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Dietary calcium limits size and growth of nestling tree swallows *Tachycineta bicolor* in a non-acidified landscape

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Much previous research has focussed on the role of food supply in determining the growth and the survival of avian offspring. More recently, acid deposition in some ecosystems has demonstrated that in addition to energy, birds also need to acquire sufficient nutrients such as calcium to be successful. Whether procurement of adequate levels of calcium can limit reproductive success in areas that have not been impacted by acid rain remains equivocal. We tested whether calcium affected reproductive success of tree swallows *Tachycineta bicolor* by feeding extra calcium to nestlings during the brood-rearing period. Our manipulation did not enhance the survival of offspring, however, provisioning of extra calcium resulted in nestlings showing enhanced rates of growth of mass (all nests) and of ninth primary flight feathers (nests with after-second year female parents), compared to control nestlings. Calcium supplementation also resulted in nestlings having longer feathers and tarsi at age 16 days, and there was evidence that some nestlings receiving extra calcium were heavier at 16 days old. As offspring that have faster growth, or that are in good condition at fledging, often survive better after leaving the nest, these results suggest that calcium availability can limit fitness. Our results are noteworthy because our experiment was conducted in an area with abundant soil calcium where acid deposition has not occurred. The role of calcium in limiting the reproductive performance of avian species may therefore be more pervasive than previously thought.

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Raising altricial offspring is an energetically expensive activity for parent birds, and their ability to adequately provision young may be a key determinant of their fitness (Drent and Daan 1980). Indeed, Lack (1947) hypothesized that the ability of parents to provide food for growing offspring would ultimately determine clutch size. Congruent with these ideas, there is abundant evidence confirming the importance of food supply in determining reproductive rates (reviews in Boutin 1990, Martin 1995), and parental behaviour (Dawson and Bortolotti 2002) of birds. However, Barclay (1994) hypothesized that among flying vertebrates (birds and bats), procuring limited nutrients such as calcium may be a more important factor than acquisition of energy in limiting reproductive success. Birds need to obtain calcium in sufficient quantities during laying, to form egg shells, and again during brood rearing to ensure proper skeletal development of their rapidly growing offspring. It is now well-documented that the diets of insectivorous and granivorous birds are insufficient to meet these demands for calcium (Graveland and van Gijzen 1994, Taliaferro et al. 2001). While some birds are able to overcome this problem by storing and mobilizing calcium from specialized medullary bone to form eggs (Dacke et al. 1993), small birds may be unable to do so (Krementz and Ankney 1995, Pahl et al. 1997). In fact, among some species of passerines, the calcium content of a clutch of eggs can be similar to, or even exceed that of the entire skeleton of the female (Graveland and van Gijzen 1994, Reynolds 1997). As a result, birds actively forage for calcium-rich items such as snail shells both during egg laying and brood rearing (Bureš and Weidinger 2001; references in Reynolds 1997).

In recent years, the deposition of acidic precipitation in various ecosystems has illustrated the importance of calcium limitation in the reproduction of birds. Acid deposition, especially in base-poor areas, causes a reduction in available soil calcium (Ramsay and Houston 1999; but see Mahoney et al. 1997, Ormerod and Rundle 1998), and an associated decline in the abundance of calcium-rich prey items, such as snails (Graveland et al. 1994, Graveland and van der Wal 1996), that insectivorous and granivorous birds need to meet their calcium demands. In areas of Europe and North America where such changes have occurred, research has shown that birds perform poorly, both in terms of producing eggs and the growth of their offspring (Drent and Woldendorp 1989), and in some cases, these effects can be reversed by providing supplemental calcium (Graveland et al. 1994, Graveland and Drent 1997). Such results led Graveland (1996) to speculate that calcium limitation may be a general phenomenon, and impose reproductive constraints on birds even in areas that have not suffered acid deposition. In such habitats, calcium could directly impact reproduction by determining growth of offspring or the ability of females to form eggs, and indirectly by forcing parents to trade-off procuring energy versus calcium or making birds more susceptible to predation while they forage for calcium on the ground (Johnson and Barclay 1996). However, results of studies conducted in non-acidified landscapes have yielded conflicting results. For example, Poulin and Brigham (2001) were unable to detect any significant effects of calcium supplementation on growth of purple martins *Progne subis*. While Johnson and Barclay (1996) found some benefits of calcium supplementation, they concluded that calcium limitation was not an important factor influencing reproduction of house wrens *Troglodytes aedon* on their study area in Wyoming. In contrast, great tits *Parus major* supplemented with calcium in a non-acidified area initiated egg laying earlier, laid more eggs and as a result fledged more young (Mänd et al. 2000, Tilgar et al. 2002). Similarly, Tilgar et al. (1999), and Mänd and Tilgar (2003), showed that extra calcium allowed pied flycatchers *Ficedula hypoleuca* to lay larger eggs and to produce young with longer tarsi.

In this paper, we explore how calcium affects growth, size and survival of nestling tree swallows *Tachycineta bicolor*. Patterns of growth in tree swallows have been well-studied, and most investigators have shown that variation in food supply (Quinney et al. 1986, McCarty and Winkler 1999, McCarty 2001), as well as nest microclimate (R. D. Dawson, unpubl. data), are key factors determining growth rates. Research conducted in an acidified landscape has also shown that tree swallows fledged more young, and offspring grew better, as wetland pH increased (Blancher and McNicol 1991). However, it was not clear whether these effects were due to differences among wetlands in food or calcium availability (Blancher and McNicol 1991). In the present study, we performed an experiment to investigate how calcium influences performance of nestlings. We directly fed nestlings calcium throughout the brood-rearing period and compared them to a group of control nestlings. We provide evidence that calcium can influence growth and size of offspring, even in a non-acidified area with abundant soil calcium such as our study area.

Materials and methods

We studied tree swallows breeding in nest boxes from May to August 2002 on an approximately 800 km^2 study site near Vanderhoof, British Columbia, Canada (54° N, 124° W). Our study site is a matrix of open agricultural areas mixed with small patches of coniferous and deciduous trees, and is interspersed with small wetlands. This area has not been impacted by anthropogenic acid deposition, and has abundant soil calcium (Arocena and Sanborn 1999). Tree swallows arrived in the area in early May, and began nest construction and egg laying in late May. Nest boxes were mounted 3 m above the ground on electrical poles, and were located approximately 800m apart and 5–10 m from roads. We visited nest boxes every 2 to 3 days prior to egg laying; once a clutch had been initiated, we continued to visit the nest every 2 days until laying was completed. Once a clutch was complete, we weighed each egg to the nearest 0.01 g using a digital scale and subsequently calculated mean egg mass for each clutch. We began visiting nest boxes every day near the predicted hatching date to determine when the first nestling emerged from the egg, and the number of eggs that hatched.

Once hatching was completed, adult swallows were captured in the nest box. Each adult was banded, weighed (nearest 0.25 g), and the length of its ninth primary flight feather measured (nearest 0.5 mm). We used plumage colouration to classify females as being either in their second year (SY), or older (after-second year: ASY; details in Hussell 1983). At this time, each nest was also sequentially allocated to either a control or a treatment group; the offspring in the latter nests received supplemental calcium during brood rearing (details below). The sequential allocation of nests to treatment or control groups allowed us to control for potential seasonal effects associated with hatching date. In addition, some nests used in the present study were also part of a previous investigation of the potential role of calcium in limiting egg production of tree swallows (Bidwell and Dawson 2005). The parents at these nests had received crushed oystershell as soon as they had arrived on the study area in spring until they had completed their clutches. As soon as clutches were completed, all traces of oystershell were removed. When allocating nests to treatment and control groups for the present study, we evenly distributed those nests that had been supplemented prior to clutch completion between control and treatment groups. In our analyses, we also tested whether any residual effects of supplementation prior to clutch completion existed, thus ensuring that our groups were directly comparable (see below).

Nestlings in the treatment group received supplemental calcium in the form of pulverized oystershell suspended in water, which we fed to them every other day from 4 days post-hatching until 14 days post-hatching. Using a feeding tube and a plastic syringe we provided each nestling with a 0.2 ml dose of this aqueous suspension, which contained approximately 53 mg of oystershell. Oystershell contains about 97.5% $CaCO_3$ (38% calcium) so each nestling received about 20 mg of calcium every other day or about 120 mg of calcium over the course of the experiment. Graveland and van Gijzen (1994) showed that the calcium content of adult great tits was approximately 190mg. Adult tree swallows are similar in body mass to great tits, so we estimate that we provided approximately 60% of the calcium contained in the body of an adult tree swallow. Oystershell is a common supplement for domestic poultry, has been used to study calcium use by wild birds (Johnson and Barclay 1996) and is similar in composition to the snail shells that are commonly found in nests of tree swallows. Graveland and van Gijzen (1994) also suggested that $CaCO_3$ is easier for birds to metabolize than calcium found in insects. Control nestlings were provided an equivalent amount of water according to the same schedule.

We measured each individual nestling every two days, beginning at 4 days post-hatching and continuing until 16 days post-hatching. We measured mass with a spring scale (nearest 0.25 g), length of ninth primary flight feather with a ruler (nearest 0.5 mm) and length of the tarsus using digital calipers (nearest 0.01 mm). Each nestling's tarsus was measured 3 times, and the mean value calculated. We kept track of individual chicks within a nest by marking the legs of each nestling with a unique colour combination using a non-toxic pen. Nestlings were banded when they were 10 or 12 days old. We made a final visit to each nest box 22 days after hatching to determine if any nestlings failed to fledge. To investigate whether providing extra calcium had consequences for growth of offspring, we calculated growth curves for mass, ninth primary and tarsus. We first calculated the means by nest for mass, length of ninth primary and length of tarsus at each age from 4 to 16 days old. For each data set, we used iterative least-squares non-linear curve fitting procedures to fit logistic and Gompertz models, ultimately selecting the model that produced the best fit (i.e., the model that explained the most variation in the data). For growth rates of mass, we used the logistic model, which has the form:

$$\mathrm{M(x)} = \mathrm{a}/1 + \mathrm{be}^{-\mathrm{cx}}$$

where M(x) is the mass at age x, a is asymptotic mass, b is the inflection point, and c is the growth rate constant. To describe growth of the tarsus and ninth primaries, we used the Gompertz model which takes the form:

$$\mathrm{T(x)} = \mathrm{ae}^{-\mathrm{e}^{\mathrm{bc}-\mathrm{x}}}$$

where T(x) is length of the structure at age x, a is asymptotic length, b is the inflection point, and c is the growth rate constant. Both logistic and Gompertz models are commonly used to calculate growth rate curves for passerines (McCarty 2001). We calculated growth rates only for nests with complete measurements every second day from ages 4 to 16 days; in several cases, we did not obtain complete measurements (e.g., due to inclement weather), and so our sample sizes differ among analyses.

Because some of the nests used in the present study were also part of another investigation where calcium was provided to parents prior to and during egg laying (see above), we needed to ensure that this did not result in biases for our present study. To address this, we first used analysis of variance to compare whether there were differences in brood size, nestling mass, or length of tarsus and ninth primary, between our control and calcium-supplemented nests prior to the commencement of feeding calcium to offspring. In addition, in all other analyses, we included the presence or absence of calcium supplementation during prelaying as a potential factor. This variable did not contribute significantly to any model, and so was subsequently dropped from the analyses.

To test whether growth rate constants for mass, tarsus and ninth primary were affected by calcium supplementation during the brood-rearing period, and whether calcium supplementation affected the body mass or size of tarsus and ninth primary at 16 days post-hatching (just prior to offspring leaving the nest), we used analysis of covariance (ANCOVA). These analyses used Type III sums of squares and included calcium treatment as the explanatory variable of interest. In addition, we also included in the analysis the age of the female parent (SY or ASY), mass and ninth primary length of both parents, brood size, mean egg mass and hatching date as potential covariates. Nests where some offspring had died before age 16 days were excluded from the data set as we did not want to introduce the confounding effect of brood reduction in these analyses. Initial models also included all interactions involving calcium supplementation. A stepwise backward procedure was then used to eliminate all non-significant interactions and terms in the model, although we always retained the variable of interest, calcium supplementation, in the final model.

We also investigated in several ways whether supplemental calcium affected the fledgling success of tree swallows. We used a Fisher's Exact test to determine whether there were differences between treatment and control groups in the proportion of nests that experienced brood reduction, where brood reduction is defined as having one or more offspring die between hatching and fledging. Next, we used an analysis similar to those for size and growth of offspring (ANCOVA) to test whether the number of young fledged differed between groups. This analysis included age of the female parent, mass and ninth primary length of both parents, brood size at hatching, mean egg mass and hatching date as additional explanatory variables. Non-significant terms and interactions were removed from the model using a backward stepwise procedure.

All analyses were performed using SPSS (Norušis 1993), and SAS (SAS Institute 1990) software. We present means as 0 ± 1 SE. Although one may predict a priori that calcium supplementation should have positive effects on growth and size of offspring, as well the fledging success, we took a conservative approach and used two-tailed tests throughout, and considered results significant at the 0.05 level.

Results

We gathered data from 18 nests where offspring received extra calcium during our experiment, while another 18 nests served as controls. Prior to commencing our experiment, we could detect no significant differences in brood size, or in mass or tarsus length of offspring, between calcium-supplemented and control nests (all P-values >0.34). Similarly, there were no differences between treatment and control nestlings in length of ninth primary feathers at age 6 days ($P = 0.67$), the first day we measured primaries. These results suggest that there were no pre-existing biases in our sample.

Overall, extra calcium did not appear to significantly enhance offspring survival. All 36 nests fledged at least 1 young. Brood reduction occurred at 6/18 calcium-supplemented nests and 3/18 control nests; these proportions were not significantly different (Fisher's Exact test, $P = 0.44$). Similarly, after controlling for the number of nestlings hatched ($F_{1,28} = 151.70$, $P < 0.0001$), we could find no difference between treatments in the number of young fledged ($F_{1,28} = 0.20$, $P = 0.66$). This analysis did show that the number of young fledged was positively related to mean egg mass ($F_{1,28} = 5.26$, $P = 0.03$), as well as ninth primary flight feathers of male parents ($F_{1,28} = 10.91$, $P < 0.01$).

We found that providing extra calcium to chicks increased the rate of growth for mass ($F_{1,20} = 5.27$, $P = 0.03$; Fig. 1). Growth of mass was also higher among younger (SY) females than older females (ASY; $F_{1,20} = 5.14$, $P = 0.04$). Analysis of growth rate of ninth primary feathers suggested no significant effect of calcium supplementation ($F_{1,20} = 1.62$, $P = 0.22$), nor was female age an important variable ($F_{1,20} = 0.53$, $P = 0.48$). However, we also detected a significant treatment by female

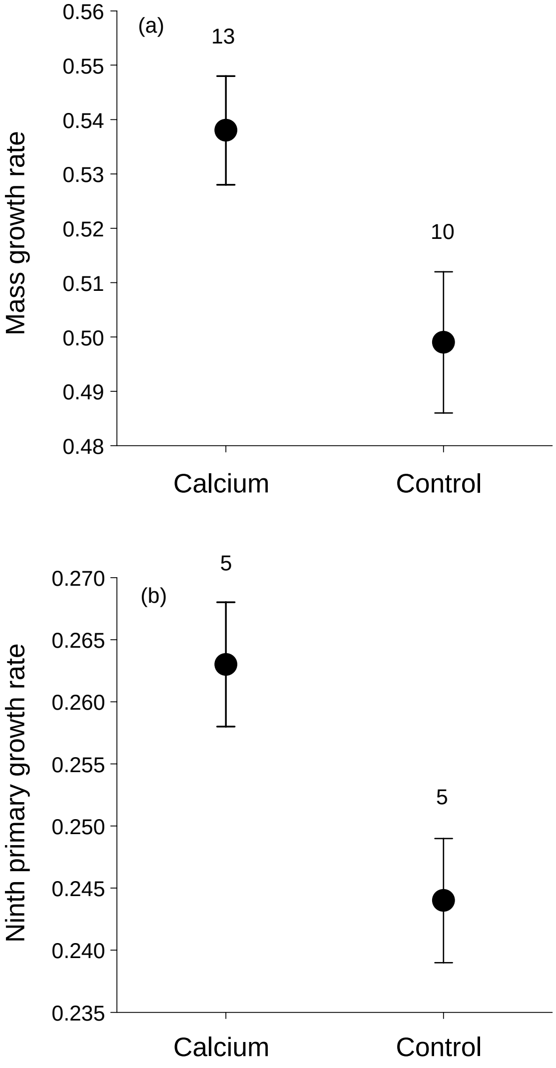

Fig. 1. Mean (±SE) rate of growth of: (a) mass, and (b) ninth primary flight feather of nestling tree swallows according to whether they were provided with supplemental calcium during the brood rearing period, or acted as a control. Samples sizes are indicated above error bars and refer to number of nests. Data for ninth primary of nestlings are presented only for nests with older (after-second year) adult females. See Materials and methods for calculations of growth rates.

age interaction ($F_{1,20} = 5.55$, $P = 0.03$), so we analyzed data separately by female age. Among SY females, there was no significant effect of calcium supplementation on growth of their offspring's ninth primaries ($F_{1,12} = 0.64$, $P = 0.44$), but offspring of ASY females provided with calcium grew their primaries significantly faster than did offspring of control ASY females ($F_{1,8} = 6.62$, $P = 0.03$; Fig. 1). Growth rates of tarsi were not influenced by calcium supplementation ($F_{1,21} = 0.06$, $P = 0.81$), but growth rates declined significantly as hatching dates became later in the season ($F_{1,21} = 4.80$, $P = 0.04$).

Our analysis showed no significant effect of calcium supplementation on offspring mass at age 16 days ($F_{1,23} = 1.31$, $P = 0.27$). However, inspection of our data revealed that chicks were very light on day 16 in two nests that received calcium supplementation. To further investigate how these two data points influenced our results, we first performed a maximum normal residual test (Snedecor and Cochran 1989) and determined them to be outliers ($P < 0.05$). When these two data points were omitted from the analysis, calcium-supplemented nestlings were significantly heavier at age 16 days than control nestlings ($F_{1,21} = 6.93$, $P = 0.02$). We have plotted these data, including the outliers, in Fig. 2. These results suggest that while calcium can have beneficial effects for offspring mass, other factors that we have not tested for can also significantly influence mass. Length of ninth primary flight feathers of offspring at 16 days of age was significantly longer in calcium supplemented birds ($F_{1,22} = 9.22$, $P < 0.01$; Fig. 3), and was positively related to the length of the female parent's ninth primary ($F_{1,22} = 5.68$, $P = 0.03$). Finally, nestlings that received supplemental calcium had longer tarsi at age 16 days ($F_{1,21} = 8.45$, $P < 0.01$; Fig. 3); length of tarsi was also negatively related to mass of the female parent ($F_{1,21} = 4.38$, $P = 0.049$), and there was some suggestion that young SY females produced young with longer tarsi than did older ASY females, although these results were not quite significant ($F_{1,21} = 4.17$, $P = 0.054$).

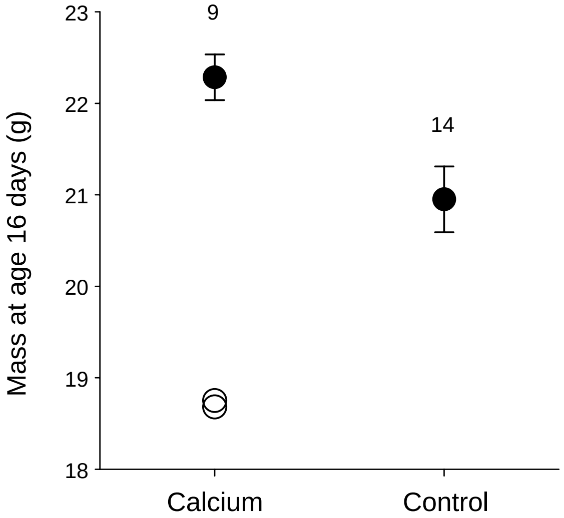

Fig. 2. Mean (±SE) mass of nestling tree swallows at age 16 days for nests receiving supplemental calcium versus control nests. Sample sizes are given above error bars and refer to number of nests. Significant differences between groups disappear when two outliers (open circles) are included in the data set. See text for further discussion.

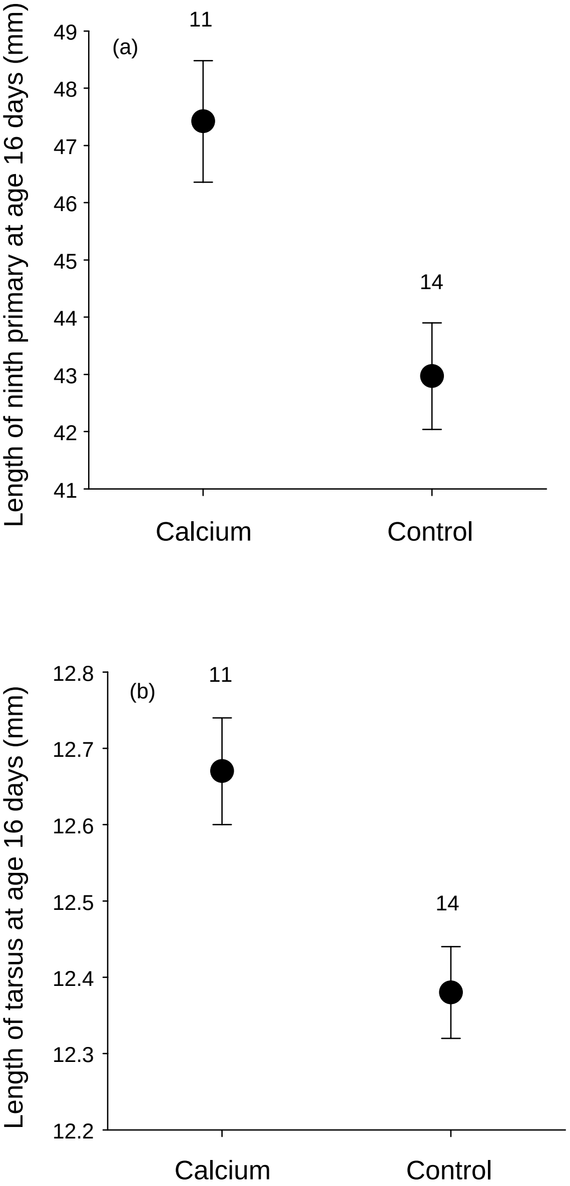

Fig. 3. Differences between calcium-supplemented and control nests in: (a) length of ninth primary feather, and (b) length of tarsus of nestling tree swallows at age 16 days. Means (±SE) are presented after controlling for significant covariates in models (see Results). Sample sizes above error bars refers to number of nests.

Discussion

Our experiment provides evidence that calcium can limit performance of avian offspring. Nestling tree swallows that received extra dietary calcium during the brood-rearing period had enhanced rates of growth for both mass and ninth primary feathers, and were larger at age 16 days than were control nestlings. While other studies have found that supplementing calcium in the diets of insectivorous birds has beneficial consequences for reproductive success (Graveland et al. 1994, Graveland 1996, Graveland and van der Wal 1996, Graveland and Drent 1997, Weimer and Schmidt 1998, Mänd et al. 2000, Mänd and Tilgar 2003; but see Mahony et al. 1997, Ramsay and Houston 1999), the vast majority of research has been conducted in areas suffering from acid deposition or in areas where calcium is not abundant. In contrast, Tilgar et al. (2002) have recently shown that great tits were limited by calcium in an area of Estonia where acid deposition has not impacted the ecosystem, and so calcium is relatively abundant. When provided with extra calcium, tits hatched more eggs and their offspring had longer tarsi. There was also a non-significant trend for supplemented birds to fledge more young, although initial differences in number of young hatched in the calcium-supplemented group was not controlled for in their analysis so this effect is unlikely to be the result of calcium having survival effects post-hatching. The effects detected in our study were much more pronounced than in the work of Tilgar et al.'s (2002), who required very large sample sizes before they were able to detect a significant influence of calcium. Nonetheless, to our knowledge, only our study and that of Tilgar et al. (2002) have shown calcium to be an important determinant of offspring quality in areas where calcium is abundant.

Calcium has the potential to limit nestling growth and survival both direct and indirectly. For example, calcium might directly limit the growth of skeletal structures, whereas indirect effects may result from parents having to trade-off time searching for energy rich food items in favour of searching for calcium-rich objects. In our study, nestlings provided with extra calcium had significantly faster growth of mass and primary flight feathers (Fig. 1). It seems more likely that these effects were manifest because of indirect effects of calcium. By having to spend less time searching for calcium, parents would be able to provision offspring to a greater extent than would control parents. Tree swallows, and other aerial insectivores, may be particularly affected by this trade-off because although they forage for food in the air, they must spend time on the ground searching for calcium-rich items (Dhondt and Hochachka 2001), and so extra calcium cannot be opportunistically obtained during normal foraging bouts. Even if calcium is available for breeding birds, they may have to fly long distances (St. Louis and Breebaart 1991) or devote significant time searching to obtain it. For example, Turner (1982) showed that barn swallows *Hirundo rustica* spend significantly more time foraging to meet their calcium requirements than they need to meet energy demands.

Trade-offs between foraging for regular prey items and searching for calcium can also explain the significant results for calcium supplementation on length of ninth primary at 16 days of age, and also for potential effects on mass of offspring at this age (Figs 2 and 3). The results that we detected for mass of offspring at 16 days old deserves further attention. Our initial analysis showed no difference in offspring mass between calcium-supplemented and control nests; however, inspection of our data set revealed the presence of two nests in the calcium group with very light nestlings. (Fig. 2). When these two outliers were removed from the analysis, there were significant differences between calcium and control nests. While we are uncomfortable simply eliminating these data from the analysis and concluding that calcium has wide-ranging implications for offspring mass, this situation does shed light on patterns of offspring growth. Clearly, some broods benefited from extra calcium, yet others were in poor condition despite our supplementation. This illustrates that while calcium can be important for offspring quality, other factors such as food supply or microclimate can mask or even override these effects.

We could find no effect of calcium supplementation on growth rates of tarsi. However, we did show that nestlings in our calcium supplementation group had longer tarsi at age 16 days. Hence calcium did not allow chicks to grow their tarsi at a faster rate but did allow them to achieve larger size. Tarsi of tree swallows usually reach adult size by approximately 8–9 days old (McCarty 2001), so our results show that calcium significantly affected some aspects of adult structural size. Longer tarsi have been noted previously in other studies (Mänd et al. 2000, Tilgar et al. 2002, Mänd and Tilgar 2003), and probably result from direct effects of calcium. However, it is unclear why growth of this structure was not also directly affected by calcium. Because reasonably well-developed legs would be beneficial for competition with siblings to jockey for position when parents make feeding visits to the nest (Dutta et al. 1998), it may be that growth of tarsi is already at a physiological maximum. Nonetheless, bone growth is a complex process and the factors that affect it are not well-understood (Carrier and Auriemma 1992).

The results from several of our analyses suggested that there may be differences in characteristics of offspring that are attributable to age of the female parent. However, for both growth of mass and length of tarsus at age 16 days (these latter results only approached significance), we showed that younger second-year (SY) female parents had offspring that performed better than offspring of older, after-second year (ASY) females. These results were unexpected, as we would have expected older, presumably more experienced, females to perform better. We are unable to provide an explanation for these results, and our experiment was designed to evaluate the potential effects of extra calcium on offspring quality as opposed to effects manifested through variation in female age. More research is needed to fully understand these patterns.

Despite the beneficial effects of supplemental calcium on size and growth of nestlings tree swallows, we could detect no significant difference between calcium-supplemented and control nests either in brood size at fledging, or in the proportion of nests that experienced brood reduction. It may be that while calcium is important for some aspects of offspring performance, other resources such as energy may be a more important determinant of survival. Our analyses of the number of nestlings at fledging did show, however, that egg size was positively related to brood size. Neonates from larger eggs often have larger body size and more nutrient reserves, which could enhance survival during the first few days following hatching if parents are unable to provide enough food (Williams 1994). However, we are unable to determine if enhanced survival is a direct result of egg size per se, or due to other characteristics that are correlated with egg size. For example, it may be that high-quality females are able to both lay large eggs and raise large broods. If this is the case, then large brood size may be a consequence of female quality as opposed to large egg size.

In conclusion, extra calcium allowed nestling tree swallows to have faster rates of growth and have larger size at age 16 days. Our previous research on this study area has also shown that calcium provided prior to laying can limit egg production of tree swallows, both through egg size and total clutch mass (Bidwell and Dawson 2005). In addition, we have shown calcium supplementation prior to laying enhances hatching success (Bidwell and Dawson 2005). To date, only one other study has been able to demonstrate calcium limitation of birds in non-acidified areas with abundant soil calcium (Tilgar et al. 2002). Even though we could not find significant effects of calcium supplementation on offspring survival while in the nest, the effects we did detect could still have fitness consequences. Faster growth could allow nestlings to fledge sooner, and so reduce the amount of time they are vulnerable to predators while in the nest (Lack 1968). Similarly, studies of passerine birds have shown that condition of nestlings at fledging is positively related to their probability of recruitment (Merilä and Wiggins 1995). In addition, McCarty (2001) has shown that tree swallows with high rates of growth for mass, wing and tarsus had a higher probability of being recaptured in subsequent breeding seasons (see also Tinbergen and Boerlijst 1990). To fully understand limitations on reproductive output, it may be informative for researchers to consider how factors other than energy, such as calcium limitation, affects birds, even in areas with abundant calcium or where acid deposition has not impacted ecosystems.

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