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CALCIUM AVAILABILITY LIMITS REPRODUCTIVE OUTPUT OF TREE SWALLOWS (*TACHYCINETA BICOLOR*) IN A NONACIDIFIED LANDSCAPE

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Abstract.—Breeding birds require high levels of energy and certain nutrients, such as calcium. The extent to which calcium limits reproduction in wild birds is unclear. We performed a supplementation experiment to determine whether calcium limits the reproductive output of free-ranging insectivorous Tree Swallows (*Tachycineta bicolor*), a species whose usual diet contains little calcium. Providing supplemental calcium in the form of crushed oyster shell did not affect clutch initiation date, but it caused birds that had not started constructing a nest when we first detected them on the study area to begin laying sooner, which suggests that calcium reduced the length of the prelaying period. Supplemented females produced larger eggs, and that effect was most pronounced among females in good body condition. There was a trend for supplemented birds to produce larger clutches, and their clutches had significantly greater total mass than those of control birds. Supplemented birds, in particular those breeding late in the season, also hatched significantly more eggs. Our results suggest that calcium availability may limit some aspects of avian reproduction, even in nonacidified landscapes like our study area, where levels of calcium in the soil are high. *Received 8 September 2003, accepted 23 September 2004.*

Key words: calcium limitation, clutch initiation date, clutch size, egg size, hatching success, nutrient limitation.

La Disponibilidad de Calcio Limita el Rendimiento Reproductivo de *Tachycineta bicolor* en un Paisaje no Acidificado

Resumen.—Durante la época reproductiva, las aves requieren niveles altos de energía y de ciertos nutrientes como el calcio. La importancia del calcio como limitante de la reproducción de las aves silvestres no está claramente establecida. En este estudio realizamos un experimento de suplementación para determinar si el calcio limita el rendimiento reproductivo de golondrinas silvestres *Tachycineta bicolor*, una especie insectívora cuya dieta usual contiene poco calcio. La provisión de calcio suplementario en forma de conchas de ostra maceradas no afectó la fecha de iniciación de las nidadas, pero causó que aves que no habían empezado a construir un nido cuando las detectamos por primera vez empezaran a poner huevos más temprano, lo que sugiere que el calcio redujo la duración del período pre-postura. Las hembras que recibieron calcio suplementario produjeron huevos más grandes, un efecto que fue más pronunciado en las hembras con buena condición corporal. Existió una tendencia a que las aves que recibieron calcio suplementario produjeran nidadas más grandes y sus nidadas tuvieron una masa total significativamente mayor

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que las de las aves control. Las aves que recibieron el suplemento, en particular las que se reprodujeron tarde en la época reproductiva, también presentaron significativamente más huevos eclosionados. Nuestros resultados sugieren que la disponibilidad de calcio puede limitar algunos aspectos de la reproducción de las aves, aún en paisajes no acidificados como nuestra área de estudio, donde los niveles de calcio en el suelo son altos.

Animals require higher levels of energy and certain nutrients during reproduction and growth than they do for maintenance (Robbins 1993). Birds require calcium more than any other mineral, especially during egg formation and skeletal growth (Klasing 1998). But the demand for calcium in wild birds—unlike protein and energy requirements—has received relatively little attention (Graveland and van Gijzen 1994, Dhondt and Hochachka 2001). During egg formation, female birds require 10–15× more calcium than a similar-sized mammal undergoing gestation, and most of that calcium is used to form the eggshell (Simkiss 1967, Klasing 1998). Birds are unique in depositing calcium in nonstructural medullary bone located in the marrow cavities of the leg bones; some birds, such as Galliformes, mobilize that labile reserve during egg formation (Clunies et al. 1992). Clutches of many passerine birds, however, contain as much or more calcium than the entire skeleton of the breeding female, so most of the calcium needed for egg production must come from exogenous sources (Graveland and van Gijzen 1994, Johnson and Barclay 1996, Pahl et al. 1997).

Reliance on dietary calcium for eggshell formation may not be problematic for raptorial birds that ingest bones; however, the usual food sources of most insectivorous, granivorous, and frugivorous passerines provide little calcium (Robbins 1993, Graveland and van Gijzen 1994). For example, calcium content of aerial insects is ~0.35% by dry weight (Turner 1982, Mänd et al. 2000), and female insectivorous birds can obtain only ~25% of their calcium requirements from such food sources (Graveland and van Gijzen 1994). Many female passerines compensate for low levels of calcium in their usual food by supplementing their diets with calcium-rich objects, such as snail shells, eggshells, and other calcareous grit (Mayoh and Zach 1986, St. Louis and Breebaart 1991, Graveland 1996).

Because insectivorous passerines require large amounts of calcium during egg production and their usual food sources provide little of it, the nutrient's availability may limit reproductive output and ultimately reproductive success. Indeed, studies have demonstrated negative effects of calcium limitation on a multitude of reproductive variables in captive birds, and in free-living birds in anthropogenically and naturally acidified landscapes (Holford and Roby 1993, St. Louis and Barlow 1993, Graveland et al. 1994, Mänd et al. 2000). There is little calcium available in soils of acidified lansdscapes; hence, birds inhabiting those areas have relatively few sources of calcium supplements, such as snail shells (Graveland et al. 1994). Although Johnson and Barclay (1996) suggested that egg-related reproductive variables may be less sensitive to calcium limitation in nonacidified landscapes where calcium is abundant in soils, studies of calcium limitation on the reproductive output of aerial insectivores have not been conducted in such environments. Aerial insectivores, such as swallows, may be particularly limited by calcium availability, because they often lack suitable mobility on the ground (Robertson et al. 1992) to obtain supplemental sources of calcium.

We performed an experiment to test the hypothesis that calcium availability limits reproductive output of insectivorous birds in a nonacidified, calcium-rich landscape. By supplementing pairs of Tree Swallows (*Tachycineta bicolor*) with crushed oyster shell and comparing their reproductive output to control pairs, we tested whether calcium supplementation affected clutch initiation date, clutch size, egg size and shell thickness, and hatching and fledging success. We show that calcium availability can limit some aspects of reproductive output of insectivorous birds, even in nonacidified landscapes with high levels of soil calcium.

Methods

We studied breeding Tree Swallows from May to August 2002 on an ~800 km^2 study site near Vanderhoof, British Columbia, Canada

(54°N, 124°W). The study site has not been affected by anthropogenic acid deposition (Rodhe et al. 2002), and it is characterized by having abundant calcium. For example, Arocena and Sanborn (1999) reported that the exchangeable calcium in the soil O-horizon was 22.11 $cmol_c\ kg^{-1}$ on our study area. In comparison, the exchangeable calcium is 6.75 $cmol_c\ kg^{-1}$ in the litter at Hubbard Brook Experimental Forest, New Hampshire, an area that is well known to be base-poor, with relatively little calcium available (Likens et al. 1998). Tree Swallows arrived on our study site during early May, and nest construction and egg laying began in mid- to late May. The study site is composed of open agricultural areas mixed with small patches of coniferous and deciduous trees and small wetlands. Tree Swallows bred in nest boxes mounted 3 m above the ground on electrical poles. Nest boxes were located ~800 m apart and 5–10 m from gravel roads.

Starting in early May, we visited each nest box every 2–3 days. As soon as we detected Tree Swallows in the area around the nest box, we included the box in our experiment. We first determined whether Tree Swallows had begun bringing nesting material into boxes (most birds had placed only a few blades of grass in boxes when they were detected). Next, we sequentially assigned each box with nesting materials to either a treatment or a control group. The same protocol of sequentially allocating boxes to treatment or control groups was used for boxes to which Tree Swallows had not yet brought nesting material. That method allowed us to control for (1) potential seasonal effects associated with egg production and (2) stage of nest construction of birds when they entered our study.

We supplemented treatment nests with crushed oyster shell as soon as they were allocated to the group, and supplementation continued until egg laying ceased. Oyster shell consists of ~97.5% $CaCO_3$ (38% calcium) and is a common supplement for domestic poultry. Oyster shell has also been used to study calcium use by wild birds (e.g. Johnson and Barclay 1996) and is similar in composition to the snail shells that are commonly found in nests of Tree Swallows (R. D. Dawson unpubl. data). We provided treatment pairs with *ad libitum* oyster shell in three ways: in small paper cups attached to the inside of boxes, on the ground in feeding trays in front of boxes (e.g. Dhondt and Hochachka 2001), and scattered on the edge of the road near each box. Pieces of oyster shell in cups in the nest boxes was of uniform diameter (~2 mm), whereas shell in the feeding trays and along the road was variable in size (1–10 mm in diameter). The range of size of the oyster shell we provided was comparable to the grit size normally used by Tree Swallows (see Mayoh and Zach 1986). Additionally, we provided a small amount of crushed and shattered rib bone from moose (*Alces alces*) near the feeding tray of each treatment nest. Because of the large size of our study area, it was not logistically feasible to systematically observe birds at supplemented nest boxes to ensure that they used the oyster shell; however, several lines of evidence suggest that they did. Tree Swallows were observed, on several occasions, picking up grit on the roadways in the vicinity of the oyster shell we provided. Oyster shell in cups placed in nest boxes was also disturbed in each of the supplemented nests in the study. Additionally, on a different study area, we found pieces of oyster shell in the nesting material of 100% of nests (n = 37, R. D. Dawson unpubl. data); Tree Swallows at that second site were procuring oyster shell from several small pens where poultry were kept. Empty paper cups were attached to the insides of control boxes, and we placed feeding trays filled with gravel on the ground in a manner similar to treatment nests. Control nests were visited at the same frequency as treatment nests. The closest distance between a control nest and a supplemented nest was 0.45 km, but most were much farther apart (mean ± SE = 1.22 ± 0.20 km). Although it is possible that control birds consumed some of the calcium we provided, distances between control and supplemented boxes in our study were much greater than in previous studies (e.g. Tilgar et al. 2002, Mänd and Tilgar 2003). Given the large distance between nest boxes, we are reasonably confident that control pairs did not have access to the calcium sources provided to treatment nests.

The frequency of our visits to the study area in spring allowed us to determine the date on which Tree Swallows were first seen around individual nests boxes, which we used as an estimate of arrival date on the study area. Our visits to the nest boxes also allowed us to determine date of clutch initiation. Once we were certain a clutch was complete, we estimated egg size by weighing each egg to the nearest 0.01 g using a digital scale and subsequently calculating mean egg mass for individual clutches. Clutches were weighed on the second day of incubation; though it is well known that eggs lose mass throughout incubation, that should not have biased our results, because other research has shown that mass of individual eggs on day of laying is highly correlated with mass on day 2 of incubation in Tree Swallows (r^2 = 0.93, P < 0.0001, n = 57; P.-P. Bitton and R. D. Dawson unpubl. data). We visited boxes every 1–2 days near the predicted hatching date to determine when the first nestling emerged from the egg, and number of eggs that hatched. When possible, we collected pieces of eggshells from hatched eggs, and subsequently used a digital micrometer to determine thickness of eggshells (nearest 0.0025 mm). Adult Tree Swallows were captured in the nest box as soon as all eggs had hatched; each bird was banded and weighed (nearest 0.25 g), and the length of its ninth primary was measured (nearest 0.5 mm). We used plumage coloration to classify females as being either in their second year (SY) or older (after second year [ASY]) (details in Hussell 1983).

Data Analysis

We tested for effects of supplemental calcium on clutch initiation date, egg and clutch size, total egg mass, eggshell thickness, number of eggs that hatched, number of young fledged, as well as body mass of parents at the conclusion of the incubation period. For all of the above variables, we first performed preliminary single-factor analyses to investigate how each was affected by potential factors and covariates. For each dependent variable, we then employed analysis of variance (ANOVA) or analysis of covariance (ANCOVA) as appropriate, with calcium treatment as a main effect and any other variables identified in the above analyses. Initial models also included first-order interactions. We used a stepwise backward procedure to eliminate all nonsignificant interactions and terms. Final models always included the variable of interest: calcium supplementation. We also investigated whether extra calcium influenced the probability that birds occupying territories around nest boxes successfully initiated breeding (i.e. laid eggs), using Fisher's exact tests.

All analyses were performed using SPSS (Norušis 2000) and SAS, version 6 (SAS Institute, Cary, North Carolina). We present results as means ± 1 SE. Although one may predict *a priori* that calcium supplementation should increase reproductive output, we took a conservative approach and used two-tailed tests throughout, and considered results significant at the 0.05 level.

Results

During the course of the study, we provided supplemental calcium at 30 nest boxes; an additional 29 boxes served as controls. Presence of supplemental calcium did not influence a pair's decision to lay eggs or abandon their attempt (22 of 29 control pairs laid eggs, 27 of 30 supplemented pairs laid eggs; Fisher's exact test: P = 0.18). There was also some suggestion that birds that had already begun nest building when we first discovered them were more likely to lay eggs (27 of 29) than those that had not brought nesting materials (22 of 30; Fisher's exact test: P = 0.08).

Analysis of covariance showed that supplemental calcium did not directly influence clutch initiation date (F = 0.22, df = 1 and 35, P = 0.65; Table 1), but birds that had already brought nesting material into boxes when we detected them initiated laying earlier (F = 7.92, df = 1 and 35, P < 0.01), as did those birds arriving earlier in the season on our study site (covariate: F = 142.82, df = 1 and 35, P < 0.0001). There was also a significant interaction between calcium supplementation and the presence or absence of nesting material (interaction: F = 4.93, df = 1 and 35, P = 0.03). To further investigate that interaction, we analyzed data separately for birds with and without access to supplemental calcium. We found that control birds with nesting material initiated their clutches, on average, 6.0 days before those without nesting material (F = 12.63, df = 1 and 15, P < 0.01). In contrast, among calcium-supplemented birds, there was only a 0.5-day difference in clutch initiation dates between birds with and without nesting material (F = 0.18, df = 1 and 19, P = 0.68), which suggests that calcium reduced the length of the prelaying period among that group.

Calcium-supplemented females produced larger eggs than control females (F = 4.87, df = 1 and 37, P = 0.03; Table 1); and contrary to our expectation, young females (SY) laid significantly larger eggs than older (ASY) females (F = 5.17, df = 1 and 37, P = 0.03). The

TABLE 1. Reproductive output of Tree Swallows breeding in central British Columbia, Canada, that were supplemented with calcium from their arrival on the study area until the commencement of incubation, and of control pairs. Means (± SE) and *P* values for differences between groups are presented, after controlling for significant covariates in models (see text). Sample sizes are indicated in parentheses and refer to number of nests.

	Control	Treatment	*P*
Clutch initiation date [a]	161.5 ± 0.8 (18)	161.0 ± 0.7 (22)	0.65
Egg mass (g)	1.67 ± 0.02 (20)	1.70 ± 0.02 (22)	0.03
Eggshell thickness (mm)	0.677 ± 0.003 (13)	0.687 ± 0.004 (15)	0.51
Clutch size	5.57 ± 0.15 (20)	5.91 ± 0.14 (22)	0.098
Total clutch mass (g)	9.28 ± 0.26 (20)	10.02 ± 0.24 (22)	0.04
Number of eggs hatched	4.79 ± 0.21 (20)	5.02 ± 0.21 (22)	0.02
Brood size at age 16	4.85 ± 0.16 (9)	4.80 ± 0.17 (8)	0.84

[a] 1 = 1 January.

analysis also showed that egg size increased significantly as female mass increased ($F = 10.56$, df = 1 and 37, $P = 0.02$). However, there was a significant interaction between female mass and calcium supplementation ($F = 5.17$, df = 1 and 37, $P = 0.03$), which suggests that the slopes of those relationships differed for control and supplemented birds (Fig. 1). When we analyzed data separately for treatment and control groups, egg size increased significantly with female mass in the supplemented group ($r = 0.52$, $P = 0.01$, $n = 24$ nests); but no such relationship existed for control nests ($r = 0.13$, $P = 0.58$, $n = 21$ nests; Fig. 1). We did not detect a significant difference in thickness of egg shells between calcium-supplemented and control females ($F = 0.44$, df = 1 and 26, $P = 0.51$; Table 1).

Clutch size increased as birds bred earlier in the season ($F = 21.09$, df = 1 and 37, $P < 0.001$), was larger among older (ASY) than among second-year females ($F = 9.66$, df = 1 and 37, $P < 0.01$), and increased with length of a female's ninth primary flight feather ($F = 10.07$, df = 1 and 37, $P < 0.01$), which suggests that structurally larger females produced more eggs. The analysis also suggested that females supplemented with calcium laid more eggs than control females ($F = 2.87$, df = 1 and 37, $P = 0.098$; Table 1). Analysis of total mass of clutches showed that calcium-supplemented females laid significantly larger total mass of eggs than control birds ($F = 4.57$, df = 1 and 37, $P = 0.04$; Table 1), and the same factors that influenced clutch size also affected total clutch mass (female age: $F = 5.14$, df = 1 and 37, $P = 0.03$; length of ninth primary: $F = 12.54$, df = 1 and 37, $P < 0.01$; clutch initiation date: $F = 16.69$, df = 1 and 37, $P < 0.001$).

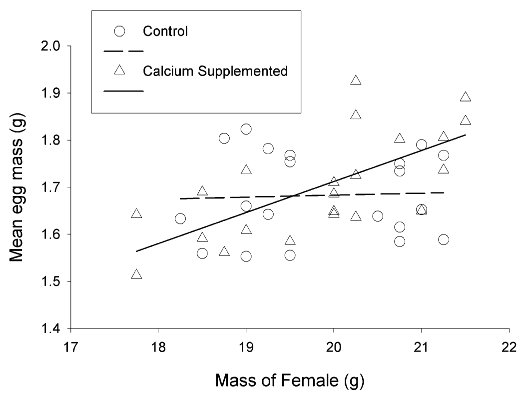

FIG. 1. Relationship between mass of female Tree Swallows and mean mass of eggs they laid, according to whether they received supplemental calcium prior to and during laying or served as a control.

Female Tree Swallows with larger clutches also hatched more eggs ($F = 5.80$, df = 1 and 34, $P = 0.02$), as did older females ($F = 7.42$, df = 1 and 34, $P = 0.01$) and those with longer ninth primaries ($F = 4.10$, df = 1 and 34, $P = 0.05$). Although the analysis also showed that females supplemented with calcium hatched more eggs than control females ($F = 6.35$, df = 1 and 34, $P = 0.02$; Table 1), we detected a significant interaction between calcium supplementation and hatching date ($F = 6.52$, df = 1 and 34, $P = 0.02$) and between female age and length of the ninth primary ($F = 7.62$, df = 1 and 34, $P < 0.01$). Inspection of the data suggested that the interaction between calcium supplementation and hatching date resulted from number of eggs hatched by control birds declining significantly with later hatching date, whereas no such relationship occurred for supplemented birds (Fig. 2). Correlation analyses performed separately for treatment and control birds confirmed those relationships (control: r = –0.70, P < 0.0001, n = 21 nests; treatment: r = –0.04, P = 0.87, n = 25 nests). Interaction between female age and length of the ninth primary suggested that among young females (SY), body size had a positive effect on their ability to incubate and hatch eggs (r = 0.59, P = 0.02, n = 26 nests). In contrast, hatching success of older females (ASY) was unrelated to their body size (r = –0.02, P = 0.93, n = 16 nests).

As expected, pairs of Tree Swallows with larger broods at hatching also had larger broods 16 days after hatching (F = 59.82, df = 1 and 14, P < 0.001), but calcium-supplemented pairs did not have larger broods than control pairs at that time (F = 0.04, df = 1 and 14, P = 0.84; Table 1). Sample sizes were small for the analysis because some of the nests used in the study were also manipulated during brood rearing as part of a separate investigation (Dawson and Bidwell 2005), and so were excluded from the data set.

Finally, there was no effect of calcium supplementation on mass of female (F = 0.03, df = 1 and 43, P = 0.87) or male parents at hatching (F = 0.01, df = 1 and 33, P = 0.98), though males with longer ninth primaries were heavier (F = 8.48, df = 1 and 33, P < 0.01). Those results confirm that positive effects detected on egg production and number of eggs hatched were attributable to calcium supplementation *per se* and not to the fact that calcium-supplemented parents were in better condition than control parents.

Discussion

Providing supplemental calcium to Tree Swallows on our study site significantly affected their reproductive output in several ways. Calcium-supplemented birds that had not begun nest construction when first detected on the study area initiated clutches earlier and so had reduced prelaying periods. Supplemented females also produced larger eggs, and that effect was more pronounced if a female was heavier and therefore presumably in good body condition (Fig. 1). There was also a nonsignifcant trend for supplemented females to lay more eggs than control females, and as a result, total clutch mass of supplemented

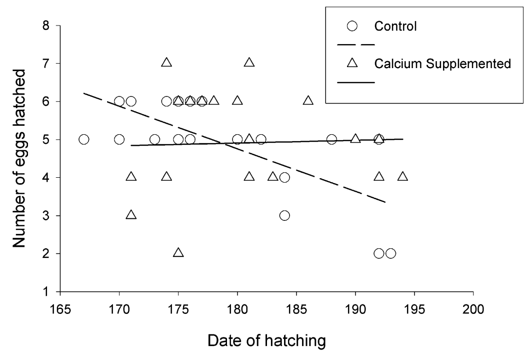

Fig. 2. Number of eggs hatched by pairs of Tree Swallows that received supplemental calcium or acted as a control versus date of hatching (1 = 1 January).

birds was significantly larger than that of control birds (Table 1). Finally, supplementation allowed birds—particularly those breeding late in the season—to hatch more eggs (Fig. 2). Our results demonstrate that calcium availability affects reproductive output of insectivorous birds in landscapes that have relatively high levels of calcium in the soil, and that have not been altered by anthropogenically induced increases in acidity (Arocena and Sanborn 1999, Rodhe et al. 2002).

Although Mänd et al. (2000) showed that extra calcium allowed Great Tits (*Parus major*) to breed earlier in the season than controls, other work on that species has been unable to find such an effect (Graveland and Drent (1997). In our study, supplementation did not have an overall effect on clutch initiation date (Table 1); however, when we controlled for the stage of nest construction when pairs were allocated to the study, our analysis revealed that supplementation allowed birds without nesting materials to initiate clutches earlier and thus have shorter prelaying periods. Birds that had brought nesting materials to the box when we detected them would have been further along in the breeding cycle than birds without nest materials. As a consequence, calcium supplementation allowed birds to proceed to egg laying more quickly than control birds, which suggests that the timing of calcium acquisition may also be important. That suggestion is supported by Graveland and Berends (1997), who found that 90% of the calcium used for formation of eggshells was consumed during the laying period. Ultimately, that effect would cause the offspring of supplemented birds to fledge earlier, with potentially beneficial consequences for postfledgling survival (e.g. Verboven and Visser 1998).

Tilgar et al. (1999) and Mänd and Tilgar (2003) recently demonstrated that access to extra calcium caused Pied Flycatchers (*Ficedula hypoleuca*) to lay larger eggs than those without calcium, though Mänd et al. (2000) did not detect that effect in Great Tits. Our results showed that calcium supplementation caused significant increases in mean mass of eggs laid by Tree Swallows (Table 1). Furthermore, heavier females produced heavier eggs when supplemented with calcium, whereas no such relationship existed among control birds (Fig. 1), which suggests that females in good body condition benefit more from extra calcium. We suggest that calcium supplementation allows females with larger body reserves to allocate more of their nutrients toward production of larger eggs, because calcium may no longer constrain eggshell formation and thus the size of the egg. Although some studies have demonstrated that young hatched from larger eggs may have a higher probability of surviving than those from smaller eggs (e.g. Schifferli 1973, but see Reed et al. 1999), we were unable to detect any effect of extra calcium on the number of offspring surviving to fledging (Table 1).

Effects of calcium on clutch size are equivocal; some studies have found no effect (e.g. St. Louis and Barlow 1993, Graveland and Drent 1997), whereas others have demonstrated nonsignificant trends for supplemented females to produce larger clutches (Johnson and Barclay 1996, Mänd et al. 2000). One study has recently demonstrated that calcium-supplemented Great Tits laid larger clutches than control birds (Tilgar et al. 2002). Our results were not significant, but there was a trend for larger clutches among supplemented birds, which suggests that nutrients like calcium could also be an important factor in the evolution of clutch size in altricial species like Tree Swallows (Carey 1996). However, many other factors can affect clutch size, and further work is required to more precisely determine the role of calcium limitation in those relationships.

Another important contribution to reproductive success is hatching success. If eggs are laid that fail to hatch, not only do parents raise fewer offspring, but females have wasted resources on those inviable eggs. Graveland and Drent (1997) determined that calcium supplementation in an acidified landscape increased hatching success in Great Tits and also reduced the incidence of defective eggshells. We showed, after controlling for clutch size, that Tree Swallows supplemented with calcium hatched more eggs than control pairs (Table 1), and those effects were more pronounced among late-breeding birds (Fig. 2). The reasons for that differential hatching success are unclear. Graveland et al. (1994) and Graveland and Drent (1997) attributed hatching failures to calcium deficiencies causing birds to lay eggs with thin, porous shells. In our study, eggshell thickness did not differ between treatment and control groups (Table 1), so that factor cannot explain why control birds experienced greater hatch failure. However, our data may have been inadequate to investigate that relationship, because we only measured eggshells from eggs that hatched. Differences in eggshell thickness may have been detected if we had examined the shells of eggs that failed to hatch; we do not have data to test that possibility.

Effects of calcium on reproduction of birds can manifest themselves in both direct and indirect ways. Direct effects are the result of females being unable to acquire enough calcium to form eggshells; in such cases, calcium may limit reproduction as much as energy or other nutrients. Direct effects are most likely to occur in environments with extremely low levels of calcium, where one might predict females to lay defective, inviable eggs or no eggs at all (Graveland et al. 1994, Graveland and Drent 1997). Graveland and Drent (1997) suggested that such effects may be most common in areas where calcium availability has declined recently and in which birds lack the ability to adaptively respond to low levels of calcium. Alternatively, indirect limitation occurs if low levels of calcium affect a bird's ability to acquire some other limited resource (e.g. energy), which in turn delays or prevents it from successfully reproducing, or reduces reproductive output. Moreover, Graveland and Drent (1997) suggested that such delays in breeding and reduced ouput may be evolutionary adaptations to low levels of calcium in nonacidified but calcium-poor environments.

We suggest that the effects of calcium limitation are most appropriately evaluated in light of a gradient of environmental calcium availability. In extremely calcium-poor areas, such as those with recent acid deposition, low levels of calcium may directly affect reproductive output. In calcium-rich areas, calcium should mainly limit reproduction indirectly, if at all (Graveland and Berends 1997). Most environments, including our study site, lie between the two ends of that spectrum. We found effects related to egg viability (e.g. hatching success) as well as timing of breeding, egg size, and clutch size, and so our results are consistent with both direct and indirect effects. We have also recently shown that calcium availability for nestlings limits their size and growth while in the nest (Dawson and Bidwell 2005). Taken together, our studies support the idea that reproduction of birds may be limited by calcium, even in environments where it is relatively abundant.

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