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MALE AND FEMALE REPRODUCTIVE SUCCESS IN A THREATENED POLYGYNOUS SPECIES: THE STRANGE-TAILED TYRANT, *ALECTRURUS RISORA*

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Abstract. The Strange-tailed Tyrant (*Alectrurus risora*) is an endangered obligate grassland bird that inhabits savannas, wet grasslands and marshes in southern Paraguay and northeastern Argentina. We evaluated the extent of social polygyny, main measures of reproduction (clutch size, hatching success, and chick survival), and factors that influence nest success in this species. We also estimated the reproductive success of females and males by measuring the number and fate of nesting attempts by banded females and the number of females per a male's territory. More than 80% of the males were polygynous. Males defended contiguous territories of 2–2.5 ha that included the territories of up to four females. Females built the nest, incubated the eggs, and brooded and fed the chicks. On average, successful nests fledged 2.3 chicks. Nest survival over the entire cycle was 0.23 and decreased with nest age and time of breeding. Most females made two or three nesting attempts per breeding season and bred in the same area for 2 or 3 consecutive years. In contrast, males rarely were seen in the same area more than 1 year, suggesting sexual differences in mortality. As a result of this, the reproductive success of females and males was similar. Our findings indicate that although males are highly polygynous and nest success is low, the high turnover of males in successive breeding seasons and the high probability of females' renesting within and in successive breeding seasons reduce the variance in reproductive success of both sexes.

Key words: *Alectrurus risora*, MARK, mating systems, nest survival, reproductive success, Strange-tailed Tyrant.

Éxito Reproductivo de Machos y Hembras en una Especie Poligínica Amenazada: *Alectrurus risora*

Resumen. *Alectrurus risora* es un ave amenazada de pastizal que habita sabanas, pastizales húmedos y bañados en el sur de Paraguay y noreste de Argentina. Evaluamos el grado de poliginia social, los principales parámetros reproductivos (tamaño de puesta, éxito de eclosión y supervivencia de pichones) y los factores que influyen el éxito de anidación en esta especie. También estimamos el éxito de anidación de hembras y machos midiendo el número y destino de los intentos de anidación de hembras marcadas y del número de hembras en los territorios de los machos. Más del 80% de los machos fueron poligínicos. Los machos defendieron territorios contiguos de 2–2.5 ha que incluyeron los territorios de hasta cuatro hembras. Las hembras construyeron el nido, incubaron los huevos y empollaron y alimentaron a los pichones. En promedio, los nidos exitosos produjeron 2.3 volantones. La supervivencia de los nidos a lo largo del ciclo de anidación fue de 0.23 y disminuyó con la edad del nido y la fecha de la temporada reproductiva. La mayoría de las hembras tuvo 2–3 intentos de anidación por temporada reproductiva y anidó en la misma área 2–3 años consecutivos. Por el contrario, los machos raramente fueron vistos en la misma área más de un año, lo que sugiere diferencias sexuales en la mortalidad. Como resultado de esto, el éxito reproductivo durante el periodo de estudio fue similar para hembras y machos. Nuestros resultados indican que si bien en esta especie los machos son altamente poligínicos y las hembras tienen un bajo éxito de anidación, el alto recambio de machos entre temporadas reproductivas y la alta probabilidad de anidación repetida de hembras dentro y entre temporadas reproductivas reducen la varianza en el éxito reproductivo de machos y hembras.

INTRODUCTION

The tyrant flycatchers (Tyrannidae) are endemic to the New World, reach their highest diversity in the Neotropical Region, and constitute one of the world's most diverse bird families, with 429 species and 104 genera recognized (Fitzpatrick 2004). The breeding biology of this family is known mainly

from some of the species of the North Temperate Zone and tropics; information on representatives of the subtropics or South Temperate Zone is scarcer.

Within Tyrannidae the subfamily Fluvicolinae includes, among others, the genera *Fluvicola*, *Alectrurus*, *Knipolegus*, *Hymenops*, *Muscisaxicola*, *Xolmis*, and *Agriornis* (Ohlson et al. 2008, Tello et al. 2009). These flycatchers evolved in open

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habitats and occupy grasslands, steppes, and wetlands along the Andes, in Patagonia, and on the Pampas at the west and south of South America (Ohlson et al. 2008). They share some characteristics such as large bodies, sexual dimorphism, complex aerial displays and foraging techniques (Traylor and Fitzpatrick 1982, Fitzpatrick 1985, 2004).

The Strange-tailed Tyrant (*Alectrurus risora*) is a highly sexually dimorphic fluvicoline that inhabits savannas, wet grasslands, and marshes in southern Paraguay and northeastern Argentina (Ridgely and Tudor 1994). Males have a long tail with modified outer feathers, contrasting black-and-white plumage, and during the breeding season notable bare red skin on the throat, while females have brown plumage with an outer pair of rectrices that are also elongated and terminate in a racket (Ridgely and Tudor 1994). On the basis of observations of a group of unbanded breeding birds it has been suggested that this species is polygynous (Traylor and Fitzpatrick 1982). This observation is particularly interesting, as the predominant mating system of tyrant flycatchers, in both temperate and tropical latitudes, is social monogamy, and polygyny is unknown among the Fluvicolinae (Fitzpatrick 2004).

Variation in the extent of sexual dimorphism and dichromatism among birds is traditionally attributed to sexual selection and differences in the social mating system (Andersson 1994, Owens and Hartley 1998). Species under intense sexual selection may be more vulnerable to extinction because sexual selection may oppose natural selection, favoring traits that promote males' reproductive success at the expense of survival (Andersson 1994, Sorci et al. 1998, Doherty et al. 2003). Furthermore, in birds mortality of males is positively associated with the extent of polygyny (Liker and Székely 2005) and with sexual size dimorphism and male plumage brightness (Promislow et al. 1992). These findings have led to the general view that local extinction rates are higher for dichromatic and polygynous birds than for monochromatic and monogamous birds.

The Strange-tailed Tyrant is an endangered bird that depends exclusively on grassland for nesting and feeding (Vickery et al. 1999, Fitzpatrick 2004). During the last century its original range has contracted by 90% in association with the conversion of natural grasslands to agriculture (Di Giacomo and Di Giacomo 2004). At present it is classified as "vulnerable," and further range contractions and declines in abundance are expected because suitable habitat is undergoing extensive agricultural intensification and afforestation (Collar et al. 1992, 1994, BirdLife International 2008).

For effective conservation measures for threatened and declining species to be identified, information on their breeding biology and reproductive performance is essential. In spite of the conservation status of the Strange-tailed Tyrant, there is a remarkable lack of information on basic aspects of its biology, such as its mating system, main reproductive statistics, and nesting success, that may help to assess its risk of

extinction (Birdlife International 2008). For example, polygyny is expected to produce variance in male reproductive success higher than that of alternative mating systems (Stiver et al. 2008), and in populations of constant size an increase in the variance in reproductive success of either sex will reduce effective population size (Hill 1972, Hedrick 2005), which is thought to increase extinction risk (Frankham et al. 2002, Frankham 2005). In passerines, nest survival depends mainly on nest predation (Ricklefs 1969, Martin 1993). Nest predation is particularly important in neotropical species, which suffer high predation rates but attempt many nests per year (Martin 1996). In turn, nest predation may depend on nest-site characteristics (Martin and Roper 1988), parental activity at the nest (Skutch 1949, Roper and Goldstein 1997, Martin et al. 2000), and progression of the breeding season (Davis 2005, Grant et al. 2005). Information on the genetic mating system, nest-predation rates, number of nests attempted per breeding season, and chicks fledged per successful attempt is necessary male and female reproductive success to be estimated. This knowledge may help the viability of the remaining populations of the Strange-tailed Tyrant and the main factors that affect that viability to be assessed (Morris and Doak 2002) and conservation programs for the species to be optimized (i.e., Duca et al. 2009).

In this study we analyzed a large set of observational data on a banded population of the Strange-tailed Tyrant to study the species' social mating system and evaluate the extent of its polygyny. We also measured clutch size, hatching success, chick survival, and how they vary through the breeding season, examined the correlates of nesting success, and estimated the reproductive success of females and males by measuring the number and fate of nests attempted by banded females and the number of females per male's territory. On the basis of the previous report of polygyny in this species (Traylor and Fitzpatrick 1982), we expected reduced or no parental care by the male and male-biased mortality. We also expected high rates of nest predation and a long breeding season with several attempts at renesting by the same female, as observed in other subtropical birds (Martin 1996, Stutchbury and Morton 2001).

METHODS

STUDY SITE AND DATA COLLECTION

The study was carried out at Reserva El Bagual in the province of Formosa, Argentina (26° 18' 17.5" S; 58° 49' 51.1" W) during the breeding season (early September to mid-January) from 2000–2001 to 2007–2008. This reserve is an open savanna, 3300 ha in size, located in the eastern, or humid, Chaco (Cabrera and Willink 1980). Within this reserve there are no large exotic herbivores, and the main large native herbivore is the Marsh Deer (*Blastocerus dichotomus*). Average annual rainfall for the period 2000–2007 was 1245 ± 243 mm (mean \pm SD, range 1038–1702 mm), with mean monthly rainfall

varying from 40 mm in midwinter (July) to 215 mm in early autumn (April). Mean monthly rainfall during the breeding season varied from 120 mm (January) to 180 mm (November). Mean annual temperature was approximately 22 °C, and mean monthly temperatures varied from 16.9 °C in July to 26.7 °C in January. During the study period there were two accidental fires (March 2001 and April 2003) and one prescribed fire (August 2006) that affected part of the reserve, including our study plot (for details see Di Giacomo et al. 2011).

We studied the Strange-tailed Tyrant in a grassland plot of 50 ha located along a small stream. This grassland is dominated by two species of tall grasses (0.8–1.2 m in height): *Imperata brasiliensis* and *Elionurus muticus* (Andropogoneae). In 30 ha of this plot we erected poles (2 m in height) every 100 m, forming a grid of 300 × 1000 m (30 squares of 100 × 100 m). We used this grid to delimit the territories of banded males and females (Bibby et al. 1992).

Using mist nets, we captured males during the nonbreeding season and females during both the nonbreeding and breeding seasons. We banded 8 males and 17 females on the tarsus with a numbered aluminum band and a combination of colored plastic bands. We considered that a male held a territory if it remained more than 4 weeks in the area (Vickery et al. 1992). Males were consistent in the use of their territory throughout the breeding season. We noted territorial males during visits to nests (every 2 or 3 days), and we recorded their positions through focal observations of 1 hr (one observation every 20–30 days and 4 or 5 observations per male through the breeding season). We used all these records to delimit the breeding territory as the minimum convex polygon.

We found nests by observing females' nesting behavior (Martin and Geupel 1993) or by flushing females during systematic searches for nests within the 30-ha study area. During the study, we found 199 active nests with eggs, 13 in 2000–2001, 22 in 2001–2002, 29 in 2002–2003, 25 in 2003–2004, 38 in 2004–2005, 22 in 2005–2006, 27 in 2006–2007, and 23 in 2007–2008. These nests were found during construction ($n = 41$), laying ($n = 12$), incubation ($n = 122$), and after hatching ($n = 24$). We are confident that we found the majority of the nests, as there were only two cases during the study period in which we observed fledglings with a female whose nest we had not previously found.

We recorded the plant species in which the nest was constructed and the nest's height. We marked eggs with waterproof ink, and in some nests we also measured egg length and width with a caliper (± 0.1 mm) and weighed them with a 10-g Pesola scale to the nearest 0.1 g. We visited nests every 2 or 3 days until the chicks fledged or the nest failed. During visits we recorded the number of eggs and chicks. After the chicks hatched, we marked them on the tarsus with waterproof ink and weighed them with 10- and 30-g Pesola scales to the nearest 0.1 and 0.2 g, respectively. We banded chicks when they were 8–10 days of age.

We video-recorded nest activity with a Sony Hi8 CCD video camera placed 3–4 m far from the nest. Video records lasted between 2 and 4 hr and were made between 07:00 and 11:00. We video-recorded 5 nests during incubation (total 10 hr), 19 nests when chicks were 2 or 3 days of age (60 hr), and 11 nests when chicks were 6–8 days of age (36 hr). We recorded nest activity during the breeding seasons 2004–2005, 2005–2006 and 2006–2007. Three of the video-recorded females were unbanded. However, because females are territorial (see Results) and the recorded nests were distant from each other, it is unlikely that we video-recorded the same female more than once.

DATA ANALYSIS

Clutch size, hatching success, and chick survival. We estimated clutch size from nests found during construction and laying in which laying was ultimately completed. We considered a clutch complete when the number of eggs remained constant for at least 2 consecutive days. Because eggs belonging to the same clutch are not statistically independent, we first averaged the measures of the clutch and report these averages. We estimated the incubation period as the time elapsed since the laying of the last egg and the hatching of the last chick in clutches where all eggs hatched (Nice 1954). We calculated hatching success as the number of hatchlings divided by the number of eggs present in the nest at the time of hatching and chick survival as the number of fledglings divided by the number of hatchlings. For the calculations of hatching success and chick survival we considered only nests found during construction, laying, or incubation that hatched and fledged chicks, respectively.

Parental care. We reviewed videotapes in the laboratory and identified the sex of the parent and the times (to the nearest second) it landed at, entered, exited, and departed from the nest. We calculated the frequency of visits to the nest (per hour), the average length of the visits (sec), and the proportion of time spent at the nest.

Nest survival. We considered a nest as depredated if all the eggs or chicks disappeared between two consecutive visits and deserted if the eggs were cold to the touch for two consecutive visits and the female did not attend the nest. We estimated nesting success by the daily survival rate (DSR) generated by program MARK (White and Burnham 1999). From the original data set we excluded two nests for which data for nest-survival analysis were insufficient and one of unknown fate ($n = 196$ nests). All dates were scaled so that day 1 was the clutch-initiation date of the earliest nest in our sample (11 September). We calculated overall nest survival as DSR^t , where t is the length of the nesting cycle. From nests monitored from the start of laying until the chicks fledged we found the length of the nesting cycle was 32 days (see Results).

We used MARK to examine some of the factors that affect nest survival. We built candidate models with combinations of

five nest covariates that are known to affect nest survival. The covariates we used were nest age (days elapsed since the laying of the first egg on day 0), start date (days elapsed since the start of the breeding season, 1 September), plant height (height of the plant in which the nest was built), nest height (distance from the ground to the top of the nest), and whether our study plot was burned or not by an accidental or prescribed fire during the previous nonbreeding season. We included year as a random effect. We limited the analyses to a set of eight a priori models that examined the effects of the selected covariates. We compared the various candidate models with the simplest null-hypothesis model of constant survival, $S(\cdot)$ in MARK notation. For filling in missing cells in the data matrix we used mean values of the covariate. We selected MARK's default options of sin for the constant-survival model and the logit-link function for models incorporating covariates (Dinsmore et al. 2002). We evaluated support for competing models within the set of candidate models with the Akaike information criterion (AIC) corrected for small samples sizes (AIC_c , Burnham and Anderson 2002). We considered the model with the lowest AIC_c value as the best fit to the data. An assumption of the nest-survival model in MARK is that nest fates are independent (Dinsmore et al. 2002). We assumed independence of a female's successive nesting attempts during the same breeding season on the basis that the survival of nests was not associated with the order of the nesting attempt (13 of 34, 10 of 28, and 3 of 9 successful nests among first, second and third nesting attempts; chi-squared test: $\chi^2_2 = 0.09$, $P = 0.96$).

STATISTICAL ANALYSIS

For most analyses we used nonparametric statistics because samples were relatively small and the data were not distributed normally after standard transformations. We analyzed differences among years with a Kruskal–Wallis test and differences through the breeding season with Spearman rank correlations. To compare the clutch size and hatching success of different nests of banded females we used Wilcoxon signed-rank tests. Similarly, we used Wilcoxon signed-rank tests to compare the length and frequency of females' visits to the nest when chicks were 2–3 and 6–8 days of age. For statistical tests we used StatView 5.0 (SAS Institute 1998) with α set at 0.05. Values reported are means \pm SE.

RESULTS

BREEDING BEHAVIOR AND MATING SYSTEM

By the end of July, males occupied contiguous territories and started performing flight displays. We observed between five and seven males at our study plot (30 ha) each year. On average, the size of a male's territory was 2.3 ± 0.1 ha ($n = 24$ territories, Table 1). Nearly 80% (19/24) of the males were socially polygynous (i.e., there was more than one female on their territories). The number of females per male's territory was 2.1 ± 0.15 ($n = 24$ territorial males, range 1–4 females per male), while the number of nesting attempts per breeding season within each male's territory was 4.5 ± 0.5 (range 2–12, Table 1). Males and females maintained the same territories throughout the breeding season. In addition, females that nested in consecutive breeding seasons did so in the same territory or close to it (see below), but most males occupied their territories for one breeding season only (number of banded individuals that renested in consecutive years, females: 11/15, males: 1/6; Fisher's exact test, $P < 0.05$).

NEST BUILDING, EGG LAYING, AND INCUBATION

The first nesting attempt began on 11 September (2002), the last on 16 January (2005). Most nests (76%) were attempted during October and November with two peaks, one in October, the other at the end of November (Fig. 1). The second peak corresponded to second attempts of females whose first attempt failed (see below).

Nest construction ($n = 16$ nests) took 7–14 days, and in all cases only the female carried nest material. Nests were built in tall grasses such as *Imperata brasiliensis* (96/157 nests), *Paspalum plicatulum* (9/157 nests), *Elionurus muticus* (8/157 nests) and *Andropogon selloanus* (7/157 nests), among others, at an average height of 31.8 ± 1.3 cm (range 0–80 cm, $n = 153$ nests).

Females generally laid eggs every 48 hr between 07:00 and 09:00, but approximately 30% of the females laid the third egg 24 hr after laying the second one. Eggs were immaculate white with a length of 21.8 ± 0.1 mm (range 20.4–23.3 mm, $n = 36$ nests), a width of 16.8 ± 0.1 mm (range 15.9–17.4 mm, $n = 36$ nests), and a mass of 3.0 ± 0.1 g (range 2.7–3.3 g, $n = 35$ nests). Egg size did not vary with time of breeding (length: Spearman $\rho = 0.08$, $P = 0.49$, $n = 36$; width: Spearman

TABLE 1. Number of male and female Strange-tailed Tyrants (*Alectrurus risora*), size of males' territories (in ha), and number of nests attempted per breeding season (September–January). Data from a 30-ha study plot at Reserva El Bagual, Formosa, Argentina, during the breeding seasons 2004–2005 to 2007–2008.

Breeding season	Number of males	Number of females	Total number of nests	Size of male's territory	Number of females per male	Number of nests per female	Number of nests per male
2004–2005	7	15	38	2.1 ± 0.2	2.1 (1–3)	2.5 (1–4)	5.4 (4–7)
2005–2006	7	13	22	2.4 ± 0.3	1.9 (1–3)	1.7 (1–3)	3.1 (2–5)
2006–2007	5	11	27	2.5 ± 0.3	2.2 (1–4)	2.5 (2–4)	5.4 (2–12)
2007–2008	5	14	23	2.3 ± 0.3	2.8 (1–4)	1.6 (1–2)	4.6 (2–6)

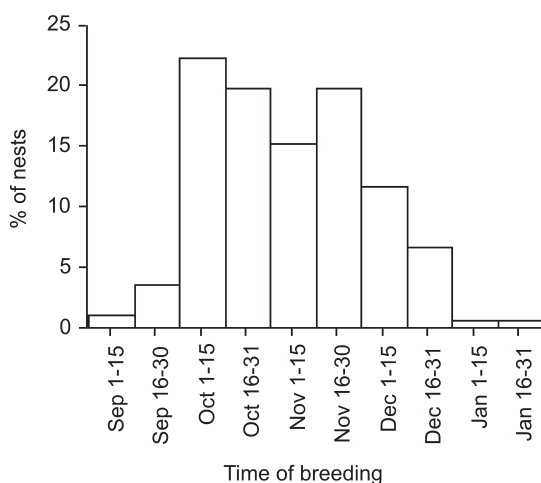


FIGURE 1. Percentage of nests initiated through the breeding season by female Strange-tailed Tyrants, on the basis of 199 nests followed through the breeding seasons 2000–2001 to 2007–2008 at Reserva El Bagual, Formosa Province, Argentina.

$\rho = -0.06$, $P = 0.71$, $n = 36$ nests). Clutch size was on average 2.9 ± 0.03 eggs ($n = 163$ nests) and did not differ from year to year (Kruskal–Wallis test: $H_7 = 9.4$, $P = 0.22$, $n = 163$ nests). Because females attempted several nests in a breeding season (see below), we repeated this analysis, including only the first attempt per breeding season by banded females. Clutch size was 3.0 ± 0.06 eggs (range 2–4, $n = 32$ nests) and did not differ by year (Kruskal–Wallis test: $H_3 = 6.2$, $P = 0.10$, $n = 32$ nests).

Clutch size decreased with time of the breeding season (Spearman $\rho = -0.18$, $P = 0.02$, $n = 163$ nests). We observed the same result when we compared attempts by the same female within one breeding season (first nest 3.0 ± 0.07 eggs; second nest 2.64 ± 0.11 eggs; Wilcoxon signed-rank test: $z = -2.83$, $P = 0.005$, $n = 22$ females; time elapsed between nesting attempts 44.0 ± 3.5 days). Incubation started with the laying of the penultimate egg, lasted 17.0 ± 0.6 days (range 16–18 days, $n = 23$ nests), and was done exclusively by the female. Females spent $32.7 \pm 1.5\%$ of their time in the nest ($n = 5$ nests). On average, the length to the nest was 364.4 ± 172.6 sec, and the frequency of visits was 3.3 ± 0.4 hr⁻¹.

HATCHING AND CHICK GROWTH AND SURVIVAL

Hatching was asynchronous, with the first two eggs (or three in clutches of four eggs) hatching synchronously, the last hatching 1 day later. Hatching success was on average 0.86 ± 0.02 ($n = 110$ nests) and did not differ by year (Kruskal–Wallis test: $H_7 = 10.9$, $P = 0.14$) or through the breeding season (correlation between hatching success and hatching day: Spearman $\rho = -0.02$, $P = 0.85$, $n = 110$ nests). There was no difference in hatching success between first and second nests (0.91 ± 0.16 vs. 0.91 ± 0.22 , $n = 11$ banded females that completed incubation in two consecutive nesting attempts; Wilcoxon signed-rank test: $z = 0.45$, $P = 0.65$).

Recently hatched chicks had orange skin with dense and long (10–15 mm) white down on the head, back, and underparts. The mouth was orange with yellow flanges. Chick mass at hatching was 2.8 ± 0.1 g ($n = 16$ nests). The chicks remained in the nest for 12–14 days, and their mass at day 12 was 19.2 ± 0.3 g ($n = 4$ nests). We observed brood reduction in 9 of 42 nests (seven nests with three hatched chicks and two nests with two hatched chicks). In all cases brood reduction involved the chick that hatched last. On average, chick survival in successful nests (nests from which one or more chicks fledged) was 0.89 ± 0.04 ($n = 42$ nests) and did not differ by year (Kruskal–Wallis test: $H_7 = 2.1$, $P = 0.96$) or through the breeding season (correlation between chick survival and day of hatching: Spearman $\rho = -0.25$, $P = 0.10$, $n = 42$ nests). Similarly, chick survival in banded females' first nests was 0.83 ± 0.05 ($n = 21$ nests) and did not differ by year (Kruskal–Wallis test: $H_3 = 1.4$, $P = 0.70$) or through the breeding season (Spearman $\rho = -0.26$, $P = 0.24$, $n = 21$ nests). Successful nests fledged on average 2.29 ± 0.12 chicks ($n = 42$ nests).

PARENTAL CARE DURING THE NESTLING STAGE

Only females brooded and fed the chicks. Figure 2 shows the length and frequency of visits to the nest when chicks were 2–3 and 6–8 days of age. When chicks were 2–3 days of age, females spent $26 \pm 3\%$ of their time in the nest ($n = 19$ nests). At this age the length of visits to the nest was negatively associated with air temperature (Spearman $\rho = -0.47$, $P = 0.04$, $n = 19$ nests), but there was no association between temperature and frequency of visits (Spearman $\rho = 0.09$, $P = 0.73$). When chicks were 6–8 days of age, females spent $10 \pm 2\%$ of their time in the nest ($n = 11$ nests). During this period the length and frequency of the visits were not associated with

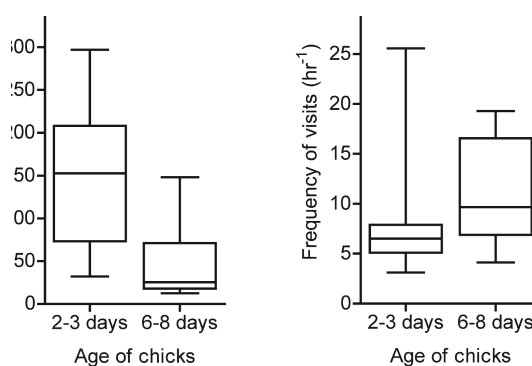


FIGURE 2. Box-and-whiskers plots showing the median, lower and upper quartiles, and smallest and largest observations of length (A) and frequency (B) of visits to nests by female Strange-tailed Tyrants at Reserva El Bagual, Formosa Province, Argentina. Data correspond to 19 and 11 nests with chicks 2–3 and 6–8 days of age, respectively.

temperature (Spearman $\rho = 0.2$, $P = 0.55$ and $\rho = -0.55$, $P = 0.10$, respectively; $n = 11$ nests in both cases). We compared the length and frequency of visits to six nests monitored when the chicks were 2–3 and 6–8 days of age. Visits were longer when chicks were 2–3 than when they were 6–8 days of age, but the frequency of visits did not differ with age of chicks (Wilcoxon signed-rank test, $z = -2.0$, $P = 0.05$, and $z = -1.36$, $P = 0.17$, respectively). The female fed the chicks for approximately 30 days after they fledged ($n = 9$ females).

NEST SURVIVAL

For the 8 years of our study the average daily nest-survival rate (DSR) was 0.955 ± 0.004 ($n = 196$ nests) and the cumulative probability of nest survival through the nesting cycle was 0.23. The length of the cycle was 32 days, on the basis of laying on alternate days, incubation starting with the laying of the second egg and lasting 17 days, and chicks fledging after 12 days. Models that incorporated nest age, start date, and year as covariates were better than null models with constant survival, $S(\cdot)$, while models that incorporated burn, height of plant and height of nest as covariates were worse than null models with constant survival (Table 2). The model best supported for explaining nest survival included nest age (Table 2). This model showed a decrease in DSR with age of the nest (mainly after hatching). Another well-supported model ($\Delta AIC_c < 2$) combined nest age and start date and showed a decrease in DSR with age of the nest and time of breeding (Fig. 3).

TABLE 2. Support for models predicting daily survival rates through the nesting cycle of Strange-tailed Tyrant nests at Reserva El Bagual, Formosa, Argentina, during the breeding seasons 2000–2001 to 2007–2008. Models are based on Akaike’s information criterion corrected for small samples sizes (AIC_c). We compared the different models with the null-hypothesis model of constant survival, $S(\cdot)$. ΔAIC_c = difference in AIC_c between each model and the top model; deviance = difference in the -2 log-likelihood between each model and the saturated model; K = number of parameters in the model; w_i = Akaike weight, a measure of the relative support of each model within the set of candidate models. See Methods section for definition of model covariates.

Model	ΔAIC_c	Deviance	K	w_i
$S(\text{nest age})$	0.0 ^a	837.8	2	0.71
$S(\text{nest age} + \text{start date})$	1.8	837.6	3	0.29
$S(\text{year})$	35.7	861.4	8	0.00
$S(\text{start date})$	38.3	876.1	2	0.00
$S(\cdot)$	39.4	879.2	1	0.00
$S(\text{burn})$	40.6	878.4	2	0.00
$S(\text{height plant})$	40.8	878.5	2	0.00
$S(\text{height nest})$	41.3	879.1	2	0.00

^a $AIC_c = 841.8$.

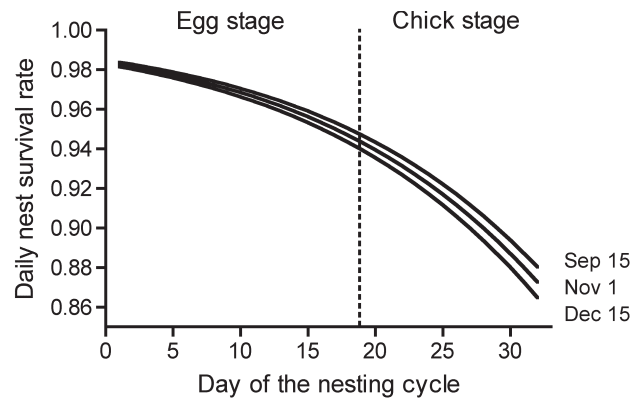


FIGURE 3. Daily survival rates (DSR) of nests of the Strange-tailed Tyrant, through the 32-day nesting cycle, calculated with software MARK for a model including age of the nest and time of breeding as predictor variables. The three curves correspond to DSR modeled for nests at which laying started early in the breeding season (15 September, upper curve), at the peak of the breeding season (1 November, middle curve), and late in the breeding season (15 December, lower curve).

Seventy-five percent of nest failures (104/139) were the result of predation. The remaining cases (35/139) were nest abandonments, mainly as a result of heavy rains that flooded the grassland.

RENESTING WITHIN AND IN SUCCESSIVE BREEDING SEASONS

During the breeding seasons 2004–2005 to 2007–2008 we followed the nesting of 17 banded females. Six females were followed one breeding season only, five females for two consecutive breeding seasons, five females for three consecutive breeding seasons and one female over all four breeding seasons, totaling 35 female-years. In 30 of these 35 cases (86%) we observed more than one nesting attempt during a breeding season. The average number of nests attempted per female per breeding season was 2.3 ± 0.1 (range 1–4, $n = 35$). In 19 of the 30 cases of renesting, the second attempt was preceded by nest failure (nest abandoned or depredated), but in the other cases (11/30) it occurred after a successful nest. In 9 of the latter cases the time elapsed between consecutive nesting attempts varied from 9 to 23 days. As the length of the post-fledging period is 30 days, these renestings likely occurred after depredation of the young of the previous nest. In the other two cases renesting occurred after 30 and 38 days and the second attempt was also successful (chicks fledged).

On average, the time elapsed between the first and the second attempt was 17.0 ± 2.1 days (range 2–49 days, $n = 30$ renestings). The distance between successive nests by the same female during a breeding season was 18.5 ± 3.6 m (range 5–40 m, $n = 14$ renestings). Seven of eight females banded in the first year (2004) renested in the same plot in more than one

year (two females in two consecutive years, four females in three consecutive years, and one female all four years, average 2.6 breeding seasons per female). In these cases the distance between the last nest of one breeding season and the first one of the next breeding season was on average 67.2 ± 6 m. The number of nests attempted per breeding season by these “older” females was 2.2 ± 0.2 (range 1–4, $n = 20$ female-years).

REPRODUCTIVE SUCCESS OF MALES AND FEMALES

We estimated the reproductive success of males and females from our sample of banded individuals. For this estimation we assumed that the territorial male fathered all the chicks in the nests within its territory. Although this assumption is probably invalid, the degree to which it is invalid is unknown at present (see Discussion). Males fledged on average 2.58 ± 0.61 chicks per breeding season (range 0–12 chicks, variance 7.15, $n = 19$ males), while females fledged 1.6 ± 0.29 (range 0–6 chicks, variance 2.95, $n = 35$ female-years), but this difference was not significant (Mann–Whitney U test: $z = -1.54$, $P = 0.12$). Because most females (11/17) bred in more than one breeding season, the average number of chicks fledged per female during the study period was 3.04 ± 0.74 (range 0–10, $n = 17$ females).

DISCUSSION

This study provides the first complete account of the breeding behavior and reproductive success of the threatened Strange-tailed Tyrant. Our results show that (1) this species has a socially polygynous mating system, with males holding territories with two females on average, (2) parental care is provided exclusively by the female, which builds the nest, incubates the eggs, and broods and feeds the chicks without the male’s assistance, (3) successful nests fledge on average 2.3 chicks, (4) nest survival through the nesting cycle is 0.23 and decreases with nest age and the time of breeding within a season, (5) most females attempt two or three nests per breeding season, and (6) females bred in the same area over several years, but males rarely were seen in the same area more than one year, which is consistent with the hypothesis of male-biased mortality.

BREEDING BEHAVIOR AND MATING SYSTEM

Our observations confirm that the Strange-tailed Tyrant is a socially polygynous species, as suggested by Traylor and Fitzpatrick (1982). Nearly 80% of the males had more than one female in their territories, indicating high levels of social polygyny in our population. In addition, video records and observations of focal nests showed that males did not provide any form of parental care.

The predominant mating system of tyrant flycatchers in both temperate and tropical zones is social monogamy

(Fitzpatrick 2004). In this family, social polygyny is rare, with a few examples in the genera *Empidonax* in North America (Prescott 1986, Briskie and Sealy 1987, Davidson and Allison 2003, Pearson et al. 2006) and *Mionectes* in the neotropics (Snow and Snow 1979, Wescott and Smith 1994, Pizo and Aleixo 1998). Regarding parental care, in most tyrant flycatchers the female builds the nest, incubates the eggs, and broods the chicks, but usually both sexes feed the chicks (Fitzpatrick 2004). Biparental care also characterizes the polygynous species of *Empidonax* (Prescott 1986, Briskie and Sealy 1994) but not the lek-breeding *Mionectes*. Thus the Strange-tailed Tyrant is the first example of a nonlekking tyrant flycatcher with extended social polygyny and uniparental female care.

We found that females that nested in consecutive breeding seasons did so in the same area, but we rarely observed males breeding in the same area in consecutive years. Because we never observed these males in other areas of the reserve, we consider it likely that they died between breeding seasons, although we cannot rule out dispersal as a cause of low rates of males returning. This apparent difference in survival between males and females could be related to increased detectability or reduced movement due to the male’s exaggerated ornaments, as has been observed in other sexually dimorphic (Promislow et al. 1992) and polygynous (Liker and Székely 2005) species. The fact that females settle on the same territory (or close to it) in consecutive years, regardless of which male is occupying that territory, raises the question of how important sexual selection is in terms of mate choice in this species. One possibility is that the best males consistently hold the best territories and therefore females holding the best territories are choosing the best males indirectly. Alternatively, the genetic mating system may not reflect the social one (i.e., females may have extra-pair fertilizations with good-quality males). Accordingly, preliminary genetic analysis of eight microsatellite loci confirmed that most males were polygynous but also revealed extra-pair fertilizations (Mahler et al., unpubl. data).

BREEDING BIOLOGY AND NESTING SUCCESS

The size of the Strange-tailed Tyrant’s clutch was relatively constant (three eggs in most clutches) but decreased through the breeding season. This reduction in clutch size could be an adaptive response to the increase in the risk of nest predation with time of breeding, as suggested by Eggers et al. (2006). Alternatively, it could be a consequence of lower availability of food as a result of increased temperature and decreased precipitation at the end of the breeding season or poor physiological condition of the female as a result of previous investment.

Nest survival decreased with age of the nest. This trend has also been observed in grassland passerines of North America (Martin et al. 2000, Grant et al. 2005, Lloyd and Martin 2005) and Africa (Muchai and du Plessis 2005). Similarly, Auer et al. (2007) found that in four neotropical forest tyrants, predation rates were higher during the nestling stage than

during incubation. Skutch (1949) hypothesized that increased parental activity could raise the risk of nest predation because nest predators use parental activity to find nests. Our results are consistent with Skutch's hypothesis, as frequency of visits to the nest increased from 3 hr⁻¹ during incubation to 7–11 hr⁻¹ during the nestling stage, and this increase was associated with a decrease in daily nest-survival rates. Alternatively, the higher nest mortality at this stage could result from more active and louder chicks that make the nest more conspicuous to predators.

Daily nest-survival rates also decreased with time of breeding. This temporal pattern has been observed in other ground-nesting grassland passerines in North America (Davis 2005, Grant et al. 2005) and has been attributed to various causes. Grant et al. (2005) reported that nesting success at the end of the breeding season decreased as a result of an increase in the local abundance of predators. In other grassland species, the peak of breeding was associated with the emergence of insects, and the decrease in nesting success was likely the result of lower prey availability (Jones and Cornely 2002, Knapton 1994). Because we do not have data on seasonal variation in predators or arthropod prey, we cannot test these hypotheses. Other studies have shown an association between protective cover and nesting success in some grassland species (Davis 2005). Similarly, at our study site the end of the Strange-tailed Tyrant's breeding season coincides with a seasonal drought that reduces protective cover (growth of C4 grasses is arrested), which could decrease nest concealment.

RENESTING BY FEMALES

Tropical and subtropical birds have longer breeding seasons than their temperate-zone counterparts (Stutchbury and Morton 2001), which may allow them to attempt several nests (and eventually second broods) in a breeding season. Accordingly, we found the Strange-tailed Tyrant has a long breeding season (approximately 4 months), and during that period some females attempted up to four successive nests. Most renesting occurred after a failed attempt, but approximately 30% of the cases of renesting we observed were by females that had fledged chicks. We also observed a few cases in which the female made two successful nesting attempts in the same breeding season. However, because of the length of the post-fledging period, only two of 35 cases of renesting could be considered second broods (i.e., renesting after a successful first brood). Thus, like most tyrant flycatchers (Fitzpatrick 2004), the Strange-tailed Tyrant generally raises a single brood per breeding season.

Among subtropical tyrants, Lopes and Marini (2005) recorded several cases of renesting by the Suiriri Flycatcher (*Suiriri affinis*) and the Chapada Flycatcher (*S. islerorum*). Similarly, Medeiros and Marini (2007) reported that pairs of Lesser Elaenia (*Elaenia chiriquensis*) whose nests failed at the beginning of the breeding season often renested and in

some cases had second broods. One difference between these species and the Strange-tailed Tyrant is that the former have biparental care while the latter has uniparental care by the female only, making renesting more costly for the female.

MATING SYSTEM AND REPRODUCTIVE SUCCESS OF MALES AND FEMALES

Although nearly 80% of the male Strange-tailed Tyrants we studied were polygynous, in most cases they bred in our study area in only one breeding season. By contrast, most females bred in the same area for two or three consecutive breeding seasons. As a result, the reproductive success of banded individuals during our 4-year study was similar for females and males (approximately 3 chicks per individual).

Polygyny is expected to produce higher variance in males' reproductive success (and lower effective population size) because fewer males monopolize more mates (Stiver et al. 2008). However, the high rate of turnover of male Strange-tailed Tyrants increased the number of males that contributed genetically to the next generation. Variance in females' reproductive success depends more on the proportion of females that reproduce and the variance in offspring produced per successful female than on the numbers of mates (Frankham et al., 2002, Stiver et al. 2008). Although nest survival was relatively low (only 23% of the nesting attempts were successful), 86% of the females renested after nest failure. This high probability of renesting reduced the variance in the number of offspring produced per female per breeding season. In addition, because most females bred for two or three consecutive breeding seasons, the variance in the number of chicks fledged per female was low (only two of the 17 banded females did not fledge any chicks during the study period). Further studies of the extent to which reproduction of males is skewed (i.e., extra-pair fertilizations), the post-fledgling survival of juveniles, and the annual survival rates and dispersal patterns of females and males may help us to estimate the effective population size and to predict the risk of extinction of threatened populations of the Strange-tailed Tyrant.

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