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 (Diaz, 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 (Diaz, 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 (Rios et al., 2012a, b), or water (Carillo et al., 2007). Birds may also avoid seeds based on toxic components (Marone et al., 2008; Rios 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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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 type 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>
<thead>
<tr>
<th>Seed Type</th>
<th>Moisture (%)</th>
<th>Ash (%)</th>
<th>Fat (%)</th>
<th>Protein (%)</th>
<th>Weight (mg)</th>
<th>Volume (mm$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaranth</td>
<td>2.15</td>
<td>3.08</td>
<td>7.62</td>
<td>18.32</td>
<td>0.71</td>
<td>4.32</td>
</tr>
<tr>
<td>Canola</td>
<td>2.47</td>
<td>3.67</td>
<td>38.75</td>
<td>22.48</td>
<td>3.46</td>
<td>5.41</td>
</tr>
<tr>
<td>Niger</td>
<td>3.23</td>
<td>3.98</td>
<td>34.87</td>
<td>22.86</td>
<td>4.02</td>
<td>6.44</td>
</tr>
<tr>
<td>Red Millet</td>
<td>4.97</td>
<td>2.79</td>
<td>4.23</td>
<td>14.40</td>
<td>4.69</td>
<td>10.49</td>
</tr>
<tr>
<td>Yellow Millet</td>
<td>6.06</td>
<td>2.66</td>
<td>4.19</td>
<td>13.25</td>
<td>6.28</td>
<td>13.42</td>
</tr>
<tr>
<td>Canary Grass</td>
<td>5.67</td>
<td>8.68</td>
<td>7.05</td>
<td>15.92</td>
<td>7.41</td>
<td>15.40</td>
</tr>
<tr>
<td>Sorghum</td>
<td>5.48</td>
<td>0.74</td>
<td>3.30</td>
<td>10.62</td>
<td>31.62</td>
<td>45.54</td>
</tr>
<tr>
<td>Wheat</td>
<td>4.00</td>
<td>1.66</td>
<td>2.72</td>
<td>16.02</td>
<td>33.44</td>
<td>46.62</td>
</tr>
<tr>
<td>Sunflower</td>
<td>2.17</td>
<td>2.77</td>
<td>38.73</td>
<td>18.18</td>
<td>55.21</td>
<td>165.57</td>
</tr>
</tbody>
</table>

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

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. Na fase I se ofreció uma mezcla de nueve semillas comerciais por diferentes períodos de tiempo. 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 importância de incluir características da casca das sementes e do tempo de manipulação.
the trials was determined at random for each of the five birds. Feeding time in Phase 2 was 45 min, because on day 1 of Phase 1 birds consumed very little in 30 min.

A linear mixed model was fitted to analyze the amount (g) of seeds consumed. Consumption was log-transformed to fulfill 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 30 min. With a longer feeding time (6 h), 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 (mm³) 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.

In Phase 2 there was a significant interaction effect between seed type and trial (F<sub>10,68</sub> = 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. 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

### TABLE II

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

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.
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 ±107.4mm³) or body weight (mean= 24.3 ±1.0g) among the experimentally 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 Puhlmann, 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 (Diaz, 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 grainivorous 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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