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Effect of Nutritional Content on Artificially Supplied Seed Utilization of Wintering Birds in a Mixed Forest, South Korea

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Key words
Behavior, Digital camera, Fat, Feeder, Food type

ABSTRACT

This study was conducted to clarify the effect of nutritional content on artificially supplied seed utilization of wintering birds in a mixed forest in South Korea. The dominant tree species in this forest were Japanese red pine (*Pinus densiflora*), Mongolian oak (*Quercus mongolica*), Japanese emperor oak (*Quercus dentate*). At the study site, we selected 6 plots and set up 3 feeders in each plot. The feeders were located 1.5 m above the ground and spaced 1 m apart. We selected 3 types of food resources (kidney beans, brown soybeans, and peanuts) based on their energy per 100 g. We supplied 200 g of each food type at the feeders. Feeders were recorded with a digital camera (HDR AS15, Sony, Tokyo, Japan) for 2 h. This was conducted 3 times per day. The videos were then analyzed to determine the frequency of visits, duration of stay at the feeder, frequency of pecking on food items, and number of consumed food items. Moreover, social behaviors were analyzed. In this study, we used peanuts as high-fat food type. Peanuts were consumed at the highest frequency by marsh tits (*Poecile palustris*), great tits (*Parus major*), and Eurasian nuthatches (*Sitta europaea*). In addition, the type of food, temperature, and metabolic energy requirement affected food utilization in marsh tits and great tits. In our study, some evidence was found that wintering birds in temperate zones prefer high-energy food items. Limited food availability during winter affects social hierarchies.

INTRODUCTION

Food utilization differs due to various causes such as the type and amount of food resources in the habitat, fluctuations in energy demand within an organism's life cycle, and the digestion efficiency, taste, and color of food (Samuni-Blank *et al*., 2013). Understanding species-specific food preferences is crucial for understanding habitat adaptations, as both the type and amount of food resources and the local species composition in a habitat vary with one another (Hinsely *et al*., 2002; Chatterjee and Basu, 2018).

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The choice of food also differs seasonally. In the case of Passeriformes that live in temperate regions, invertebrates such as caterpillars and other insects were the primary food sources used while brooding young (Chamberlain *et al*., 2005; Johansen *et al*., 2014). However, there is a difference in the type and amount of food resources that occur in a given season due to changes in temperature, humidity, and available plants (Koenig and Knops, 2001; Thomson *et al*., 2012; Sánchez-Reyes *et al*., 2019). As a result, the utilization rate of vegetative food increases in autumn and winter (Behmer *et al*., 2001).

For birds in northern temperate zones in particular, access to sufficient food resources is likely to vary between seasons (Plummer *et al*., 2013). In winter, these birds face a limited quality and quantity of habitat factors (Carrascal *et al*., 2012). This includes a dramatic reduction in arthropod populations as well as reduced foraging opportunities caused by snow cover (Walter and Gosler, 2001; Renner *et al*., 2012). Winter survival depends on obtaining enough food for self-maintenance (Cresswell *et al*., 2010), and wintering birds need large amounts of energy to maintain homeostasis. Because of only a few daylight h and low temperatures, birds experience increased energy losses and prefer high-energy foods (Johansen *et al*., 2014).

It is well known that food availability in wintering sites influences survival and productivity in migratory birds. Previous studies of food preferences in winter have examined the role of seed size, nutritional content, and handling time, as well as bird bill size (Ríos *et al*., 2012; Johansen *et al*., 2014). The feeding preferences of wintering birds have been related to the amount of fat needed to maintain homeostasis (Desmond *et al*., 2008). Moreover, high-carbohydrate foods may be preferred, as they can be easily digested and used as energy sources (Brown *et al*., 2012).

The provisioning of anthropogenic food to wild birds is a popular method for conserving bird communities (Ewen *et al*., 2014; Wilcoxen *et al*., 2015). Moreover, winter food supplementation may influence the body condition of birds in the subsequent breeding season, potentially being reflected in their reproductive success (Plummer *et al*., 2017). Supplementary foods may help birds overcome short periods of food availability in winter. In particular, feeders may be an important tool for offering predictable and abundant food resources to meet high energy demands in winter (Carrascal and Polo, 1999; Carrascal *et al*., 2012).

The purpose of this study was to identify the food preferences of wintering birds. We set out to investigate the effect of nutritional content on artificially supplied seed utilization of birds in a mixed forest of South Korea.

MATERIALS AND METHODS

This study was carried out from November 2018 to February 2019 in a mixed forest at Chung-Ang University in Ansung, Gyeonggi Province, South Korea. This area was dominated by Japanese red pine (*Pinus densiflora*), Mongolian oak (*Quercus mongolica*), and Japanese emperor oak (*Quercus dentate*). A HOBO data logger was placed at the center of the study area. During this study, temperatures ranged from -7.18°C to 8.60°C, with the average temperature being -0.61°C.

We selected six plots in the study area, with each plot being separated by at least 700 m. Three feeders were set up in each plot. The feeders were located above 1.5 m above the ground and spaced 1 m apart. The size of the feeder was 2 cm × 30 cm × 30 cm (height × width × length). We selected three types of food resources (kidney bean, brown soybean, and peanut) based on their energy per 100 g. These resources have different ratios of carbohydrates, proteins, and fats (Ministry of Food and Drug Safety, 2016, Table I). To reduce the effect of food size on birds' food preference, we randomly selected 1000 seeds for each food type. We measured the length, depth, and weight of seeds of each food type using Vernier calipers (530-123, Mitutoyo, Kawasaki, Japan) and a digital balance (FX-200i, AND Labtech, Gimpo, South Korea). There were no differences in food size and weight among food types (Table II). Thirty days prior to the experiment's start, we added food to the feeder to make local birds aware of the food. We supplied 200 g of each food type on the feeder. At the end of each experiment, we measured the amount of consumed food.

Table I. Differences in the nutritional content of kidney beans, brown soybeans, and peanuts (Ministry of Food and Drug Safety, 2016).

	Kidney bean	Brown soybean	Peanut
Carbohydrate (%)	64.00	30.60	17.10
Protein (%)	21.00	35.00	26.10
Fat (%)	1.00	17.20	49.10

Table II. Differences in the size and weight of kidney beans, brown soybeans, and peanuts, with results from an analysis of variance.

	Kidney bean	Brown soybean	Peanut	χ^2	p
Length (mm)	16.88±0.10	17.92±0.08	17.02±0.19	0.53	0.59
Depth (mm)	8.34±0.06	8.65±0.06	8.28±0.18	2.74	0.07
Weight (g)	0.56±0.01	0.54±0.01	0.58±0.01	2.79	0.06

To assess the interaction between birds' morphological characteristics and feeding behavior, we captured birds using a mist net. Mist nets were set up around feeders and the body length, tarsus length, head to bill length, bill to skull length, tail length, wing length, and weighed body mass of captured birds were measured. Same researcher measured the traits with same instruction to decrease the measuring deviation. Different combinations of colored bands were placed on the tarsus of each captured bird to enable individual identification. We calculated maintenance energy expenditure (MEE) based on weight (W, g) (Harper, 2000).

$$MEE\ (kcal/day) = 0.50W^{1.1}$$

We supplied the feeders with food items and recorded feeders using a digital camera (HDR AS15, Sony, Tokyo, Japan) for 2 h. The videos were then analyzed in a laboratory. To minimize the influence of inclement weather, such as snow, clouds, and mist, on the foraging behavior of birds, videos were only recorded on sunny days. We analyzed the frequency of visits, duration of stay at the feeder, frequency of pecking on food items, and number of consumed food items using a Sony Vegas Pro 13.0. We calculated the number of consumed food items based on the average weight of each food item.

When two or more individuals were present at the same feeder, the social behaviors were recorded (Hwang, 2020). Social behavior among individuals was classified into one of three types:

1. One individual approaching the others, spreading its wings, or inflating its feathers, or one individual attacking the others with its beak or claws
2. Moving or leaving the feeder when the others approach it
3. No response to the others

Relative aggression was calculated by analyzing individual social behaviors (Haythorpe *et al*., 2012). To calculate a relative aggression score, we used the following formulae:

$E_{agg} = (ab_x/AB) \times A$

$NE_{agg} = A - E_{agg}$

In these formulae, E_{agg} is the predicted occurrence of aggressive behaviors of X species, and ab_x is visit frequency of X species confirmed at one point. AB represents the frequency of visits of all birds identified at one point. A is the frequency of total aggressive behaviors identified at one point. NE_{agg} is a value that predicts that species X will not behave aggressively. It uses a value excluding the value expected that species X will behave aggressively from the total aggressive behavior identified at one point.

The relative aggression (RA) of each species was calculated as follow:

$RA = [(E_{agg} - Q_{agg})^2 / E_{agg}] + [(NE_{agg} - NO_{agg})^2 / NE_{agg}]$

O_{agg} represents the number of times species X initiated an aggressive behavior, while NO_{agg} expresses number of times species X did not initiate an aggressive behavior. When the frequency of actual aggression was lower than the expected value (E_{agg}), the relative aggression value was expressed as a negative number, and when frequency of aggressive behavior was higher, it was expressed as a positive number.

To investigate differences in the feeding behavior of marsh tits, great tits, and Eurasian nuthatches, we used a one-factor repeated-measures ANOVA. If each foraging behavior differed based on species, we ran a Bonferroni post-hoc test. We tested the effect of variables on the food choices of wintering birds with an analysis of covariance (ANCOVA). Before running the ANCOVA, we used a correlation analysis to examine associations among variables such as wintering bird morphological characteristics, food type, and temperature. Frequency of visits on the feeder was significantly correlated with temperature, food type, and MEE. Therefore, these variables were included as covariates in the corresponding analyses. The ANCOVA was performed with the package 'datarium' in R.

RESULTS

During this study, the feeders were used 165,120 times. Of the 13 species that used the feeders, great tits showed the highest visit frequency, visiting feeders 57,355 times. Marsh tits and Eurasian nuthatches visited 45,901 and 39,245 times, respectively.

All three of these bird species visited the peanut feeder at higher frequencies. In particular, marsh tits (ANOVA, $\chi^2 = 9.78$, $p = 0.01$), great tits ($\chi^2 = 6.71$, $p = 0.04$), and Eurasian nuthatches ($\chi^2 = 44.63$, $p < 0.01$) mostly visited the peanut feeder. The frequency of visits did not differ between brown soybean and kidney bean feeders for marsh tits (Mann–Whitney U test, Z = 0.55, $p = 0.84$), great tits (Z = 1.11, $p = 0.46$), or Eurasian nuthatches (Z = 2.54, $p = 0.55$). Time spent on the feeder per visit was longer on the kidney bean feeder for marsh tits ($\chi^2 = 27.25$, $p < 0.01$) and great tits ($\chi^2 = 27.25$, $p < 0.01$). For all wintering birds, the frequency of pecking for food items was the highest at the peanut feeder and the lowest at the brown soybean feeder. The amount of consumed food differed among food types. Marsh tits ($\chi^2 = 945.88$, $p < 0.01$), great tits ($\chi^2 = 3146.09$, $p < 0.01$), and Eurasian nuthatches ($\chi^2 = 2941.79$, $p < 0.01$) preferred peanuts. Marsh tits did not use kidney bean and brown soybean feeders. Great tits and Eurasian nuthatches pecked occasionally at kidney beans, and did not use brown soybean feeders (Table III).

Analysis of the factors influencing food utilization revealed that marsh tits were influenced by food type and the interaction between food type and MEE, while great tits were influenced by the type of food resource, MEE, and the interaction between food resource and MEE. On the other hand, type of food, MEE, and temperature did not affect the food utilization of Eurasian nuthatches during the winter season (Table IV).

In the analysis of interspecific interactions, Eurasian nuthatches were more aggressive than other species. Eurasian nuthatch relative aggression values were higher than those of marsh tits and great tits ($\chi^2 = 11.39$, $p < 0.01$), while marsh tits and great tits did not differ in their relative aggression value (Z = 2.39, $p = 0.57$). While using feeder, Eurasian nuthatches were dominant compared to other bird species. If Eurasian nuthatches were feeding at a peanut feeder, marsh tits and great tits stayed on other feeders (Fig. 1).

Table III. Differences in the feeding behavior of marsh tits (*Poecile palustris*), great tits *(Parus major*), and Eurasian nuthatches (*Sitta europaea*) at feeders with different food types, with results from an analysis of variance.

Species	Feeding behavior	Kidney bean	Brown soybean	Peanut	χ^2	p
Marsh tit	Frequency of visit (no/hr)	1.65 ± 0.17	1.56 ± 0.16	12.14 ± 1.31	9.78	0.01
	Duration of visit (s/visit)	65.01 ± 4.77	45.22 ± 3.77	38.01 ± 4.81	27.25	< 0.01
	Frequency of pecking (no/visit)	0.10 ± 0.07	0.04 ± 0.04	2.89 ± 0.25	1171.88	< 0.01
	Feeding amount (g/visit)	0.00 ± 0.00	0.00 ± 0.00	0.37 ± 0.02	945.88	< 0.01
	Foraging success (%)	6.67 ± 6.67	16.67±16.67	46.39 ± 3.09	58.78	< 0.01
Great tit	Frequency of visit (no/hr)	3.43 ± 0.36	3.73 ± 0.38	15.33 ± 1.47	6.71	0.03
	Duration of visit (s/visit)	95.49 ± 5.80	63.89 ± 4.79	48.70 ± 4.04	27.25	< 0.01
	Frequency of pecking (no/visit)	0.25 ± 0.02	0.08 ± 0.08	1.20 ± 0.07	2197.92	< 0.01
	Feeding amount (g/visit)	0.06 ± 0.04	0.00 ± 0.00	0.46 ± 0.02	3146.09	< 0.01
	Foraging success (%)	35.30±16.84	0.00 ± 0.00	84.27 ± 2.34	530.14	< 0.01
Eurasian nuthatch	Frequency of visit (no/hr)	0.79 ± 0.11	0.93 ± 0.14	16.25 ± 1.85	44.63	< 0.01
	Duration of visit (s/visit)	33.09±4.23	27.15 ± 3.39	40.66 ± 3.65	7.38	0.03
	Frequency of pecking (no/visit)	0.80 ± 0.42	0.08 ± 0.08	3.78 ± 0.29	780.88	< 0.01
	Feeding amount (g/visit)	0.06 ± 0.04	0.00 ± 0.00	0.57 ± 0.01	2941.79	< 0.01
	Foraging success (%)	12.86 ± 9.69	0.00 ± 0.00	53.16 ± 2.67	138.22	< 0.01

Table IV. Relationship between feeder visitation and factors influencing food selection in marsh tits (*Poecile palustris*), great tits (*Parus major*), and Eurasian nuthatches (*Sitta europaea*), with results from an analysis of co-variance.

Species	Source	d.f.	Mean square	F	p
Marsh tit	Food type	2	198.11	9.76	<0.01
	MEE	1	1.09	1.53	0.22
	Temperature	1	4.78	0.24	0.63
	Food type × Temperature	2	8.91	0.44	0.51
	Food type × MEE	2	77.50	3.82	<0.05
	MEE × Temperature	1	6.57	0.32	0.57
	Food type×MEE×Temperature	2	13.38	0.66	0.42
Great tit	Food type	2	15.88	10.84	<0.01
	MEE	1	6.28	4.29	0.04
	Temperature	1	0.16	0.11	0.74
	Food type × Temperature	2	0.31	0.21	0.65
	Food type × MEE	2	13.40	9.15	<0.01
	MEE × Temperature	1	0.17	0.12	0.73
	Food×MEE×Temperature	2	0.20	0.14	0.71
Eurasian nuthatch	Food type	2	8.35	0.13	0.71
	MEE	1	0.31	0.01	0.94
	Temperature	1	1.35	0.02	0.88
	Food type × Temperature	2	5.67	0.09	0.76
	Food type × MEE	2	1.05	0.02	0.90
	MEE × Temperature	1	3.10	0.05	0.82
	Food×MEE×Temperature	2	14.99	0.24	0.62

MEE, maintenance energy expenditure.

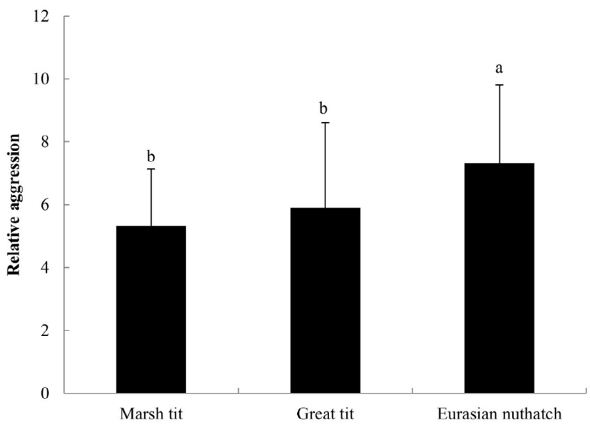

Fig. 1. Differences in relative aggression values of marsh tits (*Poecile palastris*), great tits (*Parus major*), and Eurasian nuthatches (*Sitta europaea*), with results from an analysis of variance.

DISCUSSION

The wintering season is a threat to the survival of most birds living in temperate regions. The low temperatures during this time increase the energy consumption necessary for homeostasis. As a result, birds require a tremendous amount of energy during this period (Johansen *et al*., 2014). As predicted, wintering birds preferred fat-rich and, to a lesser extent, carbohydrate-rich food, likely because of their increased energy requirements. According to the optimal foraging theory, wintering birds should prefer foods with high energy content because these foods maximize energy intake while minimizing energy expenditure (Renner *et al*., 2012).

In this study, we used peanuts as a high-fat food type. Peanuts were preferred at the highest frequency by marsh tits, great tits, and Eurasian nuthatches. In addition, the type of food, temperature, and metabolic energy requirement affected food utilization in marsh tits and great tits. Compared with kidney bean and brown soybean feeder, peanut feeders experienced higher frequencies of visits and pecking, as well as greater food consumption and foraging success. Thus, overall, birds preferred the peanut feeder, which offered more calories indicating that peanuts represented the optimal choice (Støstad *et al*., 2017). Dietary fat is assumed to be especially beneficial in increasing individuals' survival rate, especially in uncertain foraging environments (Rogers and Heath-Coss, 2003).

In a harsh wintering food condition, these type of high contents of food could be a nutrient source for wild birds at urban parks. However, the food provision should be considered with installation of food plates with a species-specific condition environment in the wild to minimize the negative effect of bird feeding.

In the case of Eurasian nuthatch, factors affecting food utilization were not identified. This could be attributed to the fact that Eurasian nuthatches had a competitive advantage over great tits and marsh tits, as well as the species-specific behavior of storing food during the winter. One study found that, in competitions for food, a bird with a lower hierarchy typically strives to avoid competition with a higher-order individual (Francis *et al*., 2018). Accordingly, when the higher-order individual was using the feeder, lower-order individuals waited for the higher-order individual's feeding to end rather than simultaneously feeding. Social rank was related to the bodyweight of the individual, with heavier individuals having a higher order than light individuals (Bergman and Moore, 2003). In this study, relative aggression values of Eurasian nuthatches at feeders were higher than those of great tits and marsh tits.

While the Eurasian nuthatch was feeding at the peanut feeder, great tits and marsh tits stayed on feeders without Eurasian nuthatches. However, after Eurasian nuthatches left the feeder, marsh tits and great tits began using the feeder. Moreover, in previous work, Eurasian nuthatches have been observed storing their food in tree trunks and under fallen leaves during autumn and winter periods (Galván, 2017). In summary, Eurasian nuthatches, which possessed a higher social rank than great tits and marsh tits, stayed on dominant feeder and had a greater chance of acquiring food.

In our study, some evidence was found that wintering birds in temperate zones prefer high-energy food items. Limited food during the winter season is known to affect social hierarchies. However, this study was conducted in a restricted area over a short period of time. Conducting similar experiments at different sites would clarify the variables influencing the feeding behavior of wintering birds. Further work should focus on how winter feeding may be used to benefit birds at the individual and population levels.

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IRB approval

IBR was obtained from Institutional Animal Care and Use Committee, Chung-Ang University (approval number: CAU 2017-00095).

Statement of conflict of interest

The authors have declared no conflict of interests.

REFERENCES

Behmer, S.T., Raubenheimer, D. and Simpson, S.J., 2001. Frequency-dependent food selection in locusts: A geometric analysis of the role of nutrient balancing. *Anim. Behav*., **61**: 995–1005. https://doi.org/10.1006/anbe.2000.1695

Bergman, D.A. and Moore, P.A., 2003. Field observation of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. *Biol. Bull*., **205**: 26–35. https://doi.org/10.2307/1543442

Brown, M., Downs, C.T. and Johnson, S.D., 2012. African red-winged starling prefers hexose sugar solutions, but do not like them too sweet. *J. Ornithol*., **153**: 265–272. https://doi.org/10.1007/s10336-011-0739-5

Carrascal, L.M., and Polo, V., 1999. Coal tits, *Parus ater*, lose weight in response to chases by predators. *Anim. Behav*., **58**: 281–285. https://doi.org/10.1006/anbe.1999.1142

Carrascal, L.M., Seoane, J. and Villén-Pérez, S., 2012. Temperature and food constraints in wintering birds an experimental approach in montane Mediterranean oakwoods. *Commun. Ecol*., **13**: 221–229. https://doi.org/10.1556/ComEc.13.2012.2.12

Chamberlain, D.E., Vickery, J.A., Glue, D.E., Robinson, R.A., Conway, G.J., Woodburn, R.J.W. and Cannon, A., 2005. Annual and seasonal trends in the use of garden feeders by birds in winter. *Int. J. Avian*

Sci., **47**: 563–575. https://doi.org/10.1111/j.1474-919x.2005.00430.x

Chatterjee, S. and Basu, P., 2018. Food preferences determine habitat selection at multiple scales: Implication for bird conservation in tropical forests. *Anim. Conserv.*, **21**: 332–342. https://doi.org/10.1111/acv.12397

Cresswell, W., Lind, J., and Quinn, J.L., 2010. Predator-hunting success and prey vulnerability: Quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *J. Anim. Ecol.*, **79**: 556–562. https://doi.org/10.1111/j.1365-2656.2010.01671.x

Desmond, M.J., Mendez-Gonzalez, C., and Abbott, L.B., 2008. Winter diets and seed selection of granivorous birds in southwestern New Mexico. *Stud. Avian Biol.*, **37**: 101–112.

Ewen, J.G., Walker, L., Canessa, S., and Groombridge, J.J., 2014. Improving supplementary feeding in species conservation. *Conserv. Biol.*, **29**: 341–349. https://doi.org/10.1111/cobi.12410

Francis, M.L., Plummer, K.E., Hythgoe, B.A., Macallan, C., Currie, T.E. and Blount, J.D., 2018. Effects of supplementary feeding on interspecific dominance hierarchies in garden birds. *PLoS One*, **13**: e0202152. https://doi.org/10.1371/journal.pone.0202152

Galván, I., 2017. Condition-dependence of pheomelanin-based coloration in nuthatches *Sitta europaea* suggests a detoxifying function: implications for the evolution of juvenile plumage patterns. *Sci. Rep.*, **7**: 9138. https://doi.org/10.1038/s41598-017-09771-4

Harper, E.J., 2000. Estimating the energy needs of pet birds. *J. Avian Med. Surg.*, **14**: 95–102. https://doi.org/10.1647/1082-6742(2000)014[0095:ETENOP]2.0.CO;2

Haythorpe, K.M., Sulikowski, D. and Burke, D., 2012. Relative levels of food aggression displayed by common mynas when foraging with other bird species in suburbia. *EMU Austral. Ornithol.*, **112**: 129–136. https://doi.org/10.1071/MU11046

Hinsely, S.A., Hill, R.A., Gaveau, D.L.A. and Bellamy, P.E., 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Funct. Ecol.*, **16**: 851–857. https://doi.org/10.1046/j.1365-2435.2002.00697.x

Hwang, H.S., 2020. *Characteristics of food selection and competition for wintering birds*. PhD dissertation, Chung-Ang University, Seoul, Korea.

Johansen, S.M., Horn, D.J. and Wilcoxen, T.E., 2014. Factors influencing seed species selection by wild birds at feeders. *Wilson J. Ornithol.*, **126**: 374–381. https://doi.org/10.1676/13-066.1

Koenig, W.D. and Knops, J.M.H., 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.*, **70**: 609–620. https://doi.org/10.1046/j.1365-2656.2001.00516.x

Ministry of Food and Drug Safety, 2016. *Food nutrients data base*. Cheongju, Republic of Korea.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. and Blount, J.D., 2013. Winter food provisioning reduces future breeding performance in a wild bird. *Sci. Rep.*, **3**: 6. https://doi.org/10.1038/srep02002

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. and Blount, J.D., 2017. Effects of winter food provisioning on the phenotypes of breeding blue tits. *Ecol. Evol.*, **8**: 5059–5068. https://doi.org/10.1002/ece3.4048

Renner, S.C., Baur, S., Possler, A., Winkler, J., Kalko, E.K.V., Bates, P.J.J. and Mello, M.A.R., 2012. Food preferences of winter bird communities in different forest types. *PLoS One*, **7**: e53121. https://doi.org/10.1371/journal.pone.0053121

Ríos, J.M., Mangione, A.M. and Marone, L., 2012. Tolerance to dietary phenolics and diet breath in three seed-eating birds: Implications for graminivory. *J. exp. Zool.*, **317**: 425–433. https://doi.org/10.1002/jez.1735

Rogers, C.M. and Heath-Coss, R., 2003. Effect of experimentally altered food abundance on fat reserves of wintering birds. *J. Anim. Ecol.*, **72**: 822–830. https://doi.org/10.1046/j.1365-2656.2003.00754.x

Samuni-Blank, M., Dearing, M.D., Karasov, W.H., Gerchman, Y., Kohl, K.D., Lymberakis, P., Kurnath, P. and Arad, Z., 2013. Physiological and behavioural effects of fruit toxins on seed-predating versus seed-dispersing congeneric rodents. *J. exp. Biol.*, **216**: 3667–3673. https://doi.org/10.1242/jeb.089664

Sánchez-Reyes, J.U., Niño-Maldonado, S., Clark, S.M., Barrientos-Lozano, L. and Almaguer-Sierra, P., 2019. Successional and seasonal changes of leaf beetles and their indicator value in a fragmented low thorn forest of northeastern Mexico (Coleoptera, Chrysomelidae). *Zookeys*, **825**: 71–103. https://doi.org/10.3897/zookeys.825.30455

Støstad, H.N., Aldwinckle, P., Allan, A. and Arnold, K.E., 2017. Foraging on human-derived foods by urban bird species. *Bird Study*, **64**: 178–186. https://doi.org/10.1080/00063657.2017.1311836

Thomson, R.M., Brose, U., Dunne, J.A., Hall, Jr, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romaunk, T.N., Stouffer, D.B. and Tylianakis, J.M., 2012. Food webs: Reconciling the structure and function of biodiversity. *Trends Ecol. Evol.*, **27**: 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Walther, B.A. and Gosler, G., 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*). *Oecologia*, **129**: 312–320. https://doi.org/10.1007/s004420100713

Wilcoxen, T.E., Horn, D.J., Hogan, B.M., Hubble, C.N., Huber, S.J., Flamm, J., Knott, M., Lundstrom, L., Salik, F., Wassenhove, S.J. and Wrobel, E.R., 2015. Effects of bird-feeding activities on the health of wild birds. *Conserv. Physiol.*, **3**: cov058. https://doi.org/10.1093/conphys/cov058