J. Field Ornithol., 68(1):91–97

THE BREEDING BIOLOGY OF THE PIED WATER-TYRANT AND ITS INTERACTIONS WITH THE SHINY COWBIRD IN VENEZUELA

ALEXANDER CRUZ AND ROBERT W. ANDREWS
Environmental, Population, and Organismic Biology Department
University of Colorado
Boulder, Colorado 80309-0334 USA

Abstract.—We studied the breeding biology of the Pied Water-Tyrant (*Fluvicola pica*) in a seasonally inundated savanna in the llanos of western Venezuela. A total of 123 nests was located in the wet season (June–October). The water-tyrant nested mainly in trees and shrubs near water in the early part of the wet season (86%), but nested primarily in emergent marsh vegetation during the latter part (84%). The species was heavily parasitized (53% of nests) by the Shiny Cowbird (*Molothrus bonariensis*). The rate of parasitism was nearly equal in both tree/shrub nests and marsh nests, and declined only late in the season. Parasitized nests were more frequently abandoned (60%) than nonparasitized nests (30%). The number of host eggs in nests was nearly equal in non-parasitized (2.42) and parasitized nests (2.51). The number of cowbird eggs (1.23) was less than the number of host eggs in parasitized nests. Of 37 non-parasitized clutches of the Pied Water-Tyrant, 18 (49%) produced nestlings and 7 (19%) produced fledglings, and of 47 parasitized clutches, 2 (4%) produced nestlings and fledglings. Given the high level of parasitism on the Pied Water-Tyrant, it should be considered a major Shiny Cowbird host in the llanos of Venezuela. The Pied Water-Tyrant, however, does not appear to be an optimal host as only 3 of 47 parasitized nests in which the outcome was known successfully fledged cowbird young.

LA BIOLOGÍA REPRODUCTIVA DE *FLUVICOLA PICA* Y SU INTERACCIÓN CON *MOLOTHRUS BONARIENSIS* EN VENEZUELA

Sinopsis.—Estudiamos la biología reproductiva de *Fluvicola pica* en una sabana estacionalmente inundada en los llanos del oeste de Venezuela. En la temporada húmeda (junio–octubre) se localizaron un total de 123 nidos. En la parte temprana de la temporada húmeda la especie anidó principalmente en árboles y arbustos cerca del agua (86%), pero anidó principalmente en vegetación pantanosa emergente durante el final de temporada (84%). La especie fué intensamente parasitada (53% de los nidos) por *Molothrus bonariensis*. La razón de parasitismo fué prácticamente igual tanto en árboles/arbustos como en nidos de pantanos, y declinó solo al final de la temporada. Los nidos parasitados fueron abandonados más frecuentemente (60%) que los no parasitados (30%). En número de huevos de la especie hosperdera por nido fué casi igual en los nidos no-parasitados (2.42) y en los parasitados (2.51). El número de huevos de *Molothrus* (1.23) fué menor que el número de huevos de *Fluvicola* en nidos parasitados. De 37 camadas no parasitadas de *Fluvicola pica*, 18 (49%) produjeron pichones y 7 (19%) produjeron volantones, mientras que de 47 camadas parasitadas, 2 (4%) produjeron pichones y volantones. Debe considerarse *Fluvicola pica* como uno de los hosperderos principales de *Molthrus bonariensis* en los llanos de Venezuela dado el alto nivel del parasitismo detectado. Sin embargo, *Fluvicola pica* no parece ser un hospedero óptimo ya que solo 3 de 47 nidos parasitados en los cuales se conoce el éxito sacaron volantones de *Molothrus*.

The Pied Water-Tyrant (*Fluvicola pica*) occurs as a breeding species from central Panama and Trinidad to northern Argentina, Uruguay, and southern Brazil (ffrench 1980, Lefebvre et al. 1992, Meyer De Schauensee 1966, Narosky and Yzurieta 1987). Throughout its range, the water-tyrant is associated with wetland areas (Cruz and Andrews 1989, ffrench 1980).

The Shiny Cowbird (*Molothrus bonariensis*) is a generalized brood parasite found from South America to Florida (Cruz et al. 1989; Cruz et al.,

in press). In many areas of South America, including Venezuela, the Shiny Cowbird is sympatric with the Pied Water-Tyrant (Cruz and Andrews 1989). In this paper, we describe the reproductive biology of the Pied Water-Tyrant in the llanos (flooded savanna) of Venezuela. We provide data on timing of breeding, clutch size, and reproductive success. We also discuss the frequency and impact of Shiny Cowbird brood parasitism on the reproductive success of Pied Water-Tyrants. This research was part of a larger study of Shiny Cowbird and its host relationships in northern South America and the Caribbean basin.

STUDY SITES AND METHODS

Study areas.—We made observations at Hato El Frío (7°35′–7°55′N, 68°45′–69°00′W), a cattle ranch in northern Apure state, Venezuela. It covers 78,000 ha at an elevation of 65–75 m. The land is flat and the climate is characterized by slight annual temperature variations and by well-defined rainy and dry seasons. At Mantecal (approximately 49 km southwest of Hato El Frío), annual precipitation varied from 1314–2980 mm, with an average of 1645 mm. About 90% of the rain falls in the May–October rainy season. The December–March dry season is virtually or entirely rainless; April and November are transitional months.

Hato El Frío is situated in a flooded savanna. Much of the ranch is covered by savannas and water bodies; only about 20% is wooded. Data were collected in *esteros* and *caños* habitats. *Esteros* are alluvial bottom savannas found in depressions up to 2-m deep. They are flooded throughout the wet season and retain water in the dry seasons. *Caños* are riverine overflow channels which also retain water in the dry season. Search time was approximately equal between these two habitats.

Methods.—Observations were made from 12 Aug.–28 Nov. 1982 and 5 Jun.–2 Nov. 1983. Nests were located by daily searches. After a nest was found, it was checked every 2–4 d until it failed or young were successfully fledged. Only nests with water-tyrant or cowbird eggs and of which the final outcomes were known were included in the analysis of nesting success. Nest contents were recorded at the time of each check, and the data were used to determine clutch sizes, nesting successes, and levels of parasitism. If the nest failed, the area was searched for evidence of the cause of failure (e.g., punctured eggs, damaged to the nest). Nest appearance and mode of disturbance were used to determine whether nests were disturbed by predators. A chi-squared test was used to determine if there were difference in the proportion of nests parasitized in caño and estero habitats, and if there were differences in the reproductive success of unparasitized and parasitized Pied Water-Tyrant nests. A two-tailed Students *t*-test was used to determine if there were differences in the clutch size for unparasitized and parasitized nests. We located 123 nests in esteros and caños habitats, 95 of which were used to calculate clutch size and a smaller subset (84 nests) were used to determine reproductive success.

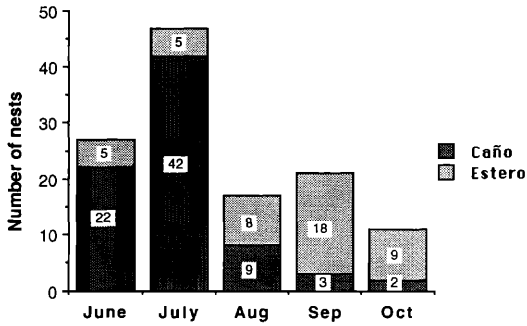

FIGURE 1. Distribution of Pied Water-Tyrant nests in caño and estero habitats during the breeding season. Actual number of nests depicted inside of bars.

RESULTS

Timing of breeding.—During the study period, nesting Pied Water-Tyrants were recorded from June to October (Fig. 1). The number of nests and the number of new nests discovered peaked in July, and subsequently declined from August through October.

Nest and nest placement.—Nest were globular, 6–11 cm front to back ($\bar{x}$ = 8.0 cm, n = 22), 6–13-cm wide ($\bar{x}$ = 8.5 cm, n = 22), and 10–15-cm high ($\bar{x}$ = 13 cm, n = 22), with 2–8-cm diameter entrance ($\bar{x}$ = 4.5 cm) near the top. The cavity depth was 3–6 cm ($\bar{x}$ = 5 cm, n = 14), and was lined with grasses, spider-webs, and feathers (usually of egrets). Both members of the pair constructed the nest.

Toward the early part of the rainy season (June–July), most nests (86.5%, n = 64/74) were located in trees (33%), shrubs (7%), or *Mimosa piagra* thickets (60%) in caño habitats (Fig. 1). As the season progressed (September and October) and stiff emergent vegetation grew, nests were more often placed within such vegetation in esteros (84%, n = 27/32). In the esteros, the most commonly used plant was *Echinodurus paniculatos* (75%) and *Sesbania* (25%). The average height of nest over ground was 170 cm (n = 27), and the height over water was 50 cm (n = 54).

Shiny Cowbirds parasitized 53% (54/102) of nests (Table 1). No significant differences were found in frequency of parasitism of nests found in caño (58%, 26/45) and estero (49%, 28/57) habitats (X^2 = 0.45, df = 1, $P < 0.05$). Frequency of parasitism was high (Fig. 2).

Clutch sizes and eggs.—Eggs were laid at daily intervals. Mean host clutch size (±SD) was 2.42 ± 0.80 in 43 unparasitized nests and 2.51 ± 0.80 in 52 parasitized nests. Water-tyrant clutch sizes in parasitized and unparasitized nests were not significantly different (t = 0.40, n = 95, $P > 0.05$).

Pied Water-Tyrant eggs are oblong, oval, and white with a wreath of red-brown spots and blotches, mostly at the larger end but a few random marks elsewhere (n = 43). Mean weight of 122 eggs was 1.6 g (1.0–2.2 g), and they measured 18.02 × 12.91 mm (15.60–19.94 × 11.75–14.00, n = 122).

TABLE 1. Host reproductive success of parasitized and unparasitized Pied Water-Tyrant nests at Hato El Frío, Venezuela.

Nest data	Unparasitized	Parasitized
Total number of nests	48	54
Nests used in determining reproductive success	37	47
Number of nests hatching at least one young	18	2
Number of nests fledging at least one young	7	2
Number of eggs laid	98	118
Average clutch size	2.65	2.52
Number of eggs hatched	34	8
Number of young fledged	14	3
Nest hatching success[a]	0.4865 (18/37)	0.0426 (2/47)
Egg hatching success (no. hatched/no. eggs laid)	0.3469 (34/98)	0.0678 (8/118)
Egg fledgling success (no. fledged/no. eggs laid)	0.1429 (14/98)	0.0263 (3/118)

[a] Proportion of nests hatching at least one host young.

The average number of cowbird eggs found in tyrant nests was 1.23 ± 0.425 SD (n = 52), with the number ranging from 1–2 eggs. Shiny Cowbird eggs in water-tyrant nests were larger and noticeably more rounded than water-tyrant eggs. The background color was white to red-brown with cloudy red-brown marbling and mottling over the entire egg. Mean weight of 56 cowbird eggs was 3.3 g (2.0–4.2), and they measured 21.62 × 17.08 mm (20.05–23.85 × 16.70–18.30, n = 43).

Nesting success.—The overall nest success of the Pied Water-Tyrant was affected by parasitism (Table 1, X^2 = 24.8, df = 1, $P < 0.05$). In unparasitized nests, 34 of the 98 eggs (35%) laid were successfully hatched (Table 1). In parasitized nests, 8 of the 118 eggs (7%) laid were successfully hatched (Table 1).

Nest hatching success was higher (48.7%) in non-parasitized than in parasitized nests (4.3%) (X^2 = 20.1, df = 1, $P < 0.05$). Egg hatching

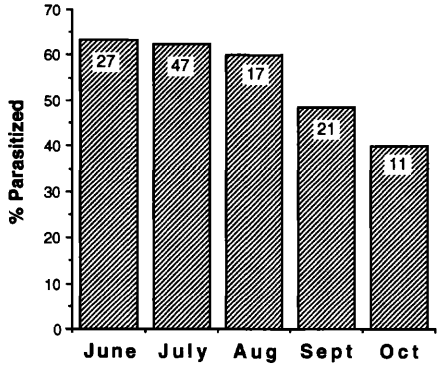

FIGURE 2. Frequency of Shiny Cowbird parasitism in relation to the time of breeding of Pied Water-Tyrants. Number of nests parasitized shown inside of bars.

TABLE 2. Cowbird reproductive success in parasitized Pied Water-Tyrant nests at Hato El Frío, Venezuela.

Nest data	Parasitized
Number of nests	47
Number of nests hatching at least one young	3
Number of eggs laid	59
Average clutch size	1.26
Number of eggs hatched	3
Number of young fledged	3
Nest hatching success[a]	0.0638 (3/47)
Nest fledgling success[b]	0.0638 (3/52)
Egg hatching success (no. hatched/no. eggs laid)	0.0508 (3/59)
Egg fledgling success (no. fledged/no. eggs laid)	0.0469 (3/64)

[a] Proportion of nests hatching at least one host young.
[b] Proportion of clutches laid that fledged at least one host young.

success in nonparasitized nests (35%) was significantly greater than egg hatching success in parasitized nests (6.8%), ($X^2 = 24.8$, df = 1, $P < 0.05$). Egg fledgling success in nonparasitized nests (14.3%) was higher than parasitized nests (3%), ($X^2 = 8.6$, df = 1, $P < 0.05$).

Parasitized nests were more frequently abandoned (59.6%, $n = 28/47$) than nonparasitized nests (30%, $n = 11/37$) ($X^2 = 12.6$, df = 1, $P < 0.05$). Many of the abandoned parasitized ($n = 12$) and nonparasitized nests ($n = 5$) had broken eggs.

Factors other than parasitism contributing to the low nest success included predation (11 nonparasitized and 9 parasitized nests) in which the nest or its contents disappeared, and host eggs and nestlings ($n = 50$) that did not hatch.

Cowbird nesting success.—Cowbird reproductive success in water-tyrant nests was very low (Table 2), with only 3 of 47 nests producing young. Nest abandonment by Pied Water-Tyrants played an important role in this low nesting success. However, all three cowbird eggs that hatched fledged young.

DISCUSSION

Timing of breeding.—Llanos appear to be one of the most marked examples of a seasonal tropical ecosystem. Rainfall is concentrated in 4–6 mo, and the dry season is 4 mo or more. Consequently, the annual cycles of plants and animals are highly seasonal. In seasonal areas of the tropics, passerines are primarily wet-season breeders (Cruz and Andrews 1989; Lefebvre et al. 1992; Poulin et al. 1992, 1993; Snow and Snow 1964). During the wet season, we found Pied Water-Tyrant nests in all months, except November. In an earlier study in the same region, Ramo and Busto (1984) found 4 of 28 Pied Water-Tyrant nests in November, but none in April. Our combined data suggest that the breeding season extends from at least June to November. The actual timing may vary from year to year, as the start of the rainy season is variable; it may be as early as late March or as late as June or even July (Cruz and Andrews 1989; Thomas 1985,

pers. obs.). The timing of breeding in this species may have evolved to match the seasonal flush of insects (Cruz and Andrews 1989), which have been documented in the llanos (Lefebvre et al. 1992, Poulin et al. 1992, 1993, Travieso et al. 1977, Wolda 1978).

Nesting success and brood parasitism.—Although the Pied Water-Tyrant has been reported as a Shiny Cowbird host in Argentina, Guyana, Surinam, and Trinidad (Friedmann 1929, Friedmann et al. 1977, Friedmann and Kiff 1985, Haverschmidt 1965), most studies report low levels of parasitism. Friedmann (1929) found no parasitized nests among 20 seen in Argentina, and ffrench (1980) said the species is "sometimes" parasitized in Trinidad. The low cowbird fledgling success indicates that the Pied Water-Tyrant is not an optimal cowbird host. Before our study there were no reports of this species rearing cowbird chicks successfully.

Pied Water-Tyrants in the llanos of Apure, however, are affected by Shiny Cowbirds. Pied Water-Tyrants accept cowbird eggs, and nests that were parasitized had significantly lower nesting success than nonparasitized nests. We also found parasitized nests of the Rusty-backed Spinetail (*Cranioleuca vulpina*), White-headed Marsh Tyrant (*Arundinicola leucocephala*), Bicolored Wren (*Campylorhyncus griseus*), Yellow-hooded Blackbird (*Agelaius icterocephalus*), Red-breasted Blackbird (*Leistes militaris*), and Carib Grackle (*Quiscalus lugubris*) (Cruz and Andrews 1989; Ramo and Busto 1980, 1981), but the number of parasitized Pied Water-Tyrant nests was greater than the combined parasitized nests of the other host species.

As noted by Piper (1994), deforestation and conversion of most of the land in the llanos of Apure has probably favored increased of Shiny Cowbirds. The increase in cowbirds might, at least in part, explain the differences in frequencies of brood parasitism between our study and that of Ramo and Busto (1980, 1981). Based on data gathered before 1980, Ramo and Busto found a frequency of parasitism of 10.7% (3 of 28 nests) at El Frío, while we observed a frequency of parasitism of 52.0% (54 of 102 nests). In addition, unlike our study, none of the parasitized nests found by Ramo and Busto produced either cowbird or host young.

In our study, nest desertion was more frequent in parasitized nests than in nonparasitized nests. These desertions may have been a response of the Pied-Water tyrant to a reduction in clutch size as a result of egg breakage or egg removal by cowbirds. Desertion will result in the loss of the entire clutch and would appear to be a poor anti-parasite strategy. However, most Pied-Water Tyrants can produce more than one clutch per season (Borrero 1973, this study). Since reproductive success from parasitized nests is low, and raising a cowbird is energetically costly to the parents, the option of renesting would be a desirable one for an acceptor species like the Pied Water-Tyrant.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation Grant PRM-8112194 to the Univ. of Colorado, A. Cruz, principal investigator. Logistical assistance was provided by the Maldonado family (owners of Hato El Frío), the Sociedad de Ciencias Naturales La Salle (op-

erators of Estacíon Biológica El Frío, J. Ayarzagüena, director), and by E. Herrera, E. La Marca, C. and M. Lilyestrom, S. Reid, and D. Taphorn. Useful discussion in the field were given by B. Busto, C. Casler, M. de Visscher, C. Parrish, and C. Ramo. N. Wischnewsky assisted with the field work, and R. Rondeau identified many plants.

LITERATURE CITED

BORRERO, J. I. 1973. Sobre la historia natural de la Viudita, *Fluvicola pica* (Boddaert) (Tyrannidae). Ardeola 19:69–87.

CRUZ, A., AND R. W. ANDREWS. 1989. Observations on the breeding biology of passerines in a seasonally flooded savanna in Venezuela. Wilson Bull. 10:62–76.

———, J. W. WILEY, T. K. NAKAMURA, AND W. POST. 1989. The Shiny Cowbird in the Caribbean region—biogeographical and ecological implications. Pp. 519–540, *in* Biogeography of the West Indies-past, present, and future. Sandhill Crane Press, Gainesville, Florida.

———, J. W. PRATHER, W. POST, AND J. W. WILEY. In press. The spread of Shiny and Brown-headed Cowbirds in the Florida region. *In* North American Research Workshop on the Ecology and Management of Cowbirds.

FFRENCH, R. P. 1980. A guide to the birds of Trinidad and Tobago, 3rd ed. Harrowood Books, Valley Forge, Pennsylvania. 450 pp.

FRIEDMANN, H. 1929. The cowbirds. A study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois. 421 pp.

———, L. F. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge of host relations of the cowbirds. Smithson. Contrib. Zool. 235:1–75.

———, AND L. F. KIFF. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2:226–302.

HAVERSCHMIDT, F. F. 1965. *Molothrus bonariensis* parasitizing *Fluvicola pica* and *Arundicola leucocephala* in Surinam. Auk 82:508–509.

LEFEBVRE, G., B. POULIN, AND R. MCNEIL. 1992. Settlement period and function of long-term territory in tropical mangrove passerines. Condor 94:84–92.

MEYER DE SCHAUENSEE, R. 1966. The Species of Birds of South America with their distribution. Livingston Publ. Co., Wynnewood, Pennsylvania. 418 pp.

NAROSKY, T., AND D. YZURIETA. 1987. Guia para la idenficacion de las aves de Argentina y Uruguay. Vazquez Mazzini Editores, Buenos Aires, Argentina. 345 pp.

PIPER, W. H. 1994. Courtship, copulation, nesting behavior and brood parasitism in the Venezuelan Stripe-backed Wren. Condor 96:654–671.

POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73:2295–2309.

———, ———, AND ———. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. Ibis 135:432–441.

RAMO, C., AND B. BUSTO. 1980. Biología reproductiva de la Viudita (*Fluvicola pica*) en el llano venezolano. Natura 86:22–25.

——— AND ———. 1981. La reproducción de un ave parásito: el tordo-mirlo (*Molothrus bonariensis*) en los llanos de Apure (Venezuela). Doñana Acta Vert. 8:215–224.

——— AND ———. 1984. Nidificación de los Passeriformes en los llanos de Apure (Venezuela). Biotropica 16:59–68.

SNOW, D. W., AND B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad landbirds. Zoologica 49:1–39.

THOMAS, B. T. 1985. Coexistence and behavior differences among the three Western Hemisphere storks. Pp. 921–931, *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Wrigley, and F. G. Buckley, eds. Neotropical Ornithology. Ornithol. Monogr. No. 36.

TRAVIESO, G., VILLAROEL, AND J. PACHECO. 1977. Análisis de la commanded de insectos de la sabana del Módulo Experimental de Mantecal, Estado Apure. Acta Cientifica Venezolana 27:69–70.

WOLDA, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Anim. Ecol. 47:369–381.

Received 27 Nov. 1995; accepted 3 Apr. 1996.