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Article

Eggshell consumption in different reproductive stages and broods of the Western Bluebird, *Sialia mexicana*

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SUMMARY

Calcium is an essential micronutrient to egg production and reproductive success in birds. Its availability at the start of the reproductive cycle is especially important to passerines (perching birds, namely songbirds) since they do not store calcium when not reproducing. To date, no data has been published to illustrate whether Western Bluebirds would consume provisioned eggshells, during which phases and to what degree in the reproductive cycle consumption might occur, and whether the amount consumed would vary between broods in a single season. We hypothesized that Western Bluebirds would consume the highest amount of eggshells during nest-building and egg-laying and that consumption would be greater during the first brood. Western Bluebirds breeding in nest boxes hanging in trees were provided eggshells in small containers attached to the roof of the box. Differences in average consumption between reproductive stages were significant. The greatest consumption was seen during the Pre-hatch phase (nest-building, egg-laying, and incubation), and less during the Post-hatch phase (nestling and fledgling). This was likely in preparation for and to replenish calcium needed during egg-laying in both broods. Average consumption between two broods produced by a single breeding pair was not significantly different. However, there was significant variation in the amount of consumption between breeding pairs. This high variation suggests that birds may have different strategies for obtaining and consuming calcium.

INTRODUCTION

Calcium is a vital mineral for wildlife, including reptiles (1), mammals, and birds (2). It is essential for biological processes such as growth and maintenance of the skeleton and teeth, eggshell development, and muscle contractions (3). Calcium can come in many forms in the environment, including mollusk shells, eggshells, calcium-rich soil, and vertebrate bones (2). Available calcium sources have become increasingly scarce for birds, especially near urbanized areas (4, 5). Human activities introduce acidic substances (e.g., acid rain) as well as heavy metals into the surrounding environment, causing the dissolution of calcium in soil (4). For birds, calcium plays a crucial role during the breeding season in the form of egg development and initiation of breeding (6). Great Tits (*Parus major*) provided with snail shells or eggshells abandoned the nest less frequently and had fewer shell abnormalities as compared to non-supplemented females in a calcium-poor environment (4). In addition, European Pied Flycatchers (*Ficedula hypoleuca*) and Great Tits provided with snail shells or eggshells exhibited increased egg volume, eggshell thickness, and earlier start of breeding compared to unsupplemented birds in calcium-deficient soils (7). Calcium can also affect reproductive success. For example, calcium supplemented House Wrens (*Troglodytes aedon*) laid more eggs per clutch than non-supplemented birds (8).

Obtaining sufficient calcium is a time-consuming behavior, even in calcium-rich environments (5), so there may be an incentive for birds to consume readily available calcium instead of searching for other sources. Songbirds typically only retain enough calcium for routine metabolic needs and do not store calcium in the medullary bone as with other avian species (9, 10). External sources of calcium are also crucial to insect-eating birds, as arthropods are not a sufficient source of calcium for eggshell formation, amounting to about 5–10% of the needed calcium even in calcium-rich areas (11). Therefore, it is likely that songbirds need additional calcium via external sources during the breeding season. One study of Eastern Bluebirds (*Sialia sialis*) reported that females sometimes eat eggshells of their own hatchlings (12). For the Western Bluebird, the clutch size of first broods (4.94 eggs) is significantly larger than second brood clutches (4.06 eggs) (13), and more eggs would require more calcium consumption for eggshell formation. However, it is unknown when in the breeding process birds need to consume this additional calcium and if consumption is greater in one of the broods.

The Western Bluebird is an ideal passerine species for this study because they readily use nest boxes, and the reproductive stages can be easily observed and determined. Historically, they have almost exclusively nested in natural or woodpecker-made cavities in dead trees (13). As a result of the removal of dead trees due to urbanization and current U.S. Forest Service practices in our national forests, Western Bluebirds, especially populations in urbanized Southern California, have become reliant on artificial nest boxes that are hung in trees or placed on metal poles by volunteers (13). Western Bluebird monitors check the boxes weekly from March to August, the breeding season of the Western Bluebird. Within that time period, they typically have one to two broods, and exceptionally three broods (13). There are five main reproductive stages that take place with each successful brood: nest-building, egg-laying (the range is 2–8 eggs, but 4–5 eggs are the most frequent), incubation, hatchlings, and fledging. No data has been published yet on how calcium consumption changes between these stages. Incubation is done by the female, although there is one anecdotal sighting of a male incubating a clutch that was thought to be possibly erroneous (13). The duration of each stage is variable, depending on each nesting pair and environmental conditions. Nest-building usually takes 3–7 days and is done mainly by the female. Rainstorms or sudden cold weather can interrupt this process, which causes nest-building to be significantly drawn out. Egg-laying takes about 5–6 days and incubation 12–17 days. Hatchlings take 18–25 days to fledge, or in other words, to have developed sufficient wing feathers to leave the nest. After fledging, the juveniles remain with the parents for about two weeks. Some then depart, but others can continue to reside in the parents' territory as nest helpers for up to four years (13).

External sources of calcium are then essential for avian reproductive success, especially during egg development. While research has been done on calcium supplementation in passerines and, more specifically, insect-eating birds and its effects on reproductive success, differences between consumption in different reproductive stages and broods have not been studied. Therefore, we investigated how eggshell consumption differed throughout the reproductive stages and broods of the Western Bluebird (*Sialia mexicana*). By providing Western Bluebirds with supplemental eggshells throughout their entire breeding season, we hypothesized that most eggshell consumption by the Western Bluebird would take place before and during egg-laying because the female would be preparing for and replenishing calcium. We additionally hypothesized that more consumption would be seen during the first brood compared to the second because a greater clutch size in the first brood would require more calcium. Greatest consumption was seen in the nest-building, egg-laying, and incubation stages, likely in preparation for and replenishing for egg-laying. Average eggshell consumption was not significantly different between the two broods. Consumption between breeding pairs was significantly variable, suggesting that birds have different strategies for obtaining calcium.

RESULTS

We measured the eggshell consumption by 52 Western Bluebird nests (each consisting of a breeding pair and their nestlings) weekly from March to August. Nest box activity was also checked weekly to determine reproductive stage (nest-building, egg-laying, incubation, nestling, fledging) and status (breeding success). Data was subsampled into groups, with Brood 1 consisting of all nests in Brood 1 (n = 40), Brood 1s consisting of all nests in Brood 1 with corresponding Brood 2 nests (n = 13), and Brood 2 consisting of all nests in Brood 2 (n = 13) (**Table 1**). Reproductive stages were grouped into Pre-hatch (includes: nest-building, egg-laying, and incubation) and Post-hatch (includes: hatching and fledging).

Timing of eggshell consumption in reproductive stages

We measured consumption of eggshells between reproductive stages in Brood 1, 1s, and 2. The average eggshell consumption between reproductive stages (Pre-hatch and Post-hatch) in Brood 1 were significantly different (p-value = 0.01, **Table 2a**). There was no significant difference in average eggshell consumption between stages in Brood 1s. Average consumption was about 1.5 times greater when the Pre-hatch mean eggshell consumption was compared to that during the Post-hatch stage for Brood 1 (p-value = 0.01) (**Table 2a**). Average consumption between reproductive stages in Brood 2 was also not significantly different (**Table 2a**).

Individual variation in eggshell consumption

Additionally, we determined individual variation in consumption of eggshells between nests. Average eggshell consumption between individual nests in Brood 1 varied significantly (p-value = 3.82E-08, **Table 2b**). Some nests consumed almost no eggshells, whereas others consumed a moderate amount (**Figure 1**). A few nests consumed very large amounts, up to a total of 12 g through the rearing of an entire brood (**Figure 1**). Average consumption was not variable for Brood 1s nests (n = 13), whereas average eggshell consumption between individual nests was significantly different for Brood 2 consisting of the same 13 nests (**Table 2b**).

Brood comparisons in eggshell consumption

Furthermore, we measured the consumption of eggshells

	Brood 1			Brood 1s			Brood 2		
	Total	Pre-hatch	Post-hatch	Total	Pre-hatch	Post-hatch	Total	Pre-hatch	Post-hatch
Sample size	40	40	40	13	13	13	13	13	13
Population mean eggshell consumption (g)	0.47	0.59	0.28	0.58	0.77	0.50	0.53	0.62	0.58
Standard deviation	0.42	0.67	0.60	0.59	0.90	0.93	0.34	0.56	0.45

Table 1: Sample size, eggshell consumption, and standard deviation of reproductive stages. Sample size, average eggshell consumption, and standard deviation for each grouping (Pre-hatch, Post-hatch, and total for each brood).

2a	Timing of consumption in reproductive stages		
	Brood 1	Brood 1s	Brood 2
Test	Two-sided Wilcoxin signed rank test	Two-sided Wilcoxin signed rank test	Two-sided Wilcoxin signed rank test
p-value	0.00	0.20	0.68
Bonferroni-corrected *p*-value	0.01	1	1
Bonferroni-corrected significance	significant	not significant	not significant

2b	Differences in consumption between nests		
	Brood 1	Brood 1s	Brood 2
Test	One-sample t-test	One-sample t-test	One-sample t-test
p-value	4.24E-09	0.01	0.00
t-value	-7.57	-3.30	-4.02
Bonferroni-corrected *p*-value	3.82E-08	0.06	0.02
Bonferroni-corrected significance	significant	not significant	significant

2c	Comparison of brood consumption in reproductive stages		Comparison of average eggshell consumption between broods
	Pre-hatch	Post-hatch	
	Brood 1s vs Brood 2		Brood 1s vs Brood 2
Test	Two-sided Wilcoxin signed rank test	Two-sided Wilcoxin signed rank test	Paired *t*-test
p-value	0.97	0.23	0.55
t-value (if applicable)	N/A	N/A	-0.60
Bonferroni-corrected p-value	1	1	1
Bonferroni-corrected significance	not significant	not significant	not significant

Table 2: Test results for individual variation and timing of consumption in reproductive stages and broods. For each test, the type of test, *p*-value, *t*-value (if applicable), Bonferroni-corrected *p*-value, and Bonferroni-corrected significance is given. These tests have been grouped together in sub-tables based on the purpose of the test. (2a) Differences in average consumption between nests in Brood 1 (n = 40), Brood 1s (n = 13), and Brood 2 (n = 13). (2b) Timing of consumption between reproductive stages (Pre-hatch and Post-hatch) in Brood 1, Brood 1s, and Brood 2. (2c) Comparison of average eggshell consumption in broods between reproductive stages (Pre-hatch and Post-hatch) and the comparison of average consumption between broods.

between the two broods. We found there was no difference in average eggshell consumption between the two different broods or for individual nests (*p*-value = 1, **Table 2c**). Nor were there differences in average eggshell consumption between broods within a reproductive stage (*p*-value = 1, **Table 2c**), suggesting that brood number may have little impact on eggshell consumption.

DISCUSSION

The highest eggshell consumption observed was in the pre-hatching stage (includes: nest building, egg laying, and incubation). Consumption seen during nest building was likely in preparation for the egg laying stage. It is reasonable to assume that consumption seen in egg laying was either to partially replenish calcium from the last egg laid or to prepare for laying the next egg. The low consumption seen in the nestling and fledgling stage may have been due to caretaking demands on the female. This provides a plausible

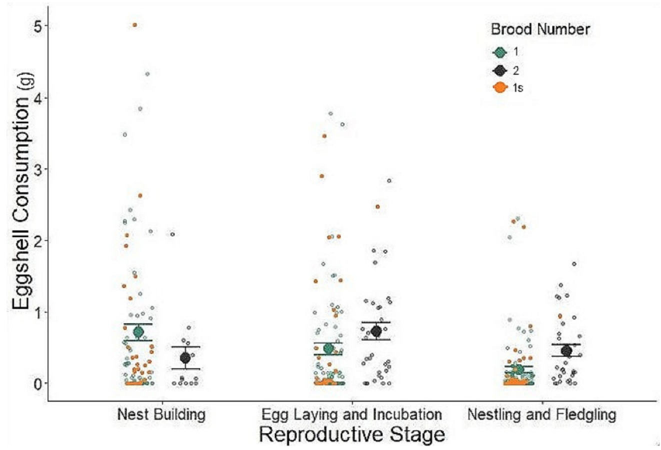

Figure 1: Eggshell consumption in different reproductive stages. Means of consumption in grams of different stages in the two broods with standard error bars and raw weekly data overlaid.

explanation for an increase in eggshell consumption at the onset of a second brood. Coincidentally, in the nestling phase, it is not well documented whether females (and males) feed their own eggshells to nestlings or if nestlings consume the eggshells themselves, in addition to incidental calcium present in arthropod prey which provide 5–10% of calcium needed for skeletal growth (11). Given the lack of available data from larger sampling, it is also unknown if females that lay a second brood consume a greater amount of eggshells during the nestling and fledgling stages of the first brood than was demonstrated in this small study.

Contrary to our second hypothesis, brood number had little, if any effect on the average amount of eggshells consumed. The original hypothesis was that greater consumption would be seen in Brood 1 was based on a study showing that the average clutch size of first broods is usually significantly larger (~25%) than the average size of second brood clutches (13). These results indicate that it is likely that the timing of consumption (which reproductive stage consumption took place) within a brood was of greater importance to the quality of the eggs than it was to the specific brood in which the eggs were produced.

Ostensibly, the measured eggshell consumption for a nest box is attributed to all of the individual birds inhabiting it (adult female, adult male, and nestlings). However, the conclusions drawn in this study are largely based on the premise that the female is the primary consumer of the eggshells. Most, if not all, eggshell consumption can be attributed to the female, because she is the only one who needs calcium to produce sufficiently thick eggshells. Females have a compelling need for calcium from external sources such as the provisioned eggshells, because passerines do not store calcium in the medullary bone (9), and only 5–10% of the needed calcium for egg-laying is found in their regular diet (11). Additionally, when eggshell consumption was observed (n=4) (on separate occasions by three volunteers and myself) we noted that only females consumed pieces of eggshells. The likelihood of eggshell consumption by males is extremely low because they can obtain sufficient calcium for bone maintenance and other metabolic functions through their diet of arthropods (5). A study on Great Tits showed that snail shell consumption by females was negligible (~4 mg per day) in the two week pre-laying period, but then increased to an average of ~65 mg per day during egg-laying (5). It is reasonable to infer that snail shell consumption by males was minimal throughout the nesting period. Adult birds may also feed eggshells to their nestlings, as calcium is important for skeletal growth.

Although it is possible that birds outside of the breeding pair would consume the eggshells, we find this to be highly unlikely. Bluebirds are extremely aggressive in the breeding season, especially the males, who fiercely defend their territories (which includes their nest box and eggshell container) (13) from other Western Bluebirds and other birds. A much more well-studied congener, the Eastern Bluebird (*Sialia sialis*), will fight until severe injury or death to defend their territories (12). No containers showed signs of tampering by a larger bird or possibly small mammal. Additionally, the nest boxes where no bluebirds nested (n=6), no consumption over the margin of measurement error (0.05 g) was seen. Further research, possibly with trail cameras positioned to watch the top of the occupied nest boxes throughout the breeding season, is needed to definitively prove that the adult female is the primary consumer of the eggshells. Additionally, this would show that no other bluebirds, other species of birds, or small mammals consume or tamper with the eggshells.

The results showed that there were significant differences in the average amount of eggshells consumed by each nest and some variation in the timing in which the eggshells were consumed. Also, some birds chose to consume no eggshells at all, suggesting that they relied on other sources of calcium. Other birds obtained a fraction of their needed calcium from the offered eggshells, but mostly obtained calcium elsewhere. To contrast, a few birds heavily relied on the offered eggshells for calcium, as indicated by the few nests with high average consumption. This could imply that birds from each nest have different strategies in terms of when to consume calcium, which calcium sources to choose, and how much calcium is obtained from each source.

The decision to choose a particular strategy may be heavily influenced by a bluebird pair's experience, the location of the nest box (which affects the availability of calcium and likely changes what and where calcium sources are), and individual choice. For example, some birds may tend to stay away from calcium provided by humans, whereas others consume offered eggshells because they may have limited sources. Birds with limited choices may choose to consume provided eggshells because they would otherwise lose valuable foraging time searching for calcium (14). Additionally, birds that reside in places with more acidic soils may choose supplemented eggshells. Some studies have shown that natural calcium sources can be severely reduced by increased acidity of the soil (15) and can result in birds losing both calcium-rich soil and snail shells as sources. Some sources of calcium may be more easily eaten and absorbed or have more calcium content than other sources (16, 17). Furthermore, the novel container high off the ground may have deterred some bluebirds from consuming the eggshells. This possibility can be extrapolated from one study (18), which illustrated that thrushes (such as bluebirds) which typically forage on the ground show a tendency to seek calcium sources found on the ground when given a choice between containers on the ground or platforms. Further study is needed to determine under what circumstances birds are more inclined to consume human offered eggshells and which strategy, if any, is more successful than the others.

MATERIALS AND METHODS

This study was conducted from March to August 2020 on 52 nest boxes in 9 cities in Orange County, California. Volunteers from the Southern California Bluebird Club assisted with data collection. Chicken eggs were commercially purchased, rinsed, air dried, and baked at 121°C for 10 minutes to sterilize the eggshells and safeguard the birds' health. After eggshells cooled, they were crushed to small pieces, roughly 0.25 cm^2.

Eggshells were provided in a small white plastic container with a dime-sized hole cut on the clear lid to allow for easy access of eggshells by bluebirds, but to limit larger birds and mammals from tampering with the eggshells. A thumbtack was used to create four evenly spaced pinholes on the bottom of the container as drainage in case of rain. Volunteers were not allowed to put mealworms on or near the box to limit variables and avoid attracting other birds or animals. As a general practice, monitors avoided putting boxes where non-avian predators are known to exist. No other bird or mammal was seen on the boxes and eggshell containers were not altered, damaged, or missing. In boxes where no birds nested (n = 6), no consumption greater than the margin of measurement error (0.05 g) was observed.

The container was affixed to the top of each nest box using two pieces of velcro. Each container had 5 g of eggshells. Eggshell consumption was measured each week by subtracting the remaining amount of eggshells from the starting 5 g. Afterwards, the eggshell containers were replenished to 5 g. Although bluebirds never consumed this amount of eggshells in a single week, a surplus ensured that birds would have more than enough. Western Bluebird nest boxes were monitored to determine the reproductive stage (based on nesting material, laying of eggs, presence of hatchlings, and evidence of successful fledging) and nesting success. Nests were checked on a weekly basis between dawn and dusk, except during periods of severe rainfall that occurred in March, April, and May 2020. Wet eggshells could not be accurately weighed and monitors did not check nest boxes during heavy rain or high winds for safety reasons. This resulted in some instances of unequal sampling during those periods. Variability in the timing of reproductive stages also contributed to unequal sampling. All volunteers used standardized nest boxes with dimensions pre-established by the North American Bluebird Society, Cornell Nestwatch Project, and the National Audubon Society to keep out invasive species.

All volunteers in this experiment were supplied with a Brifit Digital Mini Scale which could weigh items up to 200 g with a readability of 0.01 g (d = 0.01 g), and included a 100 g calibrated weight. While all scales used by the volunteers were the same model, there were 17 individual units. To alleviate concerns in measurement differences between scales we conducted measurement trials with all of the units prior to distribution. A calibrated Mettler Toledo Precision Balance Scale (capacity 120 g, d = 0.001 g) was used to create a test weight of 12.350 g (7.350 g for container; 5.000 g for eggshells) to check for measurement variations between units. We calibrated each of the 17 scales using the 100 g calibration weight included with each scale (which would be used throughout the experiment by each volunteer), and then conducted trials on each scale with the test weight. Scales with the lowest weight reading were designated as the baseline (0.00 g) reading. We found that the results between the units ranged from 0.00 g to 0.05 g, thus the highest measurement differential was used to establish the margin of measurement error of 0.05 g. Therefore, nests with average consumption of less than 0.05 g were excluded from the study (n=4). While these data points were interesting, we decided to exclude them from the statistical analysis because they did not provide relevant data for the questions on timing of eggshell consumption that we studied.

Data Analysis

The average eggshell consumption by each nest (a mated pair of bluebirds and their nestlings), regardless of reproductive stage or brood number, was first calculated to check the data for accuracy and outliers. Due to instances of unequal sampling of individual nests (as described above), consumption was subsampled (the data was grouped as to allow for comparison) and analyzed to test each hypothesis. Subsampled groups are as follows: Brood 1 consisting of all nests in Brood 1 (n = 40), Brood 1s consisting of all nests in Brood 1 with their corresponding Brood 2 nests (n = 13), and Brood 2 consisting of all nests in Brood 2 (n = 13). Eggshell consumption was normalized for between-nest comparisons by calculating the average consumption for each nest and for each subsample category. The eggshell consumption data did not follow a standard normal distribution. Subsampled data that compared brood eggshell consumption followed a log-normal distribution and was log transformed. Non-parametric statistics were used to analyze the comparison of average eggshell consumption between reproductive stages. Statistical analyses were run in MATLAB (R2019b, MathWorks, Natick, MA, USA) and significance was taken at $\alpha = 0.05$. A Bonferroni correction was applied post-hoc (n = 9, corrected significance alpha = 0.005). Sample sizes, average eggshell consumption, and standard deviation for each stage and each group are outlined in **Table 1**.

Timing of eggshell consumption in reproductive stages

We hypothesized that a higher average eggshell consumption would be seen before and during egg-laying when the female would be preparing for and laying eggs. Data was collected for five reproductive stages (nest-building, egg-laying, incubation, nestling, and fledgling) that are typically recognized when monitoring Western Bluebirds (or any other species of cavity-nesting bird). However, due to unequal sampling of nests throughout reproductive stages, our analysis grouped reproduction into two stages: Pre-hatching, which included nest-building, egg-laying, and incubation, and Post-hatching, which included the nestling and fledgling stages. Paired *t*-tests were used to compare average eggshell consumption between reproductive stages within a brood and between the two broods across different stages. Using a two-sided Wilcoxon signed rank test, the average eggshell consumption of all broods between stages was compared.

Individual variation in eggshell consumption

We hypothesized that there would be high individual variation in eggshell consumption as the nest boxes are found in different localities that may have varying availability of calcium resources. Average eggshell consumption between individual nests in Brood 1, Brood 1s, and Brood 2 was compared using one-sample *t*-test.

Brood comparisons in eggshell consumption

We hypothesized that bluebirds would require more calcium during the first, and typically larger sized, brood compared to the second brood. Brood 1 consisted of all nests in Brood 1 (n = 40), and Brood 1s consisted of all nests in Brood 1 with a corresponding Brood 2 nest (n = 13). Brood 2 consisted of all nests in Brood 2 (n = 13). The average eggshell consumption between the two broods was compared with a paired *t*-test.

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