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Does Seasonal Rainfall Act as a Molt Constraint in African Sunbirds? The Role of Climate in the Adaptation and Evolution of Delayed Plumage Maturation

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DOES SEASONAL RAINFALL ACT AS A MOLT CONSTRAINT IN AFRICAN SUNBIRDS? THE ROLE OF CLIMATE IN THE ADAPTATION AND EVOLUTION OF DELAYED PLUMAGE MATURATION

by

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ABSTRACT

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Delayed plumage maturation (DPM) is a phenomenon in which birds retain immature plumage until their second breeding season despite reaching sexual maturity earlier. This study investigated DPM in Amethyst Sunbirds (*Chalcomitra amethystina*) and Scarlest-chested Sunbirds (*Chalcomitra senegalensis*). I used museum specimens to describe duration, intensity and scheduling of molt in immature and adult males. I hypothesized that in these African Sunbirds 1) rainfall seasonality acts as a molt constraint and 2) molt intensity and duration differ between age groups. I found that while primary molt was initiated during the rainy season, body molt occurred at low intensities throughout the year. Age-based differences in molt intensity and duration were largely inconclusive. I also documented the occurrence of interrupted molt, which indicates that molt is energetically constrained. Low intensity and interrupted molt may be adaptive strategies which allow balance among molt, nomadic movements and opportunistic breeding in a changing and unpredictable environment.

PREFACE

Edited portions of this thesis will be submitted for publication in the Auk, a quarterly journal of ornithology published by the American Ornithologists' Union. Formatting for this thesis follows guidelines posed by the Auk and by the Graduate School of the University of Memphis. Tables are interspersed within the text and figures are placed in an appendix following the text.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Delayed plumage maturation: definition and hypotheses. - Delayed plumage maturation (DPM) is a phenomenon in which a male bird retains a dull (i.e. more cryptic) subadult plumage over its first winter and the following breeding season or longer. Curiously, these males in their first breeding season are often sexually mature and can potentially produce their own offspring (Rohwer et al.1980, Procter-Gray and Holmes 1981, Flood 1984, Foster 1987). This raises questions about the adaptive significance of the dull plumage and the selective pressures that influenced its evolution.

Early studies of DPM produced a number of hypotheses regarding its evolution through both behavioral (Lyon and Montgomerie 1986) and physiological selective pressures (molt constraint hypothesis: Rohwer and Butcher 1988). These hypotheses are commonly split into two groups: summer and winter adaptation hypotheses. Summer adaptation hypotheses (SAH) suggest that retention of the female-like plumage during the young male's first summer is naturally selected for because of forces that are present during the first breeding season (for reviews on these hypotheses see Lyon and Montgomerie 1986 and Montgomerie and Lyon 1986). These include, among others, the cryptic hypothesis, the status-signaling hypothesis, and the female mimicry hypothesis. The cryptic hypothesis explains that dull plumage is less visible to predators and will be selected for despite its negative effect on the first summer breeding success (Rohwer 1983). The status-signaling hypothesis, suggests that the dull plumage is an honest signal of subordinance to adult males (Rohwer 1975, Ketterson 1979, Rohwer and Ewald 1981, Lyon and Montgomerie 1986, Conover et al. 2000, Vergara 2007). Finally, the female mimicry hypothesis (Rohwer et al. 1980, Rohwer 1983, Vergara 2007) proposes that the dull plumage of the young males fools adult males into believing the young males are actually females. As a result, the older males will not chase off the young males, which can then establish territories.

The winter adaptation hypotheses (WAH), on the other hand, suggest that sub-adult plumages are adaptive in the winter. These hypotheses are reviewed in Rohwer and Butcher (1988). Given that fitness gains derived from this dull plumage allow for better individual over-winter survival, it is possible to experimentally test the WAH. Although over-winter survival is relatively difficult to measure, it has been assessed in a study of North Island Robins (*Petroica longipes*; Berggren et al. 2004). That study found support for the WAH, although the authors note that current selective forces may be different than those that were responsible for the evolution of the trait.

This poses the question: why is the dull plumage retained during the breeding season if it is only adaptive during the winter? Rohwer and Butcher (1988) proposed the molt constraints hypothesis which suggests that energetic constraints have prevented the evolution of two (or more) complete body molts/year in some species. The process of molt is known to be energetically expensive: studies have found that basal metabolic rate increases during molt (reviewed in Payne 1972, see also Dietz et al. 1992, Lindström et al. 1993, Vezina et al. 2009, but not found in Brown and Bryant 1996). This rise in metabolic rate reflects not only the cost of protein (keratin) synthesis but also thermoregulatory costs (Lustick 1970, Vezina et al. 2009), and the recrudescence of the integument (i.e. pulp formation: this includes an increase in vascularization of activated feather follicles, and an increase in blood volume: see Lillie 1940, DeGraw and Kern 1985) (Payne 1972, Murphy and King 1992).

The energetic cost of feather synthesis differs among species (Lindström et al. 1993). In particular, bright plumages, and those that are high in melanin (as is the case for this study's focal species) may be even more energetically expensive to grow than dull female-like plumages. Studies have demonstrated a link between plumage brightness (quality) and the energetic state of an individual. For example, in Eastern Bluebirds (*Sialia sialis*), an increase in parental effort negatively affects the individual's ability to produce colorful plumage in the next successive molt (Siefferman 2005). Similarly, in Eurasian Kestrels the proportion of nestlings with predominantly gray coloration (greater melanin content) was higher in years with abundant prey (Fargallo et al. 2007).

If the molt constraints hypothesis accurately represents what happens in nature, how come so many individual birds are able to successfully grow bright breeding plumages (or in the case of the study species: colorful iridescent feathers and black/dark brown feathers with high melanin content)? An intuitive answer is that there are fundamental age-based differences that allow adults to over-come the energetic constraints. This may occur through increased foraging efficiency, which develops as juveniles grow into adults. These differences in foraging efficiency between juveniles and adults are a result of two main factors: maturity (of the beak, skeleto-muscular system, and neurological functioning) and experience (learning of foraging skills) (reviewed in Marchetti and Price 1989, see also Orians 1969, Watson and Hatch 1999, and Vanderhoff and Eatson 2008).

An important consideration in this study is the degree to which, and what aspects of molt, is heritable. Although research on this subject is not extensive, the conclusions that have been reached are consistent across studies and support the assumption that molt patterns are heritable traits (Berthold et al. 1994, Larsson 1996, Helm and Gwinner 1999). For instance, studies that cross-bred individuals from different populations of Blackcaps (*Sylvia atricapilla*) and Stonechats (*Saxicola torquata*) produced offspring with molt patterns that were intermediate to those of the parental populations (Berthold et al. 1994, Helm and Gwinner 1999, respectively). For the purpose of this study, I will assume that any molt patterns observed in the study taxa are affected by a combination of genetic inheritance and environmental effects.

Delayed plumage maturation and seasonality. - The traditional hypotheses to explain delayed plumage maturation are focused on temperate North American passerines and are categorized in a winter/summer seasonal context that is not applicable to tropical species. The molt constraint hypothesis in particular highlights how delayed plumage maturation may be a result of a young bird's inability to acquire the resources necessary to perform the energetically expensive act of molt. In this model, the dull plumage is adaptive during the winter, and limited resources (or a reduced capability to exploit the available resources) during this time prohibit an additional molt before the following breeding season.

The occurrence of delayed plumage maturation, however, has also been noted in species that reside outside of the temperate zone and do not experience a significant summer versus winter season. Numerous species of African Sunbirds, for example, exhibit delayed plumage maturation (Cheke et al*.* 2001). Many of these Sunbirds are found in the tropical and subtropical savannah regions of sub-Saharan Africa where seasons are largely identified by changes in rainfall. These seasonal changes in rainfall may create fluctuating resource availability. Individuals must then balance molt with other energy demanding life history events such as breeding and migration. One key focus of this study was to determine whether molt patterns in two species of African Sunbirds that exhibit delayed plumage maturation are constrained by rainfall patterns.

I hypothesize that rainfall patterns can indirectly act to constrain molt through its effects on resource availability. I further hypothesize that adults, who have more developed foraging skills (Marchetti and Price 1989) and are better able to secure resources, complete the energetically expensive act of molt more efficiently than do immature individuals. Any difference in molt intensity or scheduling would likely be related to a difference in the trade offs (such as delaying expensive plumage maturation to increase survival at the cost of reduced breeding fitness) inherent at different life stages.

Sub-Sahara Africa: overview and climate. - The tropical and subtropical savannah of Africa cover about 65% of the continent and occur in areas with strongly seasonal climates with well-defined wet and dry seasons (Adams et al*.* 1996). Continuous grass cover is characteristic, and tree/bush cover varies (Leroux 2001). Normal annual range in temperature across the savannah regions is small relative to temperate ranges. In areas just south of the Sahara Desert (10^{o} N to10^{o} S latitude) the temperature range between the hottest and coldest months is about 3-6^{o}C (5-10^{o}F). In southern African savannahs (about 10^{o} to 35^{o} S latitude), normal annual temperature range increases slightly to 6-11^{o}C (10-20^{o}F) except at the Kalahari Desert and basin region, for which the range is 11-22^{o}C (20-40^{o}F) (Veregin 2005).

Seasonality in these savannah regions is more strongly related to rainfall than temperature. In most savannah regions in Africa, there is a single wet season, with the exception of Eastern equatorial Africa, which has two wet seasons. Within the ranges of the study taxa there are areas that experience long dry spells (greater than six months) or short dry spells (three months) and significant amount of variation in average rainfall during any one month (Adams et al. 1996).

Study taxa. - The focal species for this study were two African passerines in the family Nectariniidae: *Chalcomitra amethystina* (Amethyst Sunbird) and *C. senegalensis* (Scarlet-chested Sunbird). These species are appropriate for a study of DPM because they are numerous, widespread across Africa (see Figs. 1 and 2 for distribution maps), and display DPM. Additionally, immature males of these species are readily distinguishable from adults and females (Cheke et al*.* 2001). The timing of breeding is variable across their ranges, and some may nest twice a year in six month intervals (Cheke et al. 2001). The Amethyst Sunbird is a nomad and partial migrant, while the migratory patterns of the Scarlet-chested Sunbird are complex and varied across its range with some groups remaining sedentary (Cheke et al. 2001). Both model species forage on insects and nectar (Cheke et al. 2001). Insect abundance increases during the savannah rainy season (Dingle and Khamala 1972) and according to a study of nectar availability and use by birds at Zaria, Nigeria (Pettet 1977), the Scarlet-chested Sunbird feeds on various nectar-producing plants species, switching to a different species when the flowering period of one species ends.

Molt and delayed plumage maturation in Sunbirds. - Relative to European/African migrants and North/South American migrants, little has been written about molt in African species. Mackworth-Praed and Grant (1945) used the British Museum Sunbird collection to report on molt in the Sunbirds of eastern Africa (Amethyst Sunbirds from Sudan, Kenya, Tanzania, Malawi, Mozambique, Zimbabwe and Zambia; Scarlet-chested Sunbirds from Eritrea, Ethiopia, Sudan, Uganda, Kenya, Tanzania, Democratic Republic of the Congo, Zambia, and Malawi). A review of molt in southern African passerines by Craig (1983) includes a brief summary of the molt of Scarlet-chested and Amethyst Sunbirds in Malawi. Molt information from the western parts of Africa is more limited as only one study on molt in Scarlet-chested Sunbirds at a single study site in Nigeria exists (McGregor et al. 2007). Figures 1 and 2 make note of regions (roughly) where molt has and has not been studied in these species.

The current published knowledge of molt and delayed plumage maturation will be introduced and summarized first for the Scarlet-chested Sunbird and then for the Amethyst Sunbird. Based on the following information, it is clear that molt patterns in these species merit further study to cover their entire ranges. Only such an effort will allow a broader picture that more conclusively describes molt patterns, sequence and variation.

Based on past publications it is uncertain whether or not molt is seasonal in the Scarlet-chested Sunbird. For example, Macworth-Praed and Grant (1945) and Craig (1983) concluded that there is no seasonal molt pattern in the Scarlet-chested Sunbird because there was evidence of molt throughout the year. McGregor et al. (2007), however, found that 73% of the Scarlet-chested Sunbirds of the Amurum Community Forest Reserve in Nigeria (09°52'N 08°58'E) molted during the dry season and estimated primary molt duration at 248 days.

Other molt patterns of note include the possible existence of an eclipse plumage and interrupted molt in Scarlet-chested Sunbirds. In this species there are reports of males in a nonbreeding "eclipse" plumage that resembles the dull-female plumage (Craig 1983, Cheke et al. 2001). Other publications, however, state that males molt from one bright breeding plumage to the next without a dull non-breeding plumage (Mackworth-Praed and Grant 1945, del Hoyo et al. 2009). Interrupted molt was reported to be common in remiges as a centrifugal pattern of tail molt was noted: this pattern, in which the innermost feathers are lost first and proceed to the outermost, is common to most passerines (Niles 1972, Ginn 1975, Pyle et al. 1987).

In regards to delayed plumage maturation, Craig (1983) reported that the male Scarlet-chested Sunbirds in Malawi undergo two complete molts before they acquire definitive adult plumage at about two years of age. Cheke et al. (2001) described the gradual transformation into adult plumage with some of the red feathers appearing first, then a blotchy body with the metallic crown feathers appearing last.

In the Amethyst Sunbird, Mackworth-Praed and Grant (1945) concluded that there is no seasonal molt pattern because in southeastern African countries molt was recorded in most months of the year (e. g., Malawi: February, May, and June; Mozambique: January, March, and July; Zambia/Zimbabwe: April, May, August, and September). Craig (1983) suggested that adults in Malawi may undergo two molts per annual cycle: once from April to June and again in December and January. Juvenile Amethyst Sunbirds of Malawi are thought to go through two complete molts before they attain the definitive adult plumage (Craig 1983). No references to eclipse plumages in the Amethyst Sunbird have been noted with the exception of Cheke et al. (2001) who reported an eclipse plumage in a captive male.

At a broader level, African Sunbirds (family *Nectariniidae*) are an interesting family in which to study delayed plumage maturation because there is a considerable amount of variability in both the occurrence of delayed plumage maturation and non-breeding plumages. With regard to molt schedule and plumage types, African Sunbird species can be classified into three groups (Mackworth-Praed and Grant 1945, Cheke et al. 2001, del Hoyo et al. 2009). Males of species in the first group do not have an intermediate immature plumage (~24 species see Appendix B). The young males of this group molt directly from juvenile plumage into breeding plumage and there is no evidence of delayed plumage maturation. This group is also characterized by the presence of an eclipse plumage during the non-breeding season.

Species of the second group have an intermediate immature plumage that is similar to the dull plumage of the females, but do not have an eclipse plumage (~ 14 species, see Appendix B). They molt from breeding plumage to breeding plumage as adults. According to Mackworth-Praed and Grant (1945), both the Amethyst Sunbird and the Scarlet-chested Sunbird are included in this group.

The final group is made up of species that lack both delayed plumage maturation and eclipse plumage (~70 species, see Appendix B). Humphrey and Parkes (1959) noted that "This family thus presents one of the most challenging problems in the study of plumage succession."

Significance. - Tests of the molt constraint hypothesis have focused largely on species from temperate localities where seasonal temperature changes create limitations on timing of annual events such as breeding, migrating, and molting as a function of fluctuations in resource availability. DPM, however, also occurs in bird taxa with geographic ranges that are characterized by stable (by comparison) seasonal temperatures. This suggests that other variables may also constrain molt. This study investigates the degree to which molt is constrained by seasonal rainfall. If molt is constrained by rainfall then perhaps the molt constraints hypothesis can be applied to explain (in part) DPM of taxa in the savannah regions.

METHODS

I used museum specimens to describe the sequence and patterns of molt in both Sunbird species across their ranges. The molt data were also paired with publicly available climate data to test for correlations between molt and climatic variables, such as amount of rainfall.

Molt nomenclature. - Molt terminology follows Humphrey and Parkes (1959), with modifications from Rohwer et al. (1992). This terminology names molts by the plumage (or feather generation) that they produce with clarity because these terms are independent of seasons, reproductive status, and age of the bird (Palmer 1972). For example, instead of classifying a two-molt cycle as "pre- and post-nuptial" molt (Dwight 1900), these molts are referred to as "prebasic" (gives rise to the basic plumage) and "prealternate" (gives rise to the alternate plumage). When there is only one molt per cycle, it is said that the bird molts from basic to basic plumage.

Museum specimens. - I examined 470 male specimens (167 *C. amethystina* and 303 *C. senegalensis*). Some specimens were acquired on loan from the Field Museum of Natural History and the Los Angeles County Museum of Natural History. I measured the remaining specimens on site at the Natural History Museum at Tring in the United Kingdom. I took several molt and morphological measurements and recorded associated locality and date as noted on each specimen tag. Morphological measurements included the lengths of the right tarsus, right wing, and tail, as well as several bill measurements (length, depth, and width). Measurements were taken with digital calipers as described in Pyle et al. (1987). Specific molt scoring methods are to follow.

If no latitude/longitude coordinates were noted on the specimen tag, I approximated these coordinates with the available locality data and the use of Google Maps (http://maps.google.com/). If no specific locality could be conclusively identified based on the locality data, then the specimen was not included in any climate-related analyses. If a specimen had no collection date noted on the tag it was excluded from all analyses.

Species identification, nomenclature, and aging. - Species identification, nomenclature, and aging followed Cheke et al*.* (2001). Both species are sexually dimorphic, show geographic variation, and males exhibit delayed plumage maturation.

The Amethyst Sunbird nominate adult male has a blackish-brown plumage with an iridescent coppery-purple throat and shoulders. The crown has a large light green patch with a silvery sheen. The immature male displays a subadult plumage that is similar to the female (grayish-brown above, pale gray-below with mottling) but is easily distinguished by its purple throat.

The Scarlet-chested Sunbird nominate adult male also has a blackish body, but has a vermillion breast and the crown, throat, and malar stripe are metallic green. This species can be confused with the mostly allopatric, but closely related Hunter's Sunbird (*C. hunteri*). Hunter's Sunbird can be distinguished by its iridescent violet upper-tail coverts.The immature nominate male Scarlet-chested Sunbird has a subadult plumage with dull brown above and pale yellow belly with brown mottling. The immature male can be distinguished from the adult female by its red breast, metallic green chin, and green throat (Cheke et al*.* 2001).

Both the Amethyst and Scarlet-chested Sunbirds display geographic variation in plumages. These plumage variations are reflected in the subspecific divisions and nomenclature. Each specimen used in this study was identified to subspecies to investigate any differences in molt patterns at this level.

The Amethyst Sunbird has three recognized subspecies divisions: *C. a. amethystina*, *C. a. deminuta,* and *C. a. kirkii*. *C. a. deminuta* differs slightly from *C. a. amesthystina* by its shorter bill while *C. a. kirkii* males lack the purplish-violet plumage coloring of the upper-tail coverts, which is present in the other two subspecies (Cheke et al*.* 2001). Delineated range maps show the approximate ranges of the subspecies (see Fig. 1 and 2).

The Scarlet-chested Sunbird (*C. senegalensis*) has five designated subspecies: *C. s. senegalensis*, *C. s. acik*, *C. s. cruentata*, *C. s. gutturalis*, and *C.s. lamperti* (see Fig. 1 and 2). All groups have the characteristic red breast, green crown, and green moustacials. Two subspecies, however, *C. s. gutturalis* and *C. s. cruentata*, are unique because they have a metallic violet shoulder-spot on the lesser wing coverts. Additionally, *C. s. cruentata* has a black throat which distinguishes it from all other subspecies. The nominate differs from *C. s. acik* and *C. s. lamperti* by its heavier metallic blue barring on the chest. *C. s. acik* and *C. s. lamperti* are the most difficult to differentiate. Reportedly, *C .s. acik* has a shorter bill than *C. s. lamperti* (Cheke et al. 2001), but I found considerable overlap in bill size where their ranges meet so I am, therefore, unsure of the validity of this measure in designating subspecies status. As a result, I was unable to assign to subspecies a number of specimens that could have been either *C. s. acik* or *C. s. lamperti*.

Molt scoring. - Scoring of molt follows Rohwer (1986; see also Voelker and Rohwer 1998) with a few alterations. Specimens were closely examined under a magnifying lamp and a forceps or probe was used to gently lift feathers and locate emerging feathers. I estimated percentage of feather re-growth on the body, wings, and tail. Molt of flight feathers (both remiges and rectrices) were scored on a scale from 0 to 1.0. A score of 0 indicates an old feather, and scores between 0.1 and 1.0 represent the fraction of growth that the bird had completed at the time of its collection. For example, if a new flight feather had grown to half of its possible length it would be assigned a score of 0.5. All primaries (except P10 which is significantly reduced in size), secondaries, tertials, and rectrices were scored. Total primary molt scores (sum of all individual primary feather scores) and total flight feather scores (sum of all individual flight feather scores) were calculated for each specimen.

For molt occurring in the remaining feathers, I focused on seven areas: the throat/chin/malar/moustache area, breast, belly, crown, back, rump/upper tail coverts, and wing coverts. Unlike in Rohwer (1986), tail and wing coverts are included because both areas display color variations that partly differentiate sub-species in both study species and also because these regions may play an important role in signaling. I estimated the percentage of emerging feathers and score the feathers in these seven areas using the following scale: 0 = no emerging feathers, 10 = 1-20% of feathers in development, 30 = 21-40% of feathers in development, 50 = 41-60%, 70 = 61-80%, and 90 = 81-100%. Accidental feather loss indicated by distinctly non-symmetrical loss in flight feathers, and small patches of emerging feathers of all the same age (Rohwer 1986) were excluded from the molt score estimations. An average body molt score (the average of all seven body area molt scores) was calculated for each specimen.

Climate data. - Climate data made public by the Climatic Research Unit of the University of East Anglia was used to investigate possible correlations between molt and climate variables (see http://www.cru.uea.ac.uk/). I used the CRU TS 2.1 dataset which is a global 0.5^o resolution grid that covers the global land surface (Mitchell and Jones 2005). It has both temperature (daily minimum, maximum, and average) and precipitation data that are interpolated from station data. Monthly values are available for each grid point for the years 1901-2002 which covered the majority of the specimens assessed. I chose to use these interpolated data because actual site measurements are localized and do not adequately cover the large ranges of the study taxa.

Each grid point of the globe for this dataset is assigned an (x,y) coordinate, allowing the latitude/longitude coordinate for each specimen to be 'transformed' to the (x,y) CRU TS 2.1 coordinate. I then extracted the climate data of interest for each specimen including: the amount of precipitation in the month prior to collection and the minimum daily temperature of the month the specimen was collected.

Analyses: general molt study. - I estimated general patterns of body feather replacement and described flight feather molt series in both immature and adult male Amethyst and Scarlet-chested Sunbirds. By definition, a flight feather molt series can be described by a single replacement rule (Langston and Rohwer 1996, Voelker and Rohwer 1998). If a feather or group of feathers is not replaced according to the rule that describes the replacement of the remainder of the series then that feather or feather group is categorized as a separate molt series. For example, Langston and Rohwer (1995) found that Laysan (*Diomedea immutablis*) and Black-footed Albatrosses (*Diomedea nigripes*) replace their primaries in two molt series. In these species primary molt initiates in the middle (the nodal feathers vary) and proceeds bidirectionally (i.e. the outer feathers are replaced in a proximal to distal pattern and the inner primaries are replaced distal to proximal). In passerines, it is common for the primaries P1-P9 to consist of one molt series.

Molt series in the study species were established following the technique by Yuri and Rohwer (1997) and as used in Voelker and Rohwer (1998). Each growing (focal) feather was categorized into one of four groups: 1) nodal, 2) terminal, 3) proximal to distal and 4) distal to proximal. A feather that is the first to be replaced in a molt series is categorized as the “nodal feather,” which in the case of passerine primaries is often the P1 feather. The “terminal feather” is the last feather to be replaced in a molt series. The other two categories describe the direction of growth in the series: proximal to distal (inner feathers of the series that are closer to the body are lost and grown first) or distal to proximal (outer feathers further from the body are lost and grown first). Directionality can be determined by observing adjacent feathers. If for example, the focal feather P4 is half grown, P5 is worn and P3 is fresh then it is clear that P4 should be placed in the proximal to distal category (Yuri and Rohwer 1997, Voelker and Rohwer 1998).

I also assessed the timing of primary molt in relation to body molt. Primary molt score was plotted against body molt score for each species (separately). Only specimens in the process of molting their primaries were included in this analysis (follows Yuri and Rohwer 1997).

Analyses: primary molt duration. - I estimated the duration of primary molt in the study taxa by using Pimm’s (1976) regression method as used in Voelker and Rohwer (1998). Various groupings of specimens were used to best determine molt duration in these widespread species and to detect potential differences in molt duration. Only specimens with a primary molt score of > 0 were included in the analyses. Specimens with accidental molt (any feathers growing out of sequence or non-symmetrically) were excluded from these analyses.

First, I grouped specimens by subspecies and considered age groups (immature and adult specimens in prebasic molt) separately. Because this resulted in some groups with very small sample sizes I next grouped specimens simply by species. The molt patterns in this large grouping of Scarlet-chested Sunbirds were difficult to interpret, likely because the latitudinal range of the Scarlet-chested Sunbird extends considerably above and below the equator (*C. amethystina* specimens ranged from 34.0^{o} S to 2.3^{o} N latitude while *C. senegalensis* specimens ranged from 25.4^{o} S to 15.1^{o} N latitude). Latitudinal variation in molt has been shown in other species (Mewaldt and King 1978). In the sunbird ranges, northern-most latitudes experience the height of the rainy season in August and September, while the southern-latitudes rainy season occurs in December and January (Thompson 1975). In light of this I ran additional regression analyses on these individuals after assembling them into northern and southern groups (i.e. north or south of the equator).

Analyses: molt intensity. - I also described a related aspect of molt duration, which is molt intensity (defined for this study as the number or % of feathers growing in at one time). I compared the average body molt scores (which reflect the % of body feathers on a specimen that were growing at the time of collection) with a t-test using SPSS 16.0 (SPSS for Windows 2007), and took into account whether or not the assumption of equal variance was met when drawing conclusions.

Analyses: seasonality of molt and relation to climate variables. - To illustrate whether or not molt was seasonal in the Amethyst or Scarlet-chested Sunbird, I plotted molt score (body and primaries) against the day of year the specimen was collected. If molt is seasonal (whether because of climate or in avoidance of a breeding season) then body molt scores of individuals should approximately initiate, peak and taper off in concert. The relationship of primary molt scores should be linear (Pimm 1976).

Following this, I used multiple regression to predict molt score (dependent variable) in response to two climate variables: precipitation and minimum temperature. The precipitation variable represents the total amount of precipitation in the month prior to month the specimen was collected. This variable was selected because there is probably a lag between rainfall and resource availability which results from rainfall. The minimum temperature variable is the minimum daily temperature of the month the specimen was collected. If one of the variables was not significantly correlated with primary molt score then it was removed from the model. I grouped specimens by species and lumped adult and immature specimens (those in the first prebasic molt) together.

When using multiple regression analysis, I checked for multicollinearity. Multicollinearity of variables is a concern because it can inflate the variance of regression coefficients. This can result in the erroneous exclusion of significant predictor variables when building the model

(Legendre and Legendre 1998, Graham 2003). I used the Variance Inflation Factor (VIF) to determine in each model if minimum temperature and precipitation were collinear. VIF thresholds of 4 and 10 are suggested in the literature (O'Brien 2007). The VIF in the models reported in this study were all around a score of one, well below either of the suggested thresholds. Therefore, multicollinearity was not a concern for this study.

RESULTS

General molt study. - Flight feathers in both the Scarlet-chested and Amethyst Sunbird were replaced in patterns that are common to passerines. Primaries are replaced in a descending mode (proximal P1 to distal P10, see Table 1) while secondaries are replaced starting with S1 moving sequentially inward to S6 (Table 2). The order of tertial replacement can vary, but the central S8 is commonly lost first before S7 and S9 (Table 2). S7 and S9 may grow simultaneously or sequentially, often with S9 more advanced than S7. S8 is often growing simultaneously with S1, and is generally slightly advanced. Growth of S9 was observed when S1 and S2 were growing. When replacement of S7 follows S9 rather than simultaneous replacement, S7 is seen growing at the same time as S2-S5, but most commonly with S3 or S4.

TABLE 1. Primary feather replacement sequence in Amethyst and Scarlet-chested Sunbirds. (Procedure follows Yuri and Rohwer 1997, Voelker and Rohwer 1998.) The numbers represent the number of specimens found displaying the noted feather replacement pattern. Note that P1 and P2 seem to have been dropped at the same time in *C. amethystina* FMNH201896.

	Focal feather								
	P1	P2	P3	P4	P5	P6	P7	P8	P9
Amethyst Sunbird (*Chalcomitra amethystina)*									
Proximal to distal		3	8	2	10	4	12	12	
Distal to proximal									
Nodal feathers	3	1							
Terminal feathers									16
Scarlet-chested Sunbird (*Chalcomitra senegalensis)*									
Proximal to distal		7	11	9	9	11	10	11	
Distal to proximal									
Nodal feathers	6								
Terminal feathers									25

TABLE 2. Secondary feather replacement sequence in Amethyst and Scarlet-chested Sunbirds. (Procedure follows Voelker and Rohwer 1998, and Yuri and Rohwer 1997.) The numbers represent the number of specimens found displaying the noted feather replacement pattern.

	Focal feather								
	S9	S8	S7	S6	S5	S4	S3	S2	S1
Amethyst Sunbird (*Chalcomitra amethystina)*									
Proximal to distal									
Distal to proximal		2			6	11	10	2	
Nodal feathers		4	2						5
Terminal feathers	5		15	7					
Scarlet-chested Sunbird (*Chalcomitra senegalensis)*									
Proximal to distal		1							
Distal to proximal					13	15	7	9	
Nodal feathers	1	14	3						15
Terminal feathers	7	3	6	21					

In general, rectrices are replaced centrifugally (central R1 to outer R6, see Table 3). A few Scarlet-chested Sunbird specimens proved to be exceptions to this pattern as they showed evidence of rapid loss of the central R1 and R2 feathers, appearing to have been dropped at the same time (FMNH399628, FMNH206261, FMNH117211, and FMNH439376). Two specimens showed evidence that R6 was dropped prior to R5 while R4 was growing (*C. senegalensis* BMNH 1915.12.24.1125 and *C. amethystina* BMNH 1905.12.29.1675). In these cases R6 was categorized as nodal and as a separate molt series. One *C. amethystina* specimen (BMNH 1933.7.14.392) had an exceptionally strange molt sequence as R1 was half grown, with R2 missing, worn R3 and R4, R5 nearly fully grown, and R6 full-grown. While this pattern could have been the product of accidental loss, it should be noted that the pattern was symmetrical, so it may in fact be an anomaly.

Flight feather molt in general was symmetrical; however, it was not uncommon for one side to be slightly more advanced than the other. I found no evidence to support the existence of eclipse plumages in either of these species (i.e., no male in the definitive basic plumage was ever recorded growing any dull female-like plumage). Most birds (immature and adults combined) in the process of primary molt were also molting body feathers (Amethyst Sunbird 89%, Scarlet-chested Sunbird 88%, Fig. 3).

TABLE 3. Tail feather replacement sequence in Amethyst and Scarlet-chested Sunbirds. (Procedure follows Voelker and Rohwer 1998, and Yuri and Rohwer 1997.) The numbers represent the number of specimens found displaying the noted feather replacement pattern.

	Focal feather					
	R1	R2	R3	R4	R5	R6
Amethyst Sunbird (*Chalcomitra amethystina)*						
Proximal to distal		3	8	9	7	
Distal to proximal					1	
Nodal feathers	5					2
Terminal feathers						5
Scarlet-chested Sunbird (*Chalcomitra senegalensis)*						
Proximal to distal		11	9	10	11	
Distal to proximal						
Nodal feathers	13	4				1
Terminal feathers					1	5

Before going into detail about the body molt sequence in the study species it is important to note that the progression through these body molt sequences when viewing each species as a whole was evident throughout the year (Fig. 4 and Fig. 5). This is likely attributable to the wide-distributional range of both species and how they experience seasonal changes at different times, but the low intensity of molt may also play a part.

In the male Amethyst Sunbird the molt sequence is as follows: the natal downy feather coat is replaced in the prejuvenal molt by the first true feather coat, the juvenal plumage. These feathers are all female-like and none resemble the definitive adult male feather coat. Part or all of this plumage is replaced by a supplemental plumage through a presupplemental molt. During the presupplemental molt all body areas observed in specimens were growing dull female-like feathers except the throat which was growing iridescent purple feathers that resemble those of the definitive adult male feather coat. The following prebasic molt replaces all the crown, breast, belly, back, rump, and wing coverts and also replaces all or part of the throat feathers. Only one specimen in prebasic molt was observed growing female-like dull feathers. These brownish-yellow feathers were growing on the rump of this specimen, but not in any other body area. Once the definitive basic feather coat is attained, the adult males transition from one basic plumage to the next basic plumage. These low intensity molt transitions were observed throughout the year, though sampling of juveniles is sparse at the beginning and end of the year (Fig. 4A). This could correlate with breeding season patterns. There are also very few samples of immature specimens from mid-July to the end of October.

The molt sequence in the male Scarlet-chested Sunbird is much the same: natal plumage is lost through the prejuvenal molt and this first set of true feathers is the juvenal plumage. The juvenal plumage is replaced by the supplemental plumage in a presupplemental molt. In regards to delayed plumage maturation hypotheses it is important to note that during the presupplemental molt some or all of the juvenal belly, crown, back, rump, and wing coverts are replaced with fresh female-like feathers. The new supplemental feather coat of young males is set apart from the female plumage by a red chest and green throat. This red chest of the immature males, however, is not as extensive as in adult males.

The next molt that occurs is the sequence is the prebasic molt that will result in the definitive adult male plumage. All of the female-like dull gray-brown feathers of the crown are replaced with green feathers and the remaining brown or mottled yellow feathers are replaced with black, dark brown, or reddish brown feathers (geographic variation). Some or all the breast, throat, and moustachial feathers are replaced.

Unlike in the Amethyst Sunbird, the occurrence of interrupted molt is relatively common in young male Scarlet-chested Sunbirds in subadult plumage. Out of 39 male Sunbirds recorded in the process of prebasic molt, 14 (36%) showed evidence of interrupted molt (Table 4). Interrupted molt is often associated with migration (or nomadic movements), and opportunistic breeding (Avery 1985, Thompson 1988, Young 1991, Craig 1996). The presence of interrupted molt in the scarlet-chested sunbird indicates the presence of a molt constraint.

TABLE 4. Breakdown of interrupted prebasic molt observed in Scarlet-chested Sunbirds

Number of specimens	Interrupted molt observed
2	Flight feather molt in progress, but body molt interrupted
2	Body feather molt in progress, but flight feather molt interrupted
4	Interrupted body molt with all fresh or all worn flight feathers
6	Interrupted body and flight feather molt

There were also a few specimens that are worth mentioning specifically because they do not fit the predominant molt sequence. One individual seemed to skip the presupplemental molt and supplemental plumage and go straight into prebasic molt (*C. s. cruentata* BMNH 1946.5.2637). The first red chest feathers were emerging at the same time the black belly, back, rump, and wing covert feathers in this specimen. Also out of the ordinary were two specimens that were in the process of presupplemental molt in all body areas, but were also growing green crown feathers (*C. s. lamperti* FMNH 117260 and *C. s. gutturalis*: FMNH 202033). The appearance of these green crown feathers was abnormal because they generally first appear in the prebasic molt.

Age class comparisons: primary molt duration. - In my initial attempts to estimate molt duration in adult and immature Sunbirds I grouped individuals first by subspecies and later by 10^{o} latitude blocks. Sample sizes for the immature individuals were too small to estimate molt with these divisions. Molt duration could be estimated for some groups of adults, but was not possible for all groups (Tables 5 and 6). The small sample sizes in each of these groups are a concern and may have resulted in erroneous duration estimations.

When the Amethyst Sunbird specimens were all grouped together there was a clear linear primary molt score trend (Fig. 6A). Duration of adult primary molt was estimated to be 141 days (Feb 9 to Jun 30). Sample sizes for the immature Amethyst Sunbirds in prebasic molt when grouped in any way were too small to estimate the duration of molt with any regression models. Primary molt patterns for Scarlet-chested Sunbirds were unclear when all were grouped together (Fig. 6B), but it was possible to estimate molt duration for both adult and immature Scarlet-chested Sunbirds when they were partitioned into north and south (of the equator) groups (Fig. 7). When broken into these groups it was evident that molt wrapped around from one year and into the next which necessitated data adjustment to clarify the linear pattern of primary molt.

In the northern adult Scarlet-chested Sunbirds, molt was estimated to take 244 days to complete (June 7 to February 6) while in immature birds molt took nearly a year to complete (358 days; April 29 to April 22 of the following year). In the southern hemisphere adults, molt duration was calculated to be over a year (416 days) but was estimated at only 172 days in immature specimens. There was a lack of immature specimens in early stages of primary molt in the southern group, however, so this estimation may be erroneous.

Age class comparisons: molt intensity. - To determine whether molt intensity differed between adult and immature Amethyst Sunbirds I used a t-test to compare mean molt intensity in each group. There was no statistical difference in molt intensity between these groups (adult n = 77, $\bar{x}$ = 8.5; immature n = 24, $\bar{x}$ = 6.1; P = 0.127 where unequal variance was assumed). The Scarlet-chested Sunbirds shows a similar story. There is no statistical difference in the molt intensity of body feathers between adult and immature individuals (adult n = 109, $\bar{x}$ =6.7; immature n = 45, $\bar{x}$ = 6.6; P = 0.907 equal variances assumed). So both the adults growing dark melanin dense feathers and more extensive patches of iridescent feathers and the immature individuals growing light grayish brown feathers and some smaller iridescent patches showed similar intensities of molt. It is interesting to note on average, the individuals in the process of molting their body feathers were actively growing less than 10% of their feather coat at any one time. This is relevant to the molt constraint discussion

Note that the specimens used for this test were collected during many different months of the year, but collection bias likely resulted in a nonrandom sampling throughout the year. This may have affected the outcome. These results should be regarded as preliminary and not conclusive.

Seasonality of molt and relation to climate variables. - Figures 8 and 9 illustrate the precipitation patterns throughout the year. These graphs were made by plotting the amount of estimated rainfall in the month of the year the specimen was collected. The patterns for the Amethyst Sunbird, although assembled from dates over a span of a hundred years, still fit the expected characteristic average rain patterns with rainy seasons just below the equator around March and November (Fig. 8A), heavy rains in January for between 10 and 20 degrees south latitude (Fig. 8B), and much smaller relative rainy peaks in the very southern tip of Africa (Fig. 8C). Rain patterns experienced by the Scarlet-chested Sunbird also match expectations.

TABLE 5. Summary of molt duration in each subspecies

Subspecies	N[a]	Ex[b]	Sig[c]	Equation[d]	Start[e]	End[f]	Length[g]
C. a. amethystina	3	16	-	-	-	-	-
C. a .deminuta	9	24	P = 0.036	D = 5.149m + 94.952	Day 95: Apr 5	Day 187: July 6	92 days
C. a. kirkii	20	36	P = 0.048	D = 8.249m + 37.386	Day 37: Feb 6	Day 186: July 5	149 days
C. s. acik	4	27	-	-	-	-	-
C. s. cruentata	9	28	P = 0.044	D = 6.967m + 287.01	Day 287: Oct 14	Day 47: Feb 16	125 days
C. s. gutturalis	9	48	-	-	-	-	-
C. s. lamperti	4	22	-	-	-	-	-
C. s. senegalensis	8	35	P = 0.003	D = 10.064m + 202.123	Day 202: Jul 21	Day 18: Jan 18	181 days

[a] N = the number of individuals actively molting primaries
[b] Ex = the number of individuals not molting and excluded from the analyses
[c] Sig = the P value of the regression model
[d] Equation = the regression equation that describes the relationship between primary molt score and day of year where D = day of year and m = primary molt score
[e] Start = the approximate date primary molt is initiated
[f] End = the approximate end date of primary molt
[g] Length = the estimated duration of primary molt

TABLE 6. Summary of molt duration in each species grouped by latitude

Species	Latitude range	N[a]	Ex[b]	Sig[c]	Equation[d]	Start[e]	End[f]	Length[g]
C. amethystina	0 to -10	7	16	-	-	-	-	-
	-10 to -20	11	27	P = 0.002	D = 10.551m + 13.44	Day 13: Jan 13	Day 203: Jul 22	190 days
	-20 to -30	4	13	-	-	-	-	-
C. senegalensis	20 to 10	7	31	P =0.000	D = 18.851m +97.828	Day 98: Apr 8	Day 72: Mar 13	339 days
	10 to 0	8	38	-	-	-	-	-
	0 to -10	7	78	-	-	-	-	-
	-10 to -20	3	10	-	-	-	-	-

[a] N = the number of individuals actively molting primaries
[b] Ex = the number of individuals not molting and excluded from the analyses
[c] Sig = the P value of the regression model
[d] Equation = the regression equation that describes the relationship between primary molt score and day of year where D = day of year and m = primary molt score
[e] Start = the approximate date primary molt is initiated
[f] End = the approximate end date of primary molt
[g] Length = the estimated duration of primary molt

Plotting body molt score against the day of year with specimens split into 10° latitude blocks showed relatively low intensity body molt (mostly scores of 15 and lower) throughout the year with a few exceptions in both species. For Amethyst Sunbirds at 10 to 20° S there was a spike in the body molt scores (up to a score of about 30) in July (Fig. 10A) and at 0 to 10° S latitude there was a spike in late February/early March (Fig. 10B). A few Scarlet-chested Sunbird specimens had higher molt (scores of about 20) from between May to July at latitudes 10 to 0° N (Fig. 10C). Just a bit below the equator from 0 to 10° S in the Scarlet chested Sunbird there was one adult with pronounced molt in December (score of 50) and a few other adults with extensive molt in March (scores of 25; Fig. 10D).

Scheduling of primary replacement during the first prebasic molt (immature birds), and definitive prebasic molt (adults) are compiled and shown graphically in figure 6A for Amethyst Sunbirds and in figures 6B and 7 for Scarlet-chested Sunbirds. Immature and adult birds are shown together in each figure for comparison. Note that the day of year (independent) is plotted on the y-axis and primary molt score on the x-axis following Pimm (1976) for the estimation of molt duration.

After plotting the primary molt against day of year to assess yearly molt patterns, multiple regression analyses were performed to check for any specific correlations of primary molt score with two climate variables: minimum temperature and precipitation. In Amethyst Sunbirds primary molt score showed a slightly negative relationship (coefficient = -0.033) with precipitation (n = 23, P = 0.02, R^2 = 0.209) and was not significantly related to minimum temperature. Body molt score in Amethyst Sunbirds was not related to either climate variable. Primary molt score in Scarlet-chested Sunbirds also showed a slightly negative relationship (coefficient = -0.353) with precipitation (n = 46, P = 0.016, R^2 = 0.124), and no significant relationship with minimum temperature.

In conclusion, primary molt score in both the Amethyst and Scarlet-chested Sunbirds is significantly related to preciptation but not minimum temperature, but relatively little variation in primary molt score can be described by this climate variable (R^2 values = 0.209 and 0.124

respectively). There is a slight response to seasonal change in rainfall: individuals initiate molt in times when there is relatively more precipitation and as molt progresses, precipitation decreases.

DISCUSSION

Molt sequence. - Primaries in both study species were molted in a simple descendent sequence that is common in passerines (Voelker 2000, Yuri and Rohwer 1997). Complex patterns, such as stepwise, multiple series, and repeated molt have been described in larger nonpasserines including a number of seabirds (cormorants, tropicbirds, terns, pelicans, frigatebirds and solids, see Bridge 2006; and alcids, see Thompson et al. 1998), as well as in falcons and parrots (Stresemann and Stresemann 1960, and Forshaw and Cooper 1989 respectively as cited in Thompson et al. 1998). In stepwise molt a second wave of primary molt initiates before the first is completed (Langston and Rohwer 1995). Repeated molt describes a pattern where a variable number of remiges are molted two or three times in a year (Bridge et al. 2007). Multiple series molts have also been described where two molt series (initiating at different nodal feathers) proceed simultaneously. These complex primary molt strategies create smaller gaps in the wing during molt. It is suggested that these patterns may have evolved in response to flight inefficiency pressures (Bridge 2006) which may not have a great effect on smaller birds such as Sunbirds.

In both study species body molt sequence initiates with the natal feather coat which is replaced by the juvenal plumage by the prejuvenal molt. This plumage is lost in the presupplemental molt which produces the supplemental plumage. The definitive prebasic molt follows, replacing all remaining dull female-like feathers with the definitive adult plumage. Adults molt from one basic molt to the next. The majority of birds molting primaries were also molting body plumage. I did not record any evidence of an eclipse plumage in either species. Molt sequence had not previously been studied in this detail in Sunbirds. It would be interesting to find out if closely related species in the genus Chalcomitra, such as Hunter's Sunbird (*C. hunteri*), the Green-throated Sunbird (*C. rubescens*) and Socotra Sunbird (*C. balfouri*) show the same body molt sequence. While these species all lack an alternate (non-breeding/eclipse) plumage, unlike the others, the Socotra Sunbird does not have an immature (supplemental) plumage (See Appendix B and the sources cited within).

The nomenclature listed here for the sequence of body molt may need to be adjusted in regards to homology and the complexity of molt sequence patterns in the family of Sunbirds. According to Humphrey and Parkes (1959), it may be that the basic plumage has been completely suppressed in some Sunbirds, which may be the case in the Amethyst and Scarlet-chested Sunbird. Further study on a broader range of molt sequences in Sunbirds is in order.

Primary molt duration. -In the northern Scarlet-chested Sunbirds, primary molt duration appears to be longer in immature birds than in adults, and is initiated earlier. This is consistent with this study's consideration of the molt constraint hypothesis and age-based differences in foraging efficiency. It could also indicate that adults are under a more intense molt constraint than immature birds. It is likely that is more common for immature Sunbird males to be nonbreeders relative to adults. Adults may need to finish molting faster than immature birds to prevent the overlap of the costly efforts of molt and breeding. In Cassin's Auklet, for example, primary molt in the post-breeding season occurs earlier in nonbreeders (Payne 1965, Emslie et al. 1990).

While a thorough comparison of molt duration between adult and immature Sunbirds in all groups could not be completed as a result of small sample sizes: it is still interesting to consider the molt duration in the adults. Duration of molt shows considerable variation both among and within species (Keast 1968, Payne 1972, Mewaldt and King 1978, Emslie et al*.* 1990, Voelker 2004).

When Amethyst Sunbirds were all grouped together, primary molt duration was estimated at 141 days while in the Scarlet-chested Sunbird molt duration lasted 244 days in the northern latitudes and 358 days at southern latitudes. McGregor et al*.* (2007) estimated the duration of molt in the Scarlet-chested Sunbird to be 246 days long, which is very close to my estimate of northern latitude birds. The authors also considered the molt duration of the Green-headed Sunbird (*Cyanomitra verticalis*) and estimated it to be 181 days. Somewhat amazingly they found the Variable Sunbird (*Cinnyris venustus*) to have a molt duration of only 36 days. Craig's (1983) summary on molt in southern African passerines does not have an estimate of duration of wing molt in either of this study's focal species, but he reports an estimated wing molt duration for two other sunbird species, the Coppery Sunbird and the Yellowbellied (Variable) Sunbird. In the Coppery Sunbird (*Cynnyris* (*Nectarinia) cuprea*) wing molt lasts about 200 days. In the Yellowbellied Sunbird (Variable Sunbird: *Cinnyris venusta*) wing molt duration was reported to be about 95 days, which is a far spread from the estimation in McGregor et al. (2007).

I found variation in the duration of molt between subspecies. For example, duration for *C. s. cruentata* (125 days) and *C. s. senegalensis* (181 days) differed by 56 days. Because these subspecies have a similar latitudinal range (Fig. 2) this difference may not be attributable to markedly different seasons experienced by the two subspecies. Rather, this could reflect an inherent subspecies difference. However, McGregor et al. (2007) estimated molt duration to be 246 days calculated for what was very likely *C. s. senegalensis* based on the geographical location of the study site. Although speculative, such differences between studies might be due to pronounced inter-year variance in molt that could result from differential resource availability. In a year with high resource availability it is not unreasonable to expect that birds could complete molt more rapidly than in poor years.

It should be mentioned that these species brood multiple times per season (Cheke et al. 2001) and thus there are multiple cohorts of different aged birds per year. This may have confounded the attempt to determine an accurate estimation of molt duration and added error which would likely result in overestimation of molt duration. In conclusion, while it has been determined that molt duration is considerably protracted in both species; because of limited sample sizes in some groups and the issue of multiple cohorts making up the population the results should be interpreted with caution.

Molt intensity. - There is no evidence to support the hypothesis that subadult birds molt less intensely than adult birds as a result of their immaturity (or for any reason). I found no difference in molt intensity between these groups. Molt intensity in fact appears to be quite low for both groups. Low-intensity slow molt is also seen in birds of arid regions where it is thought to be adaptive because it causes relatively low physiological stress in an unpredictable or relatively resource-poor environment (Keast 1968, Zann 1985).

Intensity of molt may also be related to the type of feathers. Both the Amethyst and Scarlet-chested Sunbird have mostly black plumage. These melanin rich feathers are costly to produce (Veiga and Puerta 1996, but see McGraw et al. 2002), which may play a part in why molt intensity is so low and takes place throughout the year.

Molt schedules and seasonality. - While this study provides evidence that primary molt is correlated to the seasonal change in precipitation, body molt appears to be non-responsive to these changes and occurs at low intensity throughout the year. Based on the results of this study, it is likely that there is one very long protracted molt of the flight feathers each year.

McGregor et al*.* (2007) found that 73% of molt in the Scarlet-chested Sunbird occurred in the dry season. My results also show that while some primary molt of both Scarlet-chested and Amethyst Sunbirds occurs during the dry season, some also occurs in the wet-season (Table 7). Additionally, both species started primary molt when there was relatively higher precipitation and as the molt series progressed, the amount of rainfall decreased which largely agrees with the patterns summarized in Table 7.

According to Payne (1980), seasonal molt is characteristic of tropical African birds. The focal species of that study, the Red-billed Firefinch (*Lagonosticta senegala*), is a resident of open woodlands in south-central Africa that had very pronounced differences in breeding and molting seasons. Molt duration in this species, like the Sunbirds of my study, was long (3.5 to 4 months). It was suggested this protracted molt duration allowed the birds to have a flexible breeding season and react to unseasonal rainfall (Payne 1980).

While primary molt in Amethyst and Scarlet-chested Sunbirds was to a degree seasonal, body molt was largely unseasonal. Perhaps the study taxa do not show clear seasonal molt patterns because at some latitudes they experience low thermoregulatory costs or resources availability is relatively constant during much of the year. The firefinch previously mentioned is a granivore (Payne 1980) and it is likely that seed production is limited and temporally linked to rainfall. In contrast, the two sunbirds species under study are both nectarivorous and insectivorous (Cheke et al*.* 2001), potentially providing them a less seasonally variable resource base. Additionally, Petett (1977) showed that in Zaria, Nigeria, the flowering of five main ornithophilous species spanned most of the year in an overlapping sequence, thus providing a ready resource base throughout the year that may have allowed the evolution of an aseasonal molt in these sunbird species.

Evidence of seasonal body molt patterns may also be lacking because movements of these sunbird species within their range and across the year are complex. For example, within a population could be individuals that are sedentary, whereas others may be nomadic while others are migratory (Cheke et al*.* 2001). This conclusion is supported by Craig and Hulley (1994) who conclude their review on sunbird movements by stating, "Diversity rather than uniformity appears to be the pattern for nectarivore movements, and both inter- and intra-population variation is to be expected." These individuals within the population that pursue different strategies could potentially utilize different molt strategies confounding analysis of patterns.

Delayed plumage maturation. -Both immature Scarlet-chested and Amethyst Sunbirds refresh the dull-plumage feathers that resemble the juvenal plumage (in all but the throat/chest) in the presupplemental molt. This indicates that this dull plumage likely has an adaptive significance. There is, however, the potential for phylogenetic constraints to play a role in the retention of traits. DPM in these species could be a trait remnant carried over from a previous lineage that has not yet been removed by selection.

In terms of the molt-constraint hypothesis, the absence (or inability to detect) seasonal patterns of body molt in the study species suggests that seasonality and energetics are not a driving force in the retention of this delayed plumage maturation trait. Alternatively, despite the lack of seasonal body molt, Sunbirds may have evolved in other ways to deal with molt constraints. This study detected low levels of molt intensity in all groups and recorded interrupted molt in immature Scarlet-chested Sunbirds. Both of these strategies may be adaptations to balance energetically costly life history events.

TABLE 7. Timing of primary molt and the dry season months at different latitudes. Primary molt months (in bold) are those that correlate with the dry season months. Dry season months for each latitude range were determined using monthly surface climatology maps compiled for the years 1920-1980 by the Center for Resource and Environmental Studies (CRES) at the Australian National University and made available through the National Oceanic and Atmospheric Administration's (NOAA) African Desk of the Climate Prediction Center. These data are publicly available at: http://www.cpc.ncep.noaa.gov/products/african_desk/afr_clim/ncep/

	Latitude range	Dry season[a] months (<200mm rainfall)	Primary molt months[b]
Amethyst Sunbird	0 to 10° S	Jun-Oct	Mar, Apr, **Jun**
	10 to 20° S	Apr-Oct	Jan, Feb, Mar, **Apr, May, Jun, Jul, Sep**
	20 to 30° S	Feb-Oct	**Apr, May, Jun, Jul**
Scarlet-chested Sunbird	20 to 10° N	Nov-May	Oct, **Nov, Dec, Jan, Feb, Mar, Apr**
	10 to 0° N	Nov-Mar	**Mar**, Apr, May, Jun, Jul, Oct, **Nov, Dec**
	0 to 10° S	Jun-Oct	Mar, Apr, May, **Jun, Jul, Oct,** Nov, Dec
	10 to 20° S	Apr-Oct	Jan, Feb, Mar, **Apr, Jun, Jul, Aug, Sep**

[a]Months with < 200 mm rainfall
[b]Months where primary molt was recorded

It is also likely that the contour feathers play a larger part in social interactions such as mate-choice and signaling. DPM in these species may instead be behavioral adaptations and could be used to signal subordinance to avoid unnecessary conflict with the adult generation as suggested by the status-signaling hypothesis (Lyon and Montgomerie 1986, Montgomerie and Lyon 1986).

Conclusion. - The diverse molt strategies of sunbirds make it a very interesting family in which to study molt patterns and sequence. This study found that while body molt in general occurs as low intensity throughout the year, primary molt does show some correlation with seasonal changes in rainfall and timing of primary molt varies with latitude.

While I found limited support for the molt constraint hypothesis to explain DPM, hopefully, the data herein can serve as a foundation for future study of DMP in these species. This study did, however, detect some interesting qualities of molt in these species which may serve as evidence towards the existence of a molt constraint such as the occurrence of interrupted molt in the Scarlet-chested Sunbird and greatly protracted molt duration in both study species.

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APPENDIX A: FIGURES

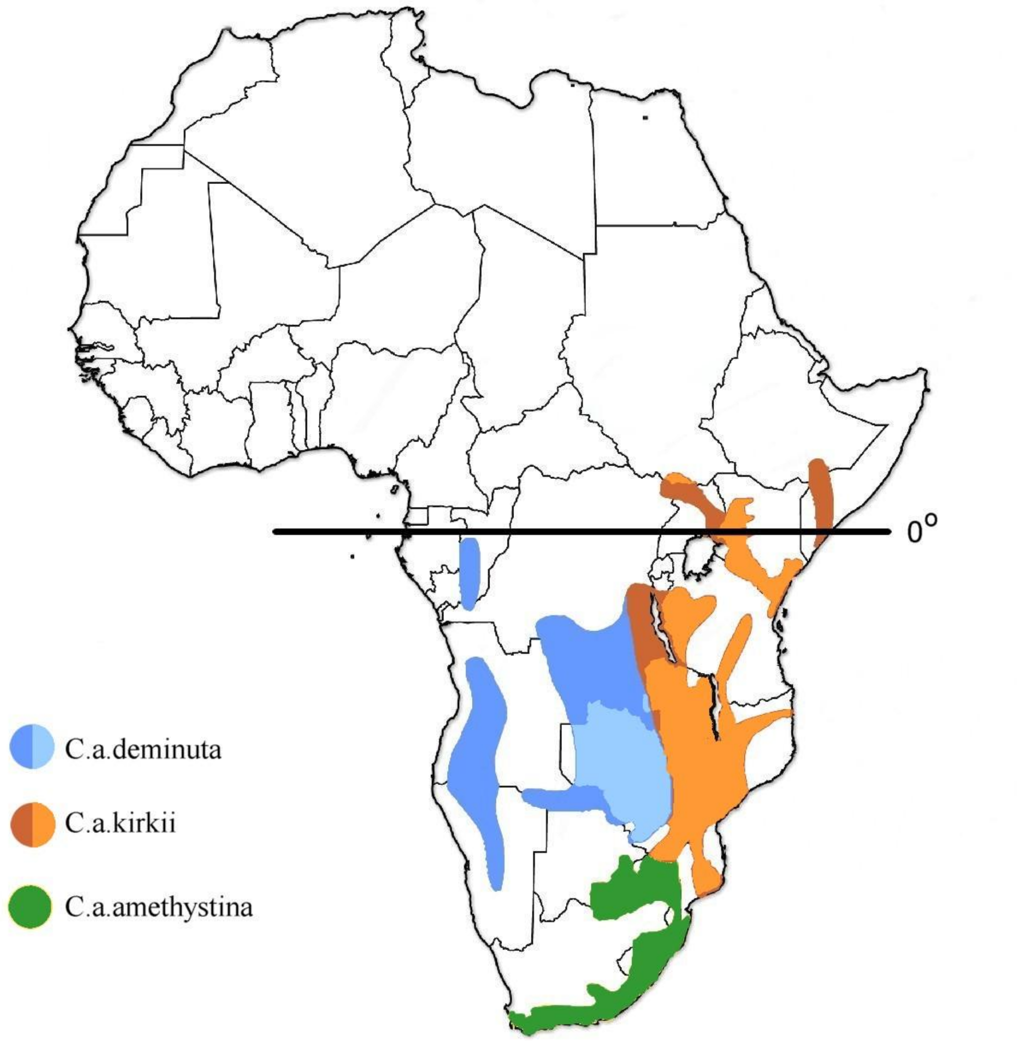

FIG. 1. Approximate range of the Amethyst Sunbird (*C. amethystina).* This map was adapted from Cheke et al*.* (2001). The estimated range of *C. a. kirkii* is in orange, *C. a. deminuta* in blue, and the nominate in green. The lighter colors represent approximate regions where molt has been studied previously in this species: light orange for *C. a. kirkii*, and light blue for *C. a. deminuta*.

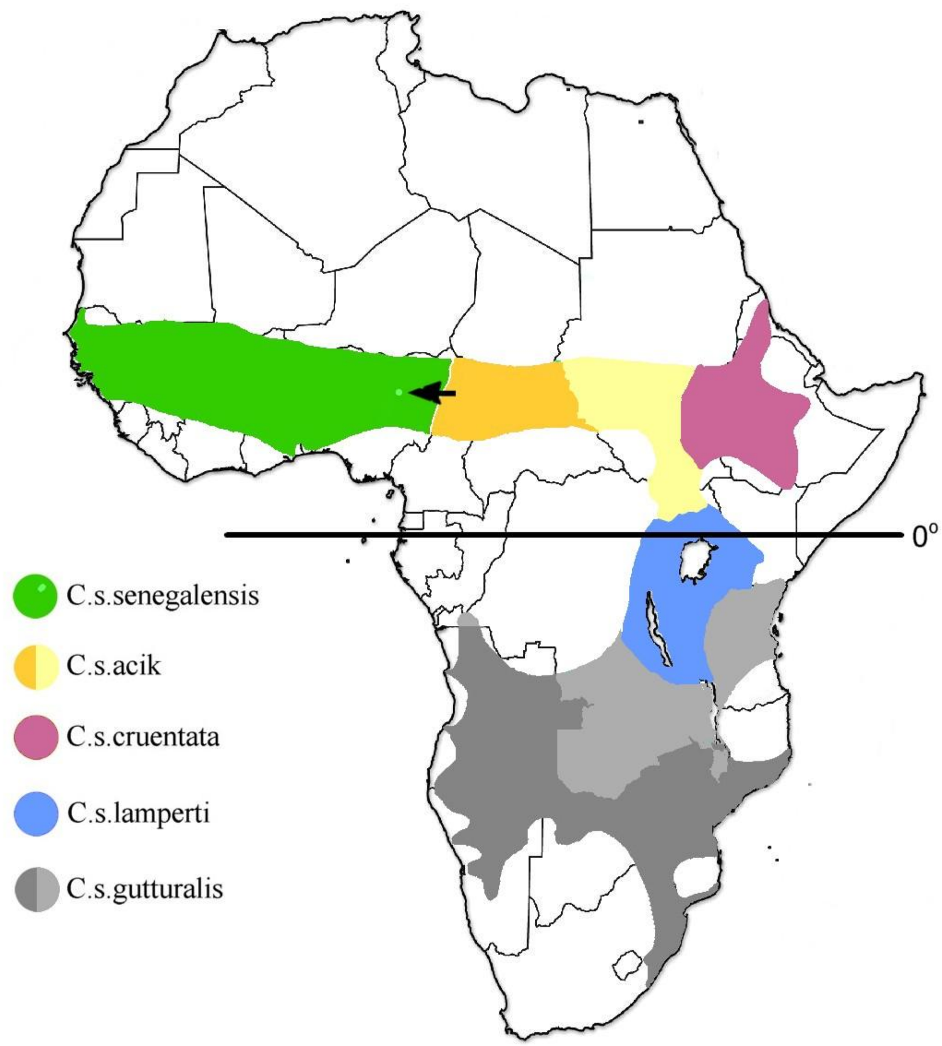

FIG. 2. Approximate range of the Scarlet-chested Sunbird (*C. senegalensis).* This map was adapted from Cheke et al. (2001). The estimated range of the nominate in green, *C.s.acik* in yellow, *C.s.cruentata* in pink, *C.s.lamperti* in blue, and *C.s.gutturalis* in gray. The lighter colors represent where molt has been studied previously in this species: the light gray regions, the light yellow regions, the entire pink region, the entire blue region, and the one western location in Nigeria in light green (pointed out by the arrow).

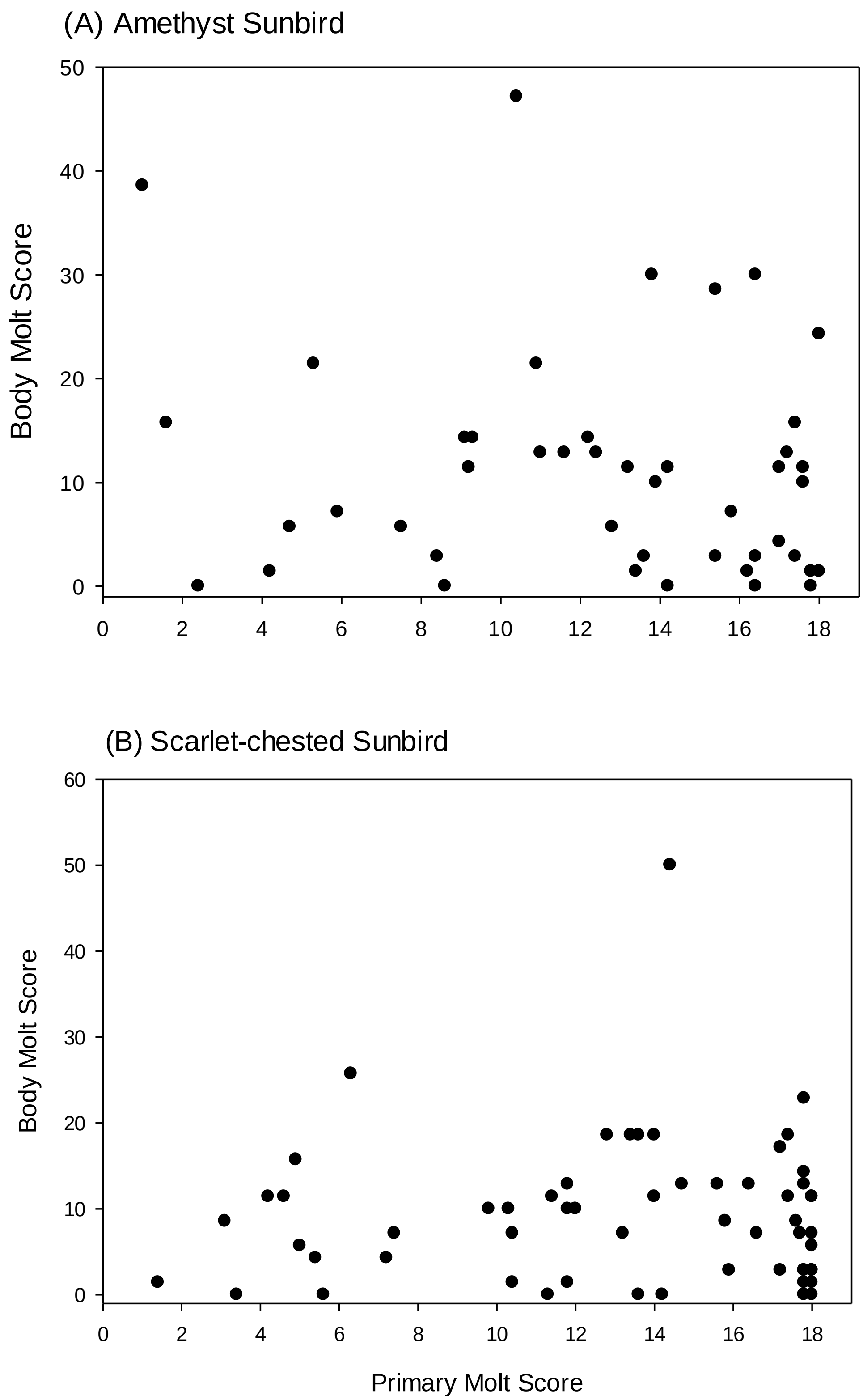

FIG. 3. Scheduling of body molt in relation to primary molt (of birds in the process of molting their primaries).

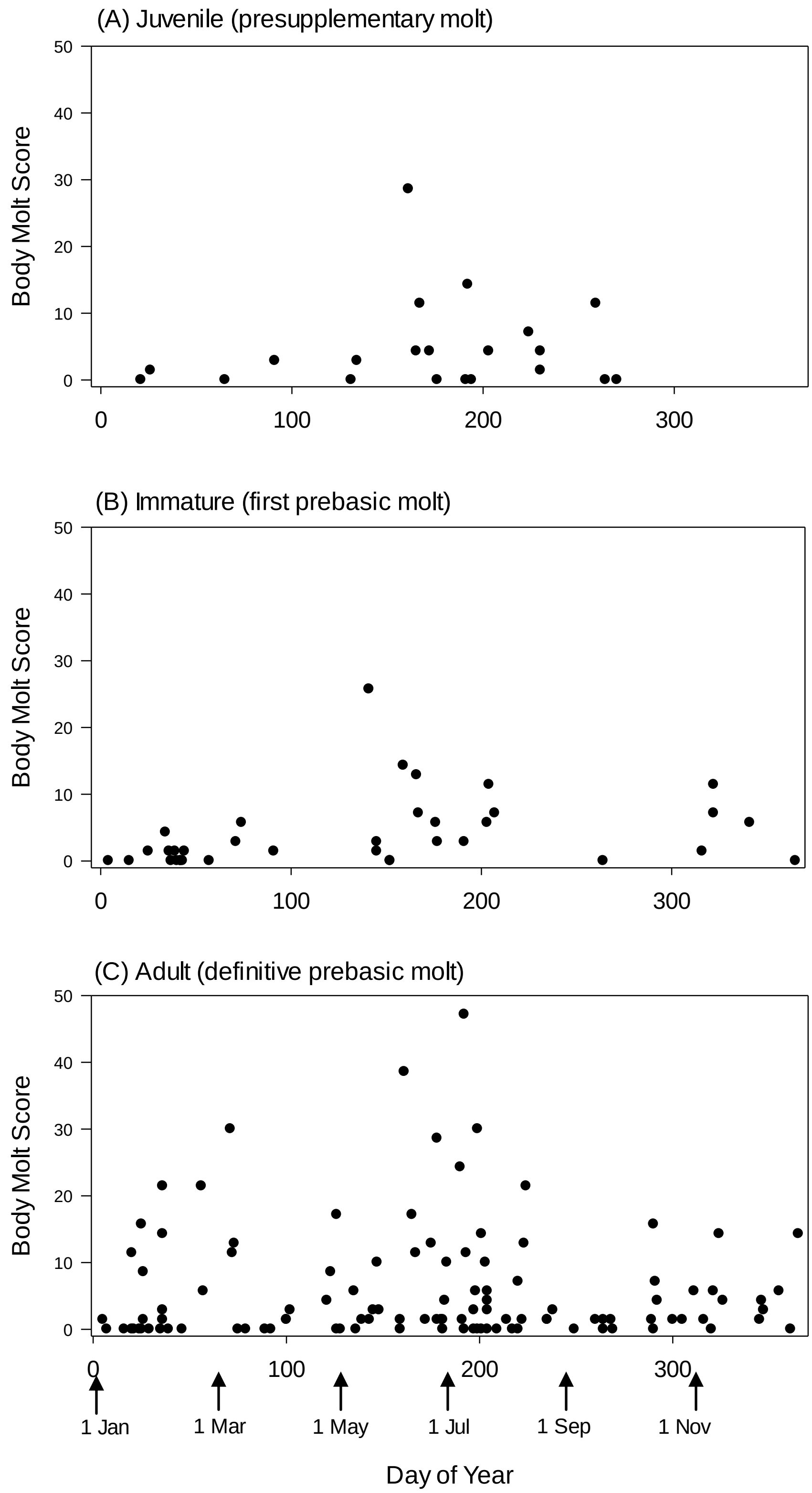

FIG. 4.Timing of body molt by age in the Amethyst Sunbird across its range. Day 1 = January 1.

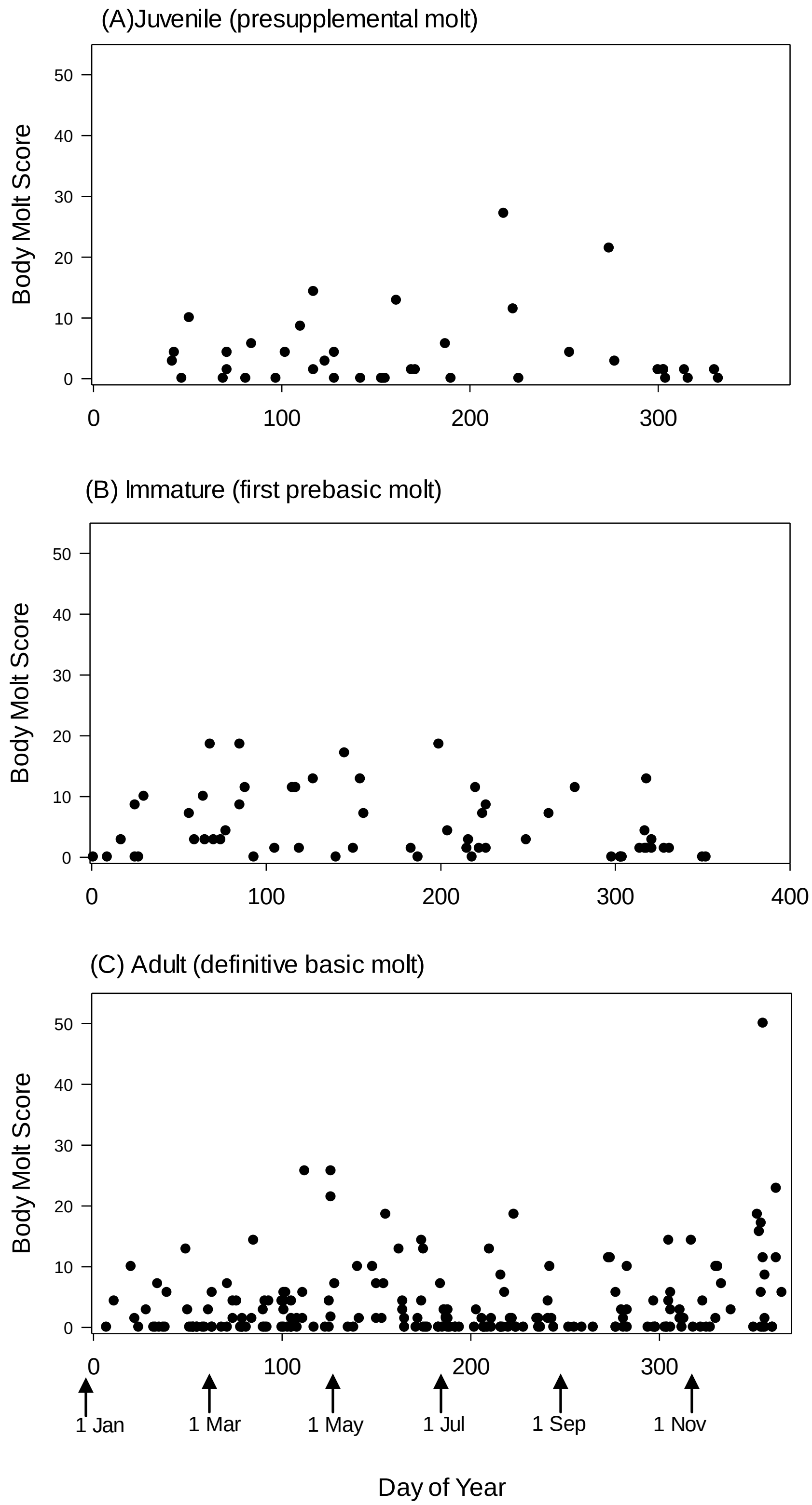

FIG. 5. Timing of body molt by age in the Scarlet-chested Sunbird. Like in the Amethyst Sunbird, evidence of body molt was recorded throughout the year across its range. Day 1 = January 1.

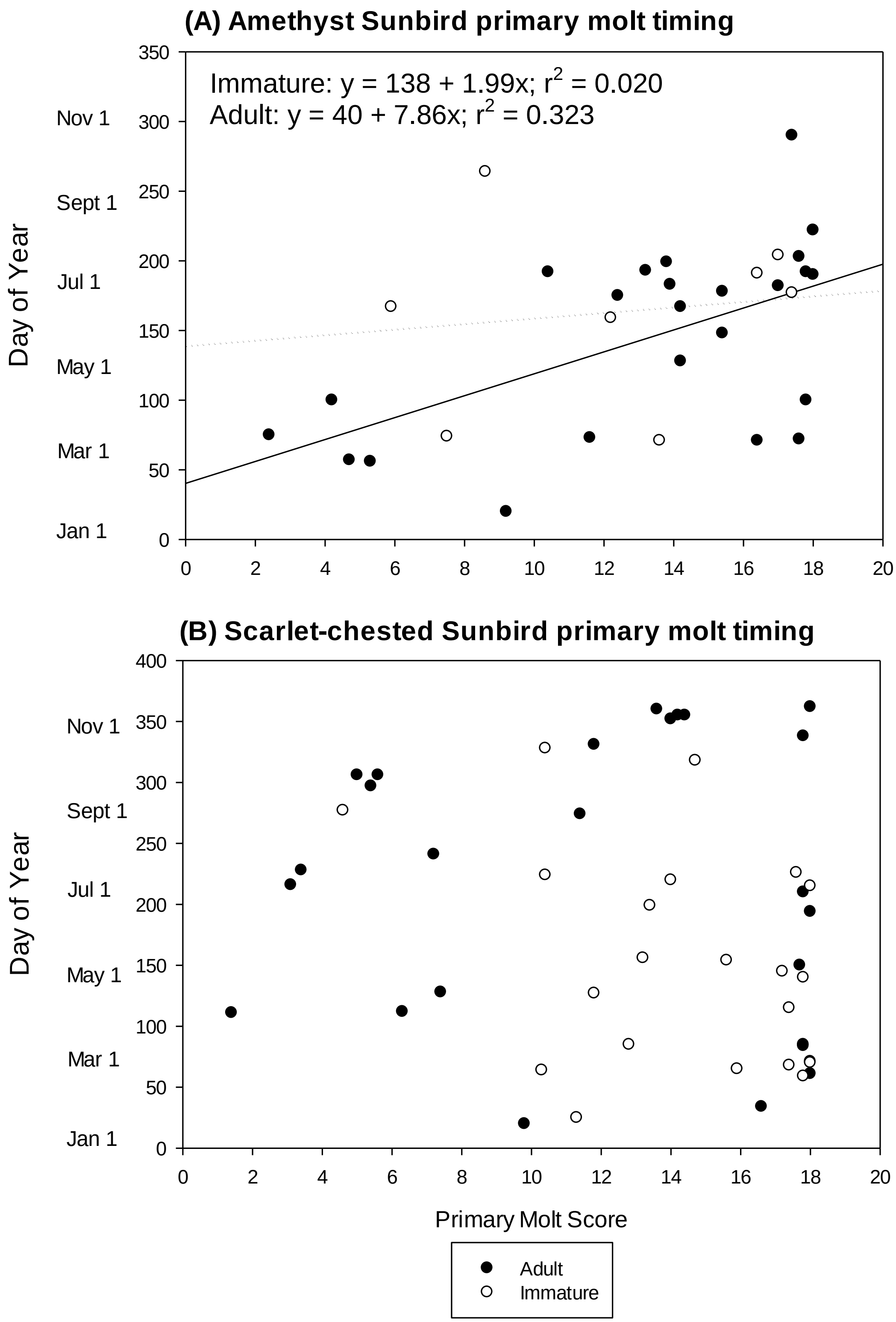

FIG. 6. Molt duration estimation for the Amethyst and Scarlet-chested Sunbird using Pimm's (1976) regression method. (A = Amethyst Sunbirds: Immature n = 8, Adult n = 24; B = Scarlet-chested Sunbirds: Immature n = 21, Adult n = 26.)

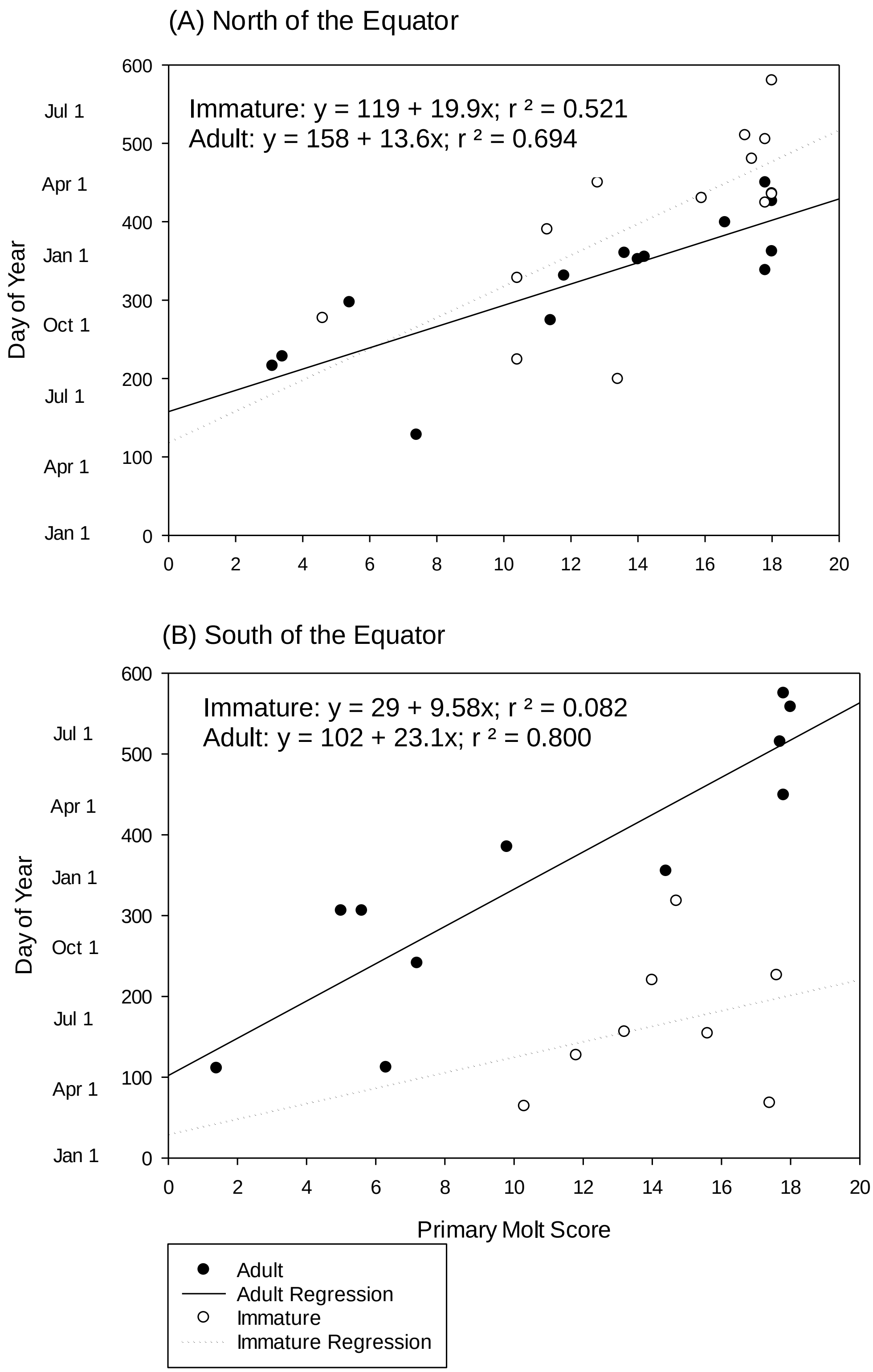

FIG. 7. Primary molt duration estimation in Scarlet-chested Sunbirds north and south of the equator. (A = north: adult n = 15, Immature n = 13; B = south: adult n = 11, Immature n = 8.)

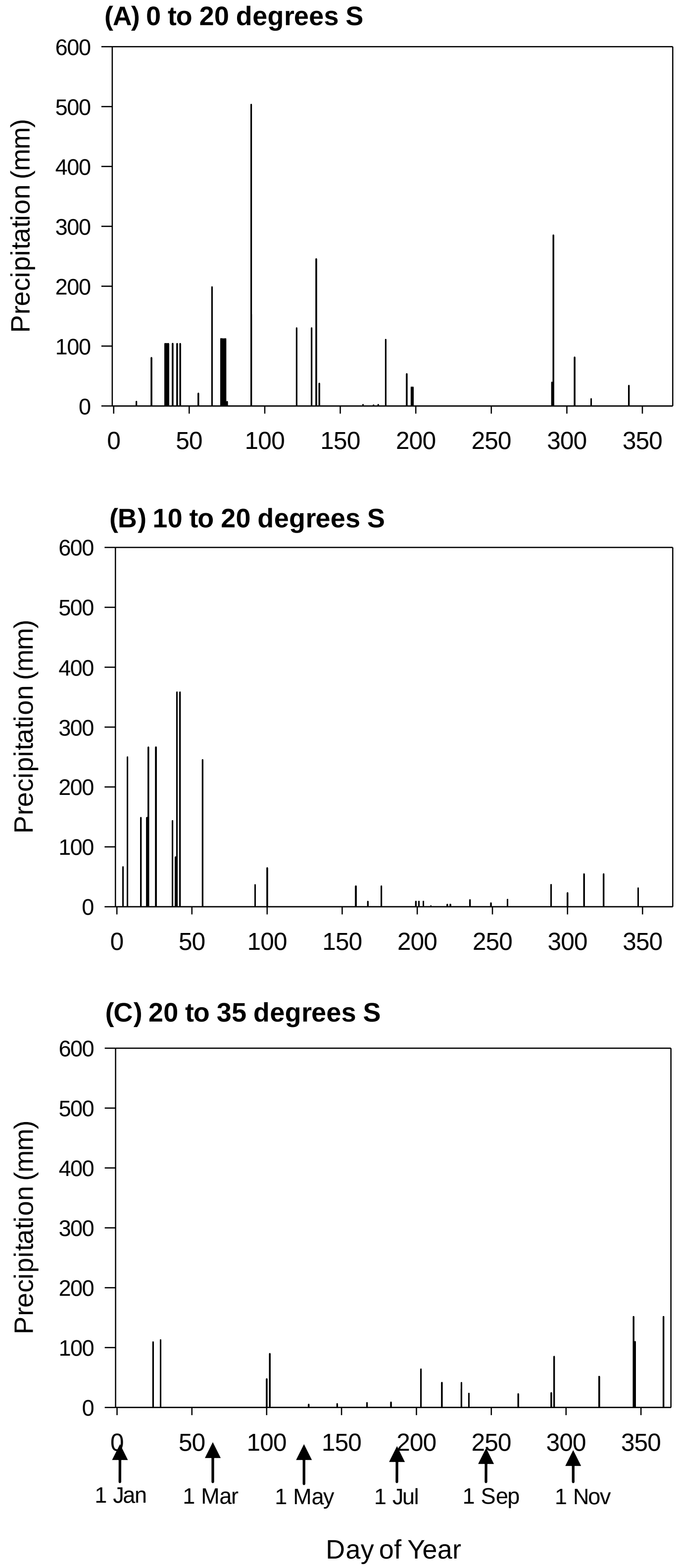

FIG. 8. Rainfall experienced by Amethyst Sunbirds across the species range. A: 0 to 10^o south latitude (n = 44), B: 10 to 20^o south latitude (n = 43), C: 20 to 35^o south latitude (n=24)

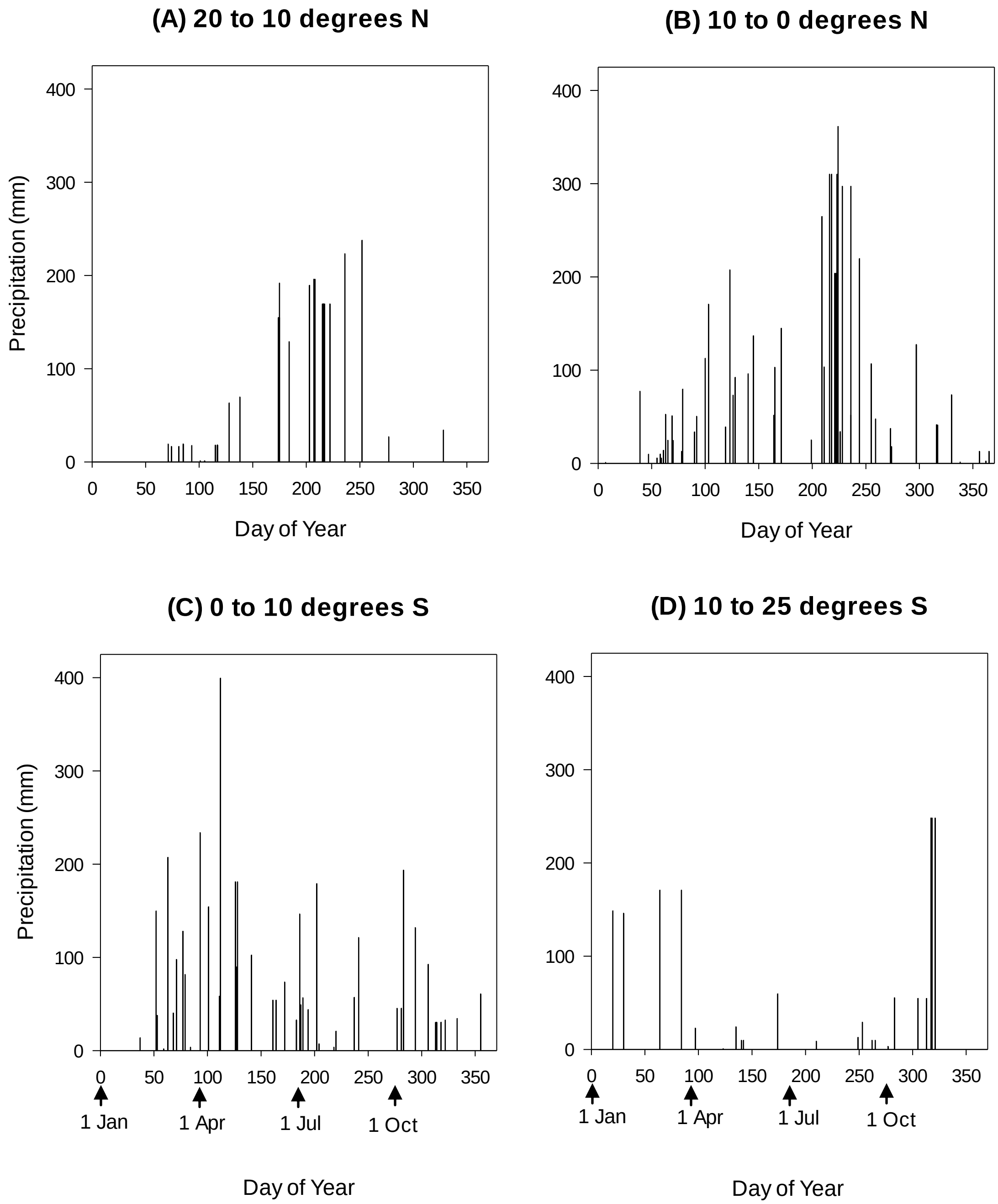

FIG. 9. Rainfall experienced by Scarlet-chested Sunbirds across the species range. A: 20 to 10^o north latitude (n=59), B: 10 to 0^o north latitude (n=64), C: 0 to 10^o south latitude (n=53), D: 10 to 25^o south latitude (n=40)

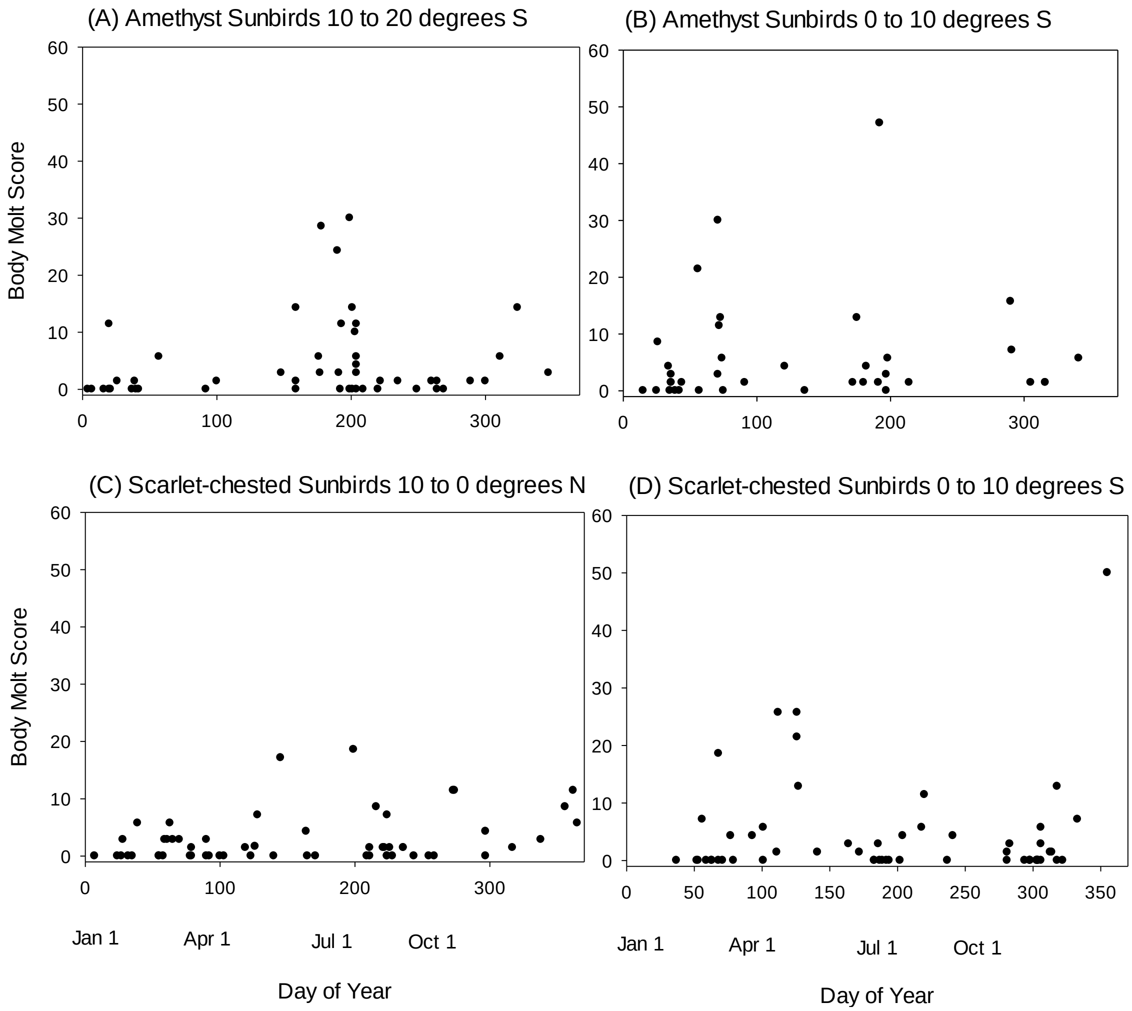

FIG. 10. Timing of body molt in Amethyst and Scarlet-chested Sunbirds split into 10^{o} latitude intervals.

APPENDIX B. Sunbird molting regimes: From Cheke et al. 2001 and del Hoyo et al. 2009 as categorized in Mackworth-Praed and Grant 1945.

Molt regime group description	Species
Group 1 No immature plumage Have non-breeding/eclipse plumage	Nectarinia Malachite Sunbird (*N. famosa*) Tacazze Sunbird (*N. tacazze*) Purple-breasted Sunbird (*N. purpureiventris*) Red-tufted Sunbird (*N. johnstoni*): nominate race, but not the subspecies Cinnyris (8 other species not listed) Beautiful Sunbird (*C. pulchellus*) Copper Sunbird (*C. cupreus*) Purple-banded Sunbird (*C. bifasciatus*) Kenya Violet-breasted Sunbird (*C. chalcomelas*) Shelley's Sunbird (*C. shelleyi*) Oustalet's Sunbird (*C. oustaleti*) Variable Sunbird (*C. venustus*) Stuhlmann's Double-collared Sunbird (*C. stuhlmanni*) Anthodiaeta Pygmy Sunbird (*A. platura*) Nile Valley Sunbird (*A. metallica*) Drepanorhynchus Golden-winged Sunbird (*D. reichenowi*) - potentially Leptocoma Crimson-backed Sunbird (*L. minima*) - potentially
Group 2 Have immature plumage No non-breeding/eclipse plumage	Anthodiaeta Collared Sunbird (*A. collaris*) - potentially Amani Sunbird (*A. pallidigaster*) Cinnyris Splendid Sunbird (*C. coccinigaster*) Shining Sunbird (*C. habessinicus*) Pemba Sunbird (*C. pemba*) Southern Double-collared Sunbird (*C. chalybeus*) Regal Sunbird (*C. regius*) Moreau's Sunbird (C. moreaui) Chalcomitra Amethyst Sunbird (*Chalcomitra amethystina*) Green-throated Sunbird (*Chalcomitra rubescens*) Scarlet-chested (*Chalcomitra senegalensis*) Hunter's Sunbird (*Chalcomitra hunteri*) Nectarinia Bocage's Sunbird (*N. bocagii*): Angolan population, but not the Congolese Aethopyga Fire-tailed Sunbird (*A. ignicauda*)

APPENDIX B. continued: Sunbird molting regimes

Molt regime group description	Species
Group 3	Aethopyga
No immature plumage	Grey-hooded Sunbird (*A. primigenia*)
No non-breeding/eclipse plumage	Apo Sunbird (*A. boltoni*)
	Lina's Sunbird (*A. linaraborae*)
	Flaming Sunbird (*A. flagrans*)
	Metallic-winged Sunbird (*A. pulcherrima*)
	Elegant Sunbird (*A. duyvenbodei*)
	Lovely Sunbird (*A. shelleyi*)
	Handsome Sunbird (*A. bella*)
	Gould's Sunbird (*A. gouldiae*)
	Green-tailed Sunbird (*A. nipalensis*)
	White-flanked Sunbird (*A. esimia*)
	Fork-tailed Sunbird (*A. christinae*)
	Black-throated Sunbird (*A. saturate*)
	Javan Sunbird (*A. mystacalis*)
	Temminck's Sunbird (*A. temminckii*)
	Anthodiaeta
	Collared Sunbird (*A. collaris*) –potentially
	Anthreptes
	(probably all but the Straight-billed Green Sunbird: *A. rectirostris*)
	Western Violet-backed Sunbird (*A. longuemarei*)
	Kenya Violet-backed Sunbird (*A. orientalis*)
	Uluguru Violet-backed Sunbird (*A. neglectus*)
	Anchieta's Sunbird (*A. anchietae*)
	Plain-backed Sunbird (*A. reichenowi*)
	Plain Sunbird (*A. simplex*)
	Brown-throated Sunbird (A. *malacensis*)
	Gray-throated Sunbird (*A. griseigularis*)
	Red-throated Sunbird (*A. rhodolaemus*)
	Mouse-brown Sunbird (*A. gabonicus*)
	Violet-tailed Sunbird (*A. aurantius*)
	Little green Sunbird (*A. seimundi*)
	Banded Sunbird (*A. rubritorques*)
	Chalcomitra
	Socotra Sunbird (*Chalcomitra balfouri*)
	Chalcoparia
	Ruby-cheeked Sunbird (*Chalcoparia singalensis*)
	Cinnyris (17 other species not listed)
	Red-chested Sunbird (*Cinnyris erythroceria*)
	Superb Sunbird (*C. superbus*)
	Mariqua Sunbird (*C. mariquensis*)
	Orange-tufted Sunbird (*C. bouvieri*)
	Eastern Double-collared Sunbird (*C. chloropygius*)

APPENDIX B. continued: Sunbird molting regimes

Molt regime group description	Species
Group 3 continued No immature plumage No non-breeding/eclipse plumage	Cyanomitra Green-headed Sunbird (*C. verticalis*) Bannerman's Sunbird (*C. bannermani*) Blue-headed Sunbird (*C. alinae*) Blue-throated brown Sunbird (*C. cyanolaema*) Cameroon Sunbird (*C. oritis*) Eastern Olive Sunbird (*C. olivacea*) Western Olive Sunbird (*C. obscura*) Deleornis Gray-headed Sunbird (*D. axillaris*) Scarlet-tufted Sunbird (*D. fraseri*) Drepanorhynchus Golden-winged Sunbird (*D. reichenowi*) – potentially Hypogramma Purple-naped Sunbird (*H. hypogrammicum*) Leptocoma (all species) Purple-rumped Sunbird (*L. zeylonica*) Crimson-backed Sunbird (*L. minima*) - potentially Purple-throated Sunbird (*L. sperata*) Black Sunbird (*L. sericea*) Copper-throated Sunbird (*L. calcostetha*) Nectarinia Bronze Sunbird (*N. kilimensis*)