NESTING BIOLOGY OF THE ANDEAN SOLITAIRE (*MYADESTES RALLOIDES*) IN NORTHEASTERN ECUADOR

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Resumen. – La anidación del Solitario Andino (*Myadestes ralloides*) en el este del Ecuador. – Estudiamos la biología reproductiva del Solitario Andino (*Myadestes ralloides*) durante 6 años en la ladera este de los Andes ecuatorianos. La actividad reproductiva dura entre Enero y Julio, con una máxima alrededor de Abril y enarbolando Marzo. Sus nidos (n = 26) eran tazas de musgo, delineadas gruesamente con escamas de helecho arborescente, y colocados en los bancos bajos o los troncos de árboles cubiertos de musgo. El tamaño de la puesta (n = 13 nidos) era entre uno (1 nido) y tres huevos (1 nido), los restantes con dos huevos. El tamaño promedio de los huevos era 24,3 por 17,1 mm (n = 28), y los índices de pérdida de agua eran 1,1%/día de su peso original. El promedio del peso fresco de huevos era 3,7 g (n = 6). El periodo de incubación de los Solitarios Andinos fue de 14–17 días y el periodo de pichones de 14–15 días. El crecimiento de pichones, expresado con parámetro K de la ecuación logística, era 0,33. Estimamos que 39% de los nidos fueron exitosos.

Abstract. – We studied the reproductive biology of Andean Solitaire (*Myadestes ralloides*) over the course of 6 years on the east slope of the Ecuadorian Andes. Breeding activity lasts from January to July, peaking around April and March. Nests (n = 26) were mossy cups, thickly lined with tree fern scales, and placed either on low banks or mossy tree trunks. Clutch size (n = 13 nests) ranged from 1 (1 nest) to 3 eggs (1 nest), most often 2. Mean egg size was 24.3 by 17.1 mm (n = 28), and mean fresh egg weight was 3.7 g (n = 6). Mean rate of mass loss was 1.1% per day of original mass. Andean Solitaires had an incubation period of 14–17 days, and a nestling period of 14–15 days. Growth rate of young expressed by the *K* parameter of the logistic equation was 0.33. We estimate a nest survival rate of 39%. *Accepted 10 December 2007.*

Key words: Andean Solitaire, *Myadestes ralloides*, cloud forest, Andes, nestling, eggs, nests, waterloss.

The Andean Solitare (*Myadestes ralloides*) is distributed at elevations of 800 to 2700 m in the Andes from northwest Venezuela to northern Bolivia (Collar 2005). Like most of the other 11 members of the genus (Collar 2003), the Andean Solitaire builds a mossy cup nest on a bank or low on a tree trunk (Miller 1963, Wallace 1965). Not surprisingly, however, there have been no detailed studies of the nesting biology of this species. Here we present our observations of Andean Solitaire reproduction over the past 6 years in northeastern Ecuador.

MATERIALS AND METHODS

From 2001 to 2007, we studied the reproductive biology of Andean Solitaire on the private
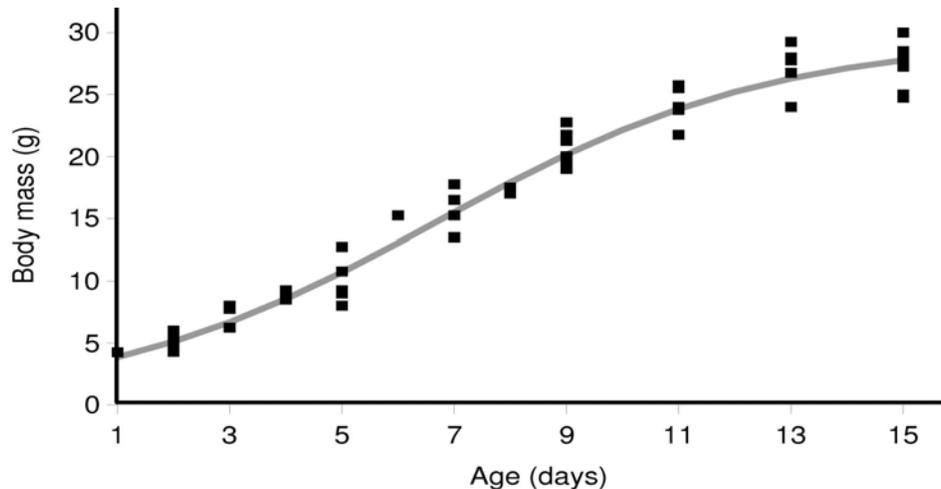
FIG. 1. Nestling growth of Andean Solitaire (*Myadestes ralloides*) at the Yanayacu Biological Station, 2000–2200 m, Napo, Ecuador. Data presented are for 10 nestlings from 6 separate nests. The day of hatching is, following Ricklefs (1976), designated as day 1. The equation of the growth curve was: mass (age) = 29.5/[1+exp(-0.33(age-6.7))].

birding reserve of Cabañas San Isidro, next to the Yanayacu Biological Station and Center for Creative Studies (00°35' S, 77°53' W), at elevations of 1950–2100 m, 5 km west of Cosanga, Napo, Ecuador. Nests were usually discovered by flushing adults from a nest, or by following adults carrying food or material. We took linear egg measurements to the nearest 0.1 mm and egg mass to the nearest 0.001 g. We weighed eggs periodically during incubation, calibrating the scale each time using a standard 50 g weight (to account for any unevenness of the scale). We placed each egg on the scale three separate times and used the mean of the three weighings. Nestlings were weighed and photographed every 3–4 days. A growth curve relating body mass to age was fitted to the logistic function, as proposed by Ricklefs (1976): mass(age) = $A/[1+e(-K(age-t))]$, where A, K, t are the parameters of growth and e is the base of the natural logarithm. We calculated the inverse measure of growth rate, the time required to grow from 10% to 90% of the asymptote, using the formula $4.4/K$. To make results comparable, we also followed Ricklefs' convention of making the day of hatching day one. The sample size was relatively small (see Fig. 1) and within-brood variation in growth rates was similar to between-brood variation, hence we treated each nestling as an independent data point.

At each approach to the nest we recorded the distance at which the incubating/brooding adult flushed from the nest, and any associated behavior. Daily survival rates of nests were calculated and compared using the methods developed by Mayfield (1975) and Johnson (1979).

RESULTS

Nests. All nests were fairly neat, mossy cups with a thick lining of tree fern scales (ramenta). Of the 26 nests encountered, 13 were built on the side of the trunk of living trees, 12 on the ground on low banks, and one on the side of a dead stump (most similar in situation to a bank nest). Nest height

ranged from 0.25 to 2.2 m (mean ± SD = 1.1 ± 0.6). Mean nest measurements cm ± SD were: outer cup diameter (n = 16), 12.7 ± 1.4; outside cup height (n = 6), 8.7 ± 0.9; inner cup diameter (n = 16), 7.3 ± 0.9; inner cup depth (n = 16), 4.1 ± 1.3.

While we did not mark individual birds, most nests were found very close to, or in some cases on top of, previous years' nests, and we suspect high nest-site fidelity. At two nests we found evidence of at least two old nests below the active one. One nest site was used at least three times during our observation period, though never on consecutive years, and one nest site was reused 3 years after the first time we found it occupied.

Eggs. Clutch size (n = 13) ranged from 1 (n = 1 nest) to 3 (n = 1 nest) eggs, most often 2 (n = 11 nests). Eggs were white with cinnamon speckling, heaviest at the larger end. They ranged in length from 22.6 to 27.0 mm, and in width from 16.6 to 18.2 mm (n = 28; mean ± SD = 24.3 ± 0.9 by 17.1 ± 0.4 mm). Mean fresh (before development) egg weight was 3.68 ± 0.15 g (n = 6). Seven eggs (n = 4 nests) lost mass at a mean rate of 1.10 ± 0.21% per day during incubation (mass loss = waterloss; Ar & Rahn 1980). Mass loss in different eggs ranged from 0.83 to 1.45% per day.

Egg laying and incubation. Eggs from one nest were laid between 08:00 h and 10:30 h, and 08:00 h and 12:45 h, on separate days. At another nest an egg was laid between 08:30 h and 14:00 h. While we did not confirm the interval between laying of eggs, we suspect that in most nests, eggs were laid 48 h apart. At a nest with three eggs, one egg was laid 4 days prior to the laying of the second, and only 24 h passed before the third egg was laid. At one nest, both eggs hatched 14 days after the second egg was laid and, at another, 13 days after the second was laid. At another nest, containing three eggs, two hatched 16–

17 days after the last egg was laid, one egg having disappeared the day before hatching. Interestingly, at this nest we found the eggs to be cold to the touch, with no evidence of an adult nearby, during 4–6 checks per day during the first 3 days after the last egg was laid, suggesting that incubation was delayed. The nest, however, was successful in fledging both young. Hatching was synchronous at all nests, thus suggesting that incubation did not begin until clutch completion.

Nestlings. Upon hatching, nestlings' skin was pink, with a yellow cloaca. Their bills were yellow-orange, with slightly paler yellow-white gapes and bright yellow mouth linings. They had sparse, long grey down plumes on the back and head. By 6 days of age, pinfeathers on all contour feather tracks were just starting to break their sheaths. Pinfeathers on the wing remained unbroken but began emerging from their sheaths soon after. Their bills had turned dusky, with a sharply contrasting bright yellow-white gape and yellow mouth lining. Eyes remained mostly closed. At 8 days of age, nestlings' eyes were open. Body contour feathers were well-emerged from their sheaths, with those on the chest and back colored chestnut and edged in black, and those on the belly colored white. Contour feathers on the head were still just emerging from their sheaths. Secondary and primary feathers had emerged 2–4 mm from their sheaths, primaries colored black and secondaries black tipped with chestnut. By 10 days of age, nestlings were well-feathered with only sparse wisps of down still attached. Wing feathers were roughly half way emerged from their sheaths, while tail feathers were only just breaking their sheaths. Dorsally, nestlings were dark brown with chestnut spotting, making them extremely cryptic when in the sun-dappled environment of the nest. Ventrally, their upper breast was dark with light chestnut spotting fading to pale grey on the mid-breast

and finally to white on the belly. At fledging, Andean Solitaires lost most or all down feathers. Outer primaries were all dark, while inner primaries and secondaries were edged in light chestnut and wing coverts were tipped with the same color. Until they are 6 or 7 days old, nestlings continue to beg while handled or in response to observer's movement or noise. By 10 days of age, however, nestlings are very alert and duck low into the nest when approached. If handled, they often hiss or make harsh cries while spreading their wings and opening their mouth to expose their bright yellow gapes.

During the period of the fastest nestling growth, between days 5 and 8 when increase in body mass was approximately linear, nestlings on average gained 2.4 g/day (Fig. 1). The asymptotic body mass attained by nestlings close to fledging equaled 29.5g, which was 92% of the body mass (32.0 g) of the only adult individual, probably the female, caught during our study. Growth rate expressed by the K parameter of the logistic equation equaled 0.33. The curve inflected at age 6.7 days and nestlings needed 13.2 days to grow from 10% to 90% of the asymptote.

One nest fledged after 14 days, and a second after 15. At five other nests we observed nestling periods of 13–14, 13–16, 14–15, 14–16, and 15–17 days. We feel it is likely that most nestlings left the nest at 14 or 15 days of age.

Nesting success. Survival rate of nests at the egg laying stage was not estimated because we had too few data; only 3 nests were checked regularly during this period. Daily survival rate during incubation was 0.950 (SE = 0.020; 16 nests observed, 113 successful days and 6 days with a predation event). Using an incubation period of 15 days, we then calculate that 46% of nests, with successful laying periods, survive until hatching. Three out of six predation events which took place within the incubation period resulted both in the destruction of the clutch and the death/injury of the adult bird (egg shells and fully-grown feathers were found on the nest). Thus it appeared that the risk of predation for the incubating adult was fairly high. If nests with feathers are assumed to have been predations on the incubating adult, the daily probability of adult survival was 0.975 (SE = 0.014, 116 successful days of incubation and 3 fatal). Thus, over the entire incubation stage, the risk of being killed was 32% (provided that only one parent incubated).

Daily survival rate at the nestling stage was 0.989 (SE = 0.011, 9 nests observed, 91 successful days and 1 day with predation). Using a 16-day nestling period (including the day of hatching), this yields an estimated 84% nest survival from hatching to fledging. Combining these data, 39% of nests in which laying is successful are predicted to fledge young.

Adult behavior at nests. We could not consistently tell adults apart in this monomorphic species, but based on adult plumage aberrations at one nest, we confirmed that only one adult participates in nest building and incubation, while both adults care for the nestlings. This observation is consistent with other members of the Turdidae where females are known to build the nest and incubate while both members feed nestlings (Collar 2003).

While incubating, adults generally sat very still as observers approached, generally flushing at less than 1 m and, on occasion, flushing only when touched. We recorded the distance at which adults flushed during incubation for 15 flushes at 13 nests. Mean flush distance (± SD) was 2.1 ± 4.4 m. On only two occasions, however, was flush distance over 1 m (10 and 15 m, respectively). From experience with many open cup-nesting passerines (HFG pers. observ.), we suspect that on these two occasions the adult was already standing and engaged in preening, nest maintenance, or

egg rolling. Engagement in any of these behaviors at the time of approach of an observer tends to induce flushing (HFG pers. observ.) Mean flush distance (± SD) without these two instances was 0.5 ± 0.4 m. During the incubation period, adults generally flushed low and silently from the nest, often spreading their tail to expose their conspicuous white tail feathers. In addition, they often flew in a slow fluttery manner, which may be interpreted as a distraction display. Adults almost never remained near the nest while an observer was present. During the nestling phase, however, flushing adults more frequently spread their tail and fluttered, sometimes while moving slowly along the ground or in low vegetation. This rarely persisted, however, and they quickly left the area. If an adult returned to the nest to find us, they often made a cat-like, growling alarm call from a concealed position.

Seasonality. We found five nests during the construction phase, in January (2), March (1), and April (2). We found nests with eggs in January (1), February (3), March (4), April (5), May (4), and June (1). Two nests discovered in April already contained nestlings. We saw adults attending fledglings, once in February, and once in May. From these data we suggest a breeding period lasting from January to July, with a peak around March and April. This roughly corresponds to the wetter season in our study area (Greeney *et al.* 2006).

DISCUSSION

Nest and egg descriptions, as well as nest site selection from eastern Ecuador correspond to those described elsewhere within Andean Solitaire's range (Miller 1963, Wallace 1965). Nest site selection also matches that of congeners (Collar 2003). After 6 years of searching for nests in our area, we have found no evidence that Andean Solitaire breeds from August to December, making this one of the most seasonal-breeding passerines in our area, and closely matching the breeding season of two other common thrushes in our area, Glossy-black Thrush (*Turdus serranus*) and Pale-eyed Thrush (*Platycichla leucops*) (HFG unpubl.).

The duration of incubation of Andean Solitaires reported here is similar to that reported for the few other *Myadestes* with this information available (Collar 2003). Unfortunately, there is almost no information on the incubation periods of other Andean thrushes, though when compared to the relatively few other Neotropical thrushes for which there is published data, a period of 13–16 or 17 days is slightly longer than most (Collar 2003). Similarly, when compared to other Neotropical thrushes, the nestling period of Andean Solitaire falls within the normal range, again perhaps on the high side (Collar 2003).

Previous studies have noted that the growth rate of nestling tropical birds is slower than in their northern relatives. For example, the *K* parameter of the growth curve in species with adult body mass less than 100 g varied between 0.278 and 0.604 in the tropics, whereas the range for the temperate zone species was 0.384 to 0.680 (Ricklefs 1976). Growth rate in nestling Andean Solitaires was slower than values reported for other tropical thrushes, including species studied in Venezuela at 1000 m a.s.l. (Ricklefs 1976; see also Appendix 1 therein). At our study site, adult Andean Solitaires are frequently seen consuming fruit (particularly Myristicaceae), and copious fruit remains were found in all nestling fecal droppings collected during nest checks (pers. observ.) We suggest that the slow growth we observed might be the result of a relatively low-protein diet fed to nestlings and relatively low, when viewed from the lowland humid tropics perspective, temperatures at the elevation of 2000 m. The large amount of fruit fed to nestlings may also provide some insight into the strong breeding season-

ality observed in this species. As the peak in fruiting in our area closely coincides with the breeding season of Andean Solitaires (HFG pers. observ.), breeding adults may be taking advantage of this abundant resource during the rearing of their young.

The 39% nest survival estimated for Andean Solitaire is within the range of survival rates observed in North America, where a similar 41% average was found among "shrub or low-foliage nesting species" (including several thrushes), listed in Appendix 1 by Martin (1995). It was slightly higher, however, than survival rates in understory open-cup nesting birds in a lowland humid forest of Panama, which averaged 32–38% (Table 2 in Robinson *et al.* 2000).

Surely, the most striking result was the high risk of predation experienced by incubating adult solitaires. The places where parents were killed while on the nest were distant from each other, thus it seems unlikely that attacks were the result of the same individual predator. Other data, from Pale-eyed Thrush, nesting in similar situations at our study site, suggest that predation on parent birds may also frequently occur in this species (unpubl.). It appears, therefore, that high adult mortality may be characteristic for thrushes in our area. If we assume that parent birds do not share incubation, we calculate that only about 50% of the incubating gender (presumably females) survive two breeding attempts. This obviously casts doubts on Ricklefs (1997) estimates of adult survivability in the tropics (around 80% annual survival in tropical montane thrushes). This interpretation should be taken with caution, however, that, as other adult thrushes often shed abundant contour feathers when stressed (i.e., in mist nets) (P.R. Martin pers. com., Greeney pers. observ.), it remains possible that some of our observations might be interpreted as predation attempts which did not necessarily end with the death of the incubating adult.

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