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**EFFECTS OF SUPPLEMENTAL CALCIUM ON THE GROWTH RATE OF AN
INSECTIVOROUS BIRD: THE PURPLE MARTIN (*Progne subis*)**

A Thesis

Submitted to the Faculty of Graduate Studies and Research

In Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in Biology

University of Regina

by

Ray G. Poulin

Regina, Saskatchewan

May, 1997

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Dr. M. Ramsay, University of Saskatchewan

by teleconference

Dr. R.M. Brigham, Supervisor

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W. Cho

Wednesday

ABSTRACT

Most insects do not contain sufficient calcium for insectivorous birds to produce eggshells or meet the needs of their growing young. Therefore, insectivorous birds must supplement their diet and the diet of their young with calcium-rich objects such as bones, eggshells, ash, mollusk shells and limestone.

In this study, I experimentally tested whether the growth rate of nestling Purple Martins (*Progne subis*) is calcium limited. Brood sizes were experimentally manipulated to contain either 4 or 5 nestlings. Nestlings in half of the nests of each brood size were force-fed a calcium supplement; the other half of the nestlings received a water placebo. I measured the growth rates of body mass, bones (wing and leg) and feathers (outer primary and outer rectrix) over the duration of the nesting period. I found no evidence that calcium-supplemented nestlings grew to a larger size or at a faster rate than control nestlings for any of the growth parameters measured in either brood size. I contend that in calcium-rich environments, parent martins are capable of providing sufficient calcium to maximize the growth of their nestlings. I suggest that the availability of calcium for egg production should serve as an assay to the number of nestlings that can be supported.

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DEDICATION

I dedicate this thesis to my family for their unconditional love and support.

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1. INTRODUCTION

1.1 Clutch size determination

Natural selection favours those individuals that make the greatest proportionate contribution to the future population. Genes that raise the reproductive capacity of their carriers afford a direct advantage; therefore, natural selection should have acted to maximize an individual's reproductive rate. However, reproductive output is also controlled by factors related to environment, physiology, morphology and competition. Thus, clutch and brood sizes represent an optimum which balances reproductive output and constraints in a manner that maximizes reproductive yield. Understanding the determinants of reproductive success is important for understanding life history constraints for an organism.

Lack (1947, 1948a, b) hypothesized that birds produce clutches of a size that maximize the number of offspring that can be raised. He also suggested that the most common brood size in a population should equal the most productive brood size (throughout this paper the term "clutch size" will refer to the number of eggs laid in a nest whereas the term "brood size" will refer to the number of nestlings in a nest). However, subsequent studies have shown clearly that in many instances the most common brood size is smaller than that which produces the most offspring (e.g. Perrins & Wynne-Edwards 1964; Boyce & Perrins 1987), suggesting that exogenous factors act to reduce reproductive success. Several interpretations have been put forth to explain the variation in avian clutch size (e.g. Cody 1966; Klomp 1970; Crossner 1977; Hogstedt 1980; Martin 1987; Martin 1993; Martin 1995) but the ultimate control of clutch size has yet to be attributed to any one factor or combination of factors.

Lack (1954) suggested that the timing of breeding should coincide with environmental conditions that confer the greatest chance of offspring survival, a consistent seasonal decline in avian reproductive success offers support for this hypothesis (e.g. Perrins 1970; Price *et al.* 1988; Daan *et al.* 1989; Cristol 1995; Ludvig *et al.* 1995; Verhulst *et al.* 1995). For example, Barba *et al.* (1995) found that Great Tits (*Parus major*) that delayed their clutch initiation by 10 days produced smaller clutches, which took longer to hatch, had lower fledging success, fledged at a smaller mass, and were less likely to recruit to the adult population the following year. Reasons postulated for seasonal variation in reproductive success include: earlier breeders are often older, more experienced birds (Saether 1990); the individual(s) are larger (Loman 1984); the individual(s) are involved in a longer-lasting pair-bond relationship (Coulson 1966); the individual(s) arrive earlier to the breeding grounds (Pinxten *et al.* 1990); they are territorial (Dhondt & Schillemans 1983); nest in a higher quality habitat (Goodburn 1991); and are better food gatherers (Newton & Marquiss 1984). However, these explanations fail to clarify the crux of the results, why do older birds, larger birds etc. have greater reproductive success?

1.2 Dependence of young on parents

When altricial birds hatch, they are completely dependent on their parents for many of the necessities of life, including thermoregulation, sanitation, protection from predators and food (O'Conner 1984). The increased effort necessary for parent birds to support larger broods is probably the most widely accepted hypothesis explaining clutch size regulation. Lack (1947) first proposed that the optimum clutch size in nidicolous (nest dwelling) birds

corresponds to the largest number of nestlings that parents can, on average, feed. The maximum parental provisioning rate is sufficient to support a particular, maximum brood size. Any increase in this maximum brood size without a proportional increase in provisioning rate will result in either a decrease in the amount of food given to each nestling, likely reducing the overall fitness of each nestling, or cause fatal starvation of some nestlings, resulting in "wasted" reproductive output by the female bird.

The most common method to assess of a bird's productive efficiency has been to manipulate natural brood sizes and record the proportion of successful fledges (e.g. Nur 1986; Gard & Bird 1992; Arnold 1993; Konarzewski 1993; Martins & Wright 1993; Pettifor 1993). Food supplements are also used in combination with brood manipulation, to determine if reproductive success is food-limited (e.g. Reyer & Westerterp 1985; Woods 1994; reviewed by Boutin 1990). In general, results support the food limitation hypothesis and demonstrate that parental provisioning rate increases with brood size (e.g. Morehouse & Brewer 1968; Best 1977; Bryant & Gardiner 1979) until broods are too large to be supported without supplemental food (e.g. Bedard & Meunier 1983; Hussell 1985). The reduced mass of nestlings in larger broods also provides evidence that parent birds are limited in their ability to supply food to their young beyond a certain point (Martin 1987).

1.3 Growth rates

Dependent on their parents, nestlings are vulnerable to mortality from exposure (e.g. Sullivan & Weathers 1992; With & Webb 1993), parasites (e.g. Moss & Camin 1970; Howe 1992; DeLope & Møller 1993; Richner & Heeb 1995), predators (e.g. Brown & Brown 1986;

Burger *et al.* 1994; Forbes *et al.* 1994) and starvation (e.g. Jones 1988; Henderson & Hart 1993). Nest predation rates in excess of 50% have been reported for a variety of nidicolous species (e.g. Colwell 1992) and translates to a 4% daily risk of mortality based on an average incubation and brooding period. Therefore, the less time a nestling spends in the nest, the greater its chance of survival (Lack 1968; Martin 1993; Martin 1995). Bosque & Bosque (1995) provide clear evidence that species which nest in areas relatively prone to predation (e.g. cup-nesters) have faster growth rates than similar-sized species nesting in areas relatively protected from predators (e.g. cavity nesters). Faster growth presumably requires a greater food demand per nestling and may limit the number of offspring that parents can rear. Martin (1995) has hypothesized that birds nesting in areas less susceptible to predators should produce large, slow-growing broods.

The young of aerial insectivorous birds grow more slowly than do the young of similar-sized species of perching insectivores (Ricklefs 1968, 1976). O'Conner (1978) suggested that these differences can be related to the reliability of the food sources during the nesting period. Inclement weather tends to reduce the abundance of airborne arthropods (Williams 1961), forcing nestling birds to withstand periods where little or no food is available. Therefore, nestlings of aerial insectivores may dedicate more energy towards building up fat reserves to survive periods of low food than to maximizing the growth rate of bones and muscle (O'Conner 1978). The tradeoff between allocated resources to growth or fat reserves may have implications on the risk of predation.

Nestling size at fledging may be an important factor affecting survival to adulthood (Garnett 1981; Perrins 1986). Altricial birds must attain $\approx 96\%$ of adult size before they are

capable of flight (Ricklefs 1979; Barclay 1994), which suggests that complete growth is a requirement for flight. Fully-calcified wing bones may be required to withstand the torque and stress forces generated during flight (Bilby & Widdowson 1979; O'Conner 1984; Carrier & Auriemma 1992; Barclay 1994). Adult size and musculature may also be required prior to flight, imposing further demands with respect to growth and growth rate (Barclay 1994). However, the necessity for large size is presumably confounded by the necessity for rapid growth, possibly limiting clutch size (Barclay 1994).

Within a nest, larger nestlings tend to out-compete siblings for access to food offered by parents (e.g. Mock & Lamey 1991). Parent birds are most likely to feed nestlings that greet them at the cavity entrance, stand the tallest, beg the loudest or have the widest gape (Henderson 1975; Smith & Montgomerie 1991; Price & Ydenberg 1995). Larger fledging size also confers an advantage on young birds, Perrins (1986) found that the body mass at which Great Tit nestlings fledged was highly correlated with their survival in subsequent years (also Garnett 1981). Especially in years with low overall nestling survival, larger fledglings have a greater survivorship rate (but see Newton & Moss 1986; Kersten & Brenninkmeijer 1995). Overall, research on clutch size determination suggests that parent birds should produce the maximum number of nestlings that they are capable of feeding at a rate that minimizes the risks of mortality associated with living in a nest.

However, the quality of the food items may be at least as important as the quantity of food (e.g. Botkin *et al.* 1973). Arguing that bone, and muscle size and strength necessary for flight, have calcium needs that far outweigh the need for other minerals or the need for energy, Barclay (1994) suggested that number of offspring that could be raised to

independence by flying vertebrates at any one time may be constrained by the ability of the parents to provide calcium to their offspring.

1.4 Effects of dietary calcium

The selection of which food(s) to consume, given a variety of choices, has been the subject of numerous theoretical and empirical studies (e.g. Schoener 1971; Pyke *et al.* 1977; Krebs 1978; Turner 1982; Stephen & Krebs 1986). Optimal foraging studies are based on the assumption that foraging animals strive to maximize the net intake of some currency (Stephens & Krebs 1986). Until recently, most studies examining the nutritional budgets of nestling passerines have been focussed on energy as caloric economies (O'Conner 1984; Ricklefs 1984; Clutton-Brock 1991). Energy is, however, only one aspect of nutritional requirements and may not be the most critical resource restricting growth rate, survival, clutch or brood size in altricial birds (Hungerford *et al.* 1993; Barclay 1994). For example, Turner (1982) calculated that Barn Swallows (*Hirundo rustica*) required four- to six-times more foraging time to meet their calcium requirements than to meet their energy needs, suggesting that calcium may be a limiting currency and one which should be incorporated into avian foraging models.

If calcium is a reproductive constraint, avian reproductive success should be lower in areas where calcium concentrations in the environment are low. Leopold (1931) first suggested that the amount of calcium in soil may influence the distribution of Ring-necked Pheasants (*Phasianus colchicus*) in North America. Since Leopold, several studies have linked the distribution and abundance of some Galliformes (e.g. pheasants and quail) to the

availability of calcium in the soil (McCann 1939, 1961 ; Dale 1954; Dale & DeWitt 1958; Sadler 1961; Greeley 1962). For example, Wilson (1959) found that Hungarian Partridge (*Perdix perdix*) breeding in New York were limited to areas where soils were of limestone origin while, Dale (1955) found that captive Ring-necked Pheasants failed to reproduce when fed granite grit but successfully reproduced when fed limestone grit. Chambers *et al.* (1966) also showed that female pheasants fed low levels of calcium produced eggs at a slower rate and showed signs of osteoporosis compared to females fed higher levels of calcium.

The importance of calcium for successful reproduction by altricial birds has been highlighted recently by anecdotal and experimental studies on the effects of acid rain (e.g. Ormerod & Tyler 1987; Graveland 1990; Blancher & McNicol 1991; Scheuhammer 1991; St. Louis & Breebaart 1991; Graveland *et al.* 1994; Graveland 1996). Calcium carbonate is the principal mineral in limestone rock and mollusk shells and dissolves readily in acidic solutions:

Areas affected by acid rain often contain reduced numbers of calcium-rich invertebrates and other sources of calcium including: bone, mollusk shells and limestone. Birds nesting in areas affected by acid rain have consistently shown reduced reproductive success (e.g. Nyholm & Myhrberg 1977; DesGranges & Rodrigue 1986; Glooschenko *et al.* 1986; Blancher & McNicol 1988; Drent & Woldendorp 1989; Ormerod *et al.* 1991; St. Louis & Barlow 1993). For example, Graveland *et al.* (1994) found that acidic soils in The Netherlands had

significantly fewer snail shells resulting in Great Tits laying a greater number of deformed eggs which were more likely to be abandoned. By supplementing parents with crushed chicken egg-shells at the nest, the effects of acidification on the breeding performance of tits was reversed. Graveland *et al.* (1994) also noted that tits nesting in acidic areas used the chicken egg-shell supplement more than tits nesting in areas with neutral soils. Similar results have been found with Tree Swallows (*Tachycineta bicolor*) nesting near acidic lakes in Ontario (St. Louis & Breebaart 1991).

Eurasian Dippers (*Cinclus cinclus*) were less abundant, foraged longer, laid eggs later in the season, had fewer eggs per clutch, thinner eggshells and slower nestling growth in areas near acidic streams compared to conspecifics nesting near circumneutral streams (Ormerod *et al.* 1988, 1991; O'Halloran *et al.* 1990). The results of these observations were attributed to reduced calcium in the diet due to an absence of calcium-rich arthropod prey such as *Gammarus* spp. Ormerod & Tyler (1993) also showed that dippers' most productive brood size was 4, regardless of the acidity of the habitat. Their second-most productive brood size was affected by stream acidity. Near acidic streams, 3 was the second-most productive brood size while near circumneutral streams, 5 was the second-most productive brood size.

Dietary calcium supplements have less effect on reproduction in areas not affected by acid rain. Johnson & Barclay (1996) supplemented House Wrens (*Troglodytes aedon*) with eggshells and found no difference in the number of eggs laid, number of young fledged or the growth rate of the young. However, they also suggest that even if birds did not face an absolute shortage of calcium within their environment, there may be significant costs in terms of time and energy spent or an increased risk of predation by foraging on the ground for

calcium-rich prey (Johnson & Barclay 1996).

1.5 Calcium demands

Birds may experience two periods of high calcium demand during their lifetime (Johnson & Barclay 1996). Females require a large amount of calcium to contribute to the formation of eggshells prior to egg laying and all nestlings require sufficient calcium to meet the high demands of skeletal growth (Robbins 1983; O'Conner 1984; Barclay 1994). However, many passerine species feed themselves and their young almost exclusively on insects, which are sufficient to meet daily caloric requirements but not sufficient to satisfy certain other nutrient needs (MacLean 1974; Krapu & Swanson 1975; Turner 1982; Studier *et al.* 1988; Allen 1989; Studier & Sevick 1992; Hungerford *et al.* 1993).

Several researchers have calculated that a diet of insects alone does not provide sufficient calcium for egg production or skeletal development in birds (e.g. MacLean 1974; Seastedt & MacLean 1977; Turner 1982; Barclay 1994; Graveland & Van Gijzen 1994). Studier & Sevick (1992) and Graveland & van Gijzen (1994) found that the calcium composition of insects in most orders is less than 0.3% dry mass. However, some terrestrial arthropods such as some larvae, spiders, millipedes and woodlice have calcified exoskeletons, making their calcium content as much as 100 times higher than other arthropods (Reichle *et al.* 1969; Graveland & van Gijzen 1994), but these wingless arthropods are largely unavailable to aerial insectivorous birds (e.g. swallows, Hirundinidae). The calcium content of fruit and pollen, other common avian food sources, are also about 0.3% of dry mass (Stanley & Linskens 1974; Herrera 1987). 0.3% calcium per dry mass is only 25 - 50% of

the estimated calcium concentration necessary for maximal growth rate among domestic chickens (Hughes & Wood-Gush 1971; National Research Council 1984).

One method of assessing relative demand for a particular nutrient is to calculate the concentration of that nutrient in the diet and compare it to the concentration of that nutrient in the feces (Hungerford *et al.* 1993). Fecal concentrations lower than a dietary concentrations suggests that the nutrient is being assimilated or that the animal may be stressed for that particular nutrient. Hungerford *et al.* (1993) tested the mineral budgets of nestling Eastern Bluebirds (*Sialia sialis*) and found that only calcium showed a positive assimilation rate. That is, the concentration of calcium in the prey items was higher than the concentration of calcium in the fecal sacs, suggesting that nestlings may be calcium stressed. Similar results were found for adult Common Poorwills (*Phalaenoptilus nuttallii*) feeding on insects in Saskatchewan (R. Brody unpubl. data).

1.6 Estimated calcium requirements

Calcium assimilation estimates are known mainly for domestic fowl and range from 50 - 70% (Hurwitz & Griminger 1961; Taylor 1962; Sturkie 1965; Graveland & van Gijzen 1994). There do not appear to be substantial differences in digestive efficiency of adult and nestling birds (Graveland & van Gijzen 1994). Therefore, assuming that passerine birds assimilate calcium at a rate similar to domestic fowl, the amount of food that must be consumed to meet the calcium requirements for growth and eggshell formation can be calculated. For example, MacLean (1974) estimated the calcium budget of four species of arctic sandpipers (*Calidris* spp.) and found that the calcium content of adults was 2.2 - 3.8%

of fat-free dry mass (avg. ≈ 0.42 g per bird), but that for an average clutch of four eggs a total of 0.8 g calcium was required. Therefore, twice as much calcium is contained in a full clutch of eggs than is contained in the entire female bird. Dipteran larvae, which constitute the main prey of adult sandpipers, contain about 0.35% calcium per dry mass, the average prey intake is 14.5 g per adult per day, therefore, assuming calcium assimilation rate of 60% (Hurwitz & Griminger 1961; Taylor 1962; Sturkie 1965; Graveland & van Gijzen 1994), adult sandpipers could gain 0.03 g of calcium per day. Even if assimilation was 100%, female sandpipers are able to attain only 25% of the necessary calcium for egg laying from dipteran larvae (MacLean 1974). Similarly, the main prey source of nestling sandpipers is adult dipterans that contain about 0.08% calcium. Before fledging (3 - 4 weeks), nestling sandpipers consume an average of 184.5 g dry mass, containing a total of 0.15 g of calcium. At an assimilation rate of 60%, nestling sandpipers can gain 0.09 g of calcium from insect prey, which represents only 21% of the calcium necessary for growth to adult size (MacLean 1974).

Van Balen (1973) and Graveland & van Gijzen (1994) examined the calcium economy of Great Tits. Birds' calcium content varied from 2.09% of dry mass at hatching (about 0.004 g) to 1.79% of dry mass (0.083 g) at day-14 and 3.22% calcium (0.196 g) in adults. Nestlings require 1.3 g dry mass of insects per day (18.2 g over 14 day nesting period) to cover energy demands, but receive a diet having an estimated calcium content of 0.3% and based on a 60% assimilation rate, therefore nestlings are only receiving about 0.03 g, or 1/3 of their calcium needs through their insect prey. Graveland *et al.* (1994) estimated that Great Tits only receive about 20% of their calcium requirements from arthropod prey. Several

other studies have shown that the average calcium concentration of insects is insufficient to meet the calcium requirements of growth in hatchling birds or eggshell formation in female birds (e.g. Meadow Pipits (*Anthus pratensis*), Skar *et al.* 1975; Lapland Longspur (*Calcarius lapponicus*) Seastedt & MacLean 1977; Rooks (*Corvus frugilegus*) Pinowski *et al.* 1983). So where and how do adult birds secure enough calcium to meet their own needs and the needs of their dependent offspring?

1.7 Calcium sources

The skeleton contains about 98% of the calcium in the avian body (Simkiss 1967). In most birds, females resorb some calcium from their medullary bone to meet the calcium requirements of shell formation during egg laying (Simkiss 1961; 1975). Medullary bone is a labile type of bone from which calcium can be mobilized much faster than from other bone types (Simkiss 1967). By converting calcium from structural bones, birds can maintain the amount of calcium in the medullary bone, even in the presence of a calcium deficient diet (Ankney & Scott 1980; Etches 1987). This provides female birds with a readily available source of calcium for egg laying. However, the skeleton can only provide a small fraction of the necessary calcium. The amount of calcium contained within a full clutch of eggs often exceeds the total calcium content in the female bird (Jones 1976; Perrins 1979; Turner 1982; Ormerod *et al.* 1988; Graveland & van Gijzen 1994; Krementz & Ankney 1995; but see Schifferli 1979; Houston *et al.* 1995). Piersma *et al.* (1996) claim that female Red Knots (*Calidris canutus*) currently hold the avian record with respect to skeletal calcium dynamics, suggesting a 50% change in skeletal mass during the egg laying period. This still would only

be enough calcium to produce half of the average clutch size for this species. Therefore, external sources of calcium are probably essential during the egg laying period for all birds. And, clearly, the female skeleton is not useful as a calcium source for growing nestlings; therefore, all calcium for growing young must also come from external sources.

To obtain extra calcium, birds will often supplement their diet and the food provided to their young with inanimate objects rich in calcium (e.g. Payne 1972; MacLean 1974; Brown 1976; Jones 1976; Seastedt & MacLean 1977; Schifferli 1979; Beasom & Pattee 1978; Ankney & Scott 1980; Barrentine 1980; Mayoh & Zach 1986; Ficken 1989; Repasky *et al.* 1991; St. Louis & Breebaart 1991; Graveland *et al.* 1994). Ingested objects have included: calcium-rich ash, bone, teeth, mollusk shells, eggshells and limestone. Calcium-rich objects offer considerably more calcium than a strict diet of insects which usually contain only 0.3% calcium per dry mass. The bones and scales of sucker (*Catostomus commersoni*), consumed by Tree Swallows (St. Louis & Breebaart 1991) contain 23% and 11.7% calcium respectively (Lockhart & Lutz 1977; Fraser & Harvey 1982). Crayfish exoskeletons contain 21% calcium (France 1987), fresh water clam shells 45% (Huebner *et al.* 1990) and chicken egg shells contain 40% calcium (Romanoff & Romanoff 1963). Wood ash is rich in calcium; CaO often comprises 50 - 75% of total wood ash.

Anecdotal evidence suggests that birds select these objects when their calcium demands are greatest. Egg-laying females consume more calcium-rich items than non-laying birds (e.g. MacLean 1974; Jones 1976) and nestlings ingest more calcium-rich items at a time of maximum skeletal growth (e.g. Bilby & Widdowson 1979). For example, MacLean (1974) found that arctic sandpipers (*Calidris* spp.) used grit, teeth and the vertebrae of Brown

Lemmings (*Lemmus trimucronatus*) as a calcium source during the period of egg laying and juvenile growth. These calcium-rich items were gathered from dead lemmings and the pellets of raptors that usually abound with the bones of small mammals. Similar behaviour has been observed in other species, including Red Crossbills, *Loxia curvirostris*, (Payne 1972) and Red-cockaded Woodpeckers, *Picoides borealis*, Repasky *et al.* 1991). During the period of egg laying, 38% (32 of 84) of female sandpipers included lemming bones in their diet compared to only 2% (3 of 162) males. After egg laying and during the period of nestling growth, only 1 of 168 adult sandpipers consumed bones and 12% (16 of 131) of young juveniles consumed lemming bones. Consumption of lemming bones by juvenile sandpipers decreased as the nestlings grew older, and neared adult size.

Mayoh & Zach (1986) found that about a third of all Tree Swallow and House Wren (*Troglodytes aedon*) nestlings had grit or mollusk shells in their stomach. No nestlings under 3 days of age had these calcium-rich objects but over 80% of older nestlings had these objects. The percent of nestlings with grit in their stomachs increased from day-3 until about day-9, then stayed constant at about 80% until a decrease just before fledging. Barrentine (1980) found that 80% of Barn Swallow nestlings had grit in their stomach and Hagvar & Ostbye (1976) found 94% of Meadow Pipit nestlings had calcium-rich items in their stomachs.

Female hummingbirds of several species consume calcium-rich ash during nesting (DesLauriers 1994). Also, female hummingbirds have also been observed selecting sugar solutions from feeders that were supplemented with a vitamin mix, rich in calcium (Carroll & Moore 1993). Similarly, Red-cockaded Woodpeckers have been observed seeking and

caching bones from raptor pellets (Repasky *et al.* 1991). This is the only record of a bird caching material for which the primary value is mineral rather than caloric.

In summary, almost all bird species appear to ingest calcium-rich items during the egg-laying and nestling period (Graveland & van Gijzen 1994). These studies suggest that female and nestling birds utilize calcium-rich objects to supplement their diet.

1.8 Estimated calcium deficiency

By using the estimated percentages of water mass, calcium concentrations and assimilation rates published for other avian species (van Balen 1973; MacLean 1974; Skar *et al.* 1975; Seastedt & MacLean 1977; Pinowski *et al.* 1983; Graveland & van Gijzen 1994; Graveland *et al.* 1994), I estimated the calcium demand for Purple Martin nestling growth to be far greater than the demand for energy.

Martins weigh approximately 2.5 g upon hatching, of which approximately 82% is water, resulting in a dry mass of 0.45 g. Based on 1% calcium concentration, hatchling martins contain an estimated 0.0045 g of calcium. Adult martins weigh approximately 55 g, approximately 71% of which is water, resulting in a dry mass of 16 g. Based on a 3 % calcium concentration in the adult body, adult martins contain an estimated 0.48 g of calcium. Therefore, over the nesting period martins must gain 15.55 g of dry mass. Assuming that purple martins assimilate energy at the same rate as other birds (70%), they must consume 22.2 g of dry mass in insects to meet their caloric needs. Over that same period, nestlings must gain 0.4755 g of calcium. Assuming that their prey (aerial insects) consists of 0.3% calcium and they can assimilate 60% of that calcium, nestlings would need to consume 264 g

to consume 264 g of dry mass (over 1 kg fresh mass!) to meet their calcium needs. This is approximately 12 times more food than is necessary to meet their caloric needs alone.

Purple Martins most commonly have 5 nestlings, if the estimates are correct, parent birds would have to bring over 50 g of dry mass (200 g of fresh mass) of insect prey to the nest every day for the 26 days of the nesting period to meet calcium needs, if insects are the only source of calcium. The mean wet mass of insect prey brought to the nest on each parental visit is approximately 0.35 g (approx. 0.0875 g dry mass, Walsh 1978). If parents fed nestlings continually for 14 hours per day for the duration of the nesting period, parents would have to make at least 40 nest visits every hour, to meet the calcium needs of their young. In reality, Purple Martins average only about 2 feeding visits per nestling per hour (Walsh 1978). How then, are Purple Martins able to successfully provide sufficient calcium to raise broods of 5 nestlings? And, does the amount of calcium provided to nestlings ultimately limit their growth rate?

1.9 Purpose and Hypotheses

Although the reproductive success of birds has been linked to calcium availability, no study has directly determined whether calcium constrains the growth rate and the fledging success of nestling passerine birds. The purpose of this study was to experimentally test the effects of calcium supplementation on the growth rate of nestling Purple Martins (*Progne subis*). Purple Martins are aerial insectivorous birds, meaning their diet is solely comprised of flying insects. Like other members of the swallow family, Purple Martins spend very little time on the ground and this may preclude them from, or at least reduce their access to,

calcium-rich objects. When combined with a calcium-poor diet (aerial insects), inaccessability of calcium may result in reduced the growth rates of nestlings and may ultimately limit their clutch size.

I tested this theory by supplementing calcium directly to nestling martins and monitoring the growth rate of bones and feathers. To date, most studies have used mass to assess the maturity or fitness level of *nestlings*. However, mass may not the main factor determining a nestlings ability to fly and/or leave the nest. I assumed that feather and bone lengths were more appropriate measures of nestling maturity. I also assumed that faster growth rates of feathers and bones would bring nestlings to adult size more rapidly, allowing them to leave the nest earlier, and that any reduction in the time spent in the nest confers a greater chance of survival.

I tested the following hypotheses:

- 1) Bones and feathers of nestlings given a calcium supplement will grow faster than bones and feathers of nestlings not given a supplement.
- 2) Bones and feathers of nestling birds given a calcium supplement will grow larger than bones and feathers of nestlings not given a supplement.
- 3) Growth rates of nestlings in nests with smaller broods will grow faster and larger than nestlings in larger broods.
- 4) Calcium supplements will benefit nestlings in larger broods more than nestlings in smaller broods.
- 5) Calcium-supplemented nestlings will fledge faster than non-supplemented nestlings.
- 6) Broods with calcium-supplemented nestlings will fledge a greater proportion of nestlings.

2. METHODS

2.1 Study species

The Purple Martin is a 50 g (Dunning 1993) insectivorous bird whose breeding range covers much of North America (Fig 1). Martins previously nested in natural or woodpecker-excavated tree cavities but for the last century have bred almost exclusively in artificial nest-houses (Allen & Nice 1952). The use of natural cavities is now limited to montane regions of southwestern North America (Stutchbury 1991a). Martins are colonial birds; several dozen pairs often nest within a single nest-house or group of nest-houses (e.g. Morton & Derrickson 1990; Stutchbury 1991a, b; Wagner *et al.* 1996). This makes them very amenable to study, providing large sample sizes and reduced searching time for researchers. Colonial living provides protection from predators (Stutchbury 1991a) but may increase susceptibility to parasites (Moss & Camin 1970; Poulin 1991; Davidar & Morton 1993).

Throughout their breeding range, Purple Martins are among the first species of insectivorous birds to return in spring and the first to leave again in autumn. After spending the winter months in Brazil and other parts of central South America east of the Andes, adults appear in southern Florida as early as mid-January. They progress ca. 3-5 degrees latitude each half month until the beginning of May when they reach their northern breeding limits in central Saskatchewan and Alberta. Mature (>1 yr old) adult males usually arrive a few days before mature females and all adults arrive within several weeks thereafter (Morton & Derrickson 1990). Nest building and breeding usually begins a month after arrival at the breeding grounds (Allen & Nice 1952). Nests are constructed from loose leaves and twigs, often held together with mud. A clutch size of 5 eggs is most common (54% of nests),

Figure 1. Geographic distribution of Purple Martins during the breeding season (Brown 1997).

followed by 4 eggs (25%) and 6 eggs (19%) respectively. Clutches have been recorded to range from 3 to 7 (Allen & Nice 1952); thus, this is a species with considerable clutch size variation and one for which the calcium limitation hypothesis is likely to be relevant. Adults tend to lay 5 eggs and subadults (1 year old) tend to lay 4 eggs (Johnston 1964; Lee 1967; Finlay 1971; Brown 1978a). After 15-19 days of incubation, eggs hatch in the order in which they were laid. Hatchlings weigh 2-3 g and are completely dependent on parents for thermoregulation, protection and feeding. Fledging and independence usually occurs after 28 days in the nest (Moss & Camin 1970).

Purple Martins are sexually dimorphic. Mature males have deep blue and black plumage over their entire body, whereas females and immatures have deep blue and black plumage dorsally and white plumage ventrally (Niles 1972). Immature (< 2 years old) male martins are nearly indistinguishable from adult females based on plumage colour (Niles 1972). Males grow adult plumage beginning at one year of age (Stutchbury 1991b). I attempted to use only the nests of adult martins in this study.

Purple Martins forage for aerial insects over open habitats, including over water and areas in urban and rural environments (AOU Checklist 1983; Brown 1997). Insects including dragonflies (Odonata), flying ants (Hymenoptera), butterflies (Lepidoptera) and flies (Diptera) are the most common prey items consumed by adults and fed to nestlings (Walsh 1978). The activity/feeding rate of martins has been shown to be adversely affected by inclement weather (Finlay 1976). Martins spend the majority of their time roosting at their nest or pursuing aerial insects; they spend very little, if any, time on the ground.

2.2 Study site

This study was conducted at the University of Oklahoma Biological Station, Marshall County, Oklahoma (33°58'N, 96°45'W). The station borders Lake Texoma, a human-made reservoir, and is surrounded by agricultural land, short-grass prairie and deciduous forest. A colony of 40-50 pairs of martins has bred in nest-houses at this location since at least 1980. The aluminum nest-houses erected at the station consist of two tiers, with six cavities per tier, for a total of 12 cavities in each nest-house. The six houses are arranged in three pairs about 80 m apart, with houses about 20 m apart within a pair. Houses are mounted 5 m high on the top of metal poles that could be easily lowered and raised. The opening to each nest-apartment is situated on a hinged door, providing easy access to the Purple Martin nests.

2.3 Procedures

To examine the effects of supplemental calcium on growth rate and reproductive success, I performed a brood manipulation/calcium supplementation experiment on Purple Martins.

Each nest was visited daily during the nest building period (April). Individual nest initiation dates were determined by the date at which the first egg appeared in a nest. To control for any seasonal effects on reproductive success, the first nest to contain eggs was assigned the calcium treatment. The second nest with eggs was assigned the control treatment, the third nest initiated was assigned the calcium treatment, and so forth (Johnson & Barclay 1996). Replacement and second clutches were not included in this experiment. I recorded the contents of all active nests at least every other day during the egg-laying and

incubation stages. I checked all nests daily late in the incubation stage to determine the hatch date for each egg.

All nestlings from a nest receiving the calcium treatment were force-fed a calcium supplement every other day from day-3 to day-21 of the nesting period, this corresponds to the time of maximum growth for most nestling birds (Mayoh & Zach 1986). Nestlings were fed a 1 mL dose of Liquid Calcium[®], administered with a pipette. Young nestlings, blind and instinctively gaping upon a touch of their beak, readily accepted the supplement. Older nestlings required a bit more patience and effort but eventually accepted their vitamins. Liquid Calcium[®] contains 20 mg (1 mEq)/mL elemental calcium from a mixture of calcium glucoheptonate (132 mg/mL) and calcium gluconate (112 mg/mL). This is an organic form of calcium sold as a human vitamin supplement, presumably digestible by mammals; I assumed that this form of calcium is also digestible by birds. Each nestling received at least 200 mg (about half of the calcium in the adult body) of supplemental calcium over the duration of the nesting period. All nestlings from control nests were force-fed 1 mL of water every other day from day-3 to day-21. There were no apparent differences in the willingness of nestlings to accept the calcium or the water.

To examine the interactions between calcium supplements and brood size, I manipulated the number of hatchlings so that all nests contained either 4 or 5 young. All relocated nestlings were 1 or 2 days old at the time of transplanting and were transplanted to broods of similar age. Brown (1978b; 1979) showed that Purple Martins are unable to distinguish their own young from others of the same age. Consistent with this, I observed no apparent discrimination by parent birds for or against adopted chicks.

After hatching, nestlings were individually marked by painting unique toe nail combinations with non-toxic black marker, allowing me to monitor individual nestlings over the nestling period. All measurements were taken between 0700h and 1200h to minimize time of day effects. Nestlings were measured every other day beginning on day-1 and concluding when a nestling was capable of flight (approximately day-25). Measurements included: body mass, bone length and feather length. Bone and feather lengths were measured with digital calipers (± 0.01 mm) and nestlings were weighed with an electronic balance (± 0.1 g). To reduce error, each bone and feather was measured three times and the average used as that day's measurement.

The bones measured included the series of bones that make up the carpometacarpus (hand), the ulna/radius (arm) and the tarsometatarsus (leg) (Fig 2). The outer primary and the outer rectrix feathers were also measured. The bones and feathers were always measured from the right side of the nestling's body.

2.4 Statistics

The data on which my statistic analyses are based represent repeated measurements, over the course of many days, from the same individual chicks. To overcome the difficulties of non-independence of such measurements, I calculated test statistics on means for individual nests. I compared the following measures of growth among calcium and control pairs: (i) maximum size, (ii) age adult size was attained and (iii) growth rate for mass, hand, arm and leg bones and primary and rectrix feathers.

Maximum size is simply the length of bone or feather at which the nestling did not grow any further. The age adult size was reached is the age that a nestling reached maximum

Figure 2. Schematic diagram of bones measured.

size. Growth rate was calculated from the plateau point on a growth curve - a combination of the maximum size and the number of days to reach that size (Fig 3).

To determine when nestlings were capable of flight, older nestlings were set on my finger as I dropped my hand quickly. A nestling was considered to be capable of flight if it could gain altitude and fly farther than a few meters. The shortest feather lengths recorded for a nestling capable of flight were used as the standard for minimum feather size necessary for fledging.

To determine the effects of calcium supplementation, I compared calcium and control treatments by brood size and initiation date using one-tailed t-tests or one-tailed analysis of variance. All means are presented ± 1 SE. Due to the number of statistical tests performed, all hypothesis were rejected at $p < 0.01$ (see Rice 1989). Power analysis was calculated for all hypotheses that failed to be rejected (Zar 1996).

Figure 3. Theoretical growth curve, demonstrating the different parameters used to assess growth in this study (maximum size, age to reach maximum size, growth rate).

3. RESULTS

In total, measurements were made at 29 nests (137 nestlings) for this experiment. Due to mortality, natural clutch size variation and variation of initiation dates, equal numbers of nests in the two treatments were not possible. In total, data for 15 calcium treatment nests, 12 with brood size 5 and 3 with brood size 4 (72 nestlings) were compared to 14 control nests, 9 with brood size 5 and 5 with brood size 4 (65 nestlings; Fig 4).

May 3 was the earliest date that any martins at my study site laid eggs. However, only nests initiated between May 4 and May 16 were included in the study. Nests initiated before May 4 and later than May 16 were excluded to minimize seasonal effects (as noted in the Introduction). In total, 45 of the 72 apartments contained Purple Martin eggs at some time before May 26. Initiation dates were normally distributed for nests included in this time period (Fig 5). Mean clutch size between May 3 and May 25 was $5.05 (\pm 0.12)$ eggs; however, there was a significant linear ($p < 0.001$, $r^2 = 0.514$) decline in clutch size with season (Fig 6).

The growth rates for all parameters of all nestlings are presented in Figure 7. The tarsus was the first bone to reach maximum length (day-14), followed by the hand bones (day-16) and the arm bones (day-16). Primary and rectrix feathers emerged on day-8. Although not fledged, nestling birds were capable of extended flight when the outer primary feather was 60 mm in length and the outer rectrix was approximately 40 mm in length. Based on feather length, nestling birds were capable of flight by day-23, although fledging rarely occurred before day-26.

Figure 4. Distribution of treatments among the 6 nest-houses, treatments (Calcium or Water), initiation date (Early, Mid, Late) and brood size (4 or 5).

Figure 5. Number of nests initiated on each date between May 3 and May 25 ($n = 45$). Only nests with 4 or 5 nestlings, initiated between May 4 and May 16, (excluding those suffering mortality) were included in this study ($n = 29$).

Figure 6. Relationship between initiation date and mean (SE) clutch size ($n=42$, $p < 0.001$, $r^2 = 0.514$). Clutch size was not determined for the 3 nests initiated on May 25; therefore, they are not included in this graph.

Figure 7. Mean (SE) growth curves for all Purple Martins nestlings (n = 137).

Growth rates for calcium-supplemented and control nestlings are presented in Figure 8. There were no significant differences in the growth rates of bones or feathers that could be attributed to the calcium treatment (Table 1). Although the power (the probability of finding that the existing difference between means is significant at the 0.05 level, given the available sample sizes and variability) to detect a significant difference was consistently low, there was no indication of even a trend suggesting calcium increased the growth rate or maximum size of any measured parameter (Table 1).

Nest-house had no significant effect (Table 2) on any of the growth rate parameters measured (Fig 9). There were also no significant effects of brood size (Fig 10) or initiation date (Fig 11) on growth rates. There was a trend for nestlings from nests with a 4 chicks to grow larger than nestlings from nests with 5 chicks (Table 3). There was also a trend for nestlings from early initiated nests to grow larger and at a faster rate than nestlings from nests initiated later in the season (Table 4). Lastly, there were no significant interaction effects between calcium treatment, brood size, initiation date or nest-house ($p > 0.01$ for all interactions) for any growth parameters.

The difference between the number of eggs parents laid and the number of nestlings they supported (the adoption effect) did not have a significant effect on growth rate or maximum size for any of the parameters measured ($p > 0.01$ for all comparisons).

Figure 8. Mean growth curves for all nestlings, comparing calcium (.....) (n = 72) and control (—) (n = 65) treatments.

Table 1. Measures of growth (body mass, hand, arm and leg bone length and primary(1°) and rectrix(tail) feather length), comparing calcium (n = 15) and water (n = 14) treatments. n/a = comparison of means does not favour the calcium treatment. therefore power test was not applicable.

Mean (± 1 SE) age at which maximum size is attained.

	Control	Calcium	Statistic	P	Power
Mass (g)	12.4 $\pm$ 0.3	12.8 $\pm$ 0.2	t = -0.987	0.334	n/a
Hand (mm)	13.8 $\pm$ 0.2	13.5 $\pm$ 0.3	t = 0.995	0.329	0.180
Arm (mm)	13.7 $\pm$ 0.2	13.3 $\pm$ 0.2	t = 1.723	0.097	0.395
Leg (mm)	9.9 $\pm$ 0.2	10.0 $\pm$ 0.1	t = -0.573	0.572	n/a
1° (mm)	22.7 $\pm$ 0.2	22.7 $\pm$ 0.1	t = -0.218	0.829	n/a
Tail (mm)	22.8 $\pm$ 0.2	22.9 $\pm$ 0.2	t = -0.417	0.663	n/a

Mean (± 1 SE) maximum size.

	Control	Calcium	Statistic	P	Power
Mass (g)	54.6 $\pm$ 1.2	53.9 $\pm$ 0.9	t = 0.434	0.668	n/a
Hand (mm)	29.4 $\pm$ 0.2	29.0 $\pm$ 0.4	t = 0.772	0.449	n/a
Arm (mm)	33.4 $\pm$ 0.2	33.4 $\pm$ 0.1	t = -0.006	0.995	0.050
Leg (mm)	15.9 $\pm$ 0.1	15.9 $\pm$ 0.1	t = 0.481	0.635	n/a

Mean (± 1 SE) growth rate, calculated as maximum size/number of days to reach maximum size.

	Control	Calcium	Statistic	P	Power
Mass (g)	4.4 $\pm$ 0.1	4.2 $\pm$ 0.1	t = 1.524	0.146	n/a
Hand (mm)	2.1 $\pm$ 0.1	2.2 $\pm$ 0.1	t = -0.482	0.634	0.092
Arm (mm)	2.4 $\pm$ 0.1	2.5 $\pm$ 0.1	t = -1.533	0.137	0.328
Leg (mm)	1.6 $\pm$ 0.1	1.6 $\pm$ 0.1	t = 0.754	0.459	n/a
1° (mm)	2.6 $\pm$ 0.1	2.6 $\pm$ 0.1	t = 0.254	0.802	n/a
Tail (mm)	1.8 $\pm$ 0.1	1.8 $\pm$ 0.1	t = 0.441	0.663	n/a

Table 2. Measures of growth (body mass, hand, arm and leg bone length and primary(1°) and rectrix(tail) feather length). comparing nest-boxes (sample size in parentheses). ANOVA. $p > 0.01$ for all tests.

Mean (± 1 SE) age at which maximum size is attained.

	Mass g	Hand mm	Arm mm	Leg mm	1° mm	Tail mm
Box A(3)	11.8 $\pm$ 0.2	14.1 $\pm$ 0.7	13.5 $\pm$ 0.2	9.5 $\pm$ 0.4	21.9 $\pm$ 0.2	22.1 $\pm$ 0.1
Box B(8)	13.5 $\pm$ 0.4	13.0 $\pm$ 0.4	13.7 $\pm$ 0.3	10.1 $\pm$ 0.2	22.6 $\pm$ 0.2	23.1 $\pm$ 0.3
Box C(1)	12.4	13.8	13.6	10.0	23.0	23.0
Box D(6)	12.2 $\pm$ 0.3	13.9 $\pm$ 0.2	13.4 $\pm$ 0.2	9.8 $\pm$ 0.1	22.8 $\pm$ 0.3	23.1 $\pm$ 0.3
Box E(5)	11.9 $\pm$ 0.3	13.7 $\pm$ 0.4	13.3 $\pm$ 0.2	10.1 $\pm$ 0.2	22.7 $\pm$ 0.3	23.1 $\pm$ 0.3
Box F(6)	12.7 $\pm$ 0.3	13.7 $\pm$ 0.2	13.6 $\pm$ 0.4	10.1 $\pm$ 0.1	23.1 $\pm$ 0.2	23.1 $\pm$ 0.1

Mean (± 1 SE) maximum size.

	Mass g	Hand mm	Arm mm	Leg mm
Box A(3)	57.9 $\pm$ 0.9	29.3 $\pm$ 0.4	33.9 $\pm$ 0.4	16.2 $\pm$ 0.3
Box B(8)	55.8 $\pm$ 0.9	29.0 $\pm$ 0.8	33.8 $\pm$ 0.1	15.9 $\pm$ 0.1
Box C(1)	53.2	29.6	33.2	16.3
Box D(6)	51.0 $\pm$ 2.1	28.9 $\pm$ 0.3	32.9 $\pm$ 0.3	15.7 $\pm$ 0.1
Box E(5)	53.1 $\pm$ 2.2	29.4 $\pm$ 0.2	33.4 $\pm$ 0.2	15.8 $\pm$ 0.1
Box F(6)	54.6 $\pm$ 1.4	29.5 $\pm$ 0.2	33.3 $\pm$ 0.2	16.0 $\pm$ 0.1

Mean (± 1 SE) growth rate, calculated as maximum size/number of days to reach maximum size.

	Mass g	Hand mm	Arm mm	Leg mm	1° mm	Tail mm
Box A(3)	4.9 $\pm$ 0.1	2.1 $\pm$ 0.1	2.5 $\pm$ 0.1	1.7 $\pm$ 0.1	2.7 $\pm$ 0.1	1.8 $\pm$ 0.1
Box B(8)	4.2 $\pm$ 0.1	2.2 $\pm$ 0.1	2.5 $\pm$ 0.1	1.6 $\pm$ 0.1	2.7 $\pm$ 0.1	1.8 $\pm$ 0.1
Box C(1)	4.3	2.1	2.4	1.6	2.6	1.7
Box D(6)	4.2 $\pm$ 0.1	2.1 $\pm$ 0.1	2.5 $\pm$ 0.1	1.6 $\pm$ 0.1	2.6 $\pm$ 0.1	1.7 $\pm$ 0.1
Box E(5)	4.4 $\pm$ 0.1	2.2 $\pm$ 0.1	2.5 $\pm$ 0.1	1.6 $\pm$ 0.1	2.6 $\pm$ 0.1	1.8 $\pm$ 0.1
Box F(6)	4.3 $\pm$ 0.1	2.2 $\pm$ 0.1	2.5 $\pm$ 0.1	1.6 $\pm$ 0.1	2.6 $\pm$ 0.1	1.7 $\pm$ 0.1

Figure 9. Mean growth curves for all nestlings, comparing all 6 nest houses.

Figure 10. Mean growth curves for all nestlings, comparing brood size 4 (—) (n = 32) and brood size 5 (---) (n = 105).

Figure 11. Mean growth curves for all nestlings, comparing early (—) (n = 66) and late (---) (n = 43) nesting birds.

Table 3. Measures of growth (body mass, hand, arm and leg bone length and primary(1°) and rectrix(tail) feather length), comparing nests with 4 nestlings (n=8) and nests with 5 nestlings (n=21). n/a = comparison of means does not favour brood size 4, therefore power test was not applicable.

Mean ($\pm$ 1 SE) age at which maximum size is attained.

	Brood 4	Brood 5	Statistic	P	Power
Mass (g)	12.5 $\pm$ 0.5	12.6 $\pm$ 0.2	t = 0.318	0.758	0.068
Hand (mm)	13.8 $\pm$ 0.3	13.5 $\pm$ 0.2	t = -0.994	0.335	n/a
Arm (mm)	13.4 $\pm$ 0.3	13.5 $\pm$ 0.1	t = 0.336	0.743	0.064
Leg (mm)	10.0 $\pm$ 0.2	10.0 $\pm$ 0.1	t = 0.108	0.915	n/a
1° (mm)	22.7 $\pm$ 0.2	22.7 $\pm$ 0.1	t = 0.348	0.733	n/a
Tail (mm)	22.8 $\pm$ 0.2	22.9 $\pm$ 0.2	t = 0.249	0.806	0.056

Mean ($\pm$ 1 SE) maximum size.

	Brood 4	Brood 5	Statistic	P	Power
Mass (g)	55.2 $\pm$ 1.5	53.8 $\pm$ 0.9	t = -0.773	0.455	0.119
Hand (mm)	29.5 $\pm$ 0.2	29.1 $\pm$ 0.3	t = -1.281	0.211	0.210
Arm (mm)	33.5 $\pm$ 0.2	33.4 $\pm$ 0.1	t = -0.379	0.710	0.066
Leg (mm)	16.0 $\pm$ 0.1	15.9 $\pm$ 0.1	t = -1.409	0.173	0.231

Mean ($\pm$ 1 SE) growth rate, calculated as maximum size/number of days to reach maximum size.

	Brood 4	Brood 5	Statistic	P	Power
Mass (g)	4.5 $\pm$ 0.2	4.3 $\pm$ 0.1	t = -1.161	0.273	0.243
Hand (mm)	2.1 $\pm$ 0.1	2.2 $\pm$ 0.1	t = 0.322	0.753	n/a
Arm (mm)	2.5 $\pm$ 0.1	2.5 $\pm$ 0.1	t = -0.460	0.653	n/a
Leg (mm)	1.6 $\pm$ 0.1	1.6 $\pm$ 0.1	t = -0.484	0.638	n/a
1° (mm)	2.7 $\pm$ 0.1	2.6 $\pm$ 0.1	t = -0.317	0.755	0.060
Tail (mm)	1.8 $\pm$ 0.1	1.8 $\pm$ 0.1	t = -0.218	0.830	n/a

Table 4. Measures of growth (body mass, hand, arm and leg bone length and primary(1°) and rectrix(tail) feather length). comparing early (n = 14) and late (n = 10) nesters. n/a = comparison of means does not favour the early nesters. therefore power test was not applicable.

Mean ($\pm$ 1 SE) age at which maximum size is attained.

	Early	Late	Statistic	P	Power
Mass (g)	13.1 $\pm$ 0.3	12.1 $\pm$ 0.3	t = 2.572	0.018	n/a
Hand (mm)	13.6 $\pm$ 0.2	13.9 $\pm$ 0.2	t = -1.245	0.226	0.230
Arm (mm)	13.6 $\pm$ 0.2	13.5 $\pm$ 0.1	t = 0.250	0.805	n/a
Leg (mm)	10.0 $\pm$ 0.1	9.8 $\pm$ 0.1	t = 1.144	0.164	n/a
1° (mm)	22.5 $\pm$ 0.2	22.9 $\pm$ 0.2	t = -1.420	0.170	0.287
Tail (mm)	22.6 $\pm$ 0.1	23.0 $\pm$ 0.2	t = -1.619	0.125	0.372

Mean ($\pm$ 1 SE) maximum size.

	Early	Late	Statistic	P	Power
Mass (g)	57.0 $\pm$ 0.5	50.9 $\pm$ 1.5	t = 3.944	0.002*	0.994
Hand (mm)	29.7 $\pm$ 0.1	28.9 $\pm$ 0.2	t = 3.149	0.006*	0.877
Arm (mm)	33.7 $\pm$ 0.1	33.1 $\pm$ 0.2	t = 2.586	0.020	0.738
Leg (mm)	15.9 $\pm$ 0.1	15.9 $\pm$ 0.1	t = 0.078	0.939	n/a

Mean ($\pm$ 1 SE) growth rate, calculated as maximum size/number of days to reach maximum size.

	Early	Late	Statistic	P	Power
Mass (g)	4.4 $\pm$ 0.1	4.2 $\pm$ 0.1	t = 1.143	0.266	0.197
Hand (mm)	2.2 $\pm$ 0.1	2.1 $\pm$ 0.1	t = 2.161	0.042	0.529
Arm (mm)	2.5 $\pm$ 0.1	2.4 $\pm$ 0.1	t = 0.713	0.483	0.105
Leg (mm)	1.6 $\pm$ 0.1	1.6 $\pm$ 0.1	t = -1.015	0.322	n/a
1° (mm)	2.7 $\pm$ 0.1	2.6 $\pm$ 0.1	t = 1.444	0.163	0.262
Tail (mm)	1.8 $\pm$ 0.1	1.7 $\pm$ 0.1	t = 1.607	0.127	0.325

Although martins were rarely observed on the ground, I found evidence that nestlings were receiving calcium-rich items from their parents. Through the course of the study a few nestlings died (for a variety of reasons unrelated to the study); I took this opportunity to examine the stomach contents of these nestlings. All 3 nestlings examined contained several calcium-rich items in their stomach, usually small sections of mollusk shell.

Of the 34 nests initiated between May 4 and May 16, 2 broods were lost to a ladder-climbing domestic cat (*Felis domesticus*) and 3 broods were lost to a pole-climbing Black Rat Snake (*Elaphe obsoleta*). Nests that lost complete broods were not included in my analysis and because more than 98% (130 fledgings of 132 eggs hatched) of the other nestlings fledged, comparing fledging rates between treatments was not useful.

4. DISCUSSION and CONCLUSIONS

4.1 Calcium

Overall, the supplementation of the diet of nestling Purple Martins with calcium resulted in no significant increase in any measure of growth. However, I cannot rule out the possibility that supplemental calcium had a small effect on some measures of growth, but sample sizes were too small to detect minute differences (Table 1). If calcium had a substantial effect, I would have expected to find at least a trend towards increased growth. The question then is, why did calcium supplementation not affect the growth of Purple Martin nestlings?

In this study, Purple Martins may not be the ideal model for testing calcium constraints on nestling growth rates. Nesting in tree cavities or nest boxes has been correlated with larger clutch sizes and slower growth rates in several bird taxa (Martin & Li 1992; Bosque & Bosque 1995), this corresponds to the lower risk of nest predation associated with nesting in a cavity (but see Nilsson 1984, 1986). Also, colonial nesting species have the advantage of detecting and deterring predators more efficiently than solitary nesting species (e.g. Hoogland & Sherman 1976). Birds that do not endure intense pressure from predators can afford a more "relaxed" growth rate which may allow larger brood sizes (Martin & Li 1992). In fact, Purple Martins do tend to support larger broods and have slower growth rates than similar sized passerines that nest in situations where there is a greater risk of predation. However, I argue that there are other factors besides the risk of predation which may minimize the amount of time spent in the nest.

For several days during this experiment, maximum daytime temperatures exceeded

35°C. Although I did not make direct measurements, I assume that 5 large nestlings inside an aluminum apartment directly exposed to the sun, must endure extremely high temperatures. On warm days, I often observed older nestlings cooling themselves on the terrace outside of their apartments. Extreme temperatures are one of the major causes of death for nestling Purple Martins (Allen & Nice 1952). I observed significant nestling mass loss during extended periods of warm weather. Therefore, minimizing the amount of time in the nest, minimizes the exposure of nestlings to extreme temperatures.

Another factor that may pressure nestlings into minimizing the amount of time in the nest is the presence of ectoparasites. Colony nesting birds, especially those in nest-boxes, often face very high levels of ectoparasite infestations (e.g. Moss & Camin 1970; Feare 1976; King *et al.* 1978; Duffy 1983). The results of such infestations are usually decreased growth rates and increased mortality of nestlings (Moss & Camin 1970; Chapman & George 1991; Arendt 1985; Brown & Brown 1986; Emlen 1986; Delannoy & Cruz 1991). In one instance, pre-fledging Purple Martins were observed leaping to their death from a nest-house, presumably to escape the great number of ectoparasites later found in their nests (Loye & Regan 1991). I observed fleas and mites in all 6 nest-houses on my study site; however, these parasites occurred in small numbers. Regardless of parasitic density, each day nestlings remain in the nest the greater energetic and survival costs they may endure.

With the risks associated with staying in the nest, why did my calcium supplements not have at least some positive effects on nestling growth? I would not have detected an effect of calcium-supplementing if I had provided calcium to nestlings in a form that could not be digested. However, I provided nestlings with organic calcium in liquid form. Liquid

Calcium® is a human vitamin, and thus I assumed the calcium it contains is digestible by mammals, but its digestibility is unproven for birds. Most natural sources of calcium used by birds are in calcium-carbonate (CaCO_3) form. However, Boreal Chickadees (*Parus hudsonicus*) and several species of hummingbird have been shown to consume ash which contains calcium in calcium oxide (CaO) form (Ficken 1989; Des Lauriers 1994). Hummingbirds have also been shown to selectively use feeders where vitamins, including calcium (presumably in liquid form), have been added (Carroll & Moore 1993). Therefore, I assume that most bird species not only have the ability to discern a variety of calcium-rich objects but they have the ability to digest calcium in many forms. Therefore, I am confident that I provided calcium to nestlings in a usable form. Of course, the only means of determining if this form of calcium is truly digestible would be to calculate assimilation rates based on differences in concentrations of calcium intake and output. Unfortunately, due to logistic constraints this experiment could not be performed.

Some sea bird species have been shown to reduce the number of provisioning bouts based on the fitness and begging vigor of the nestlings (e.g. Bolton 1995). Possibly, parent martins compensated for faster growth in the experimentally calcium-supplemented nestlings by reducing the amount of food or calcium provided to those nestlings. My experimental design was such that all nestlings in a clutch received the same treatment, thereby minimizing the effect of parents compensating for varying growth rates within a brood. Because nestlings from both control and calcium treatments received equal volumes of liquid I have no reason to believe that begging rates varied within or between nests. However, this experimental procedure assumes that parent birds did not adjust provisioning rates between treatments. I

did not collect data on provisioning rates.

I believe the most likely reason why calcium did not affect growth is that parent martins were providing sufficient food and calcium to allow nestlings to grow at or near their genetically determined maximum rate. Lake Texoma water levels were particularly low in 1996 (B. Matthews pers. comm.), creating an enlarged beach area which exposed large numbers of mollusk shells, including the remains of snails and clams, and many fish skeletons. I found small pieces of mollusk shells in the stomach contents of all 3 of dead nestlings examined. Adults may have been collecting calcium-rich objects from the beach and supplementing the diet of their young with these calcium sources, sufficiently alleviating any dietary calcium deficiency. Martins have been reported to pick up gravel (Brown 1976), but this study is the first report of Purple Martins collecting calcium-rich objects.

On average, water levels around the research station is high enough to completely submerge the beach area. This would presumably force adult martins to find calcium-rich objects elsewhere. This could have a significant influence on the foraging behaviour and reproductive success of this species. To maximize the growth rate of their young in calcium-poor habitats, I assume that martins could either fly farther and/or search longer to find calcium-rich objects. This would result in a greater energetic cost to the parents but probably more importantly would mean less time available to incubate the young and less time to pursue insects for the nestlings. This could have implications on the number of offspring that parent birds can support. Time spent searching for calcium may reduce the number of nestlings that can be supported if foraging time necessary for caloric value decreases beyond a threshold (Fig 12). Also, if incubation time is reduced, nestlings may be forced to expend

more energy to thermoregulate, further reducing their fitness and chance of survival.

A second possible effect from the increased search time necessary in calcium-poor areas is the increased susceptibility to predators. Because martins spend the majority of their time flying or roosting on their relatively protected nest, they are rarely threatened by terrestrial predators. Therefore, the only time martins are likely exposed to such predators is when they are on the ground collecting calcium-rich objects. If calcium-rich objects were scarce or small in size, martins may have to search for a longer period of time on the ground, increasing their risk of predation. Because of the proximity of calcium-rich objects, Purple Martins at my study site may have minimized the risks associated with calcium-foraging time.

Johnson & Barclay (1996) and this study both concluded that supplemental calcium fed to chicks in nests with natural brood sizes does not increase nestling growth rate or size. However, I suggest that the amount of calcium in the environment may limit the number of eggs that a female bird can lay and this may serve as an assay to the amount of calcium available for nestling growth. If there is insufficient calcium in the environment to produce eggs, then there is probably insufficient calcium in the environment to meet the requirements of nestling skeleton growth. If this hypothesis is true, then experimentally supplementing nestlings with calcium will have no affect on the growth rate of nestlings from natural brood sizes. Also, I would expect to find that birds nesting in calcium-rich environments should attempt to raise larger broods than closely related species or the same species in calcium-poor areas (e.g. Ormerod *et al.* 1991). Or, if clutch sizes are not different, then I would expect growth rates to differ. To experimentally test differences in growth, one could provide birds attempting to nest in calcium-poor areas with sufficient calcium to allow elevated egg

Figure 12. Theoretical implications of time spent by parents searching for calcium-rich objects.

production, then remove the calcium source during brooding. If calcium is limiting, we would expect reduced growth rates and/or survival of the nestlings. One could also increase brood sizes beyond the natural range while providing supplemental food. If food is limiting, parent should be able to support more offspring with the supplemental food; if calcium is limiting, larger broods will suffer reduced growth rates regardless of supplemental food.

4.2 Initiation date

Martins that initiated egg laying earlier produced larger clutches (Fig 6) and had nestlings that tended to fledge at a larger size (Table 4). In general, older birds tend to arrive at breeding grounds earlier, lay more eggs and raise larger nestlings than younger birds (e.g. Daan *et al.* 1990). Morton & Derrickson (1990) showed that older Purple Martins arrive at breeding grounds significantly earlier than younger martins. One hypothesis often suggested is that early nesters may be better food gatherers or have access to higher quality food (Newton & Marquiss 1984). I do not believe that early nesting martins had access to a higher density of insect prey than later nesters. Insect abundance (especially grasshoppers) appeared to increase as the season progressed. This would presumably have meant access to more food later in the season, allowing larger clutches to be supported. However, the first Purple Martins arrived at my study site in April, at a time when weather varied from cold and rainy to warm and sunny. Adults were capable of sustaining themselves during those harsh conditions, suggesting a high efficiency in capturing the few insects that were available. Possibly, early nesters are more efficient food gatherers or are capable of selecting "higher quality" food items.

Alternately, earlier nesting birds may have been more efficient at selecting calcium-rich prey or calcium-rich objects. Several researchers have demonstrated that providing calcium to birds before egg-laying promotes earlier nesting and larger clutch sizes (e.g. Chambers *et al.* 1966; Johnson & Barclay 1996). If some birds are more adept at selecting calcium-rich sources, they may be able to nest earlier and produce larger clutch sizes. An experiment which could be done to test this hypothesis would involve providing calcium-rich objects to later nesting birds and determine if their clutch sizes and nestling size increase to that of earlier nesting birds. Once again, I suggest that calcium may be used as an assay; if late nesting birds cannot secure enough calcium to lay a greater number of eggs, they might not have been able to provide sufficient calcium for a greater number of nestlings.

4.3 Brood size

In general, nestlings from larger broods tend to grow at a slower rate or fledge at a smaller size than nestlings from smaller broods, suggesting that the parent birds' ability to provide some resource may limit nestling growth (e.g. Daan *et al.* 1989; Cristol 1995). Although not significantly different, martin nestlings from larger broods tended to fledge at a smaller size than nestlings from smaller broods, this suggests that if parent martins were better able to provide the limiting resource that they could successfully raise more young per nesting attempt. It is apparent from this study that the parent martins' ability to provide calcium is not the factor limiting the growth of their nestlings.

4.4 Conclusion

In conclusion, this study indicates that calcium availability does not limit the growth rate of Purple Martins nesting near an abundant calcium source. Clearly though, the question of whether calcium availability constrains the growth rate of wild passerine birds cannot be answered with just one study. As suggested by Barclay (1994), a similar study on species that are far less mobile on the ground or have behaviours that may limit their access to items rich in calcium content (e.g. hummingbirds, goatsuckers) may provide different results. Also, testing the effects of calcium on species that face greater predation risks or that produce clutch sizes that may be limited by nestling growth rates, may demonstrate calcium to be more of a limiting factor. I suggest that the amount of calcium available for egg production can serve as an assay for the amount of calcium that will be available for nestling growth. That is, if the parents can't secure enough calcium to produce larger clutches they probably would have been unable to secure enough calcium to provide the nestlings. Future tests should attempt to enlarge brood sizes to unnaturally high levels and determine if parents are capable of providing sufficient food and calcium to support their growing young.

5. LITERATURE CITED

- Allen, M. E. 1989. Nutritional aspects of insectivory. Unpublished Ph.D. Thesis, Michigan State University, East Lansing.
- Allen, R. W. & Nice, M. M. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). American Midland Naturalist 47: 606-665.
- Ankney, C. D. & Scott, D. M. 1980. Changes in nutrient reserves and diet of breeding Brown-headed Cowbirds. Auk 97: 684-696.
- A.O.U. Checklist. 1983. Checklist of North American Birds. 6th ed. American Ornithologists' Union, Washington, D.C.
- Arendt, W. J. 1985. *Philornis* ectoparasitism of Pearly-eyed Thrashers. 1. Impact on growth and development and nestlings. Auk 102: 270-280.
- Arnold, T. W. 1993. Fledging success in experimentally manipulated broods of House Wrens. Wilson Bulletin 105: 448-454.
- Barba, E., Gil-Delgado, J. A. & Monrós, J. S. 1995. The costs of being late: Consequences of delaying Great Tit *Parus major* first clutches. Journal of Animal Ecology 64: 642-651.
- Barclay, R. M. R. 1994. Constraints on reproduction by flying vertebrates: Energy and calcium. American Naturalist 144: 1021-1031.
- Barrentine, C. D. 1980. Grit ingestion by nestling Barn Swallows. Journal of Field Ornithology. 51: 368-371.
- Beasom, S. L., & Pattee, O. H. 1978. Utilization of snails by Rio Grande turkey hens. Journal of Wildlife Management. 42: 916-919.
- Bedard, J. & Meunier, M. 1983. Parental care in the Savannah Sparrow. Canadian Journal of Zoology 61: 2836-2843.
- Best, L. B. 1977. Nestling biology of the Field Sparrow. Auk 94: 308-319.
- Bilby, L. W. & Widdowson, E. M. 1979. Chemical composition and growth in nestling blackbirds and thrushes. British Journal of Nutrition 25: 127-134.
- Blancher, P. J. & McNicol, D. K. 1988. Breeding biology of Tree Swallows in relation to wetland acidity. Canadian Journal of Zoology. 66: 842- 849.

- Blancher, P. J. & McNicol D. K. 1991. Tree Swallow diet in relation to wetland acidity. *Canadian Journal of Zoology* 69: 2629-2637.
- Bolton, M. 1995. Experimental evidence for regulation of food delivery to Storm Petrel, *Hydrobates pelagicus*, nestlings: The role of chick body condition. *Animal Behaviour* 50: 213-236.
- Bosque, C. & Bosque, M. T. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *American Naturalist* 145: 234-260.
- Botkin, D. B., Jordan, P. A., Dominski, A. S., Lowendorf, H. S. & Hutchinson, G. E. 1973. Sodium dynamics in a northern ecosystem (moose, wolves, plants). *Proceedings of the National Academy of Science of the USA* 70: 2745-2748.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology* 68: 203-220.
- Boyce, M. S. & Perrins, C. M. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68: 142-153.
- Brown, C. R. 1976. Use of gravel by Purple Martins. *Auk* 93: 842.
- Brown, C. R. 1978a. Clutch size and reproductive success of adult and subadult Purple Martins. *Southwestern Naturalist* 23(4): 597-604.
- Brown, C. R. 1978b. Post-fledging behavior of Purple Martins. *Wilson Bulletin* 90: 376-385.
- Brown, C. R. 1979. Chick recognition in Purple Martins (Passeriformes: Hirundinidae). *Southwestern Naturalist* 24: 683-714.
- Brown, C. R. 1997. Purple Martin (*Progne subis*). *In: The Birds of North America*, No. 287 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- Brown, C. R. & Brown, M. B. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology* 67: 1206-1218.
- Bryant, D. M. & Gardiner, A. 1979. Energetics of growth in House Martins (*Delichon urbica*). *Journal of Zoology (London)* 189: 275-304.
- Burger, L. D., Burger, L. W. & Faaborg, J. 1994. Effects of prairie fragmentation on predation on artificial nests. *Journal of Wildlife Management* 58: 249-254.

- Carrier, D. R. & Auriemma, J. 1992. A developmental constraint on the fledging time of birds. *Biological Journal of the Linnean Society* 47: 61-77.
- Carroll, S. P. & Moore, L. 1993. Hummingbirds take their vitamins. *Animal Behaviour* 46: 817-820.
- Chambers, G. D., Sadler, K. C. & Breitenbach, R. P. 1966. Effects of dietary calcium levels on egg production and bone structure of pheasants. *Journal of Wildlife Management* 30: 65-73.
- Chapman, B. R. & George, J. E. 1991. The effects of ectoparasites on Cliff Swallow growth and survival. *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (ed. by J. E. Loye & M. Zuk). Oxford University Press. pp 69-92.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.
- Colwell, M. A. 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. 94: 767-772.
- Coulson, J. C. 1966. The influence of pair-bond and age on the breeding biology of the Kittiwake Gull, *Rissa tridactyla*. *Journal of Animal Ecology* 62: 263-273.
- Cristol, D. A. 1995. Early arrival, initiation of nesting, and social status: An experimental study of breeding female Red-winged Blackbirds. *Behavioural Ecology* 6: 87-93.
- Crossner, K. A. 1977. Natural selection and clutch size in the European Starling. *Ecology* 58: 885-892.
- Daan, S., Dijkstra, C., Drent, R. & Meijer, T. 1989. Food supply and the annual timing of avian reproduction. *Proceedings of the XIX International Ornithological Congress*, edited by H. Ouellet. Ottawa Canada 1986. pp. 392-407.
- Daan, S., Dijkstra, C. & Tinbergen, J. M. 1990. Family planning in the kestrel (*Falco tinnunculus*): The ultimate control of covariation of laying date and clutch size. *Behaviour* 114: 83-116.
- Dale, F. H. 1954. Influence of calcium on the distribution of pheasants in North America. *Transactions of the North American Wildlife Conference* 19: 316-323.
- Dale, F. H. 1955. The role of calcium in reproduction of the Ring-necked Pheasant. *Journal of Wildlife Management* 19: 325-331.

- Dale, F. H. & DeWitt, J. B. 1958. Calcium, phosphorus and protein levels as factors in the distribution of the pheasant. *Transactions of the North American Wildlife Conference* 23: 291-295.
- Davidar, P. & Morton, E. S. 1993. Living with parasites: prevalence of a blood parasite and its effect on survivorship in the Purple Martin. *Auk* 110: 109-116.
- Delannoy, C. A. & Cruz, A. 1991. Prevalence and effect of philornid (*Philornis* sp., Diptera, Muscidae) ectoparasitism on survival of nestlings of a neotropical bird of prey, Puerto Rican Sharp-shinned Hawk. *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (ed. by J. E. Loye & M. Zuk). Oxford University Press. pp. 93-103.
- DeLope, F. & Møller, A. P. 1993. Effects of ectoparasites on reproduction of their swallow hosts: A cost of being multi-brooded. *Oikos* 67: 557-562.
- DesGranges, J. -L. & Rodrigue, J. 1986. Influence of acidity and competition with fish on the development of ducklings in Quebec. *Water Air Soil Pollution* 30: 743-750.
- Des Lauriers, J. R. 1994. Hummingbirds eating ashes. *Auk* 111: 755-756.
- Dhondt, A. A. & Schillemans, J. 1983. Reproductive success of the Great Tit in relation to its territorial status. *Animal Behaviour* 31: 902-912.
- Drent, P. J. & Woldendorp, J. W. 1989. Acid rain and eggshells. *Nature (London)* 339: 431.
- Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110-119.
- Dunning, J. B. Jr. 1993. *CRC Handbook of Avian Body Masses*. CRC Press, Florida.
- Emlen, J. T. 1986. Responses of breeding Cliff Swallows to nidicolous parasite infestations. *Condor* 88: 110-111.
- Etches, R. J. 1987. Calcium logistics in the laying hen. *Journal of Nutrition* 117: 619-628.
- Feare, C. J. 1976. Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infected ticks. *Ibis* 118: 112-115.
- Ficken, M. S. 1989. Boreal Chickadees eat ash high in calcium. *Wilson Bulletin* 101: 349-351.
- Finlay, J. C. 1971. Breeding biology of Purple Martins at the northern limit of their range. *Wilson Bulletin* 83: 255-269.

- Finlay, J. C. 1976. Some effects of weather on Purple Martin activity. *Auk* 93: 231-244.
- Forbes, M. R. L., Clark, R. G., Weatherhead, P. J. & Armstrong, T. 1994. Risk-taking by female ducks: Intra- and interspecific tests of nest defense theory. *Behavioural Ecology and Sociobiology* 34: 79-85.
- Fowler, G. S. 1995. Stages of age-related reproductive success in birds: Simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist* 35: 318-328.
- France, R. L. 1987. Reproductive impairment of the crayfish *Orconectes virilis* in response to acidification of Lake 223. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Suppl. 1): 97-106.
- Fraser, G. A. & Harvey, H. H. 1982. Elemental composition of bone from white sucker (*Catostomus commersoni*) in relation to lake acidification. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1289-1296.
- Gard, N. W. & Bird, D. M. 1992. Nestling growth and fledging success in manipulated American kestrel broods. *Canadian Journal of Zoology* 70: 2421-2425.
- Garnett, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits *Parus major*. *Ibis* 123: 31-41.
- Glooschenko, V., Blancher, P., Herskowitz, J., Fulthorpe, R. & Rang, S. 1986. Association of wetland acidity with reproductive parameters and insect prey of the Eastern Kingbird (*Tyrannus tyrannus*) near Sudbury, Ontario. *Water Air Soil Pollution* 30: 529-536.
- Goodburn, S. F. 1991. Territory quality or bird quality? Factors determining breeding success in the magpie, *Pica pica*. *Ibis* 133: 85-90.
- Graveland, J. 1990. Effects of acid precipitation on reproduction in birds. *Experientia* 46: 962-970.
- Graveland, J. 1996. Avian eggshell formation in calcium-rich and calcium-poor habitats: Importance of snail shells and anthropogenic calcium sources. *Canadian Journal of Zoology* 74: 1035-1044.
- Graveland, J. & Van Gijzen, T. 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeleton growth in passerines. *Ardea* 82: 299-314.

- Graveland, J., van der Wal, R., van Balen, J. & van Noordwijk, A. J. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature (London)* 368: 446-448.
- Greeley, F. 1962. Effects of calcium deficiency on laying hen pheasants. *Journal of Wildlife Management* 26: 186-193.
- Hagvar, S. & Ostbye, E. 1976. Food habits of the Meadow Pipit *Anthus pratensis* (L.) in alpine habitats at Hardangervidda, south Norway. *Norwegian Journal of Zoology* 24: 53-64.
- Henderson, B. A. 1975. Role of chick's begging behaviour in the regulation of parental feeding behaviour of *Larus glaucescens*. *Condor* 77: 488-492.
- Henderson, I. G. & Hart, P. J. B. 1993. Provisioning, parental investment and reproductive success in Jackdaws *Corvus monedula*. *Ornis Scandinavica* 24: 142-148.
- Herrera, C. M. 1987. Vertebrate-dispersed plants of the Iberian peninsula: A study of fruit characteristics. *Ecological Monographs* 57: 305-331.
- Hogstedt, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. *Science (Washington)* 210: 1148-1150.
- Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46: 33-58.
- Houston, D., Donnan, D. & Jones, P. 1995. The source of nutrients required for egg production in Zebra Finches, *Poephila guttata*. *Journal of Zoology (London)* 235: 469-483.
- Howe, F. P. 1992. Effects of *Protocalliphora braueri* (Diptera: Calliphoridae) parasitism and inclement weather on nestling Sage thrashers. *Journal of Wildlife Diseases* 28: 141-143.
- Huebner, J. D., Malley, D. F. & Donkersloot, K. 1990. Population ecology of the freshwater mussel *Anodonta grandis grandis* in a Precambrian Shield lake. *Canadian Journal of Zoology* 68: 1931-1941.
- Hughes, B. O. & Wood-Gush, D. G. M. 1971. A specific appetite for calcium in domestic chickens. *Animal Behaviour* 19: 490-499.
- Hungerford, B. S., Studier, E. H., Szuch, E. J., Pace, G. L. & Tayler, S. 1993. Aspects of caloric, nitrogen and mineral nutrition during growth in nestling Eastern Bluebirds, *Sialia sialis*. *Comparative Biochemistry and Physiology A* 106: 385-389.

- Hussell, D. J. T. 1985. Optimal hatching asynchrony in birds: Comments on Richter's critique of Clark and Wilson's model. *American Naturalist* 126: 123-128.
- Hurwitz, S. & Griminger, P. 1961. Partition of calcium and phosphorus excretion in the laying hen. *Nature (London)* 189: 759-760.
- Johnson, L. S. & Barclay, R. M. R. 1996. Effects of supplemental calcium on the reproductive output of a small passerine bird, the House Wren (*Troglodytes aedon*). *Canadian Journal of Zoology* 74: 278-282.
- Johnston, R. F. 1964. The breeding birds of Kansas. University of Kansas Publ. Museum of Natural History 12: 575-655.
- Jones, G. 1988. Concurrent demands of parent and offspring Swallows *Hirundo rustica* in a variable feeding environment. *Ornis Scandinavica* 19: 145-152.
- Jones, P. J. 1976. The utilization of calcareous grit by laying *Quelea quelea*. *Ibis* 118: 575-576.
- Kersten, M. & Brenninkmeijer, A. 1995. Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus*. *Ibis* 137: 396-404.
- King, K. A., Keith, J. O., Mitchell, C.A. & Deirans, J. E. 1978. Ticks as a factor in nest desertion of California Brown Pelicans. *Condor* 79: 507-509.
- Klomp, H. 1970. The determination of clutch-size in birds. A review. *Ardea* 58: 1-124.
- Konarzewski, M. 1993. The evolution of clutch size and hatching asynchrony in altricial birds: The effect of environmental variability, egg failure and predation. *Oikos* 67: 97-106.
- Krapu, G. L. & Swanson, G. A. 1975. Some nutritional aspects of reproduction in prairie nesting Pintails. *Journal of Wildlife Management* 39: 156-162.
- Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. *Canadian Journal of Zoology* 56: 2463-2480.
- Krementz, D. G. & Ankney, C. D. 1995. Changes in total body calcium and diet of breeding House Sparrows. *Journal of Avian Biology* 26: 162-167.
- Lack, D. 1947. The significance of clutch size I and II. *Ibis* 89: 302-352.
- Lack, D. 1948a. Natural selection of family size in the starling. *Evolution* 2: 95-110.

- Lack, D. 1948b. The significance of clutch size III. Some interspecific comparisons. *Ibis* 90: 25-45.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen .
- Lee, J. A. 1967. Relative reproductive efficiency of adult and subadult Purple Martins. *Chat* 31: 1-2.
- Leopold, A. 1931. Report on a game survey of the North Central States. Sporting Arms and Manufacturers' Institute. Madison, Wisconsin. 299 pp.
- Lockhart, W. L., & Lutz, A. 1977. Preliminary biochemical observations of fishes inhabiting an acidified lake in Ontario, Canada. *Water Air Soil Pollution* 7: 317-332.
- Loman, J. 1984. Breeding success in relation to parent size and experience in a population of the Hooded Crow. *Ornis Scandinavica* 15: 183-187.
- Loye, J. & Regan, T. W. 1991. The cliff swallow bug *Oeciacus vicarius* (Hemiptera: Cimicidae) in Florida: Ectoparasite implications for hole-nesting birds. *Medical and Veterinary Entomology* 5: 511-513.
- Ludvig, É., Vanicsek, L, Török, J. & Csörgö, T. 1995. Seasonal variation of clutch size in the European blackbird *Turdus merula*: A new ultimate explanation. *Journal of Animal Ecology* 64: 85-94.
- MacLean, S. F., Jr. 1974. Lemming bones as a source of calcium for Arctic Sandpipers (*Caladris* spp.). *Ibis* 116: 552-557.
- Martin, T. E. 1987. Food as a limit on breeding birds: A life history perspective. *Annual Review of Ecology and Systematics* 18: 453-487.
- Martin, T. E. 1993. Evolutionary determinants of clutch size in cavity-nesting birds: Nest predation or limited breeding opportunities? *American Naturalist* 142: 937-946.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101-127.
- Martin, T. E. & Li, P. 1992. Life history traits of open- vs. cavity nesting birds. *Ecology* 73: 579-592.
- Martins, T. L. F. & Wright, J. 1993. Brood reduction in response to manipulated brood sizes in the Common Swift (*Apus apus*). *Behavioural Ecology and Sociobiology* 32: 61-70.

- Mayoh, K. R. & Zach, R. 1986. Grit ingestion by nestling Tree Swallows and House Wrens. *Canadian Journal of Zoology*. 64: 2090-2093.
- McCann, L. J. 1939. Studies of the grit requirements of certain upland game birds. *Journal of Wildlife Management* 3: 31-41.
- McCann, L. J. 1961. Grit as an ecological factor. *American Midland Naturalist* 65: 187-192.
- Mock, D. W. & Lamey, T. C. 1991. The role of brood size in regulating egret sibling aggression. *American Naturalist* 138: 1015-1026.
- Morehouse, E. L. & Brewer, R. 1968. Feeding of nestling and fledgling kingbirds. *Auk* 85: 44-54.
- Morton, E. S. & Derrickson, K. C. 1990. The biological significance of age-specific return schedules in breeding Purple Martins. *Condor* 92: 1040-1050.
- Moss, W. W. & Camin, J. H. 1970. Nest parasitism, productivity and clutch size in Purple Martins. *Science* 168: 1000-1003.
- National Research Council 1984. *Nutrient Requirements of Poultry*, 8th edition. National Academy of Sciences, Washington, DC.
- Newton, I. & Marquiss, M. 1984. Seasonal trends in the breeding performance of sparrowhawks. *Journal of Animal Ecology* 53: 809-829.
- Newton, I. & Moss, D. 1986. Post-fledging survival of Sparrowhawks *Accipiter nisus* in relation to mass, brood size and brood composition at fledging. *Ibis* 128: 73-80.
- Niles, D. M. 1972. Determining age and sex of Purple Martins. *Bird Banding* 43: 137-138.
- Nilsson, S. G. 1984. The evolution of nest site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scandinavica* 15: 167-175.
- Nilsson, S. G. 1986. Evolution of hole-nesting in birds: On balancing selection pressures. *Auk* 103: 432-435.
- Nur, N. 1986. Is clutch size variation in Blue Tits (*Parus caeruleus*) adaptive? An experimental study. *Journal of Animal Ecology* 55: 983-999.
- Nyholm, N. E. I. & Myhrberg, H. E. 1977. Severe eggshell defects and impaired reproductive capacity in small passerines in Swedish Lapland. *Oikos* 29: 336-341.

- O'Conner, R. J. 1978. Growth strategies in nestling passerines. *Living Bird* 16: 209-238.
- O'Conner, R. J. 1984. *The Growth and Development of Birds*. John Wiley & Sons, New York.
- O'Halloran, J., Gribbin, S. D., Tyler, S. J. & Ormerod, S. J. 1990. The ecology of dippers *Cinclus cinclus* (L.) in relation to stream acidity in upland Wales: Time-activity budgets and energy expenditure. *Oecologia* 85: 271-280.
- Ormerod, S. J., Bull, K. R., Cummins, C. P., Tyler, S. P. & Vickery, J. A. 1988. Egg mass and shell thickness in Dippers *Cinclus cinclus* in relation to stream acidity in Wales and Scotland. *Environmental Pollution* 55: 107-121.
- Ormerod, S. J., O'Halloran, J., Gribbin, S. D. & Tyler, S. J. 1991. The ecology of Dippers *Cinclus cinclus* in relation to stream acidity in upland Wales: Breeding performance, calcium physiology and nestling growth. *Journal of Applied Ecology* 28: 419-433.
- Ormerod, S. J. & Tyler, S. J. 1987. Dippers *Cinclus cinclus* and Grey Wagtails *Motacilla cinerea* as indicators of stream acidity in upland Wales. *In: The Value of Birds*. Edited by A. W. Diamond and F. Filion. Technical Publication of the International Council for Bird Preservation. Cambridge. pp. 191-208.
- Ormerod, S. J. & Tyler, S. J. 1993. The adaptive significance of brood size and time of breeding in the dipper *Cinclus cinclus* (Aves: Passeriformes) as seen from post-fledging survival. *Journal of Zoology (London)* 231: 371-381.
- Payne, R. B. 1972. Nuts, bones and a nesting of Red Crossbills in the Panamint Mountains, California. *Condor* 74: 485-486.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255.
- Perrins, C. M. 1979. *British Tits*. Collins, London.
- Perrins, C. M. 1986. Survival of young Great Tits: Relationships with weight. *Proceedings of the XIX International Ornithological Congress*, edited by H. Ouellet. Ottawa, Canada 1986. pp 892-899.
- Perrins, C. M. & Wynne-Edwards, V. C. 1964. Survival of young Swifts in relation to brood size. *Nature (London)* 210: 1147-1148.
- Pettifor, R. A. 1993. Brood-manipulation experiments. I. The number of offspring surviving per nest in Blue Tits (*Parus caeruleus*). *Journal of Animal Ecology* 62: 131-144.

- Piersma, T., Gudmundsson, G. A., Davidson, N. C. & Morrison, R. I. G. 1996. Do arctic-breeding Red Knots (*Calidris canutus*) accumulate skeletal calcium before egg laying? Canadian Journal of Zoology 74: 2257-2261.
- Pinowski, J., Pinowska, B., Kraśnicki, K. & Tomek, T. 1983. Chemical composition of growth in nestling Rooks *Corvus frugilegus*. Ornis Scandinavica 14: 289-298.
- Pinxten, R., Eens, M. & Verheyen, R. F. 1990. Intermediate clutches in the Starling (*Sturnus vulgaris*): Replacement clutches, additional clutches of polygynous males or late first clutches? Journal für Ornithologie 131: 141-150.
- Poulin, R. 1991. Group-living and infestations by ectoparasites in passerines. Condor 93: 418-423.
- Price, K. & Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched Yellow-headed Blackbird nestlings. Behavioural Ecology and Sociobiology 37: 210-208.
- Price, T. M., Kirkpatrick, M. & Arnold, S. J. 1988. Directional selection and the evolution of breeding date in birds. Science (Washington) 240: 798-799.
- Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology 52: 137-154.
- Reichle, D. E., Shanks, M. E. & Crossley, D. A., Jr. 1969. Calcium, potassium and sodium content of forest floor arthropods. Annals of Entomological Society of America 62:57-62.
- Repasky, R. R., Blue, R. J. & Doerr, P. D. 1991. Laying Red-cockaded Woodpeckers cache bone fragments. Condor 93: 458-461.
- Reyer, H. -U., & Westerterp, K. R. 1985. Parental energy expenditure: a proximate cause of helper recruitment in the Pied Kingfisher (*Ceryle rudis*). Behavioural Ecology and Sociobiology 17: 363-369.
- Richner, H. & Heeb, P. 1995. Are clutch and brood size patterns in birds shaped by ectoparasites? Oikos 73: 435-441.
- Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110: 419-451.
- Ricklefs, R. E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118: 179-207.

- Ricklefs, R. E. 1979. Adaptation, constraint and compromise in avian postnatal development. *Biological Reviews* 54: 269-290.
- Ricklefs, R. E. 1984. Avian post-natal development. *In: Avian Biology*. Edited by Farner, D. S., King, J. R. & Parkes, K. L., Vol VII, Academic Press, New York, pp 1-83.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-224.
- Robbins, C. T. 1983. *Wildlife Feeding and Nutrition*. Academic Press, New York.
- Romanoff, A. L. & Romanoff, A. J. 1963. *The Avian Egg*. John Wiley and Sons, Inc., New York.
- Sadler, K. C. 1961. Grit selectivity by the female pheasant during egg production. *Journal of Wildlife Management* 25: 339-341.
- Saether, B. -E. 1990. Age-specific variation in reproductive performance of birds. *Current Ornithology*, edited by D. M. Power. Vol 7, Plenum Press, New York. pp 251-283.
- Scheuhammer, A. M. 1991. Effects of acidification on the availability of toxic metals and calcium to wild birds and mammals. *Environmental Pollution* 71: 329-375.
- Schifferli, L. 1979. Das Skelettgewicht des Haussperlings *Passer domesticus* während der Eiablage und bei Jungvögeln nach dem Ausfliegen. *Ornithologische Beobachter* 76: 289-292.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 11: 369-404.
- Seastedt, T. R. & MacLean, S. F., Jr. 1977. Calcium supplements in the diet of nestling Lapland Longspurs *Calcarius lapponicus* near Barrow Alaska. *Ibis* 119: 531-533.
- Simkiss, K. 1961. Calcium metabolism and avian reproduction. *Biological Review* 36: 321-367.
- Simkiss, K. 1967. *Calcium in Reproductive Physiology*. Chapman and Hall, London.
- Simkiss, K. 1975. Calcium and avian reproduction. *Symposium of the Zoological Society of London* 35: 307-337.
- Skar, H. -J., Hagvar, S., Hagen, A. & Ostbye, E. 1975. Food habits and body condition of adult and juvenile Meadow pipit (*Anthus pratensis* (L.)). *In: F. W. Wieleglaski (ed.), Fennoscandian Tundra Ecosystems*. Ecological Studies 17, Part 2: 160-173, New York, Springer-Verlag.

- Smith, H. G. & Montgomerie, R. 1991. Nestling American Robins compete with siblings by begging. *Behavioural Ecology and Sociobiology* 29: 307-312.
- Stanley, R. G. & Linskens, H. F. 1974. *Pollen Biology, Biochemistry, Management*. Springer, Berlin.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- St. Louis, V. L. & Barlow, J. C. 1993. The reproductive success of Tree Swallows nesting near experimental acidified lakes in northwestern Ontario. *Canadian Journal of Zoology* 71: 1090-1097.
- St. Louis, V. L. & Breebaart, L. 1991. Calcium supplements in the diet of nestling Tree Swallows near acid sensitive lakes. *Condor* 93: 286-294.
- Studier, E. H. & Seveck, S. H. 1992. Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. *Comparative Biochemistry and Physiology A* 103: 579-595.
- Studier, E. H., Szuch, E. J., Tompkins, T. M. & Cope, V. W. 1988. Nutritional budgets in free-living birds: Cedar Waxwings (*Bombycilla cedrorum*) feeding on Washington hawthorn fruit (*Crataegus phaenopyrum*). *Comparative Biochemistry and Physiology A* 89: 471-474.
- Sturkie, P. D. 1965. *Avian Physiology*. Cornell University Press. New York.
- Stutchbury, B. J. 1991a. Coloniality and breeding biology of Purple Martins (*Progne subis hesperia*) in Saguaro Cacti. *Condor* 93: 666-675.
- Stutchbury, B. J. 1991b. Floater behaviour and territory acquisition in male Purple Martins. *Animal Behaviour* 42: 435-443.
- Sullivan, K. A. & Weathers, W. W. 1992. Brood size and thermal environment influence field metabolism of nestling Yellow-eyed Juncos. *Auk* 109: 112-118.
- Tayler, T. G. 1962. Calcium absorption and metabolism in the laying hen. *In: Nutrition of Pigs and Poultry*. Edited by J. T. Morgan & d. Lewis. London: Butterworths. pp 148-157.
- Turner, A. K. 1982. Timing of laying by Swallows (*Hirundo rustica*) and Sand Martins (*Riparia riparia*). *Journal of Animal Ecology* 51: 29-46.

- Van Balen, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-93.
- Verhulst, S., van Balen, J. H. & Tinbergen, J. M. 1995. Seasonal decline in reproductive success of the Great Tit: Variation in time or quality? *Ecology* 76: 2392-2403.
- Wagner, R. H., Schug, M. D. & Morton, E. S. 1996. Confidence of paternity, actual paternity and paternal effort by Purple Martins. *Animal Behaviour* 52: 123-132.
- Walsh, H. 1978. Food of nestling Purple Martins. *Wilson Bulletin* 90: 248-260.
- Williams, C. B. 1961. Studies in the effects of weather conditions on activity and abundance of insect populations. *Philosophical Transactions of the Royal Society of London* 244: 331-370.
- Wilson, J. E. 1959. The status of the Hungarian Partridge in New York. *Kingbird* 9: 54-57.
- With, K. A. & Webb, D. R. 1993. Microclimate of ground nests: The relative importance of radiative cover and wind breaks for three grassland species. *Condor* 95: 401-413.
- Woods, C. P. 1994. The Loggerhead Shrike in Southwest Idaho. Unpublished M. Sc. Thesis, Boise State University, Boise, Idaho.
- Zar, J. H. 1996. *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, New Jersey. 662 pp.

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