J. Field Ornithol., 67(3):434–441

GROWTH AND PROVISIONING OF SHINY COWBIRD AND HOUSE WREN HOST NESTLINGS

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Abstract.—The brood-parasitic Shiny Cowbird (*Molothrus bonariensis*) parasitizes more than 200 species of birds throughout its range, many of which are small passerines. Growth rates of cowbird nestlings are expected to vary according to factors such as host size, total number of young in the nest, and rates of food delivery by the host. Here I report growth and provisioning rates of cowbird and host nestlings in House Wren (*Troglodytes aedon*) nests in the Cauca Valley, Colombia. Cowbirds raised singly in wren nests had high growth rates and a short nestling period. Their mass increased 10–12-fold, reaching an asymptote at age 9–10 d and fledging at 12–14 d of age. Cowbirds fledged at 65–75% of adult mass and remained small until their first molt, after which they reached adult mass. Being raised in mixed broods with wrens did not affect growth rates of cowbirds. Wrens, in contrast, increased in mass 10-fold and reached asymptotic mass, equal to adult mass, at the age of 10–11 d. They remained in the nest for an additional 7–8 d before fledging. At 10 d of age, mass of wrens in parasitized nests was significantly lower than in unparasitized nests. The mass and provisioning rates of a single cowbird were equivalent to those of a modal brood of three wrens. The combination of rapid growth and early fledging resulted in a short nestling period for cowbirds, which together with a short incubation period, form part of a suite of adaptations that allow cowbirds to outcompete their foster nestmates.

TASAS DE CRECIMIENTO Y ALIMENTACIÓN DE POLLUELOS DE *MOLOTHRUS BONARIENSIS* Y SU HOSPEDERO *TROGLODYTES AEDON*

Sinopsis.—El Chamón Parásito (*Molothrus bonariensis*) parasita más de 200 especies de aves, muchas de las cuales son paserinos pequeños. Se espera que las tasas de crecimiento de los polluelos de chamón varíen con factores tales como el tamaño del hospedero, el número total de polluelos en el nido y las tasas de alimentación. En este artículo se presentan las tasas de crecimiento y alimentación de polluelos criados en nidos de Cucarachero Común (*Troglodytes aedon*) en el Valle del Cauca, Colombia. Los tordos criados solos en nidos de cucarachero aumentaron su masa de 10 a 12 veces más y alcanzaron la asíntota de crecimiento entre los 9–10 días de edad. Los chamones abandonaron el nido a la edad de 12–14 días, con el 65–75% de la masa de los adultos y permanecieron pequeños hasta su primera muda, luego de la cual crecieron hasta el tamaño adulto. La presencia de polluelos de reyezuelo no afectó la tasa de crecimiento de los tordos. Los cucaracheros, en cambio, aumentaron de masa 10 veces y alcanzaron la asíntota, igual a la masa del adulto, en un período de 10 días. A los 10 días de edad, los polluelos de reyezuelo en nidos parasitados eran significativamente más livianos que los de nidos no parasitados y abandonaron el nido a más temprana edad. La masa y las tasas de alimentación de un polluelo de tordo fueron equivalentes a las de una nidada modal de tres polluelos de reyezuelo. El rápido crecimiento y el corto tiempo que permanecen los polluelos de tordo en el nido, junto con sus cortos períodos de incubación, conforman un conjunto de adaptaciones que le permiten a éstos obtener una ventaja en la competencia con sus hospederos.

The brood-parasitic Shiny Cowbird (*Molothrus bonariensis*) is an extreme generalist, reportedly parasitizing more than 200 species of birds throughout its range in South America and the Caribbean (Cruz et al. 1985, Friedmann and Kiff 1985). At a local level, Shiny Cowbirds are also

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generalists and parasitize many sympatric passerines (e.g., Mason 1986, Salvador 1983, Wiley 1985). With such a variety of hosts, growth rates of cowbird nestlings are expected to vary according to host size, because of differences in the rate of food provisioning by adults, and because cowbird nestlings may be exposed to competition with foster nestmates (Wiley 1986). Growth rates of cowbird nestlings are particularly likely to be affected when raised by small hosts, because the ability of adults to deliver food to one or more large cowbird nestlings, which may be added to the host's own, may be limited. The sight of a small host feeding a voracious nestling several times its size, raises questions about the host's ability to provision it and the nestling's ability to reach a adequate fledging mass (Brooke and Davies 1989).

These observations suggest that asymptotic mass of fledglings is not species-specific in cowbirds (King 1973). Indeed, cowbirds fledge with different intrapopulational asymptotic masses, apparently always lower than the adult mass (Fraga 1978, 1985; King 1973; Wiley 1986). However, with few exceptions (e.g., Wiley 1986), fledging masses have not been explicitly compared to juvenile and adult masses in previous studies. In this paper I report on growth rates of Shiny Cowbirds and their House Wren (*Troglodytes aedon*) hosts in the Cauca Valley, Colombia. I address the following questions: (1) How do growth rates of cowbirds compare to those of wrens, which are four times smaller than the cowbirds? (2) How do fledging masses of cowbirds compare to adult masses? (3) How are growth rates of both species affected by being raised in mixed broods? and (4) How much parental effort, measured as feeding rates, does a cowbird demand from its foster parents?

STUDY AREA AND METHODS

This study was conducted at a dairy farm 28 km south of Cali (3°15'N, 76°30'W, 950 m elev.), in the Cauca Valley, Colombia, during 1989 and 1990. The study area encompassed about 25 ha of pastures with scattered shade trees and farm buildings. I mapped 14 wren territories located mostly along fence rows and around shade trees and buildings. Wrens nested in a variety of natural and semi-natural cavities, such as holes in bamboo (*Guadua angustifolia*) fence posts and other artificial structures, bromeliads, and on the ground in dense clumps of tall grass. To facilitate data collection, I placed wood nest boxes (10 × 10 × 15 cm) in most wren territories. Most breeding wrens were trapped in nest boxes or captured with mist nets, weighed with 50-g (0.5-g precision) Pesola spring scales, and banded. Adult and juvenile cowbirds were captured with mist nets, weighed with 300-g (1.0-g precision) scales, and banded.

I recorded the breeding activities of wrens in the 14 mapped territories. Once eggs hatched, I visited nests between 0630 and 0900, at intervals of 1–3 d to obtain data on nestling growth. Day of hatching was defined as day 0. Nestlings were weighed with 10-g (0.2-g precision) or 50-g (0.5-g precision) scales. When chicks were well-feathered, I visited nests daily to determine age of fledging but stopped handling chicks to avoid prema-

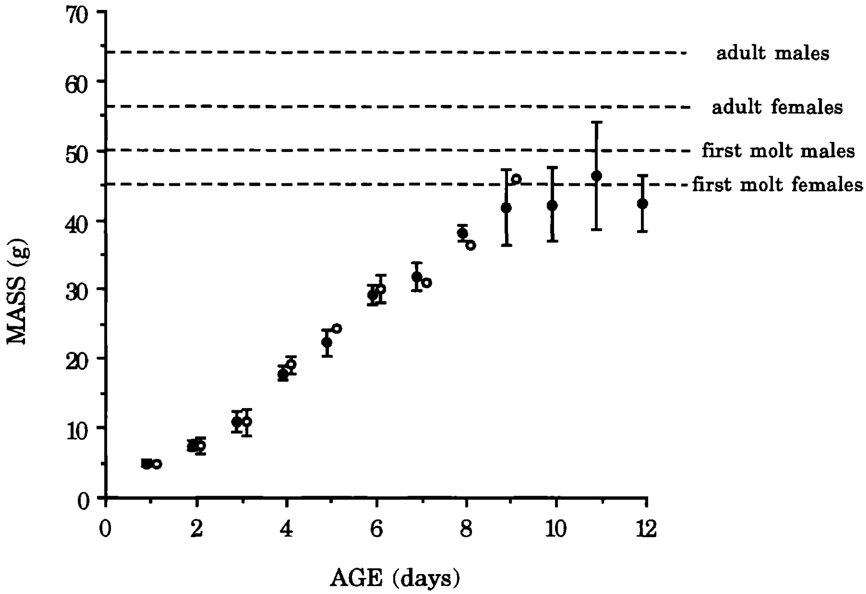

FIGURE 1. Growth curves of Shiny Cowbird nestlings raised in wren nests (mean ± SD). Solid dots indicate cowbird nestlings raised alone (n = 5–12). Open dots indicate nestlings raised in mixed broods (n = 1–4). Horizontal lines indicate average masses of adult and juvenile cowbirds (see text).

ture fledging. For comparisons of growth rates I used the logistic growth constant K, calculated as described by Ricklefs (1967).

To determine whether cowbird nestlings demand more food than a normal wren brood, I compared hourly feeding rates of broods of a single cowbird nestling with those of modal wren broods of three nestlings. I made observations with a 20× telescope, hiding behind a tree at distances of 15–20 m. Comparisons were made when nestlings were 5- and 10-d-old. I defined age of the wren brood as the age of the oldest nestling (spread of hatch was usually less than 24 h). Observations of feeding rates were made between 0800 and 1000.

RESULTS

Shiny Cowbird nestlings raised alone in wren nests had high growth rates (Fig. 1). Their mass at hatching averaged 3.5 ± 0.18 g (n = 5) and increased 10–12-fold during the 12–14-d nestling period. Nestlings reached an asymptotic mass at age 9–10 d and fledged at age 12 (n = 6) or 14 (n = 3) d. An asymptote of 42.0 g gave the best straight line fit for the logistic conversion factors as a function of age, which yielded a growth constant of K = 0.568 d^{-1}. Variation in mass among same-age nestlings was small until age 8 d, when nestlings had reached about 90% of the asymptotic mass, but subsequently it increased dramatically (Fig. 1).

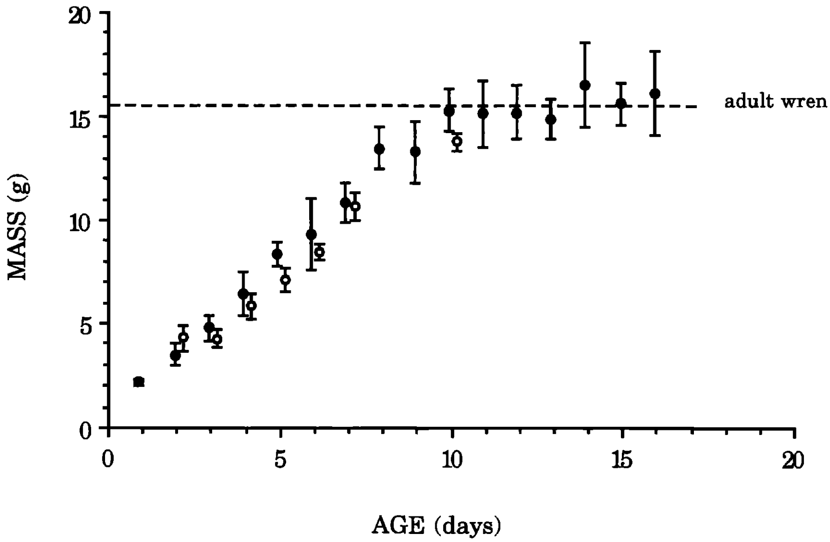

FIGURE 2. Growth curves of House Wrens in unparasitized (solid dots; n = 6–12) and parasitized nests (open dots; n = 4). The horizontal line indicates average adult mass.

Cowbirds fledged at 65–75% of adult mass and apparently increased little in mass until their first molt (Fig. 1). Females undergoing their first molt when mist-netted (with sheathed feathers and mixed juvenal-adult plumage) had a mean mass of 45.2 ± 4.4 g (n = 9), while two males captured in mixed juvenal-adult plumage had masses of 49 and 51 g. Cowbirds increased substantially in mass afterward. Adult masses were 55.6 ± 3.8 g (n = 24) for females and 63.7 ± 1.3 g (n = 5) for males. The time periods involved from fledging to molting are unknown.

In 4 out of 17 parasitized nests for which I obtained growth data, a cowbird was raised together with 1–3 wren nestlings. Being raised in mixed broods did not affect cowbirds; their masses were not different from masses of cowbirds raised alone (fixed-effects ANOVA with unbalanced cells, $F_{1,33} = 0.02$, $P = 0.8$; Fig. 1).

In spite of their smaller size, wrens in unparasitized nests had lower growth rates and longer nestling periods than cowbirds (Fig. 2). Wrens hatched with a mean mass of 1.6 ± 0.14 g (n = 12) and increased in mass 10-fold during the nestling period. They reached an asymptotic mass equal to adult mass at an age of 10–11 d and fledged at the age of 17–18 d. Using adult mass (15.4 ± 1.1 g, n = 16) as asymptotic value, I obtained a logistic growth rate of $K = 0.464\ d^{-1}$.

Masses of wren nestlings in parasitized nests differed significantly from those in unparasitized nests ($F_{1,41} = 32.2$, $P < 0.01$). At 10 d of age, masses of nestlings in parasitized nests were lower than masses of nestlings in unparasitized nests (Fig. 2). I did not obtain further mass data on these nestlings, but they all fledged at 14–15 d of age.

TABLE 1. Mass of a cowbird nestling raised alone, compared to the total mass of a brood of three wrens, at ages 5 and 10 d. Numbers in table are mean and SD.

Age (d)	Cowbird (n = 9)	Wrens (n = 4)[a]	P[b]
5	21.5 ± 1.9	23.6 ± 6.1	0.7
10	39.4 ± 3.6	46.1 ± 8.8	0.3

[a] Four broods of three wren nestlings each.
[b] Mann-Whitney U-test.

For adult wrens, raising a cowbird was equivalent to raising a brood of three wrens, the modal brood size. The mass of a cowbird nestling was similar to the total mass of a 3-wren brood, both at 5 and 10 d (Table 1). Provisioning rates increased with nestling age. Feeding rates of a single cowbird nestling were comparable to those of a 3-wren brood when the young were 5- and 10-d-old (Table 2).

DISCUSSION

Cowbird nestlings grew fast and fledged with a low mass relative to adult mass. Their growth constant (K = 0.568) is higher than the value reported as typical for tropical passerines (K = 0.40; Ricklefs 1984) and even higher than the value expected from adult body size (0.347 and 0.360 for males and females, respectively; Ricklefs 1983). This growth rate resulted in a 12-fold mass increase in a 9-d period. Cowbirds fledged at only 65–75% of adult mass, and increased little in mass until their first molt, after which they grew to adult mass.

Comparison of these results with other studies is difficult because fledging and juvenile (or even adult) masses are not always reported, and different-sized subspecies of cowbirds are involved. Growth rates of Shiny Cowbirds have been found to vary both with host size and brood size (King 1973, Wiley 1986). In most cases, cowbirds fledge in short periods and at a fraction of adult mass (Fraga 1985, King 1973, Wiley 1986), although Wiley (1986) found that cowbirds raised in Greater Antillean Grackle (*Quiscalus niger*) nests fledged at the same mass as adult females.

TABLE 2. Comparison of feeding rates (number of trips per hour, by both parents and by female wren) of a cowbird raised alone versus a brood of three wrens. Numbers in table are mean and SD.

Age (d)	Cowbirds (n = 9)	Wrens (n = 4)	P[a]
Both parents			
5	9.7 ± 2.9	9.7 ± 2.5	0.9
10	15.4 ± 1.7	13.0 ± 4.8	0.7
Female			
5	4.2 ± 2.3	4.1 ± 2.3	0.8
10	7.3 ± 1.3	8.5 ± 2.3	0.5

[a] Mann-Whitney U-test.

Short nestling periods have also been reported for Brown-headed Cowbirds (*M. ater*). In contrast to Shiny Cowbirds, growth rates of Brown-headed Cowbirds have been found to be independent of host size (Ortega and Cruz 1991, Weatherhead 1989). Similarly, Weatherhead (1989) did not find differences in growth rates of male and female Brown-headed Cowbirds. I did not sex the Shiny Cowbird chicks, but the divergence in mass during the final days of the nestling period might be attributed to sexual size dimorphism (Fig. 1). The Red-winged Blackbird (*Agelaius phoeniceus*), another icterine, exhibits a similar growth pattern, in which masses of male and female nestlings diverge in the final days of the nestling period, and both sexes fledge with a low mass relative to adult mass (Olson 1992).

The growth pattern of wrens was different from that of cowbirds (see also Alvarez-López et al. 1984). The nestling period of wrens was up to 6 d longer than that of cowbirds, and wrens fledged at adult mass. Nestling periods of House Wrens may be unusually long because they are cavity nesters. However, this does not change the consequences of the difference in nestling period in relation to host-parasite dynamics, as the difference in size and growth pattern gave a definite advantage to cowbirds over wrens.

Growth of cowbirds was not affected by competition with wrens, although with some large hosts, cowbirds may be at a competitive disadvantage (e.g., Wiley and Wiley 1980). Wrens, in contrast, were negatively affected by the presence of cowbirds in the nest. When cowbirds hatched earlier than wrens, wrens failed to hatch or died soon after hatching (Kattan 1993). Only when wrens hatched earlier (because cowbird eggs were laid after incubation had begun), did they have any chance to grow. Although limited, my data suggest that wrens in parasitized nests reached a lower asymptotic mass than in unparasitized nests. More importantly, wrens in parasitized nests were forced to fledge prematurely and this may compromise their survival (Freed 1988). A similar negative impact of cowbirds on small hosts has been reported in other studies (e.g., Marvil and Cruz 1989).

Besides decreasing the immediate reproductive success of hosts, a large parasitic nestling could also have an impact on their future reproduction, by straining the adults' ability to feed it. In particular, the female's physical condition and her performance in subsequent reproductive attempts could be affected. I found that a cowbird nestling is equivalent to the biomass of three wren nestlings, and that the provisioning rate of a cowbird nestling is similar to the provisioning rate of a wren brood. Thus, a single cowbird probably does not impose an exaggerated load on wrens. Even a larger-than-normal brood may not strain the wrens' capacity, as there is evidence that experimentally enlarged broods do not produce adverse effects on House Wrens (Finke et al. 1987).

Equivalence of provisioning rates for a single parasitic nestling versus a normal host brood has also been found for cuckoos (Brooke and Davies 1989). For two species of cuckoo (*Cuculus canorus* and *Clamator glan-*

darius), there is no evidence that host size influences growth rate of parasitic young (Brooke and Davies 1989, Soler and Soler 1991). Although Reed Warblers (*Acrocephalus scirpaceus*) can increase feeding rates, as shown by their response to experimentally enlarged broods, cuckoos do not exploit this extra feeding capacity; this suggests that cuckoos are already growing at their maximum rates (Brooke and Davies 1989). Because brood parasites are not genetically related to their foster parents, it is presumably in their interest to maximize their growth rates, if it does not compromise their own survival (Brooke and Davies 1989).

The combination of rapid growth and early fledging results in a short nestling period for cowbirds. This is presumably an advantageous trait for a brood parasite and may be part of a suite of adaptations that includes a short incubation period (Briskie and Sealy 1990, Kattan 1995). By hatching earlier than their hosts, cowbirds can outcompete their nestmates in obtaining parental resources. A short incubation period allows cowbirds to hatch early, even if parasitic eggs are laid after incubation has begun (Kattan 1995). A similar advantage would be conferred by fast growth. Even if cowbirds hatch late, they can outcompete or at least catch up with their hosts, and be ready to fledge with or before their nestmates. A similar pattern of development, both pre- and post-natal, is known for cuckoos (Payne 1977, Soler and Soler 1991).

ACKNOWLEDGMENTS

I thank Sr. Alfonso Madriñán for allowing me to work on his property. This paper is part of a dissertation submitted to the University of Florida. I thank members of my graduate comittee, L. J. Guillette, D. J. Levey, S. K. Robinson, J. W. Fitzpatrick and R. A. Kiltie, for their advise. Carolina Murcia and Humberto Alvarez-López made constructive comments on the manuscript, and Natalia Gómez provided very efficient field assistance. My work was financially supported by the Instituto Vallecaucano de Investigaciones Científicas (INCIVA), the Fundación para la Promoción de la Investigación y la Tecnología (Banco de la República) and the Fondo de Investigaciones Científicas "Francisco José de Caldas" (COLCIENCIAS).

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Received 8 May 1995; accepted 20 Oct. 1995.