IMPORTANCE OF SEED CHARACTERISTICS IN DIET PREFERENCES OF GRANIVOROUS BIRDS: A PILOT STUDY WITH HOUSE SPARROWS (*Passer domesticus*)

Mieke Titulaer, Alicia Melgoza Castillo, Felipe A. Rodríguez Almeida and Jesús A. Fernández

SUMMARY

*The availability of seeds that can be consumed profitably is an important determinant of habitat quality for granivorous birds. In order to gain experience with seed selection studies in sparrows, we performed a pilot study with the objective of investigating the effect of different seed characteristics (size, color, visibility, nutrient composition) on seed selection by house sparrows (*Passer domesticus*). The pilot study consisted of seed selection experiments in two phases. In Phase I, nine commercial seed types were offered simultaneously for different time periods. Phase II consisted of six trials with different combinations of three seed types that varied on one of the three characteristics of interest. Of the characteristics under study, seed size was the only characteristic influencing seed choice. House sparrows preferred seeds of intermediate size in all trials. The results of this study provide indications for future seed selection experiments and show the importance of taking husk characteristics and handling time into account.*

Introduction

Food availability and distribution, as well as the characteristics of the available seeds in a given area, are important factors influencing habitat suitability for granivorous birds (Pulliam, 1986). The relationship between seed size and bill size and form has been found to be the main determinant of seed preferences in granivorous birds (Díaz, 1996). Larger billed birds are more efficient at handling larger seeds than smaller billed birds (Pulliam, 1983, 1985; Soobramoney and Perrin, 2007; Johansen *et al*., 2014). This does not necessarily mean that larger billed birds always select larger seeds, as they have been found to prefer smaller seeds with shorter handling times as well (Keating *et al*., 1992). However, larger billed birds generally include a wider range of seeds in their diet (Willson, 1971; Desmond *et al*., 2008). Other seed characteristics related to the chemical composition of a seed may also influence seed selection and preference, although they are usually less important than seed size (Díaz, 1996) and results are contradictory. Different bird species have been found to select seeds based on the content of energy (Valera *et al*., 2005), fat (Thompson *et al*., 1987; Molukwu *et al*., 2011), protein (Larson *et al*., 2012; Johansen *et al*., 2014), carbohydrates (Ríos *et al*., 2012a, b), or water (Carillo *et al*., 2007). Birds may also avoid seeds based on toxic components (Marone *et al*., 2008; Ríos *et al*., 2012). In fruit eating birds, color and visibility have been shown to be important in food selection as well (Schmidt *et al*., 2004; Schaefer *et al*., 2008). In granivorous birds, these seed components have not been investigated.

Here, we studied seed preferences of house sparrows (*Passer domesticus*) in a pilot study with two objectives: 1) to test experimental procedures that may be used in seed choice experiments for testing seed preferences of granivorous birds, and 2) to determine the importance of different seed characteristics, including size, color, visibility and nutrient composition, in seed selection.

Methods

The pilot study took place in November 2012. We used five adult male house sparrows captured with traps and a bird attractor around Chihuahua City, Mexico. We measured bill length, width, and depth to the nearest 0.1mm with a caliper and determined body weight (g) immediately after capture. At the end of the experiments, birds were released in the area of capture. We housed the birds in cages of 0.8×0.8×0.8m with a swing, perch, nest and *ad libitum* access to water. The birds were provided an adaptation diet consisting of a mixture of nine commercial seeds that were used in the seed selection experiments: canary grass (*Phalaris canariensis*), niger (*Guizotia abyssinica*), yellow and red millet (*Panicum miliaceum*), rapeseed (*Brassica napus*), wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), amaranth (*Amaranthus hypochondriacus*), and sunflower (*Helianthus annuus*) seeds. These seeds were chosen because of

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IMPORTANCIA DE LAS CARACTERÍSTICAS DE LAS SEMILLAS EN LAS PREFERENCIAS DE AVES GRANÍVORAS: ESTUDIO PILOTO CON EL GORRIÓN DOMÉSTICO (*Passer domesticus*)

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RESUMEN

La disponibilidad de semillas que pueden ser aprovechadas constituye un componente importante de la calidad del hábitat para las aves granívoras. Con el fin de obtener experiencia en estudios de selección de dieta en gorriones domésticos (Passer domesticus)*, se desarrolló un estudio piloto con el fin de investigar el efecto de diferentes características de las semillas (tamaño, color, visibilidad, composición de nutrientes) sobre la selección de semillas por el gorrión doméstico (*Passer domesticus*). El estudio piloto consistió de experimentos de selección de semillas en dos fases. En la fase I se ofreció una mezcla de nueve semillas comerciales por diferentes periodos de tiempo. La fase II consistió en seis pruebas con diferentes combinaciones de tres semillas que variaron únicamente en una de las características de interés. De las características bajo estudio, solo el tamaño influyó la selección de semillas. Los gorriones domésticos prefirieron semillas de tamaños intermedios en todas las pruebas. Los resultados de este estudio proveen indicaciones para futuros experimentos sobre selección de semillas, e indican la importantancia de incluir características de la cáscara de las semillas y del tiempo de manipulación.*

IMPORTÂNCIA DAS CARACTERÍSTICAS DAS SEMENTES NAS PREFERÊNCIAS DE AVES GRANÍVORAS: ESTUDO PILOTO COM O PARDAL- DOMÉSTICO (*Passer domesticus*)

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RESUMO

*A disponibilidade de sementes que podem ser aproveitadas constitui um componente importante da qualidade do habitat para as aves granívoras. Com o fim de obter experiência em estudos de seleção de dieta em pardais-domésticos (*Passer domesticus*), foi desenvolvido um estudo piloto com o fim de investigar o efeito de diferentes características das sementes (tamanho, cor, visibilidade, composição de nutrientes) sobre a seleção de sementes pelo pardal-doméstico (*Passer domesticus*). O estudo piloto consistiu de experimentos de seleção de sementes em duas fases. Na fase I se ofereceu uma mistura de nove sementes comerciais por diferentes períodos de tempo. A fase II consistiu em seis provas com diferentes combinações de três sementes que variaram unicamente em uma das características de interesse. Das características sob estudo, somente o tamanho influenciou na seleção da semente. Os pardais-domésticos preferiram sementes de tamanhos médios em todas as provas. Os resultados de este estudo fornecem indicações para futuros experimentos sobre seleção de sementes, e indicam a importantância de incluir características da casca das sementes e do tempo de manipulação.*

their variation in size and color. We measured length, width and depth of 10 seeds of each type and calculated a seed volume index (l×w×h) per species. We also determined the weight of 10 seeds of each type and calculated the mean seed weight. Nutrient content (moisture, ash, protein and fat) of the nine seeds was determined by bromatological analysis (AOAC, 1990). Information on seed size and nutrient analysis is shown in Table I.

On the experimental days, we removed all food from the cage at 17:00. The trials started at 07:00 the next day. We ran only one trial per day. After the experimental trial, birds were fed a mixture of the nine seed types until 17:00. Feeding trays with three equal compartments were used. The experiment was initiated one week after birds were captured and consisted of two phases. During Phase 1 (days 1-2), birds were presented with a mixture of 1g of each seed type equally divided over the three compartments. On day 1, feeding time was 30min and on day 2, 6h. At the end of the feeding time, the remaining seeds were removed and the consumed amount of each seed type determined as the difference in mass between the end and the beginning of the feeding period. We determined seed preferences by comparing the amount consumed of each seed species. Days 1 and 2 were evaluated separately. In Phase 2 (days 3-8), birds were offered a combination of three seeds that varied in only one of three characteristics: size, color or visibility. The compartment in which each of the three seed types was placed was determined at random. For example, to test the effect of size, we offered the birds three black seeds of different sizes. For the color effect trials, seeds were painted with an artificial colorant (McCormack) without odor or flavor. For the visibility effect trials, we used feeders in different colors (red and yellow) and offered two seed species with the same color as the feeder (no contrast, less visible) and one seed species with a different color as the one of the feeder (high contrast, more visible). The expectation was that if visibility would play a role in seed selection, birds would prefer the most contrasting seed. In total we ran six trials, two for each seed characteristic. The order of

TABLE I
WATER AND NUTRIENT CONTENT, AND SIZE OF THE NINE EXPERIMENTAL SEED SPECIES

Seed Type	Moisture (%)	Ash (%)	Fat (%)	Protein (%)	Weight (mg)	Volume (mm^3)
Amaranth	2.15	3.08	7.62	18.32	0.71	4.32
Canola	2.47	3.67	38.75	22.48	3.46	5.41
Niger	3.23	3.98	34.87	22.86	4.02	6.44
Red Millet	4.97	2.79	4.23	14.40	4.69	10.49
Yellow Millet	6.06	2.66	4.19	13.25	6.28	13.42
Canary Grass	5.67	8.68	7.05	15.92	7.41	15.40
Sorghum	5.48	0.74	3.30	10.62	31.62	45.54
Wheat	4.00	1.66	2.72	16.02	33.44	46.62
Sunflower	2.17	2.77	38.73	18.18	55.21	165.57

the trials was determined at random for each of the five birds. Feeding time in Phase 2 was 45min, because on day 1 of Phase 1 birds consumed very little in 30min.

A linear mixed model was fitted to analyze the amount (g) of seeds consumed. Consumption was log-transformed to fulfil the assumption of normality. Normality of the log transformed variable was confirmed using a Q-Q plot. Seed type, trial, and their interaction were adjusted as fixed effects. We were specifically interested in the interaction, because a significant interaction would imply that in at least one of the six trials, one of the three seeds was consumed in a different amount than the other two. In other words, it would mean that at least one of the three seeds in at least one of the six trials was preferred or avoided. Bird weight (g) and bill volume (bill length×width×depth) were added as covariates. To control for pseudo-replication, individual (bird) was included in the model as a random effect. The final model was selected through the backward elimination of non-significant terms. Analyses were run in R 2.13.1 (R Core Team, 2014) using package lme4 (Bates *et al*., 2015). *Post hoc* tests were performed to investigate statistical differences among the three seed types in each of the six trials using the general linear hypothesis (glht) function and specified contrasts.

Results and Discussion

Results of Phase 1 showed that birds preferred canary grass seeds (Table II). This was the only seed consumed when feeding time was only 30min. With a longer feeding time (6h), birds consumed mostly millet seeds after canary grass seeds were totally consumed, but one bird preferred niger seeds. Preferences did not seem to be related to fat or protein content, since the preferred seeds contained less of these nutrients than less preferred seeds (Table I). What distinguished the preferred seed types from the others was mainly their size. Volume (mm^3) of canary grass and millet seeds is intermediate among the seed types used in this experiment. Another characteristic of canary grass seeds is that the husk is less hard. Birds remove the husk from the seed before consuming it. Thus, handling time may have been shorter for canary grass.

TABLE II
AMOUNT CONSUMED (MEAN ±SD) IN PHASE 1 AND PREFERENCE RANK OF THE SEEDS

Seed Type	Consumed (g) in 30min	Consumed (g) in 6h	Preference rank
Amaranth	0.00 ±0.00	0.28 ±0.22	5
Canola	0.00 ±0.00	0.16 ±0.09	7
Niger	0.04 ±0.09	0.26 ±0.42	6
Red Millet	0.00 ±0.00	0.82 ±0.40	3
Yellow Millet	0.10 ±0.17	0.84 ±0.36	2
Canary Grass	0.50 ±0.19	1.00 ±0.00	1
Sorghum	0.00 ±0.00	0.10 ±0.10	8
Wheat	0.00 ±0.00	0.32 ±0.40	4
Sunflower	0.00 ±0.00	0.00 ±0.00	9

In Phase 2 there was a significant interaction effect between seed type and trial ($F_{10,68}$= 2.95, P=0.004), indicating that seed type had a significant influence on the amount consumed in at least one of the six trials. In the two seed size trials, there was a clear tendency for birds to prefer the intermediate (of three) seeds. The specified contrast showed that in the second seed size trial, birds preferred seeds of intermediate size over the smaller (P= 0.002) and larger (P=0.066) seeds (Figure 1). The same pattern for size effect was observed in the first seed size trial (Figure 1), although these differences were not significant (P=0.37 and 0.30, respectively). In contrast, there was no relationship between color (Figure 2) or contrast (Figure 3) and seed preference in any of the color or contrast trials (all P>0.05). Rather than preferring seeds of a specific color or seeds that contrasted most with the feeder, birds consistently preferred canary grass or millet seeds, which is consistent with preferences found in Phase 1 of the study. Note that canary grass seeds were never used in the seed size trials because in Phase 1 canary grass was the preferred seed. To prove that intermediate seed size (among the sizes of the seed types offered) was indeed a preferred seed characteristic, we decided to use other seeds of intermediate sizes than the most preferred one. In contrast, we did use canary grass in the color and contrast trials because, if these characteristics were important, birds should choose the

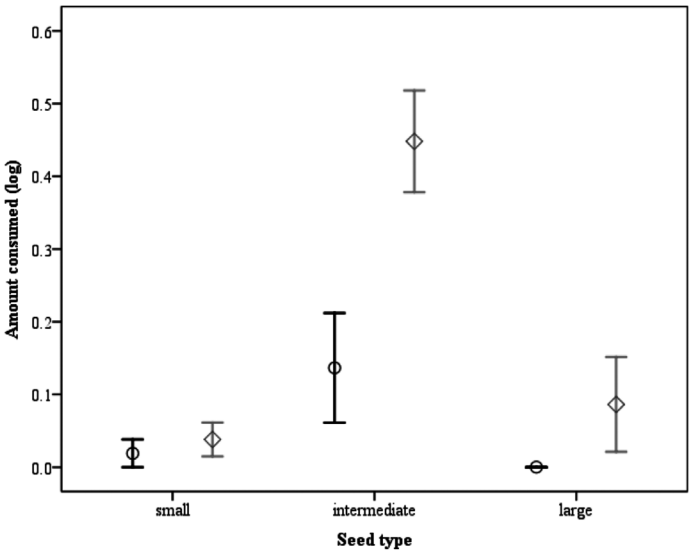

Figure 1. Mean amount consumed (±1 SE, Ln transformed) in the seed size trials. For trial 1 (black circles), small: canola; intermediate: niger; large: sunflower. For trial 2 (gray diamonds), small: amaranth; intermediate: yellow millet; large: wheat.

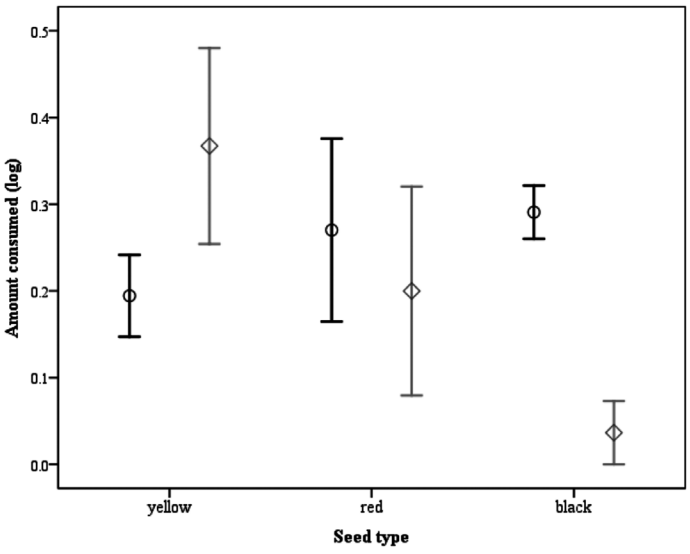

Figure 2. Mean amount consumed (±1 SE, Ln transformed) in the color trials. For trial 1 (black circles), canary grass painted yellow, red or black. For trial 2 (gray diamonds), yellow: yellow millet; red: red millet; black: canola.

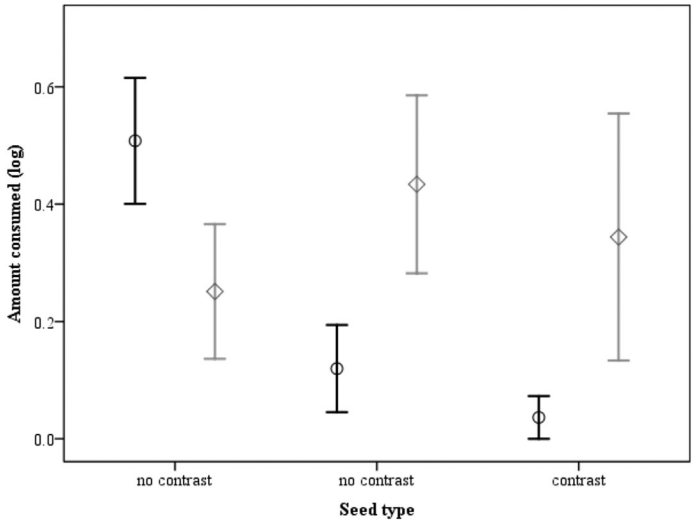

Figure 3. Mean amount consumed (±1 SE, Ln transformed) in the contrast trials. For trial 1 (black circles), no contrast: canary grass and yellow millet; contrast: niger (yellow feeder). For trial 2 (gray diamonds), no contrast: canary grass painted red and brown respectively; contrast: yellow millet (red feeder).

preferred color and most contrasting seeds instead of canary grass ones. Neither bill volume nor body weight (P>0.05) influenced seed selection. However, there was little variation in bill volume (mean= 798.7 ±107.4mm^3) or body weight (mean= 24.3 ±1.0g) among the experimental birds and these measurements are probably more useful when comparing different bird species.

In summary, we found an effect of seed size on seed preferences of five adult male house sparrows. This finding is in agreement with previous research (Willson, 1971, 1972; Pulliam, 1983; 1985; Keating *et al*., 1992; Díaz, 1994; Hrabar and Perrin, 2002). We did not find an effect of seed color or visibility on seed preference. This is in contrast to the color effect observed in fruit eating birds, where a red color is related to ripeness (Schmidt and Schaefer, 2004). Granivorous birds may not show color preferences because seed color is not consistently related to any desired nutrient content. House sparrows have relatively large bills. Preferences for intermediate seed sizes may indicate that birds are selecting the largest seeds that they can still handle efficiently (Benkman and Pulliam, 1988). In this regard, seed size rather than nutrient content seemed to influence preferences in Phase 1 of this study. Previous studies on seed selection by granivorous passerines also showed that seed size is the main characteristic influencing seed preferences, whereas seed chemical composition generally is of secondary importance (Díaz, 1996). However, husk characteristics may also play a role in handling efficiency (Van der Meij *et al*., 2004) and should be distinguished from seed size. Optimal foraging theory predicts that an animal should select food items that it can handle most efficiently as to maximize energy intake over time (Charnov, 1976; Pyke, 1984). Thus, it is possible that house sparrows are foraging optimally by selecting seeds of intermediate sizes. To test this hypothesis, we recommend that future seed preference studies make a more explicit attempt to determine handling time in relation to energy intake.

Conclusion

The results of this pilot study give insight into the design of seed selection studies with granivorous birds and provide guidelines for future studies. The results show the importance of seed size in seed preferences and point towards the necessity of measuring handling efficiency in future studies. Furthermore, the results show that it is important to take into account husk characteristics in addition to seed size to distinguish the effect of these two characteristics on handling time. Finally, it should be emphasized that this was a pilot study and that a larger sample size is required in subsequent experiments because of substantial individual variation.

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REFERENCES

AOAC (1990) *Official Methods of Analysis*. 15th ed. Association of Official Analytical Chemists. Virginia, USA.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J. Stat. Softw. 67*: 1-48.

Benkman CW, Pulliam HR (1988) The comparative feeding rates of north American sparrows and finches. *Ecology 69*: 1195-1199.

Carillo CM, Moreno E, Valera F, Barbosa A (2007) Seed selection by the trumpeter finch, *Bucanetes githagineus*. What currency does this arid-land species value? *Ann. Zool. Fenn. 44*: 377-386.

Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor. Popul. Biol. 9*: 129-136.

Desmond MJ, Mendez-Gonzalez C, Abbott LB (2008) Winter diets and seed selection of granivorous birds in southwestern New Mexico. *Stud. Avian Biol. 37*: 101-112.

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. *Comp. Biochem. Physiol. 113A*: 239-246.

Hrabar HDK, Perrin MR (2002) The effect of bill structure on seed selection by granivorous birds. *Afr. Zool. 37*: 67-80.

Johansen SM, Horn DJ, Wilcoxen TE (2014) Factors influencing seed species selection by wild birds at feeders. *Wilson J. Ornithol. 126*: 374-381.

Keating JF, Robel RJ, Adams AW, Behnke KC, Kemp KE (1992) Role of handling time in selection of extruded food morsels by two granivorous bird species. *Auk 109*: 863-868.

Larson JA, Fulbright TE, Brennan LA, Hernández F, Bryant FC (2012) Selection of seeds of an exotic and three native grasses by Northern Bobwhites (*Colinus virginianus*). *Southwest. Nat. 57*: 319-322.

Marone L, Lopez de Casenave J, Milesi FA, Cueto VR (2008) Can seed-eating birds exert top-down effects on grasses of the Monte desert? *Oikos 117*: 611-619.

Molokwu MN, Nilsson JA, Olsson O (2011) Diet selection in birds: trade-off between energetic content and digestibility of seeds. *Behav. Ecol. 22*: 639-647.

Pulliam HR (1983) Ecological community theory and the coexistence of sparrows. *Ecology 64*: 45-52.

Pulliam HR (1985) Foraging efficiency, resource partitioning, and the coexistence of sparrows. *Ecology 66*: 1829-1836.

Pulliam HR (1986) Niche expansion and contraction in a variable environment. *Am. Zool. 26*: 71-79.

Pyke GH (1984) Optimal foraging theory: A critical review. *Annu. Rev. Ecol. Systemat. 15*: 523-575.

R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Ríos JM, Mangione A, Marone L (2012a) Effects of nutritional and anti-nutritional properties of seeds on the feeding ecology of seed-eating birds of the Monte Desert, Argentina. *Condor 114*: 44-55.

Ríos JM, Mangione A, Marone L (2012b) Tolerance to dietary phenolics and diet breadth in three seed-eating birds: Implications for graminivory. *J. Exp. Zool. 317*: 425-433.

Schaefer HM, McGraw K, Catoni C (2008) Birds use fruit colour as honest signal of dietary antioxidant rewards. *Funct. Ecol. 22*: 303-310.

Schmidt V, Schaefer HM (2004) Unlearned preference for red may facilitate recognition of palatable food in young omni-

vorous birds. *Evolut. Ecol. Res. 6*: 919-925.

Schmidt V, Schaefer HM, Winkler H (2004) Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos 106*: 551-557.

Soobramoney S, Perrin MR (2007) The effect of bill structure on seed selection and handling ability of five species of granivorous birds. *Emu 107*: 169-176.

Thompson DB, Tomback DF, Cunningham MA, Baker MC (1987) Seed selection by dark-eyed juncos (*Junco hyemalis*): optimal foraging with nutrient constraints? *Oecologia 74*: 106-111.

Valera F, Wagner RH, Romero-Pujante M, Gutiérrez JE, Rey PJ (2005) Dietary specialization on high protein seeds by adult and nestling serins. *Condor 107*:29-40.

Van der Meij MAA, Griekspoor M, Bout RG (2004) The effect of seed hardness on husking time in finches. *Anim. Biol. 54*: 195-205.

Willson MF (1971) Seed selection in some North American finches. *Condor 73*: 415-429.

Willson MF (1972) Seed size preferences in finches. *Wilson Bull. 84*: 449-455.