Growth and Development of the Violaceous Euphonia and Palm Tanager in Trinidad

C. T. Collins
Department of Biological Sciences
California State University, Long Beach, CA 90840, USA
E-mail: ccollins@csulb.edu

ABSTRACT

The growth and postnatal development of Violaceous Euphonia (*Euphonia violacea*) and Palm Tanager (*Thraupis palmarum*) chicks were studied in Arima Valley, Trinidad. Like many tropical passerines, these two tanagers had lower growth rates (K = 0.462 and 0.386; $T_{10\text{-}90}$ = 9.6 and 12 days respectively) than comparable sized temperate zone species. Palm Tanagers fledged at the age of 18 days and the Euphonias between 17 and 20 days. Both species were poikilothermic at hatching and only became homeothermic at 9-10 days post hatching. Chicks of both species gaped silently which may be an anti-predator detection adaptation. The reduced mobbing by the adult tanagers may represent an adaptive response to increase adult survival and, as a result, long-term reproductive success.

Key words: *Euphonia, violacea, Thraupis, palmarum*, tanager, Trinidad, growth, thermoregulation, behaviour, begging, mobbing.

INTRODUCTION

The postnatal growth and development of nestling birds has been a long-standing interest of ornithologists. The graphical method of characterizing avian growth data and generating summary statistics (Ricklefs 1967) opened the door for broader comparative studies involving a greater diversity of species from around the world (Ricklefs 1968, 1976; Starck and Ricklefs 1998a). Despite the many field and laboratory studies in recent years, some taxa and geographical areas are still under-represented in even the most recent summary of our knowledge of avian growth (Starck and Ricklefs 1998a).

One of the early observations was that "tropical passerine birds, particularly species with small clutches, grow more slowly than passerines in temperate regions" (Ricklefs 1976:179). Although there has been a detailed analysis of this and the relationship of growth rate to other variables such as clutch size and diet (Ricklefs 1976), the available growth and life history data for some predominantly tropical bird families remain rather lean (Stutchbury and Morton 2001). Growth data are available for only 18 of 425 species (4.2 %) of flycatchers (Tyrannidae) and eight of 256 species (3.1 %) of tanagers (Emberizidae: Thraupinae). In the case of the manakins (Pipridae) there are data for only 1 of 52 (1.9 %) of the species and the large and diverse neotropical family Furnariidae (256 species) is unrepresented in the latest compendium of avian growth data (Starck and Ricklefs 1998b).

In the course of field studies of swifts I conducted in Trinidad from 1961 to 1967 (Collins 1963a, 1968a, 1968b, 2002), I was also able to obtain data on the postnatal growth and development of thermoregulation in two tanagers, the Violaceous Euphonia (= Semp, herein), *Euphonia violacea*, and Palm Tanager, *Thraupis palmarum*. Although the statistics characterizing the chick growth of these two species were included in earlier studies (Ricklefs 1968, 1976; Starck and Ricklefs 1998b), the original data on which these were based, along with data on the development of temperature regulation and additional breeding biology observations, were never placed on record and I, belatedly, do so here.

MATERIALS AND METHODS

I was able to follow the growth of four chicks in one Semp nest and seven chicks from four nests of the Palm Tanager. The single Semp nest was located at the lip of a roadside bank in the Verdant Vale area of Arima Valley. Five chicks hatched on 6 August 1962, four of which were followed for 10 of the next 15 days; one chick was collected for natal down analysis (Collins 1962). All four young presumably fledged between 21 August when the nest was last checked, and 25 August when the nest was found empty.

The four Palm Tanager nests were located in two ornamental palms on the grounds of Simla, the William Beebe Tropical Research Station in Arima Valley. One nest, followed from 6-23 May 1963, had only one viable chick; a second chick was found dead in the nest when first checked at which time they were both about 3 days old. In 1964 three nests were followed, each containing two chicks: nest 1 was followed from 6-24 June, nest 2 from 8 July to 1 August and nest 3 from 28 July until 4 August.

Nestlings were weighed with a spring balance obtained from the British Trust for Ornithology. The balance was calibrated in half-gram intervals and weights were estimated to the nearest quarter-gram. Wing and tail measurements were made with a stopped metal wing rule to the nearest 0.5 mm. The summary growth statistics for these data were generated by R. E. Ricklefs (1968) using a graphical curve-fitting procedure (Ricklefs 1967) and the logistic growth model. Included were: the overall growth rate constant K which can be used for interspecific comparisons, the asymptote of the growth curve A and T_{10-90}, an inverse measure of growth rate representing the time for growth between 10% and 90% of the asymptote.

Body temperatures were measured with a fast-registering small bulb mercury thermometer made by the Schultheis Corporation. Readings were taken with the bulb inserted about 10 mm into the cloaca. Cold stress experiments were used in 1964 as part of the investigation of nestling thermoregulatory abilities. These utilized a 20 x 15 x 13 cm (approximately) cold chamber made of foam plastic insulation material approx. 3.0 cm thick (Collins 1968: Fig. 2), which four 6 oz cans of "Skotch Ice" (refreezable liquid) kept at a temperature of approximately 5° C. Nestlings were placed individually in the chamber in the field for a period of 5 min. and their body temperatures were recorded before and after cold exposure. Even though sharp body temperature drops were recorded for very young nestlings, the tests caused no apparent ill effects.

RESULTS

At hatching, Semp chicks had only a sparse covering of 32 natal downs (neossoptiles) confined to the coronal, occipital, spinal and scapular tracts (Collins 1962). The edge of the otherwise dark bill was yellow, the gape was white, the mouth lining bright red and the legs and toes were darkly pigmented. A small egg tooth was noticed only on day 1. The eyes, which were closed at hatching, began to open at day 8 and were fully open on day 14. The dorsal skin progressively darkened during the first 6 days post hatching. Primary wing feathers first erupted through the skin on day 6 post hatching at which time the body contour feathers were still only dark streaks under the skin. By day 9 the contour pin feathers were 1.5-2.0 mm through the skin; both contour feathers and primaries began erupting from their sheaths by day 11. The contour feathers largely covered the body by day 16 but were still ensheathed at their base. By day 3 the still blind chicks gaped vigorously but silently in response to any vocal or tactile stimulus. The chicks developed rapidly and could hop and flutter short distances by day 16. Fledging took place between 16 and 20 days post hatching.

At hatching, Semp chicks weighed an average of 1.1 g. Body mass increased fourfold by day 4 and reached an average of 10.8 g by day 8 (Table 1). The rate of increase slowed thereafter and body weights varied from 13.5 to 14.5 g from days 10-15. The growth rate constant (K) was 0.460 and T_{10-90} was 9.6 days; the asymptote of the growth trajectory was 14.5 g which is the same as the average adult weight (Snow and Snow 1963a). Semp chicks' wing length was 5 mm at hatching and reached 8-9 mm by day 4. Wing length increased rapidly thereafter as the primary feathers emerged and elongated (Table 1). The wing length reached 37.5-41.0 mm (70.8 % of adult length; Snow and Snow 1963a) by day 15, the last day the chicks were handled. The rectrices first emerged on day 10 post hatching and reached a length of 9-11 mm on day 16.

Semp chicks' thermoregulatory capacity was not tested experimentally. However, on the day of hatching, their body temperatures rapidly dropped to 28.5 ° C when unbrooded; ambient temperature was probably about 24° C. This would indicate a homeothermy index (H. Visser 1998) of only 0.28. From days 3-8 their body temperature dropped from about 40° C to between 32.7 and 35.8° C during the 5-10 min. period while out of the nest being weighed and measured. During this time H increased somewhat, averaging 0.64 (n = 12, range = 0.54-0.73, SD = 0.05) which was still well below a value of $H \geq 0.80$ thus indicating homeothermy had not yet been achieved (Visser 1998). Starting on day 9 the body temperatures only dropped to 38.3-40.2 which was just 0.5-1.2 below the level recorded when they were first removed from the nest. At this time H averaged 0.95 (n = 16, range = 0.85-1.01, SD = 0.05). This rapid transition to thermoregulation occurred before the developing contour plumage offered much insulation and when the body mass was about 10-11 g which was 70-77 % of that of adults.

At hatching, Palm Tanager chicks have a moderately dense covering of 173-238 natal downs in 15 tracts and regions, including a newly defined spinal region of the spinal tract (Collins 1962; Collins and Araya 1998). The chicks had a blackish bill with a yellowish tip, ivory white gape and carmine red mouth lining. When gaping the chicks were at first silent and later only uttered a very weak peeping. A white egg tooth, observable on the upper mandible at hatching, was dark coloured but still detectable on day 5 and completely reabsorbed by day 17. The eyes, which were closed at hatching, began to open at 5-6 days and were fully open on day 9. The legs, toes and claws were unpigmented at hatching but started to darken by day 5. Feather tracts were observable by day 4 when the contour feathers were dark streaks under the skin. Primary pin feathers erupted through the skin on day 5 and the secondary and contour feathers on day 7 post hatching. Contour feathers began erupting from their sheaths on day 10. The rectrix pin feathers emerged through the skin on days 8-9

Table 1. Growth of Semp and Palm Tanager chicks. The values presented are: Mean, (range) and [sample size (n)]. ** = no data.

Semp				Palm Tanager			
Age (day)	**Mass (g)**	**wing (mm)**	**Tail (mm)**	**Age (day)**	**Mass (g)**	**Wing (mm)**	**Tail (mm)**
1	1.1 (1.0-1.12 [5]	5 (5.0-5.0) [5]	0 ** **	1	5.5 (5.0-6.0) [2]	8.5 (8.0-9.0) [2]	0 ** **
2	1.8 (1.5-2.0) [4]	5 (5.0-5.0) [4]	0 ** **	2	7.3 (6.75-8.25) [3]	9.5 (9.5-9.5) [3]	0 ** **
3	3.1 (3.0-3.25) 4	** ** **	0 ** **	3	9.6 (8.5-11.0) [5]	11.2 (11.0-11.5) [5]	0 ** **
4	** ** **	** ** **	** ** **	4	12.1 (10.5-13.8) [4]	12.8 (12.5-13.0) [4]	0 ** **
5	4.6 (4.5-5.0) [4]	8.5 (8.0-9.0) [4]	0 ** **	5	14 (13.5-14.5) [2]	15.5 (15.0-16.0) [2]	0 ** **
6	5.9 (5.75-6.25) [4]	10.1 (10.0-10.5) [4]	0 ** **	6	15.8 (15.0-16.5) [2]	18.25 (17.5-19.0) [2]	0 ** **
7	** ** **	** ** **	** ** **	7	18.25 (18.0-18.5) [2]	21.8 (20.0-23.5) [2]	0.5 (0.0-1.0) [2]
8	9.9 (9.5-10.25) [4]	15.75 (15.0-16.5) [4]	0 ** **	8	20.8 (19.8-22.3) [4]	26.5 (25.0-27.5) [4]	0.5 (0.5-0.5) [2]
9	10.8 (10.5-11.0) [4]	19.2 (18.5-20.0) [4]	0 ** **	9	21.9 (20.5-23.8) [5]	30 (27.0-32.0) [5]	1.2 (1.0-2.0) [5]
10	** ** **	** ** **	** ** **	10	23.9 (22.5-25.5) [4]	35.3 (33.0-36.5) [4]	3.1 (3.0-3.5) [4]
11	13.9 (13.5-14.3) [4]	18.7 (23.4-26.0) [4]	2.5 (1.5-3.0) [4]	11	25.9 (24.8-27.0) [4]	39.5 (37.5-40.5) [4]	5.8 (5.5-6.0) [4]
12	** ** **	** ** **	** ** **	12	26.8 (26.0-27.7) [4]	43.8 (41.0-44.5) [4]	8.5 (8.0-9.0) [4]
13	** ** **	** ** **	** ** **	13	27.7 (25.8-30.8) [4]	47.1 (46.0-48.5) [4]	11.4 (10.5-13.0) [4]
14	14.2 (13.8-14.3) [4]	33.4 (31.5-35.5) [4]	6.4 (5.5-7.0) [4]	14	27.4 (27.0-28.0) [3]	49.7 (48.5-51.0) [3]	12.5 (10.5-14.0) [3]
15	** ** **	** ** **	** ** **	15	28.5 (28.0-29.5) [4]	53.9 (53.0-55.0) [4]	16.4 (13.5-18.0) [4]
16	13.5 (13.0-14.5) [4]	39.4 (37.5-41.0) [4]	9.9 (9.0-11.0) [4]	16	28 (27.5-28.5) [2]	57.3 (57.0-57.5) [2]	19.5 (19.0-20.0) [2]
17	** ** **	** ** **	** ** **	17	30.3 (28.0-31.8) [3]	60.8 (60.0-62.5) [3]	24.1 (23.5-28.0) [3]
18	** ** **	** ** **	** ** **	18	29 ** [1]	61.5 ** [1]	23 ** [1]

and erupted through their sheaths by days 11-12. The body was mostly covered by contour feathers, except along the ventral midline by day 13 and was completely covered by day 15. The chicks developed motor skills rapidly. When placed on their side the chicks could right themselves by day 5, turn over by day 6 and begin to grasp things, such as nest material when being removed from the nest, by day 7. They could hold on to and balance on a perch by day 10 and fluttered their wings to help maintain balance on day 16. They gave a "startle" reaction to movements of nearby large objects or sounds by day 17. Fledging was on day 18 post hatching.

Palm Tanager chicks had a wing length of 8.0-9.0 mm at hatching which increased to 15.5 mm on day 5 when the primary pin feathers emerged through the skin. Thereafter, the primaries elongated and the wing length increased rapidly (3.9 mm per day) reaching 61 mm (65 % of the adult length, Snow and Snow 1963a) on day 17 just prior to fledging. The rectrices first emerged on days 8-9 and reached a length of 24-28 mm on day 17 post hatching.

At hatching, Palm Tanager chicks weighed 6.0 g and doubled this by day 4 and weighed 25 g on day 10. Their weight remained in the range of 27.5-28.5 g from days 14-17 prior to fledging (Table 1). The growth rate (K) was 0.386 and t_{10-90} was 12 days; the asymptote of the growth trajectory was 28.0 g which is only 74% of the adult body weight of 38.6 g (Snow and Snow 1963a).

Like Semp chicks, Palm Tanager chicks had very poor thermoregulatory capacity at hatching. On day 1 body temperatures quickly dropped to 32.2-33.1º C shortly after their removal from the nest. This indicates H = 0.45-0.51. From days 2-9 body temperatures dropped to 35.5-38.6º C with an average H of 0.71 (n = 37, range = 0.36-0.88, SD = 0.14). On days 8 and 9 chicks' body temperatures were higher than expected with H values of 0.75-0.88. This may have resulted from body temperature measurements being taken soon after the chicks' removal from the warm thermal environment of the nest and before enough time had elapsed for much cooling to have occurred. When subjected to 5 min. cold stress tests, days 2-9 chicks lost an average of 4.89º C (n = 15, range = 4.1-6.1, SD = 0.62) to body temperatures as low as 30.9º C. From days 10-17 body temperatures remained higher averaging 40.35º C (n = 15, range = 38.5-42.0, SD = 1.34) and lost only an average of 1.29º C when cold stressed (n = 14, range = 0.0 -3.6, SD = 1.28); one 15-day old chick increased its body temperature by 0.3º C during the test. H values for chicks ≥ day 10 averaged 0.90 (n = 27, range = 0.76 -1.00, SD = 0.07) indicating that homeothermy had been achieved (H ≥ 0.8; Visser 1998). Shivering was first noticed on day 10 at ambient temperatures of 24.6-26.8º C. As noted for the Semp chicks, the transition to thermoregulation was rapid and occurred before the contour plumage offered much insulation and when body mass, on day 10, was about 63% of that of adult Palm Tanagers.

DISCUSSION

Euphonia nests are unique within the tanagers in being domed with a side opening (Skutch 1954, 1989; Isler and Isler 1999); they may be supported by a variety of tree branches, epiphytes and even sprouts on living fence posts. Semp nests in Trinidad are typically found "at the top of a bank overlooking a path" (ffrench 1991). Palm Tanagers, like other *Thraupis* tanagers, build open cup nests but show a distinct affinity for placing their nests in the axils of palm fronds (Skutch 1954; ffrench 1991; Isler and Isler 1999). Faecal material was not removed by adult Semps and the floor of the nest and the nest opening were quite fouled with gelatinous droppings from day 10 to the time the chicks fledged. The Palm Tanager nests were generally clean, the adults presumably having carried away faecal sacs.

The reduced numbers of natal downs on the nestling Semps is not surprising. Little or no natal down is typical for chicks of passerines building domed or closed nests. This contrasts with the substantial number of downs usually found in species building open cup nests. This pattern has been documented previously for tropical flycatchers (Tyrannidae; Collins and McDaniel 1989).

At the approach of adults, both Semp and Palm Tanager chicks begged vigorously exposing the bright red mouth lining framed by the swollen white gape edges. It is notable that in both species this begging was silent or nearly silent. This is in strong contrast to the noisy begging of many temperate zone passerines which make nests and nestlings detectable at substantial distances (pers. obs.). Silent begging has also been observed in White-lined Tanagers (*Tachyphonus rufus*: pers. obs), several thrushes (*Turdus* sp.; pers. obs.), and in previous studies of the Bearded Bellbird (*Procnias averano*) in Trinidad (Snow 1970) and the Cinnamon Flycatcher (*Pyrrhomyias cinnamomea*; Collins and Ryan 1995; Ryan and Collins 1999) and Slate-throated Redstart (*Myioborus mineatus*; Collins and Ryan 1994) in Venezuela.

As noted by Ricklefs (1970) "rates of predation on eggs and nestlings of birds is about twice as high in tropical as in temperate regions." Predation accounted for 82% of all nest failures of the Western Slaty Antshrike (*Thamnophilus atrinucha*) in Panama (Roper 2005) and 80% or more for the Black and White Manakin (*Manacus manacus*; Snow 1962) and three species of thrushes (*Turdus* sp.; Snow and Snow 1963b) in Trinidad. It follows that "antipredator adaptations seem more highly developed in the tropics than in temperate and arctic regions" and thus predation should be considered to be a "strong selective force" (Ricklefs 1970; see also Ricklefs 1969). When nest losses are high "any strategy [like the silent begging noted here] which reduces the percentage loss, even by a little, will greatly increase productivity" (Snow and Lill 1974) and thus be favored by selection. Both experiments (Haskell 1994; Leach and Leonard 1997; Dearborn 1999; Moreno-Rueda 2005) and direct field observation (Perrins 1965; Redondo and Castro 1992) have shown that begging vocalizations in temperate passerines increased the mortality due to predation. Thus, predation is a "selective force that may mold the evolution of begging calls by nestlings" (Moreno-Rueda 2005) and noisy "begging may carry a significant predation cost for nestling birds" (Leach and Leonard 1997). Silent begging by tropical passerines should be viewed as yet another among the many anti-predator adaptations developed in a predator-rich environment. A reduced brood size, requiring fewer provisioning visits each of which might attract predators, could also, in part, be related to the greater array and specializations of tropical predators (Ricklefs 1969, 1970; Snow 1970).

In Costa Rica, Scarlet-rumped Tanagers (*Ramphocelus passerinii*) are active and noisy in mobbing nest predators, such as snakes, and other perceived threats (Skutch 1989). The same is true for the Red-crowned Ant-tanager (*Habia rubica*) in Trinidad (ffrench 1991, pers. obs.). Adult Semps and Palm Tanagers were much quieter. They remained nearby during the time the chicks were being handled but were not particularly active or noisy (2 to 2.5 on a response scale of 1 to 4; Ricklefs 1977); they were somewhat more agitated when larger chicks vocalized during handling. This is in sharp contrast to the intense noisy mobbing, perhaps accompanied by physical attack (4 on the response scale; Ricklefs 1977) described for other tanagers (Skutch 1989) and familiar to field workers studying most temperate zone passerines. Semp and Palm Tanagers were, however, more demonstrative than some other tropical passerines, such as manakins (Ricklefs 1977, pers. obs.) which quietly depart the vicinity of the nest with no defense or vocalizing (1 on the response scale; Ricklefs 1977). Responses, particularly at levels 3 or 4, could endanger the mobbing individual. This could be via a counter-attack from the initial predator or perhaps from another attracted to the commotion; mobbing individuals would expectedly be less vigilant at this time and potentially vulnerable to outside attack. In long-lived tropical species (Snow 1962; Snow and Lill 1974; Johnston *et al.* 1997), risking adult survival and future reproduction by mobbing or nest defense of any one nest, among perhaps many lifetime nesting attempts, would not seem to be optimal for long-term reproductive success. If any action, including predator mobbing could "decrease the individual's chance of survival by even a little" then selection should strongly support opposite behavior which is to say, behavior which would tend to increase life expectancy (Snow and Lill 1974; see also Williams 1966).

Recent field experiments using matched phylogenetically and ecologically similar species provide empirical support for the scenario developed here (the functional constraint model; Ricklefs 2000). South American species,with lower clutch sizes and higher adult survival, decreased food delivery rates to their young when faced with possible predation risk to themselves (Ghalambor and Martin 2001). North American species with larger clutches and higher adult mortality "reacted more strongly to reduce risk to their offspring" (Ghalambor and Martin 2001). Further support is provided by the observations of Roper (2005) which showed that persistent re-nesting, and a reduced re-nesting interval, following nest predation events were important influences on overall reproductive success in a long-lived species. The reduced clutch size of tropical birds may also serve to decrease the energy commitment to any one nesting attempt during a prolonged breeding season (Slagsvold 1984) and also facilitate the observed rapid re-nesting and reduced re-nesting intervals (Roper 2005).

A further analysis of the degree of mobbing and nest defense in tropical vs. temperate passerines and the relationship to different habitats, predator regimes and, particularly, adult survival, would seem to be productive.

All four Semp chicks were in the nest on day 16 but gone, presumably having fledged, by day 20. The exact age at fledging was not determined but it was presumably near the end of the 17-20 day period. In other studies three species of euphonias had a nestling period of 20-20.5 days (Ricklefs 1976). Palm Tanager chicks fledged after a nestling period of 18 days. One day-18 chick left the nest as I was reaching for it and another almost did the same. A third was present in the nest early on day 18 but had fledged on its own prior to my visit around midday.

The growth rate of both Semps ($K = 0.460$) and Palm Tanagers ($K = 0.379$) are lower than for similar sized temperate zone passerines (Ricklefs 1976). However, there is substantial overlap in the overall growth rate of temperate species (average $K = 0.502$, $n = 30$, $SD = 0.071$) and tropical species (average $K = 0.387$, $n = 51$, $SD = 0.079$; Ricklefs 1976) as well as substantially differing growth rates among congeneric species. For both temperate and tropical species groups the variation in K is greater among broods than within broods (Ricklefs 1976). The asymptotic weights of Semps (100% of adult weight) and Palm Tanagers (74% of adult weight) are within the range of values for other tropical species; however "tropical and temperate species attain similar asymptotes relative to adult body weight at the end of the nestling period" (Ricklefs 1976).

Several hypotheses have been proposed to explain the generally slower growth rates of tropical passerines, and tested to the extent possible (Ricklefs 1976). Prominent in this discussion is the role of low-nitrogen fruit in the diet of many tropical species and a possible protein deficiency limiting chick growth. However, the evidence does not support this or any one hypothesis to the exclusion of others. The debate continues.

As indicated earlier, both Semp and Palm Tanager chicks are poikilothermic at hatching. They show a rapid decrease in body temperature when unbrooded even at moderate ambient temperatures. These observations, and the cold stress experiments (on Palm Tanagers only), indicate an abrupt shift to homeothermy ($H \geq 80$) on day 9 for Semps and day 10 for Palm Tanagers. The insulative property of the plumage at this stage was still minimal. Thus in both tanager species, and possibly others, this change appears to be related more to the degree of body mass achieved and increased heat production rather than decreased heat loss. The ratio of chick body mass to adult body mass at homeothermy was 0.70-0.77 for Semps and 0.63 for Palm Tanagers; the average for 54 passerines was 0.742 (range = 0.56-1.21, SD = 0.174; Visser 1998).

The data presented here on the growth and development of tanager chicks was collected peripheral to other field studies. Accordingly they are not as complete, in some respects, as desired. Nonetheless, they contribute to the somewhat meager information available on the developmental biology of these species. Additional studies on other tropical birds, even common species, are highly desirable.

ACKNOWLEDGEMENTS

My field studies in Trinidad during 1962-1966 were supported by research awards from the Frank M. Chapman Fund of the American Museum of Natural History, New York.

REFERENCES

Collins, C. T. 1963a. The "downy" nestling plumage of swifts of the genus *Cypseloides*. *Condor*, 65: 324-328.

Collins, C. T. 1963b. The natal pterylosis of tanagers. *Bird-Banding*, 34: 36-38.

Collins, C. T. 1968a. Notes on the biology of Chapman's Swift *Chaetura chapmani* (Aves, Apodidae). *American Museum Novitates*, 2320: 1-15.

Collins, C. T. 1968b. The comparative biology of two species of swifts in Trinidad, West Indies. *Bull. Fla. St. Mus.*, 11: 257-320.

Collins, C. T. 2002. Notes on the biology of the Band-rumped Swift in Trinidad. p.138-143. *In* **Floyd E. Hayes** and **Stanley A. Temple**, eds. Studies in Trinidad and Tobago Ornithology Honouring Richard ffrench. St. Augustine, Trinidad and Tobago: Depart. of Life Sciences, Univ. of the West Indies, Occasional Paper No. 11.

Collins, C. T. and **Araya, T. A.** 1998. Natal pterylosis of tanagers II: *Tachyphonus*, *Ramphocelus* and *Tangara*. *Bull. Brit. Ornithol. Club,* 118: 172-178.

Collins, C. T. and **McDaniel, K. M.** 1989. The natal pterylosis of closed-nest building tyrant flycatchers (Aves: Tyrannidae). *Bull. So. Calif. Acad. Sci.,* 88: 127-130.

Collins, C. T. and **Ryan, T. P.** 1994. Notes on the breeding biology of the Slate-throated Redstart (*Myioborus mineatus*) in Venezuela. *Ornitologia Neotropical*, 5: 125-128.

Collins, C. T. and **Ryan, T. P.** 1995. The biology of the Cinnamon Flycatcher *Pyrrhomyias cinnamomea* in Venezuela. *Ornitologia Neotropical,* 6: 19-25.

Dearborn, D. C. 1999. Brown-headed Cowbird nestling vocalizations and risk of nest predation. *Auk,* 116: 448-457.

ffrench, R. 1991. A Guide to the Birds of Trinidad and Tobago. Ithaca: Cornell Univ. Press. 426 p.

Ghalambor, C. K. and **Martin, T. E.** 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science,* 292: 494-497.

Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. Roy. Soc., London B,* 257: 161-164.

Isler, M. I. and **Isler, P. R.** 1999. The Tanagers: Natural History, Distribution and Identification. Washington: Smithsonian Inst. Press. 406 p.

Johnston, J. P., Peach, W. J., Gregory, R. D. and **White, S. A.** 1997. Survival rates of temperate and tropical passerines: A Trinidadian perspective. *Amer. Nat.*, 150: 771-789.

Moreno-Rueda, G. 2005. A trade-off between predation risk and sibling competition in the begging behavior of Coal and Great Tits. *J. of Field Ornithology*, 76: 390-394.

Leach, S. M. and **Leonard, M. L.** 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology*, 8: 644-646.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major L. J. of Animal Ecology,* 34: 601-647.

Redondo, T. and **Castro, F.** 1992. The increase in risk of predation with begging activity in broods of Magpies, *Pica pica*. *Ibis*, 134: 180-187.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology*, 48: 978-983.

Ricklefs, R. E. 1968. Patterns of growth in birds. *Ibis*, 110: 419-451.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology,* 9: 1-48.

Ricklefs, R. E. 1970. Clutch size in birds: outcome of opposing predator prey adaptations. *Science,* 168: 599-600.

Ricklefs, R. E. 1976. Growth rates of birds in the humid New World tropics. *Ibis,* 118: 179-207.

Ricklefs, R. E. 1977. Reactions of some Panamanian birds to human intrusion at the nest. *Condor,* 79: 376-379.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian live histories. *Condor,* 102: 9-22.

Roper, J. J. 2005. Try and try again: nest predation favors persistence in a Neotropical bird. *Ornitologia Neotropical*, 16: 253-262.

Ryan, T. P. and **Collins, C. T.** 1999. Growth of a Neotropical tyrannid: the Cinnamon Flycatcher (*Pyrrhomyias cinnamomea*). *Ornitologia Neotropical*, 10: 233-237.

Skutch, A. F. 1954. Live histories of Central American birds. *Pacific Coast Avifauna,* 31: 1-448.

Skutch, A. F. 1989. Life of the Tanagers. Ithaca: Cornell Univ. Press. 111 p.

Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J. of Animal Ecology,* 52: 945-953.

Snow, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis,* 112: 299-329.

Snow, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. *Zoologica*, 47: 65-104.

Snow, D. W. and **Lill, A.** 1974. Longevity records for some Neotropical land birds. *Condor,* 76:262-267.

Snow, D. W. and **Snow, B. K.** 1963a. Weights and wing-lengths of some Trinidad birds. *Zoologica,* 48: 1-12.

Snow, D. W. and **Snow, B. K.** 1963b. Breeding and the annual cycle in three Trinidad thrushes. *Wilson Bull.*, 75: 27-41.

Starck, J. M. and **Ricklefs, R. E.** (eds.) 1998a. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. New York: Oxford Univ. Press. 441 p.

Starck, J. M. and **Ricklefs, R. E.** 1998b. Avian growth rate data set. p.381-423. *In* **J. Mathias Starck** and **Robert E. Ricklefs**, eds. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. New York: Oxford Univ. Press. 441 p.

Stutchbury, B. J. M. and **Morton, E. S.** 2001. Behavioral Ecology of Tropical Birds. San Diego: Academic Press. 165 p.

Visser, G. H. 1998. Development of temperature regulation. p.117-156. *In* **J. Mathias Starck** and **Robert E. Ricklefs**, eds. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. New York: Oxford Univ. Press. 441 p.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Amer. Nat.*, 100: 687-690.