REPRODUCTIVE RELATIONSHIPS OF THE RUFOUS-COLLARED SPARROW AND THE SHINY COWBIRD

James R. King

The Shiny Cowbird (*Molothrus bonariensis*) is a brood parasite distributed widely through Latin America from Panama to northern Patagonia. Its behavior and annual cycle are fairly well-known (Friedmann, 1929, 1963; Selander, 1964). The Rufous-collared Sparrow (*Zonotrichia capensis*) is coextensive with the Shiny Cowbird except in Patagonia and in parts of northern South America and the Lesser Antilles, and throughout its range it is an important host species (Friedmann, 1963). In certain regions it may serve as an almost exclusive host (Sick and Ottow, 1958; see also Sick, 1958), and the average level of parasitism may reach 90 percent of Rufous-collared Sparrow nests (Skinner, 1923, cited by Friedmann, 1929: 115), an incidence about double the maximum seasonal average reported for *Molothrus ater* and its main host species (*Melospiza melodia*) in North America (Friedmann, 1963: 168). Such severe parasitism must have important effects on the reproductive efficiency of the host species, but these effects in South America have been investigated quantitatively only by Sick and Ottow (1958) for the forms *M. b. bonariensis* and *Z. c. subtorquata* near Rio de Janeiro.

As a by-product of other studies of *Z. c. hypoleuca* in northwestern Argentina (King, 1972a, 1972b) I was able to obtain some information on the reproductive interactions of this species with *M. b. bonariensis*. The data are fragmentary in several respects, but nevertheless are sufficient for comparison with the results of other investigations and thus amplify our knowledge of the population ecology of the parasite and its main host.

Materials and Methods

This investigation was conducted in the province of Tucumán, northwestern Argentina, from late August 1969 to mid-June 1970. This region lies at the junction of the Gran Chaco and the eastern ranges of the Andes. Most of the observations were made in the foothill zone (ca. 550 m above sea level) near Horco Molle at about 27° S (for a detailed description see King, 1972b). This site is about 60 km north of the city of Concepción, where Friedmann made his pioneering studies of the Shiny Cowbird in 1923. Friedmann's monograph (1929) can be consulted for a thorough treatment of the distribution and habits of this species. I was in the field almost daily in the study area from September through November (the first half of the breeding season) and at least twice per week thereafter. I found 60 nests of Rufous-collared Sparrows, about half of which yielded almost complete histories. From a sample of nests the nestlings of known age were weighed daily

(± 0.1 g) in the late afternoon. Individuals were marked by nail clipping when necessary. The length of the first primary (P1) sheath (later, plus vane) was measured with a vernier caliper (ca. ± 0.2 mm). A sample of eggs was also measured (± 0.05 mm). Day 0 designates the condition of the nestlings at about the time of hatching or soon thereafter, day 1 designates the first full day (approximately) of nestling life, and so on (cf. Banks, 1959). Measurements were stopped on day 10 of nestling life to avoid disturbance of fledging. An effort was made to obtain data from the full range of nestling combinations of host and parasite, but this attempt was frequently thwarted by nest predation. The samples are therefore usually too small for useful statistical comparisons. When a statistical variation is shown with a mean value it is the standard error of the mean (SE). I have followed the common statistical convention in reporting mean values to one more significant digit than justified by the accuracy of measurement.

RESULTS AND DISCUSSION

The breeding season and cowbird movements.—In September, late in the austral winter, flocks of 100–200 Shiny Cowbirds were seen every day early in the morning flying along the foothills at the lower edge of the forest. By late September the large flocks were disbanding, and after the first week of October none larger than 24–30 individuals was seen. The cowbirds were still present in large numbers but were distributed as small localized courting parties (a female and 2–3 males, or 2 females and 3–4 males). During March, when egg-laying by the Rufous-collared Sparrow was waning, the numbers of the Shiny Cowbirds diminished rapidly; and after the end of March only two or three, and often none, were seen in a day of field work at Horco Molle. Rufous-collared Sparrows were in the region throughout the year.

The breeding season and incidence of parasitism.—The earliest clutches of eggs were completed by *Z. capensis* on about 3 October 1969, and the latest were completed on about 13 March 1970. Cowbird parasitism was light in clutches completed during the first 10 days of October (1 of 6 nests, or 14%), increased in the middle 10 days of October (3 of 4 nests, or 75%), and thereafter one or more cowbird eggs were found in all *Z. capensis* nests until 16 February (date of clutch completion). After that date, cowbirds parasitized about one-third of clutches until 26 February, and parasitized none completed after 28 February. The egg-laying season of the Shiny Cowbird thus spanned only slightly less than the entire breeding season of the Rufous-collared Sparrow in 1969–70, beginning slightly later and ending slightly earlier, and extending from mid-October to late February. This conforms approximately with the estimate Friedmann (1929: 89) made for southern Tucumán (third week of October until about the first week of January), but my records extend about 6 weeks longer. As noted above, the Shiny Cowbird practically disappeared from the foothill zone soon after the end of its egg-laying period.

Of 50 nests of *Z. capensis* at Horco Molle in which cowbird eggs could have been detected in 1969–70, 33 nests (66%) contained one or more cowbird eggs or chicks. This may be compared with 24 of 29 nests (83%) found in the plains of southern Tucumán by Friedmann (1929: 114). Similar or even higher levels of parasitism have been reported elsewhere in South America: 51 of 83 nests (61%) in coastal Brazil (Sick and Ottow, 1958); 9 of 10 nests in Minas Gerais, Brazil (Skinner, 1923, cited by Friedmann, 1929: 115); and 75 percent of nests in the same region (Moojen, 1938, cited by Friedmann, 1963: 214). In Chile, where *M. bonariensis* is a relatively recent invader, the Diuca (*Diuca diuca*) is the most common host (44 of 72 nests parasitized, or 61%), and *Z. capensis* is less heavily infested (10 of 72 nests, or 14%; Johnson, 1967). Obviously, the intensity of parasitism varies with the period of the breeding season. At Horco Molle all clutches completed between 14 October and 23 January were parasitized, although the seasonal average was 66 percent. The variation among published reports must be viewed with this in mind.

Cowbird eggs.—The eggs of *M. bonariensis* at Horco Molle averaged $23.00 \pm 0.356 \times 18.56 \pm 0.182$ mm ($n = 26$). The frequency distribution of both length and width showed apparent but not statistically significant bimodality ($P > 0.2$, by the Kolmogorov-Smirnov test; Sokal and Rholf, 1969: 573), perhaps as an expression of the dimorphism or polymorphism observed in other attributes of *M. bonariensis* eggs elsewhere in central South America (Friedmann, 1929: 83; Hoy and Ottow, 1964). The eggs I examined varied in color and pattern, but with a continuous range of variation. No immaculate eggs were found, although this condition is frequent in eastern Argentina and southeastern Brazil (Friedmann, 1929). The eggs of *Z. capensis* averaged $20.00 \pm 0.104 \times 14.90 \pm 0.059$ mm ($n = 31$ eggs, 16 nests) at Horco Molle.

Productivity of Rufous-collared Sparrows and Shiny Cowbirds

Various estimates of reproductive performance can be calculated from data obtained at Horco Molle. These are compared (Table 1) with estimates based on data reported by Sick and Ottow (1958) for coastal Brazil near Rio de Janeiro. Because of the well-known habit of *M. bonariensis* of puncturing its own eggs as well as those of its hosts (Friedmann, 1929), fully reliable estimates can be based only on nests whose histories are completely known with regard to eggs or nestlings or both.

TABLE 1

PRODUCTIVITY ESTIMATES FOR RUFOUS-COLLARED SPARROWS AND SHINY COWBIRDS SEPARATELY AND JOINTLY

	Rufous-collared Sparrows			Shiny Cowbirds
Locale and variable	With cowbirds	Without cowbirds	Both	All nests
Horco Molle				
Nest success[1]	0.32 (6/19)	0.40 (4/10)	0.34 (10/29)	0.50 (9/18)
Fledglings/nest	0.50 (9/18)	1.11 (10/9)	0.70 (19/27)	0.72 (13/18)
Fledglings/egg[2]	0.12 (4/33)	0.44 (10/23)	0.25 (14/56)	0.65 (11/17)
Fledglings/nestling[3]	0.69 (9/13)	0.83 (10/12)	0.76 (19/25)	0.81 (13/16)
Eggs hatched/laid[4]	0.38 (12/32)	0.46 (11/24)	0.41 (23/56)	0.46 (16/35)
Eggs/nest	2.29 (32/14)	2.56 (23/9)	2.39 (55/23)	2.06 (35/17)[5]
Rio de Janeiro (Sick and Ottow, 1958)				
Nest success[1]	0.20 (10/51)	0.34 (11/32)	0.25 (21/83)	0.49 (25/51)
Fledglings/nest	0.29 (15/51)	0.69 (22/32)	0.44 (37/83)	0.47 (24/51)
Fledglings/egg[2]	0.19 (15/78)[6]	0.30 (22/74)[6]	0.24 (37/152)[6]	0.26 (24/94)
Fledglings/nestling[3]	—	—	0.60 (37/62)	0.59 (24/41)
Egg hatched/laid[4]	—	—	0.41 (62/152)[6]	0.44 (41/94)
Eggs/nest	1.53 (78/51)[6]	2.31 (74/32)[6]	1.83 (152/83)[6]	1.84 (94/51)[5]

[1] Fraction of nests producing at least one fledgling.
[2] Equivalent to "egg success (total)" of Ricklefs (1969a).
[3] Equivalent to "egg success (nestlings)" of Ricklefs (1969a).
[4] Equivalent to "egg success (eggs)" of Ricklefs (1969a).
[5] Excluding nests containing only sparrow eggs.
[6] Per egg in nest at time of discovery; eggs potentially removed by cowbirds cannot be accounted for (see text).

This reduces the sample sizes below 60 (total nests found) and accounts for the variable sample sizes for Horco Molle shown in Table 1. Sick and Ottow (1958: 55) were aware of this source of error, but included in their estimates a few nests lacking complete histories, assuming that the numbers of eggs found were the same as the numbers originally laid. As they note, this means that estimates involving egg numbers as the denominator are potentially slightly above the true value, and vice versa for egg numbers in the numerator. This effect is illustrated in Table 1, where the apparent clutch size in parasitized nests is substantially lower than in nonparasitized nests, suggesting that the adult cowbirds destroyed an average of about 0.8 *Z. capensis* eggs per parasitized nest near Rio de Janeiro. A similar trend is apparent in the data for Horco Molle, where the nest histories are nevertheless complete in this respect. The trend may reflect in this case a slight tendency for *Z. capensis* to reduce clutch size in nests already containing cowbird eggs during the laying period; but the apparent reduction is not in fact statistically significant ($P > 0.05$) and none of the averages of eggs per nest differs significantly from the

TABLE 2

COMPONENTS OF MORTALITY IN *ZONOTRICHIA CAPENSIS* IN NESTS WITH AND WITHOUT PARASITISM BY *MOLOTHRUS BONARIENSIS* AT HORCO MOLLE

Component[1]	Percent daily mortality		
	Without cowbirds (1)	With cowbirds (2)	(2)/(1)
Nest mortality, M	3.66	4.56	1.25
Egg mortality, m_e	2.65	6.91	2.61
Nestling mortality, m_n	1.69	3.37	1.99
Total mortality, m	3.28	8.48	2.58

[1] Definitions and symbols according to Ricklefs (1969a).

mean clutch size (2.69 ± 0.175 eggs, $n = 35$ eggs and 13 nests) in *Z. capensis* nests not disturbed by cowbirds.

The productivity of all nests (all combinations of cowbirds and sparrows, including nonparasitized nests) was about 0.7 fledglings per nest for both cowbirds and sparrows at Horco Molle, and about 0.4–0.5 fledglings per nest for both species near Rio de Janeiro (Table 1). Thus, *Z. capensis* was nearly twice as successful, on the average, as a parent of both cowbirds and sparrows at Horco Molle than at Rio de Janeiro during the years of study in spite of the slightly greater incidence of parasitism (66% vs. 61% of nests) and the slightly greater number of cowbird eggs per parasitized nest (2.06 vs. 1.84) at Horco Molle. The productivity of Rufous-collared Sparrows for their own young was reduced by the presence of cowbird young by about 0.4 fledglings per nest at both Horco Molle and Rio de Janeiro, although the percentage reduction owing to parasitism was greater at Horco Molle (41% vs. 31%). In the case of both cowbirds and sparrows the hatching success (eggs hatched/eggs laid) was about the same at Horco Molle and Rio de Janeiro. The greater posthatching mortality of both species at Rio de Janeiro accounted for the large reduction of productivity (fledglings/nest) at Rio de Janeiro.

The effects of cowbirds on Rufous-collared Sparrows at Horco Molle can be examined in further detail through calculation of daily rates of mortality, m, from the equation $m = -(\ln P)/t$, where P is the proportion of nests, eggs, or young surviving a given span of the nesting cycle, t (Ricklefs, 1969a: 3). The value of t is based on an average egg-laying period of 2 days, an incubation period of 12 days, and a nestling period of 11 days (Miller and Miller, 1968; King, MS). The results are summarized as percentage daily mortalities in Table 2. It is evident that all components of mortality were increased by the presence of cowbird parasites, but that egg mortality was increased predominantly. This

TABLE 3

COMPARISON OF PRODUCTIVITY OF *ZONOTRICHIA CAPENSIS* AT HORCO MOLLE AND OF *Z. LEUCOPHRYS GAMBELII* IN ALASKA (66° N)

Component	*Z. capensis*[1]	*Z. l. gambelii*[2]
Nest success	0.40	0.61 (17/28)
Fledglings/nest	1.11	2.50 (70/28)
Fledglings/egg	0.44	0.53 (70/132)
Fledglings/nestlings	0.83	0.77 (70/91)
Eggs hatched/laid	0.46	0.69 (91/132)
Eggs/nest	2.56	4.71 (132/28)

[1] Without cowbird parasites; data from Table 1.
[2] Data from Williamson et al. (1966).

presumably results from the predilection of adult cowbirds for puncturing the eggs of their hosts.

The productivity of Rufous-collared Sparrows and the mortality of their nests may be compared with averages for various climatic regions summarized by Ricklefs (1969a). The study area at Horco Molle during the breeding season has a humid subtropical climate. The average total egg success (fledglings/egg laid) was 25 percent for all nests and 44 percent for nonparasitized nests at Horco Molle (Table 1). According to data analyzed by Ricklefs (1969a: 23) this variable for passerines building open nests averages 32.4 percent in the humid tropics and 46.6 percent in temperate zones. Skutch (1966) reported 30.4 percent total egg success in 23 species building open or domed nests in clearings and second growth in the humid tropics. The Rufous-collared Sparrow thus falls within the range of averages if only nonparasitized nests are considered, but below the averages if all nests are considered. A similar relationship prevails for other components of mortality (cf. Table 2, and Ricklefs, 1969a: 19).

In connection with regional variations of nesting success and mortality it is of interest to compare *Z. capensis* at Horco Molle with its congener *Z. leucophrys gambelii* on the arctic breeding grounds at 66° N. Data presented by Williamson et al. (1966) are converted to the forms used in this report and summarized together with those for nonparasitized *Z. capensis* nests in Tables 3 and 4. As may be expected from the results of previous studies of other species, the arctic form of *Zonotrichia* is more productive per nesting cycle than is the subtropical form, and raises more than twice as many fledglings. This greater productivity may have evolved concurrently with a presumably greater postnatal mortality during migration. Some insight into how this advantage (per cycle) is attained can be gathered from examination of mortality rates (Table 4). The

TABLE 4

COMPONENTS OF MORTALITY IN *ZONOTRICHIA CAPENSIS* AT HORCO MOLLE AND *Z. LEUCOPHRYS GAMBELII* IN ALASKA

Component[1]	Percent daily mortality: *Z. capensis*[2] (1)	Percent daily mortality: *Z. l. gambelii*[3] (2)	(2)/(1)
Nest mortality, M	3.66	2.08	0.57
Egg mortality, m_e	2.65	2.47	0.93
Nestling mortality, m_n	1.69	2.93	1.73
Total mortality, m	3.28	2.64	0.80
Eggs/nest	2.56	4.72	1.85

[1] Definitions and symbols according to Ricklefs (1969a).
[2] Without cowbird parasites; data from Table 1.
[3] Calculations from Ricklefs (1969a), based on data of Williamson et al. (1966).

rate of egg mortality is about the same in the two species and regions, but the daily rate of nesting mortality is, surprisingly, about 75 percent greater in *Z. leucophrys* than in *Z. capensis*. This discrepancy is more than compensated, however, by the shorter (about 1 day) nestling period and by the much greater initial clutch size in the arctic form. It should be noted in passing that the differences in nest mortality (3.66 vs. 2.08% per day) are included in the factors already discussed, and are not to be added to them.

Finally, some implications of these data for the population dynamics of *Z. capensis* can be explored briefly. Considering that 66 percent of *Z. capensis* nests were parasitized at Horco Molle in 1969–70, it can be calculated from data in Table 1 that 100 pairs of adult *Z. capensis* produced 70.7 fledged young per nesting. At this rate it is evident that the adult population can replace itself annually if an average of 2.8 broods are produced per year (or 1.8 broods in the absence of cowbird parasitism). This could be accomplished within the time available in a breeding season, and probably approximates the actual number of nesting cycles per season (King, MS).

In contrast, 100 breeding pairs of *Z. l. gambelii* at Cape Thompson, Alaska, can produce an average of 250 fledglings in one nesting cycle, or could replace their own numbers annually with an average of 0.8 cycles. There is time for only one complete nesting cycle per pair per season in this species in the arctic summer (King et al., 1966; Morton et al., 1969).

Obviously the quantitative significance of these estimates in relation to population balance depends on factors of adult and juvenile mortality that are unknown for these species and locales. The utilization

TABLE 5

GROWTH OF *ZONOTRICHIA CAPENSIS* NESTLINGS AT HORCO MOLLE[1]

Day	Body weight, g			Length of Pl[2]	
	Mean	Range	k[3]	Mean	Range
0	2.08	1.9– 2.2	—	—	
1	2.77	2.6– 3.0	0.286	—	
2	4.07	3.6– 4.7	0.385	—	
3	5.75	4.9– 6.9	0.346	—	
4	8.04	6.9– 9.1	0.335	2.1	2.0– 2.5
5	9.98	8.9–11.2	0.216	4.6	2.5– 6.4
6	12.28	11.7–14.1	0.209	9.1	7.4–10.5
7	14.34	13.1–16.2	0.179	14.7	13.0–16.2
8	15.08	14.0–16.8	0.027	20.1	18.3–22.0
9	15.30	14.3–15.5	0.013	23.9	22.2–25.3
10	15.88	14.7–17.0	0.038	27.4	25.7–29.6

[1] Broods of 3, 3, and 2 nestlings ($n = 8$ for all means).
[2] The first primary feather.
[3] Instantaneous growth-rate constant: $k = (\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_1 and W_2 = mean body weights on days t_1 and t_2.

of these data for extensive predictive purposes is further hindered by the large-scale variations that must occur between years and areas. The estimates cited in the foregoing paragraphs can apply only to the populations and seasons mentioned. Further amplifications are not justified.

POSTNATAL GROWTH OF SPARROWS AND COWBIRDS

The growth of *Z. capensis* nestlings in the absence of cowbird parasites could be followed through the entire nestling period in only three nests (successful clutches of 3, 3, and 2). The mean weights are summarized together with instantaneous growth rates and feather lengths in Table 5. It can be noted from these data that the length of the first primary feather is a more reliable criterion of age than is body weight.

The progress of nestling growth with respect to appearance and behavior did not differ from that reported in detail by Miller and Miller (1968) for *Z. capensis* in Colombia, but the pattern of weight gain differed conspicuously in one respect. The body weight of nestlings at Horco Molle reached a prefledging plateau (15.9 g) considerably below the mean adult body weight (20.6 g). That this is not merely the chance result of small sample size is indicated by the fact that recent fledglings (rectrices still with basal sheaths) caught in nets at Horco Molle also weighed less than the lightest adults (e.g. three fledglings caught in February weighed 16.2, 16.7, and 17.8 g). The *Z. capensis* Miller and Miller (1968) studied did not conform with this pattern, and two nestlings reached 19.1 and

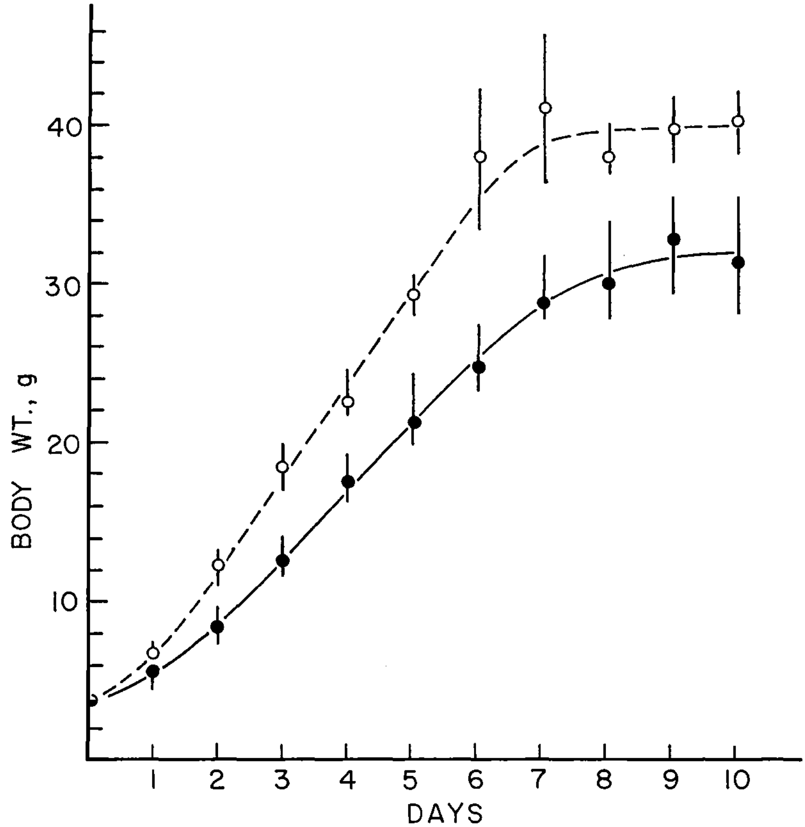

Figure 1. Growth of nestling Shiny Cowbirds (mean and range) in Rufous-collared Sparrow nests at Horco Molle. No sparrows survived beyond day 2. Upper curve: one cowbird per nest ($n = 3$). Lower curve: two cowbirds per nest (three nests, $n = 6$).

22.7 g on the 11th day of nestling life. The body weight of adults is not given in this report, but probably averages 20–21 g in Colombia. (The body weight of adult male *Z. c. australis*, supposedly the largest of the forms of this species, averages 21.92 ± 0.256 g ($n = 36$) during the breeding season in Patagonia; King, MS.) Pending the acquisition of additional data, it thus appears that nestling *Z. capensis* in Colombia leave the nest at about the adult weight. This is a nontypical condition (see beyond).

The growth rate of *Z. capensis* in the absence of cowbirds at Horco Molle (Table 5) may be compared with the rates for the North American forms *Z. leucophrys nuttalli* (Banks, 1959) and *Z. l. oriantha* (Morton

TABLE 6

GROWTH OF *MOLOTHRUS BONARIENSIS* NESTLINGS AT HORCO MOLLE[1]

Day	Body weight, g			Length of Pl[2]	
	Mean[3]	Range	k[4]	Mean[5]	Range
0	3.57	3.0– 4.2	—	—	—
1	5.60	4.2– 6.7	0.401	—	—
2	8.53	7.3– 9.8	0.421	—	—
3	12.65	11.6–14.2	0.394	1.7	1.0– 2.3
4	17.50	16.8–19.7	0.325	5.1	3.5– 6.9
5	21.28	18.9–24.8	0.196	10.9	8.9–13.9
6	24.70	22.1–27.8	0.148	17.3	15.3–21.1
7	28.90	26.8–32.0	0.157	24.4	21.8–28.1
8	29.95	27.6–34.1	0.036	31.0	29.0–34.5
9	32.97	29.1–35.3	0.097	37.1	34.6–40.0
10	31.30	28.0–36.3	-0.053	39.5	38.5–41.3

[1] Broods without *Z. capensis* nestlings.
[2] Length of first primary feather.
[3] Three broods of two each ($n = 6$).
[4] Instantaneous growth-rate constant (see Table 5).
[5] Three broods of two each plus two broods of three each ($n = 9$); no discernible differences among brood sizes with respect to feather growth.

and Carey, 1971) in central California. The total growth rate, K, from hatching to the prefledging asymptote for *Z. capensis* estimated from Ricklefs' (1967) logistic model, yields $K = 0.472$. For *Z. l. nuttalli,* Ricklefs (1968; data of Banks, 1959) estimated the growth rate as $K = 0.512$. The asymptotic weight of nestlings as a fraction of mean adult body weight is 0.77, or identical with that of *Z. capensis*. Ricklefs (1968) shows that this is the typical relationship among ground-feeding passerines in temperate as well as in tropical regions. The time interval for growth from 10 to 90 percent of adult weight ($t_{10\text{-}90}$) is 8.1 days for *Z. l. nuttalli* (Ricklefs, 1968) and 9.3 days for *Z. capensis*. The growth of *Z. capensis* is thus somewhat slower than that of *Z. l. nuttalli* in reaching the same asymptotic fraction of adult weight. This is correlated with the smaller asymptotic weight (15.9 vs. 20.5 g) and with the longer nestling period (11 vs. 10 days) of *Z. capensis*. The differences between the growth patterns of the two species, although slight, follow the trend indicated by Ricklefs (1968, 1969b). Tropical species tend to have $K =$ ca. 0.40, while temperate-zone species tend to have $K =$ ca. 0.52. Differences of nearly the magnitude found between *Z. capensis* and *Z. l. nuttalli* may also be found within species between areas and seasons (Ricklefs, 1968), and it would be premature at this time to assert that the differences found between the species of *Zonotrichia* necessarily represent specific adaptations. Data from additional nesting seasons in both regions are needed.

Data on the growth of *M. bonariensis* nestlings in nests lacking sparrows are shown in Figure 1 and Table 6 for broods of one and two nestlings. In broods of two (the commonest number) the total growth rate, K, is 0.544, and t_{10-90} is 9.3 days. For broods of one cowbird (Figure 1) the growth rate is obviously much more rapid, but the irregularities in the data at the upper flexion of the curve prevent a reliable estimate of the rate constant. It is noteworthy also that the asymptotic ratio of fledgling weight to adult body weight is evidently not species specific in these cowbirds (Figure 1). I have no data for adult body weights of *M. bonariensis* in Argentina, but probably there are definite differences of weight between sexes. It is possible but not very likely that the broods of one cowbird consisted all of males and the broods of two consisted all of females, thus accounting for the difference in the prefledging asymptotes.

Ricklefs (1968) reports $K = 0.576$ and $t_{10-90} = 7.6$ days for two nestling *Molothrus ater* in North America. The data, again, are too few to support rigorous conclusions, but suggest that cowbirds share the same trend toward slower development in tropical and subtropical regions that is found in other ground-feeding passerines.

Unfortunately, only partial nestling histories could be obtained from nests with various combinations of cowbirds and sparrows, and the data are not adequate for a thorough analysis of interactions. In cases where cowbirds hatched before the sparrows the latter typically did not gain weight normally and died on or before the 3rd day of nestling life. Sparrow nestlings were known to survive to fledging only in cases involving one cowbird and two sparrows (7 cases), one cowbird and one sparrow (5 cases), and two cowbirds and one sparrow (1 case). Two cowbird nestlings, or the equivalent thereof, evidently represent about the maximum growing biomass that a pair of adult *Z. capensis* can usually support. More than this (two cowbirds and one sparrow) is exceptional. It can be calculated from data in Tables 5 and 6 that the growth of two cowbirds is almost exactly the same as the growth of four sparrows in terms of weight gain. Four sparrow eggs is the largest number ever found at Horco Molle (about 8% of clutches), and may represent the evolutionary limit set by the capacity of the adults to support the growth of nestlings from a fully successful clutch in an average year.

Adaptive Brood Reduction?

Lack (1954: 40–41) pointed out that species of birds in which hatching is asynchronous have an opportunity to adjust brood size in relation to food availability. All the members of a brood may be fed when food is plentiful, but only the older and more active ones will receive food when

TABLE 7

EXAMPLES OF CLUTCH SIZE REDUCTION DURING THE INCUBATION STAGE IN SIX NESTS CONTAINING MIXED CLUTCHES OF *ZONOTRICHIA CAPENSIS* AND *MOLOTHRUS BONARIENSIS* AT HORCO MOLLE

	No. of eggs					
	Initial		Final[1]		Birds hatched	
	Cowbird	Sparrow	Cowbird	Sparrow	Cowbird	Sparrow
	2	2	2	0	2	0
	2	2	1	1	1	1
	1	2	1[2]	2	0	2
	5	0	2[3]	0	2	0
	2	3	2	3[4]	2	0
	2	3	2	2[5]	2	0
Means	2.33	2.00	1.67	1.34	1.50	0.50

[1] At time first nestling hatched.
[2] Egg laid 6 days after incubation began; gone from nest 5 days after sparrows hatched.
[3] Egg gone from nest on day that second cowbird hatched; a cowbird egg that was pipped on that day was gone from nest on the following day.
[4] Eggs punctured on 3rd day after cowbirds hatched; subsequently gone from nest on 4th and 5th days.
[5] One egg gone from nest on day before cowbirds hatched; two other eggs gone from nest on day following hatch.

it is short supply; the younger ones will starve to death, thus improving the chances for survival of at least some young. The mixed clutch of *Z. capensis* and *M. bonariensis* typically involves asynchronous hatching, and the results merit examination in the context of Lack's concept.

Ricklefs (1965) has provided a theoretical background for the interpretation of brood reduction and similar processes in connection with a case of apparently adaptive brood reduction in the Curve-billed Thrasher (*Toxostoma curvirostre*). The options available to a bird adjusting reproductive effort in relation to available resources can include an adjustment of clutch size, thus requiring a "prediction" of conditions occurring as much as 2 weeks later in the case of a small passerine, and can include posthatching brood reduction of the type already mentioned.

The situation for the host of a brood parasite is complicated by the fact that "clutch size," including eggs of both host and parasite, is not fully under the control of the host, but rather is partly a matter of chance. The problem of maximizing productivity by the host species for its own young is confounded by the presence of an unpredictable number of parasites. Brood size must nevertheless be adjusted to a level consistent with the ability of the host species to support the growth of the nestlings, while at the same time preserving an adequate reproductive potential for the host. The great abundance of *Z. capensis* throughout its range attests to the fact that it is successful in coping with this problem.

It is to be expected that the processes evolved by *Z. capensis* to sustain adequate productivity in the face of heavy cowbird parasitism will be complex and difficult to discern, perhaps involving elements of co-evolution with *M. bonariensis*. Only some preliminary insights are available from data obtained in the present investigation.

It was noted in many nests of *Z. capensis* at Horco Molle that sparrow eggs as well as cowbird eggs were removed from mixed clutches before the hatching of the first egg or eggs. Data for six nests whose histories are suitable in this respect (Table 7) show that the number of cowbird eggs was reduced by about 28 percent and the number of sparrow eggs was reduced by about 33 percent (0.66 eggs in both cases) on the average during the incubation period. The average number of birds finally hatched was 1.50 cowbirds and 0.50 sparrows. In terms of asymptotic weight at the time of fledging (cf. Tables 5 and 6), one cowbird is equivalent to about two sparrows, and the average nest load at the time of hatching is therefore equivalent to about 3.5 sparrows, or 1.75 cowbirds. The nest load if all eggs hatched (Table 7) would be equivalent to 4.66 sparrows, or 3.33 cowbirds.

It was suggested above on the basis of growth rates and actual brood composition that the typical pair of *Z. capensis* can successfully rear no more than the equivalent of two cowbirds or four sparrows at Horco Molle. The empirical data appear to confirm this prediction. In six nests without sparrows an average of 1.75 cowbirds were fledged (equivalent to about 3.5 sparrows). In seven nests containing both cowbird and sparrow nestlings an average of 2.0 sparrows and 0.71 cowbirds were fledged (equivalent to about 3.4 sparrows). In the latter cases the cowbirds usually hatched 2 to 4 days later than the sparrows. If these coincident averages represent the consequence of internal adjustments of brood composition to levels compatible with the ability of the adults to support nestling growth, then it is evident that the egg loss described above serves a useful purpose in reducing the commitment of adults to nestlings that they could not ultimately support to the age of fledging.

The adjustment of the initial brood size by egg loss is augmented by reduction of brood size during the nestling period. The data from Horco Molle are not adequate for a thorough appraisal, but the following cases are illustrative: (1) in a nest containing one cowbird and two sparrows a cowbird egg hatched on day 3 of the nestling period, but the cowbird nestling was gone from the nest by day 5; (2) in a nest containing two sparrow chicks a cowbird hatched on day 4 of the nestling period, but was found dead on the following day; (3) two sparrows hatched 1 day following two cowbirds, but increased in weight only to 3.1 and

3.3 g by day 4, and were gone from the nest by day 5; (4) a cowbird hatched 2 days following the hatching of two sparrows, gained weight slightly for 2 days, and was gone from the nest on the following day (two cases).

Taken together, these examples illustrate the point that nest loads tend to become adjusted to a level at or below the equivalent of two cowbirds, or four sparrows. It is an interesting speculation, in fact, that the small clutch size of *Z. capensis* relative to those of its North American congeners at similar latitudes (King, MS) may be not only a relict of recent radiation southward through equatorial regions, but also a consequence of its intense relationship with *M. bonariensis*. North American *Zonotrichia* spp. are not frequently parasitized by cowbirds (Friedmann, 1963). Through such an evolutionary adjustment *Z. capensis* may be able to reduce the energy drain of reproduction while not necessarily reducing at the same time its productivity for its own species in the presence of *M. bonariensis*.

ACKNOWLEDGMENTS

I am grateful to C. C. Olrog and to A. Willink for advice and assistance and to the officers of the Instituto Miguel Lillo (José Antonio Haedo, Director) for various courtesies. The field work was made possible by a fellowship from the John Simon Guggenheim Foundation and by sabbatical leave privileges granted by Washington State University.

SUMMARY

The relationships of the brood parasite *Molothrus bonariensis* with *Zonotrichia capensis*, its main host species, were studied through one breeding season in the foothills of the Andes in northwestern Argentina.

The egg-laying season of *M. bonariensis* overlapped at least 87 percent of the egg-laying season of *Z. capensis*. The incidence of parasitism was 66 percent of nests for the entire breeding season, and 100 percent of nests for the peak of the breeding season. The mean productivity of all nests (all combinations of cowbirds and sparrows, including nonparasitized nests) was about 0.7 fledglings per nest for both cowbirds and sparrows. The productivity of the sparrows for their own young was reduced by the presence of cowbird young by an average of about 0.4 fledglings per nest. All temporal components of mortality were increased by the presence of cowbird parasites, but egg mortality was increased to the greatest extent. This presumably reflects the predilection of the adult cowbirds for puncturing the eggs of their hosts.

Data on postnatal growth of *M. bonariensis* and *Z. capensis* and on observed brood compositions suggest that *Z. capensis* can successfully

rear a maximum of two cowbirds or four sparrows, or the equivalent thereof in various combinations. Data on the loss of eggs and young from parasitized nests suggest that there may be an adaptive reduction of nest load late in the incubation period and early in the nestling period to levels (equivalent to 3.4–3.5 sparrows) that *Z. capensis* has a reasonable chance to rear to fledging in average conditions.

Literature Cited

Banks, R. C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor, 61: 96–109.

Friedmann, H. 1929. The cowbirds. Springfield, Illinois, C. C. Thomas.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U. S. Natl. Mus., Bull. 233.

Hoy, G., and J. Ottow. 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. Auk, 81: 186–203.

Johnson, A. W. 1967. The birds of Chile, vol. 2. Buenos Aires, Platt Establecimientos Gráficos.

King, J. R. 1972a. Postnuptial and postjuvenal molt in Rufous-collared Sparrows in northwestern Argentina. Condor, 74: 5–16.

King, J. R. 1972b. Variation in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. Z. Tierpsychol., in press.

King, J. R., B. K. Follett, D. S. Farner, and M. L. Morton. 1966. Annual gonadal cycles and pituitary gonadotropins in *Zonotrichia leucophrys gambelii*. Condor, 68: 476–487.

Lack, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

Miller, A. H., and V. D. Miller. 1968. The behavioral ecology and breeding biology of the Andean Sparrow, *Zonotrichia capensis*. Caldasia, 10: 83–154.

Morton, M. L., and C. Carey. 1971. Growth and development of endothermy in the Mountain White-crowned Sparrow (Zonotrichia leucophrys oriantha). Physiol. Zool. 44: 177–189.

Morton, M. L., J. R. King, and D. S. Farner. 1969. Postnuptial and postjuvenal molt in White-crowned Sparrows in central Alaska. Condor, 62: 376–385.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor, 67: 505–510.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology, 48: 978–983.

Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis, 110: 419–451.

Ricklefs, R. E. 1969a. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool., No. 9.

Ricklefs, R. E. 1969b. Preliminary models for growth rates in altricial birds. Ecology, 50: 1031–1039.

Selander, R. K. 1964. Behavior of captive South American cowbirds. Auk, 81: 394–402.

Sick, H. 1958. Notas biológicas sôbre o Gaudério, "Molothrus bonariensis" (Gmelin) (Icteridae, Aves). Rev. Brasil. Biol., 18: 417–431.

Sick, H., and J. Ottow. 1958. Vom brasilianischen Kuhvogel, *Molothrus bonariensis*, und seinen Wirten, besonders dem Ammerfinken, *Zonotrichia capensis*. Bonn. Zool. Beitr., Heft 1/9: 40-62.

SKUTCH, A. F. 1966. A breeding census and nesting success in Central America. Ibis, 108: 1–16.
SOKAL, R. R., AND F. J. RHOLF. 1969. Biometry. San Francisco, W. H. Freeman.
WILLIAMSON, F. S. L., M. C. THOMPSON, AND J. Q. HINES. 1966. Avifaunal investigations. Pp. 437–480 *in* Environment of the Cape Thompson Region, Alaska (N. J. Wilimovsky and J. N. Wolfe, Eds.). Washington, D. C., U. S. Atomic Energy Comm.

Department of Zoology, Washington State University, Pullman, Washington 99163. Accepted 18 November 1971.