	Bill length (mm)	Bill height (mm)	Bill depth (mm)
Males (n = 6)	19.76 ± 0.78	14.17 ± 0.22	8.72 ± 0.61	7.85 ± 0.64
Females (n = 7)	18.59 ± 1.31	14.35 ± 0.49	8.67 ± 0.29	7.63 ± 0.28

Table 2. Contribution of the six seed types to the experimental mixture used in the seed preference trials. All seeds were unhusked except sunflower. Total number refers to the number of seeds fitting in a surface of 4 cm^2; length, width and mass (mean ± SD) refer to seed dimensions averaged for 30 seeds; handling time (mean ± SD) refers to the mean time a seed type is handled, averaged for the thirteen birds used in the trials (*see* Methods).

Seed types	Total number	Length (mm)	Width (mm)	Mass (mg)	Handling time (s)
Rape (*Brassica rapa*)	123	2.14 ± 0.19	1.89 ± 0.19	4.0 ± 0.12	2.29 ± 0.27
Canary (*Phalaris canariensis*)	50	5.18 ± 0.36	1.95 ± 0.23	6.5 ± 0.40	2.84 ± 0.39
Linseed (*Linum usitatissimum*)	50	4.40 ± 0.22	2.42 ± 0.10	4.8 ± 0.62	4.34 ± 0.39
Millet (*Panicum miliaceum*)	68	2.91 ± 0.13	2.43 ± 0.16	6.7 ± 0.59	6.32 ± 1.97
Oat (*Avena sativa*)	30	6.36 ± 0.41	2.09 ± 0.22	16.0 ± 0.97	11.92 ± 1.65
Sunflower (*Helianthus annuus*)	10	9.06 ± 0.89	4.35 ± 0.45	40.2 ± 1.83	19.06 ± 1.59

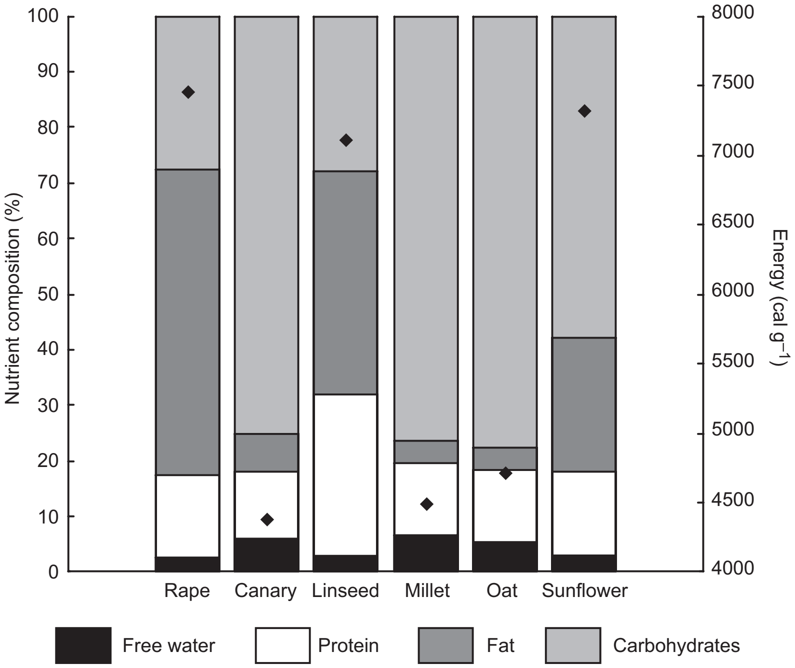

Fig. 1. Nutrient composition of seeds. Carbohydrates computed as one hundred minus percentages of free water, protein and fat. Black rhombuses inside the bars indicate energy (cal g^{-1}). Source: Willson (1971).

Seed preference trials

We sampled each bird during a period of 15 min on two different days. Samples obtained per individual were averaged prior to statistical analyses. A preliminary experiment showed that birds of this species satiated between 10–15 min after first contact with food. The minimum interval between successive replications with the same individual was 72 h. To prevent disturbance while recording data, birds were videotaped during trials. Experiments were performed between 08:00–09:00 during 12 days with similar temperature (mean ambient temperature ± SD = 21.5 ± 1.2 °C, n = 12). The feeder, placed on the floor, was a plastic dish (30 × 20 cm) filled with the experimental mixture. It was shaken in order to obtain a homogeneous distribution of seeds. During experiments birds were also offered water *ad libitum* (we believed it was the most conservative procedure in case birds selected seeds with higher water production yields. Otherwise seed selection could be interpreted as a result of water deprivation).

After each individual was sampled, the feeder was removed and the remaining seeds were counted to calculate the number of seeds consumed. When cracked seeds were found, the number of uneaten seeds was estimated from the remaining fragments. We then calculated the proportion of eaten seeds per species (by number and mass) as a percentage of the total seeds consumed.

From this experiment we determined the mean diet of our experimental population by averaging the number of each seed type consumed by the 13 birds. It was expressed in terms of proportions of seeds consumed and their nutritional and energetic intake rates (Table 3).

Handling time trials

Handling time has been demonstrated to be an important factor explaining seed selection in granivorous birds (Hespenheide 1966, Willson 1971, 1972, Hrabar & Perrin 2002). To determine whether seed preference in the trumpeter finch is affected by the time needed to handle each seed type, we performed an experiment where this variable was recorded.

Once seed preference trials were finished for all birds, we sampled individuals in a new experiment using the same aviaries. The starvation period was also the same. We sampled each individual bird on six different days, one time per day. Each of these times the bird was given a different seed type for feeding, and its behaviour while feeding was videotaped for 15 min. During these experiments birds were also offered water *ad libitum*. The feeder, placed on the floor, was a plastic dish (30 × 20 cm) filled with only one of the six following seeds: rape, millet, canary, linseed, oat, and sunflower. We used a fixed numerical sample per seed type: as many as fitted in a plain surface of 16 cm^2 (4 × 4). Data of handling time for each seed eaten was recorded from the videos using a stop watch with lap memories. Afterwards a mean derived from 15 randomly selected seed observations constituted the handling time of each type of seed for each individual bird. We defined handling time as the period since a seed was picked up until it was swallowed (Benkman 1988). For sunflower seeds no bird was able to eat more than 10 seeds before satiation. Hence, for this type of seed, we averaged handling time recorded for all seeds consumed during sampling (range: 5–10). When comparing handling time of different seeds, we averaged data obtained from all 13 individuals (*see* Table 2).

Statistics

Handling time and percentage of seeds consumed were not always normally distributed (Lilliefors tests: $p < 0.05$ except for rape and canary). Therefore, we used non-parametric tests to analyze seed preference.

Following Roa (1992) and Lockwood (1998), data of multiple-offer experiments were analysed with Friedman's ANOVA test with post-hoc multiple comparisons (Siegel & Castellan 1988, Zar 1996), because different food options were not independent (Roa 1992). However measurements of handling time of different types of seeds were independent of each other, and a Kruskal-Wallis test was used to analyze differences among seeds.

To explore the relationship between the percentages of seeds consumed and handling time, we used the TableCurve 2D software (Systat Software Inc. 2002, TableCurve 2D, ver. 5.01, Evanston, Illinois), which calculated the equation that best describes our data and its statistical fitting.

Birds' morphological measures approached a normal distribution. To examine whether morphology explained the proportion of seeds consumed by birds, we performed a Multiple Regression Analysis for the most preferred seed types (rape and canary) using a backward elimination of the independent variables. We only included these two types of seeds because they were the only seeds eaten by all individual birds during the trials. The remaining seeds were never eaten by

Table 3. Energy, fat, protein, carbohydrates, free water, and metabolic water intake rates of the mean diet consumed by the trumpeter finch (averaged for the thirteen birds sampled). The same intakes are shown for 5 hypothetical diets (*see* Methods) as percentages above (positive values) or below (negative values) the mean real diet. Total water refers to the intake rate obtained by summing up free water and metabolic water intake rates. Hypothetical diet 1 (rape and canary proportions as compared with those in the mean diet exchanged) would comprise 69.9% of canary, 23.9% of rape and 6.2% of the other seeds. Hypothetical diet 2 (the proportions of the two fastest- and the two slowest-handled seeds exchanged) would comprise 69.9% sunflower seeds, 23.9% oat and 6.2% of the rest of seed types. Hypothetical diet 3 would comprise 69.9% of oat, 23.9% of sunflower seeds and 6.2% of the remaining seed types. Hypothetical diet 4 (the proportions of the two fastest-handled seeds and the two seeds with intermediate handling times exchanged) would comprise 69.9% of millet, 23.9% of linseed and 6.2% of other seeds. Finally hypothetical diet 5 would comprise 69.9% of linseed, 23.9% of millet and 6.2% of other seeds.

	Energy (cal s^{-1})	Fat (g s^{-1})	Protein (g s^{-1})	Carbohydrates (g s^{-1})	Free water (g s^{-1})	Metabolic water (ml s^{-1})	Total water (g s^{-1})
Mean diet	11.0	5.9×10^{-4}	2.4×10^{-4}	8.5×10^{-4}	6.9×10^{-5}	1.2×10^{-3}	1.27×10^{-3}
Hypothetical diet 1	–12.6	–51.2	–1.1	49.7	46.8	–11.1	–8.0
Hypothetical diet 2	23.3	–28.9	17.0	39.6	–4.5	–7.6	–7.5
Hypothetical diet 3	–13.9	–63.2	–9.3	29.1	2.2	–23.1	–21.8
Hypothetical diet 4	–51.1	–81.2	–32.9	–13.9	–10.2	–50.9	–47.9
Hypothetical diet 5	–41.8	–55.9	–7.6	–39.3	–33.8	–45.5	–41.8

most of the sampled birds (millet was eaten only by two individuals, sunflower was eaten only by three individuals, linseed was eaten only by four individuals and oat was eaten by six individuals) which would produce unreliable results from the regression analyses due to a high number of zero values and the violation of some test assumptions. The dependent variable was either the amount of rape or the amount of canary consumed, and the independent variables were the morphological measures and bird's body mass prior to experiments. Analyses performed with the number of seeds eaten as dependent variable yielded the same results as those with their mass. Hence here, we report the results obtained in the former case. It could be argued that volume rather than number of seeds represents the appropriate variable in demonstrating seed preference. However, within our sample only three out of thirteen birds consumed sunflower (the largest seed), therefore we ruled out this possibility.

Hypothetical diets

Seeds are dry food with very low free water content (less than 8% in our experimental species; Fig. 1) but very rich in other nutrients, water being a byproduct of their metabolism (i.e., carbohydrates, fats, proteins). Our expectation for this arid land species is to select food items that maximize not only the rate of energy intake (or energy gains over a fixed time), but those simultaneously maximizing energy and water intakes (either free water and/or metabolic water gains over a fixed time). To determine whether the seed selection process in the trumpeter finch met our expectation, we compared the energetic and nutritional intakes of each seed component (energy, fat, protein, carbohydrates, free water, metabolic water and total water) from the mean diet attained for our birds with the intakes from five hypothetical diets obtained by exchanging the proportion of seeds consumed and keeping constant their total number (Table 3; for a similar approach *see* Rey & Valera [1999]). In hypothetical diet 1 the proportion of rape and canary were exchanged, seed types not differing in handling time but being different in nutrient composition. In hypothetical diets 2 and 3, the proportions of the two fastest- and the two slowest-consumed seeds in the mean diet were exchanged (Table 3). Finally, in hypothetical diets 4 and 5, the proportions of the two fastest-consumed seeds and those of intermediate handling times were exchanged (Table 3). The aim of this approach was to explore which seed component (protein, carbohydrates, fat, free water, energy) would be maximized if seed preference mediated by handling time were changed, in order to elucidate the benefits of the real mean diet in comparison with alternative hypothetical diets. We investigated whether: (i) the trumpeter finch selects seeds only to maximize energy intake, and any other nutrient intake (including free water and metabolic water) is just a consequence of the composition of seeds selected to maximize energy intake; or (ii) alternatively, the trumpeter finch selects a balanced diet optimizing energy as well as water intake. If this were the case, water production yields of seeds would also represent a "decision variable" (Stephen & Krebs 1986) for this arid land species.

Results

Trumpeter finches fed significantly more on rape and canary than on the rest of the seeds offered (Friedman ANOVA: $\chi^2 = 47.25$, df = 5, $n = 13$, $p < 0.01$; Fig. 2). These two seed types represented more than 80% of the seeds consumed for all the individuals sampled (mean = 94.31%, SD = 5.62). Thus, we included only these two seeds in multiple regression analyses.

Neither bill morphology, nor body mass were related to the proportion of seeds preferably consumed (rape: $R^2 = 0.27$, $F_{4,13} = 0.74$, $p = 0.58$; canary: $R^2 = 0.17$, $F_{4,13} = 0.41$, $p = 0.79$).

Mean handling time differed among the tested seeds (Kruskal-Wallis test: $H_{5,78} = 73.75$, $p < 0.01$). Rape and canary were the fastest-handled seeds, sunflower and oat were the slowest-handled seeds, and millet and linseed were intermediate (Fig. 3 and Table 2). There existed a nonlinear, inverse relationship between the mean handling time of the different seeds and their selectiveness by individuals. The best equation that fitted such relationship between handling time (x) and the percentage of seeds consumed

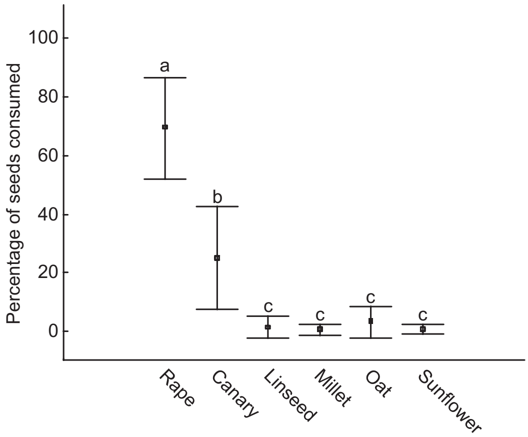

Fig. 2. Differences in the percentages of seeds eaten by trumpeter finches (mean ± SD). Similar lowercase letters near bar means homogeneous groups not statistically different at $p < 0.05$ (post-hoc multiple comparisons; *see* Methods).

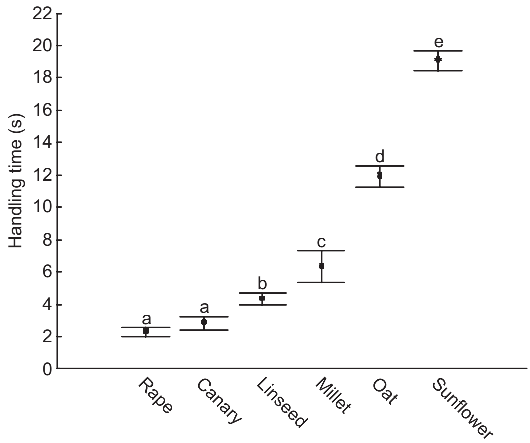

Fig. 3. Differences in handling time among the six types of seeds used in the experiment (mean ± SD). Data were averaged for the 13 trumpeter finches sampled. Similar lowercase letters near bars denote homogeneous groups not statistically different at $p < 0.05$ (post-hoc multiple comparisons; *see* Methods).

(y) was $y = -1.86 + 639.87e^{-x}$ which explained 91.26% of the variance ($p < 0.05$). It showed that birds seldom consumed seeds with longest handling times (*viz*., sunflowers and oats), but also that some seeds with intermediate handling times were not preferred (millet and linseed).

The mean diet of our trumpeter finch experimental population comprised 69.9% of rape, 23.9% of canary and 6.2% of the remaining experimental seeds, which indicates that this bird species selects those seeds with the shortest handling times. The nutritional intake rates of this mean diet are shown in Table 3, as well as the nutritional intakes for the hypothetical diets expressed as percentages above or below the mean real diet. Although the energy intake rate is higher in hypothetical diet 2 than in the mean diet (over 23%), for all hypothetical diets, total water intake rate (calculated by summing up free water and metabolic water intakes) is lower than in the mean real diet.

Discussion

The trumpeter finch feeds on rape and canary in a significantly higher proportion than it feeds on other seed types. In a large number of interspecific studies, morphological adaptations of the bill have been found to be of outmost importance determining seed choices (Newton 1967, Grant 1986, Díaz 1994, Hrabar & Perrin 2002). Far from those results, we did not find a significant effect of morphological variables on seed selection. Very likely, the amount of variability in bill dimensions at intraspecific level is smaller than that observed between species, which precludes a parallelism between relationships found at both inter- and intraspecific level (Moreno *et al.* 1997). The value of the coefficient of variation found in our study in comparison with data from other authors studying several species support this argument (CVs of bill dimensions calculated for studies using several finches species ranged from 15% to 35% (Newton 1967, Willson 1971, Díaz 1994) while CVs in our study ranged from 2% to 5%).

Seed handling time has been acknowledged to be one of the main factors determining seed preference in granivorous birds (Hespenheide 1966, Willson 1971, Willson & Harmeson 1973, Goldstein & Baker 1984, Todd *et al.* 2003). Accordingly, our results indicated that the trumpeter finch feeds preferably on seeds with the shortest handling time (rape and canary) while seeds with longest handling time were hardly consumed (sunflower and oat). However, the relationship between handling time and seed selection was not lineal. Rape and canary did not differ in handling time (Fig. 3), hence, one would expect both seeds to be selected in similar proportions. However, this was not the case. The trumpeter finch preferred rape significantly more than canary (Fig. 2). It seems that other variables apart from handling time may be playing a role in the seed selection process by the trumpeter finch.

Granivorous birds select food items with shorter handling time to maximize energy intake rate (Willson 1971, Hrabar & Perrin 2002). Energy intake rate is, therefore, a currency that plays a fundamental role in food selection (Stephen & Krebs 1986). If the trumpeter finch were selecting seeds only to maximize energy intake rate, hypothetical diet 2 (*see* Table 3) should have been obtained in our seed preference trials, as the energy gain in this hypothetical diet is higher than in the mean real diet. So, energy intake does not seem to be the only currency used by this species to assess seed value. We propose that, for this arid land passerine other currencies such as total water intake rate might also account for their food selection process.

For all hypothetical diets, metabolic water intake rate is lower than in the mean diet, but free water intake is, however, higher for hypothetical diets 1 and 3 (46.8% and 2.2%, respectively) in comparison with the mean real diet. Considering that seed water content in such a real diet is 100 times lower than the metabolic water production yields, such a percentage would not compensate the proportion of metabolic water loss (11.1% and 23.1%). In fact, for all hypothetical diets total water intake rate (obtained by summing up free water and metabolic water intake rates) is lower than in the mean real diet.

Therefore, it seems that the mean real diet in this arid land passerine is a balanced diet optimizing energy and total water intake rates at once, rather than a diet which maximizes only energy intake. This could explain why rape and canary, not differing in handling time, are selected in significantly different proportions by the trumpeter finch. It appears that in food selection process this species assesses food value through considering the time a seed needs to be handled, but also its nutrient composition, mainly its energy content and the metabolic water production yields (*see* Table 3). Birds inhabiting arid and semiarid habitats have to face low primary productivity which could constrain energy intake (Louw & Seely 1982). Therefore food selection should be highly adaptive as selected food items must maximize energy intake rate, but also must contain or produce adequate quantity of water to satisfy their metabolic requirements (MacMillen 1990).

It could be argued that hypothetical diet 2, dominated by sunflower and giving the higher energy intake is not selected because sunflower seed is too big for the birds to handle easily and quickly. Although with our experimental design we cannot rule out this possibility, it seems to be unlikely considering the species of plant on which the trumpeter finch feed preferably in the wild (e.g., *Diplotaxis* spp., *Euzomodendron bourgaeanum* and *Moricandia foetida*; Mota *et al.* 2004, own data). They belong mostly to the family Cruciferae, as the rape in this study.

Scarcity of water in arid and semiarid areas is very likely an important, selective pressure. For birds living in these areas the "struggle for existence" includes the task of maintaining an adequate state of hydration, a necessary requisite for the manifold chemical reactions that occur in a living organism (Williams & Tieleman 2001). Granivorous birds feed mostly on seeds, whose water content is, as a general rule, very low (Díaz 1996). In light of our results, we suggest that the trumpeter finch, as many other arid land animals, could obtain most of its water from its food as a byproduct of metabolism (Schmidt-Nielsen & Schmidt-Nielsen 1951). That is, it should rely much on a diet which yields high quantities of metabolic water formed during catabolism of energy substrates. Data on diet of free living trumpeter finches support this suggestion. Mota *et al.* (2004) pointed out that birds of this species have been observed feeding on *Euzomodendron bourgaeanum* and *Moricandia foetida*, two species of Cruciferae very abundant in the Spanish distribution area of the trumpeter finch. Our data agree with these observations, as we have recorded this species feeding preferably on *Diplotaxis* spp. and *Moricandia* spp. (Cruciferae), plant species with high water production yields (Carrillo *et al.* 2004).

Free water is not always available in arid and semiarid lands, so these species need to be "facultative drinkers". Bartholomew (1972) and MacMillen (1990) demonstrated that several birds of the families Fringillidae, Strildidae, Ploceidae, Alaudidae, and Platycercidae could be maintained under laboratory conditions of moderate temperatures and humidities on an air-dried seed diet without drinking water. A diet rich in fat can supply as much water as needed since water represents the element obtained through its metabolism (MacMillen & Baudinette 1993). One should be cautious, however, when explaining seed selection patterns found in the trumpeter finch, as other factors such as secondary chemical compounds might also be involved in the selection process (Greig-Smith & Willson 1985).

All animals must solve their foraging problems using some mechanisms or "rules of thumb". The trumpeter finch seems to solve its foraging problems by "taking the profitable" in terms of energy and water gain. Maximizing the energy intake rate is a widespread mechanism in animal kingdom, but maximizing the water intake rate should be considered an adaptation in arid land species that allow them to cope with water shortage of this particular type of habitats.

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References

Barne, R. M. & Levy, N. M. 1998: *Physiology*. 4th ed. — Mosby Inc., San Louis Missouri.

Bartholomew, G. A. 1972: The water economy of seed-eating birds that survive without drinking. — In: Voous, K. H. (ed.), *Proceedings of the 15th International Ornithological Congress*: 237–254. E. J. Brill, Leiden.

Benkman, C. W. 1988: Seed handling ability, bill structure, and the cost of specialization for crossbills. — *The Auk* 105: 715–719.

Benkman, C. W. & Pulliam, H. R. 1988: The comparative feeding rates of North-American sparrows and finches. — *Ecology* 69: 1195–1199.

Carrillo, C. M., Barbosa, A., Valera, F., Barrientos, R. & Moreno, E. 2007: Northward expansion of a desert bird: Effects of climate change? — *Ibis* 149: 166–169.

Carrillo, C. M., Moreno, E., Valera, F. & Barbosa, A. 2004: *Conducta de alimentación en el Camachuelo trompetero: morfología vs. composición del alimento*. — Libro de resúmenes, X Congreso Nacional y VII Iberoamericano de Etología, Almería.

Cramp, S. & Perrins, C. M. 1994: *The birds of the Western Paleartic*. — Oxford University Press, Oxford.

Davies, S. J. 1982: Behavioural adaptations of birds to environments where evaporation is high and water is in short supply. — *Comparative Biochemistry and Physiology A* 71: 557–566.

Díaz, M. 1990: Interspecific patterns of seed selection among granivorous passerines. Effects of seed size, seed nutritive value and bird morphology. — *Ibis* 132: 467–476.

Díaz, M. 1994: Variability in seed size selection by granivorous passerines. Effects of bird size, bird size variability, and ecological plasticity. — *Oecologia* 99: 1–6.

Díaz, M. 1996: Food choice by seed-eating birds in relation to seed chemistry. — *Comparative Biochemistry and Physiology A* 113: 239–246.

Endler, J. A. 1991: Interactions between predator and prey. — In Krebs, J. R. & Davis, N. B. (eds.), *Behavioural ecology: an evolutionary approach*: 169–176. Blackwell, Oxford.

Glück, E. E. 1985: Seed preference and energy intake of Goldfinches *Carduelis carduelis* in the breeding season. — *Ibis* 127: 421–429.

Goldstein, G. B. & Baker, M. C. 1984: Seed selection by juncos. — *Wilson Bulletin* 96: 458–463.

Grant, P. R. 1986: *Ecology and evolution of Darwin's finches*. — Princeton University Press, Princeton.

Greig-Smith, P. W. & Willson, M. F. 1985: Influences of seed size, nutrient composition and phenolic content on the preferences of bullfinches feeding in ash trees. — *Oikos* 44: 47–54.

Hespenheide, H. A. 1966: The selection of seed by finches. — *Wilson Bulletin* 78: 191–197.

Hrabar, H. D. K. & Perrin, M. 2002: The effect of bill structure on seed selection by granivorous birds. — *African Zoology* 37: 67–80.

Kear, J. 1962: Food selection in finches with special reference to interspecific differences. — *Proceedings of the Zoological Society of London* 138: 163–204.

Kelrick, M. I., Macmahon, J. A., Parmenter, R. R. & Sisson, D. V. 1986: Native seed preferences of shrub-steppe rodents, birds and ants: The relationships of seed attributes and seed use. — *Oecologia* 68: 327–337.

Lázaro, R., Rodrigo, F. S., Gutiérrez, L., Domingo, F. &

Puigdefábregas, J. 2001: Analysis of a 30-year rainfall record (1967–1997) in semi-arid SE Spain for implications on vegetation. — *Journal of Arid Environments* 48: 373–395.

Lockwood, J. R. I. 1998: On the statistical analysis of multiple-choice feeding preference experiments. — *Oecologia* 116: 475–481.

Louw, G. N. & Seely, M. K. 1982: *Ecology of desert organisms*. — Longman, London.

MacMillen, R. E. 1990: Water economy of granivorous birds: a predictive model. — *The Condor* 92: 379–392.

MacMillen, R. E. & Baudinette, R. V. 1993: Water economy of granivorous birds: Australian parrots. — *Functional Ecology* 7: 704–712.

Moreno, E., Barbosa, A. & Carrascal, L. M. 1997: Should congruence between intra- and interspecific ecomorphological relationships be expected? A case study with the great tit, *Parus major*. — *Proceedings of the Royal Society of London B* 264: 533–539.

Mota, J., Cabello-Piñar, J. Cerrillo, M. I. & Rodriguez-Tamayo M. L. 2004: *Subdesiertos de Almería: naturaleza de cine*. — Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.

Myton, B. A. & Ficken, R. W. 1967: Seed-size preference in chickadees and titmice in relation to ambient temperatures. — *Wilson Bulletin* 79: 319–321.

Newton, I. 1967: Adaptive radiation and feeding ecology of some British finches. — *Ibis* 109: 33–98.

Newton, I. 1972: *Finches*. — Collins, London.

Pulliam, H. R. 1985: Foraging efficiency, resource partitioning, and the coexistence of sparrow species. — *Ecology* 66: 1829–1836.

Rey, P. & Valera, F. 1999: Diet plasticity in blackcap (*Sylvia atricapilla*): The ability to overcome nutritional constraints imposed by agricultural intensification. — *Ecoscience* 6: 429–438.

Roa, R. 1992: Design and analysis of multiple-choice feeding preference experiments. — *Oecologia* 80: 82–86.

Schmidt-Nielsen, B. & Schmidt-Nielsen, K. 1951: A complete account of the water metabolism in kangaroo rats and an experimental verification. — *Journal of Cellular and Comparative Physiology* 38: 165–181.

Senar, J. C. & Pascual, J. 1997: Keel and tarsus length provide a good predictor of avian body size. — *Ardea* 85: 269–274.

Shuman, T. W., Robel, R. J., Zimmerman, J. I. & Dayton, A. D. 1990: Influence of handling time and metabolizable energy on seed selection by four emberizids. — *Southwestern Naturalist* 35: 466–468.

Siegel, S. & Castellan, N. J. 1988: *Nonparamentric statistics for the behavioral sciences*, 2nd ed. — McGraw-Hill International Editions.

Systat Software Inc. 2002. *TableCurve 2D*, ver. 5.01. — Evanston, Illinois.

Smith, T. B. 1987: Bill size polymorphism and intraspecific niche utilization in an African finch. — *Nature* 329: 717–719.

Sprenkle, J. M. & Blem, C. R. 1984: Metabolism and food selection of eastern house finches. — *Wilson Bulletin* 96: 184–195.

Stephen, D. W. & Krebs, J. R. 1986: *Foraging theory. Monographs in behavior ecology*. — Princeton University Press.

Svensson, L. 1992: *Identification guide to european passerines*. — Published by the author.

Todd, M., Felton, A. & Garnett, S. 2003: Morphological and dietary differences between common and uncommon subspecies of Crimson finch *Neochmia phaeton*, and Star finch, *Neochmia ruficanda*, in northern Australia. — *Emu* 103: 141–148.

Valera, F., Wagner, R. H., Romero, M., Gutiérrez, J. E. & Rey, P. J. 2005: Dietary specialization on high protein seeds by adult and nestling serins. — *The Condor* 107: 29–40.

Van der Meij, M. A. A. & Bout, R. G. 2000: Seed selection in the Java sparrow (*Padda oryzivora*): Preference and mechanical constraint. — *Canadian Journal of Zoology* 78: 1668–1673.

Williams, J. B. & DuPlessis, M. A. 1996: Field metabolism and water flux of sociable weavers *Philetairus socius* in the Kalahari Desert. — *Ibis* 138: 168–171.

Williams, J. B. & Tieleman, B. I. 2001: Physiological ecology and behaviour of desert birds. — In: Nolan, V. Jr. (ed.), *Current ornithology* 16: 299–353. Kluwer Academic Publishers, New York.

Williams, J. B. & Tieleman, B. I. 2005: Physiological adaptation in desert birds. — *Bioscience* 55: 416–425.

Willson, M. F. 1971: Seed selection in some North-American finches. — *The Condor* 73: 415–429.

Willson, M. F. 1972: Seed size preference in finches. — *Wilson Bulletin* 84: 449–455.

Willson, M. F. & Harmeson, J. C. 1973: Seed preferences and digestive efficiency of cardinals and song sparrows. — *The Condor* 75: 225–234.

Zar, J. H. 1996: *Biostatistical analysis*. — Prentice-Hall, New Jersey.