$$R = \int (S \cdot 39.5 \cdot M^{-1.464} \cdot L^{1.614}) \cdot 3.167 \, \delta M^{-1}$$

$$R = 26.88 \cdot S \cdot L^{1.614} \cdot (M_1^{-0.464} - M_2^{-0.464}),$$

where R = flight range (km), M_1 = body mass at the end of the flight (g), M_2 = body mass at the start (g), S = flight speed (km/h), and L = wing length (cm).

The flight ranges for the species of Table 1, for flight speeds of 75 km/h and a fattening level of 40% (fat/total mass), are predicted in Fig. 1. The first two models predict a rapidly increasing flight range with increasing body mass. In contrast, our model predicts similar flight ranges for big and small species. This result is important, because it suggests that birds with similar aerodynamic designs (shorebirds in this case) have similar flight range values. Although we concur with Summers et al. (1987) on the need for direct measurements in migratory flight, we believe that this new equation provides a more realistic approximation to the flight range capabilities of shorebird species, because it uses both body mass and aerodynamic characteristics, and at the same time allows for the decrease in body mass during the migratory flight.

T. Piersma, R. Summers, D. Raveling, and A. H. Brush provided many important comments in the original manuscript.

LITERATURE CITED

CASTRO, G. 1987. High basal metabolic rates in Sanderlings (*Calidris alba*). Willson Bull. 99: 267-268.

———, & J. P. MYERS. 1988. A statistical method to estimate the cost of flight in birds. J. Field Ornithol. 59: 369-380.

DAVIDSON, N. C. 1984. How valid are flight range estimates for Waders? Ringing & Migr. 5: 49-64.

GREENEWALT, C. H. 1975. The flight of birds. Transactions of the Am. Philos. Soc. (New Ser.) 65: 1-67.

HAYMAN, P., J. MARCHANT, & T. PRATER. 1986. Shorebirds: an identification guide to the waders of the world. London and Sydney, Croom Helm.

KENDEIGH, S. C., V. R. DOLNIK, & V. M. GAVRILOV. 1977. Avian Energetics. Pp. 127-204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). New York, Cambridge Univ. Press.

KERSTEN, M., & T. PIERSMA. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea 75: 175-187.

MCNEIL, R., & F. CAIDEUX. 1972. Numerical formulae to estimate flight range of some North American shorebirds from fresh weight and wing length. Bird-Banding 43: 107-113.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pp. 1-75 *in* Avian biology, vol. 5. (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

RAVELING, D. G., & E. A. LEFEBVRE. 1967. Energy metabolism and theoretical flight range of birds. Bird-Banding 38: 97-113.

SUMMERS, R. W., & M. WALTNER. 1978. Seasonal variations in the mass of waders in southern Africa with special reference to migration. Ostrich 50: 21-37.

———, L. G. UNDERHILL, M. WALTNER, & D. A. WHITELAW. 1987. Population, biometrics and movements of the Sanderling (*Calidris alba*) in southern Africa. Ostrich 58: 24-39.

Received 2 August 1988, accepted 22 January 1989.

Impact of Brown-headed Cowbird Parasitism on the Reproductive Success of the Solitary Vireo

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The Solitary Vireo (*Vireo solitarius*) is sympatric with the Brown-headed Cowbird (*Molothrus ater*) in eastern and western North America (A.O.U. 1983). Although the Solitary Vireo has been mentioned as an occasional cowbird host, especially in the western United States (Friedmann 1971, Friedmann et al. 1977, Friedmann and Kiff 1985), little information exists on the timing, extent, or effects of cowbird parasitism. We describe the reproductive interactions of the Brown-headed Cowbird and the Solitary Vireo (*V. s. plumbeus*) in Colorado.

Vireo nest data were collected during the summers of 1984-1986 in the foothills of the Rocky Mountains west of Boulder, Colorado. Study sites ranged from 1,800 to 2,120 m in elevation. These areas were dominated by ponderosa pines (*Pinus ponderosa*) and scattered Douglas fir (*Pseudotsuga menziesii*). The vegetation had a parklike appearance, with an open canopy and widely spaced ponderosa pines. The herb-shrub stratum was sparse and consisted of seedlings and saplings of the dominant tree species, Rocky Mountain Maple (*Acer glabrum*), willows (*Salix* spp.), chokecherry (*Prunus virginiana*), kinnikinnic (*Arctostaphylos uva-ursi*), squawbush (*Rhus trilobata*), snowberry (*Sym-*

TABLE 1. Frequency of parasitism in Solitary Vireo nests, Boulder County, Colorado, 1984-1986.

	Year			Combined years
	1984	1985	1986	
Unparasitized nests	11	12	17	40
Parasitized nests	9	12	17	38
Parasitism (%)[a]	45.0	50.0	50.0	48.7

[a] Percentage of parasitism is independent of year (G-test of independence, $G = 0.149$, $v = 2$, $P > 0.05$).

TABLE 2. Clutch sizes of Solitary Vireos in parasitized and unparasitized nests, Boulder County, Colorado, 1984-1986.

	Clutch size					
Nests	1	2	3	4	5	$\bar{x} \pm$ SD
Unparasitized			11	26	1	3.74 ± 0.50[a]
Parasitized	2	5	12	11	2	3.19 ± 1.00
Total	2	5	23	37	3	3.49 ± 0.81

[a] Differences in clutch size between unparasitized and parasitized nests significant (Wilcoxon two-sample test, $T_s = 2.65$, $P < 0.05$).

phoricarpos occidentalis), wax currant (*Ribes cereum*), juniper (*Juniperus scopulorum*), and various grass species (*Bromus, Achillia, Stipa,* and *Artemesia*).

Vireo nests were found during all stages of the nestling cycle and subsequently visited once every 2-3 days. We found 19% of the nests (15 of 78) before vireo clutch initiation. We followed the fate (parasitized, unparasitized, deserted, disturbed by a predator) of each nest. Nest appearance and mode of disturbance were used to determine whether nests were disturbed by predators. Ejection by cowbirds refers to cases in which a cowbird was suspected of tossing vireo eggs or nestlings from the nest. Nestling growth was monitored every other day by measuring body mass and lengths of radius-ulna, tibiotarsus, and 9th primary. Mass (nearest 0.1 g) was taken with 10- and 50-g Pesola spring scales; lengths (nearest 0.1 mm) were measured with a dial caliper and ruler. Only nests in which the final outcome was known were included in the analysis.

Solitary Vireos arrived about the second week in May. Most nests (81%, $n = 63/78$) were in areas where the pines were widely spaced (average of 9 ponderosa pines per 0.04 ha) and where minimal understory vegetation, other than grasses, was present. Typically, egg laying began by the last week in May, but some late nesters did not begin laying until the last week in June. Bent (1950) suggested that second brooding occurred in the Solitary Vireo, but in pairs observed throughout the nesting season, we found no second broods. Once the clutch was completed ($\bar{x} = 3.49 \pm 0.81$ SD, $n = 70$ clutches), both sexes incubated during the day, switching nest duty about every half hour. Only the female incubated at night. The eggs hatched after ca. 15 days, and both adults fed nestlings. Nestlings ($n = 102$) fledged about 13 days after hatching.

The majority (90.6%, $n = 43/47$) of cowbird eggs were laid during the vireo egg laying stage. These eggs hatched after an average incubation of 11 days, and cowbird nestlings fledged when ca. 11 days old. A total of 38 of 78 clutches (48.7%) were parasitized, with frequency of parasitism independent of year (Table 1). We determined the number of cowbird eggs per nest for 34 of 38 parasitized nests; 22 (64.7%) contained 1 cowbird egg, 11 (32.4%) contained 2 cowbird eggs, and 1 (2.9%) contained 3 cowbird eggs.

Unparasitized vireo clutches were significantly larger than parasitized clutches (Table 2). Cowbird host egg removal presumably accounts for the smaller clutch sizes of parasitized nests. Parasitized vireo nests had significantly lower hatching success (number of vireo eggs hatched per total vireo eggs laid), fledging success (number of vireo fledglings per total eggs laid), and fledgings per hatched egg (Table 3). Also, the number of vireo fledglings per nest was significantly lower in parasitized than unparasitized nests. The vireo success rates were compared to cowbird success rates (Table 3). The fledging success rate and fledging/egg hatched success rate were much higher for cowbirds than for parasitized vireos.

Nest desertion was not common in either parasitized (2 cases) or unparasitized nests (2 cases). In contrast to the Solitary Vireo, nest desertion was the most common response to cowbird parasitism by another Colorado species, the Willow Flycatcher (*Empidonax traillii*), which was effective because renesting attempts appeared to occur after the main period of cowbird parasitic activity at this high elevation (2,500 m) site (Sedgwick and Knopf 1988). Predation occurred at 8 of 29 parasitized nests and 4 of 36 unparasitized vireo nests, but the values were not significantly different ($G = 1.21$, df = 1, $P > 0.05$). Nestling starvation showed a significant difference between parasitized (10 cases) and unparasitized (0 cases) nests ($G = 13.19$, df = 1, $P < 0.001$).

Egg removal was suspected at five nests where one or more vireo eggs were missing, and a new cowbird egg was laid in the nest. In 4 of these 5 nests, broken vireo eggs were found on the ground below the nest or found stuck to pine needles in the tree. Nestling removal was suspected at 2 nests where vireo nestlings were found with injuries to head, body, and hindlimbs on the ground beneath the nests, and, in the nest, a new cowbird egg was laid.

Development of vireo chicks ($n = 10$) in parasitized nests was slower than chicks in unparasitized nests ($n = 12$) (Fig. 1). There also were differences in relative growth rates (daily change proportionate to current size) among cowbirds and vireo chicks; the cowbird chicks grew faster than vireo chicks (Fig. 1). The slower growth of vireo chicks at parasitized nests is prob-

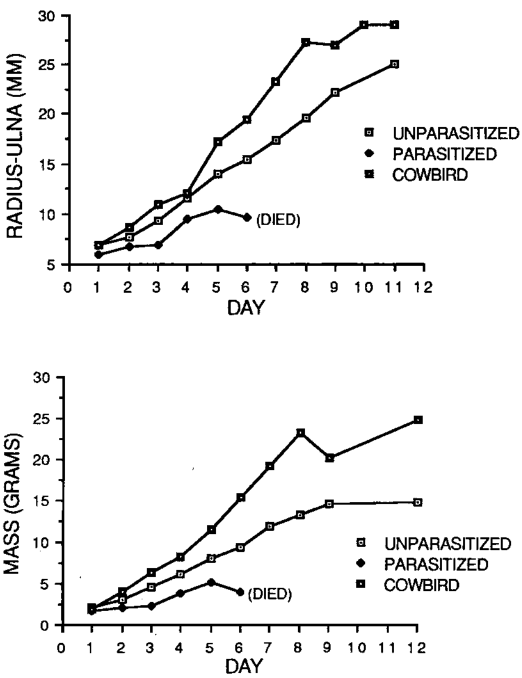

Fig. 1. Length of radius-ulna (top) and increase in mass (bottom) of cowbird and vireo nestlings in nests with and without cowbirds (1984–1985). Day 1 is the day that nestlings hatched. Mass and length are the mean mass and length of nestlings for each age.

ably related to the cowbirds' shorter incubation period. Cowbird eggs usually hatched 3 days before vireo eggs, and cowbird nestlings were substantially larger than vireos and better able to compete for food. The presence of cowbird nestlings had a negative effect on vireo growth, and none of the vireo chicks in parasitized nests survived.

We also found dead vireos, less than 1 day old, buried beneath larger and older cowbird nestlings. In these cases ($n = 7$), the newly hatched vireos may never have obtained food. We observed vireo starvation only in parasitized nests. A cowbird hatching earlier than a vireo chick has an advantage in development, particularly begging behavior. Adults may respond to the more aggressive and better developed begging responses of the cowbirds by providing them with more food than less developed host nestlings (Wiley 1982, this study).

Of 26 parasitized nests that hatched at least 1 vireo egg, 19 nests contained cowbird nestlings that were at least 2 days older than any vireos in the same nest. In these 19 nests, only 2 vireo nestlings fledged (0.11 fledglings/nest) whereas 15 cowbirds fledged (0.79 fledglings/nest). Three nests contained cowbirds the same age or younger than the vireo nestlings. These nests fledged 7 vireos and 3 cowbirds, and were successful for both vireos and cowbirds (2.33 and 1.00 fledglings/nest, respectively). In these nests, vireos had a chance to grow before cowbirds outcompeted them for food, which lowered the starvation rate. In 4 parasitized nests, no cowbirds fledged. Either the cowbird eggs were laid during the vireo nestling stage and were never incubated (3 nests), or the cowbird egg was laid during the vireo egg-laying stage but never hatched (1 nest). In the 3 cases where parasitism occurred late, only 3 vireos fledged from 3 nests (1.00 fledglings/nest). This lower success rate resulted from cowbirds removing some or all the vireo nestlings. In the nest where the cowbird egg never hatched, only 2 vireo nestlings fledged. This nest originally contained 4 vireo eggs, but 2 eggs never developed because each had a small punctured area, perhaps inflicted (either accidentally or intentionally) by the cowbird that parasitized the nest.

The numbers of cowbird eggs laid fluctuated from week to week, but neither increased nor decreased as the nesting period progressed (Pearson $r = 0.393$, n

Table 3. Nesting success in parasitized and unparasitized nests of Solitary Vireos, Boulder County, Colorado, 1984–1986.

	Vireo nests[a]			
	Unparasitized	Parasitized	All	Cowbird
No. of active nests	37	30	67	
Total eggs	126	83	209	49
Total hatched	105	51	156	29
Total fledged	87	15	102	22
Hatching success (%)	83	61[b]	75	59
Fledging success (%)	69	18[b]	49	45
Fledging/egg hatched (%)	83	29[b]	65	76
Fledging/active nest ($\bar{x}$)	2.35	0.50[c]	1.52	0.61

[a] Includes only nests found at egg-laying stage and followed to fledging or failure.

[b] Differences between parasitized and unparasitized nests significant (G-test of independence: $P < 0.001$ and $v = 1$ for hatching success ($G = 12.48$), fledging success ($G = 55.27$), and fledging/hatching success ($G = 43.25$).

[c] Differences between parasitized and unparasitized nests significant (Wilcoxon two-sample test, $T_s = 5.36$, $P < 0.001$).

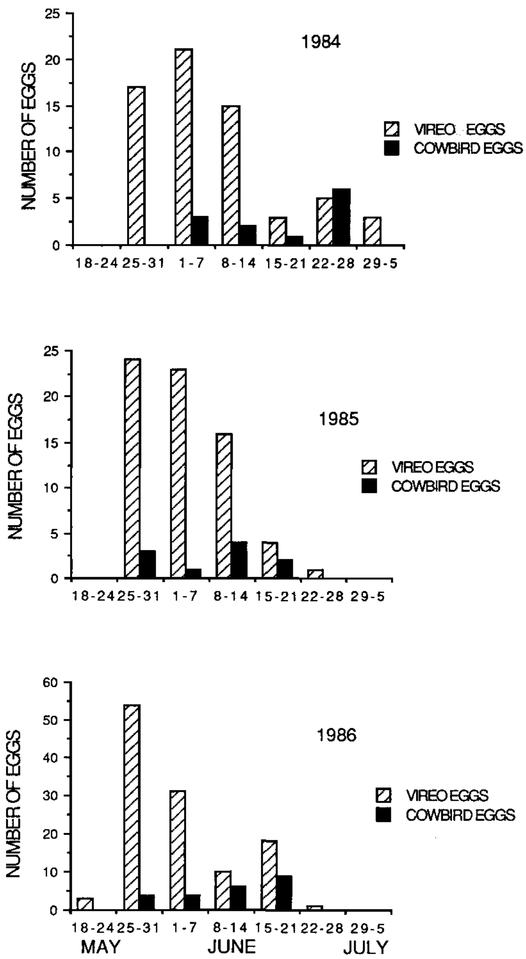

Fig. 2. Total Solitary Vireo and Brown-headed Cowbird eggs laid by week, Boulder County, Colorado, 1984–1986.

= 47, P = 0.256). For each year, the number of vireo eggs laid peaked during the last week of May or first week of June and decreased during the remainder of the nesting period (Fig. 2). During 3 yr, the number of vireo eggs laid decreased throughout the nesting season, but this decrease was not significant (Pearson $r = -0.479$, $n = 246$, $P = 0.138$). However, there were only three vireo eggs in the first time period (18–24 May) of 1986 and none in the other years (Fig. 2). Omitting this period, there was a highly significant decrease in the number of vireo eggs laid across weekly intervals (Pearson $r = -0.974$, $n = 243$, $P = 0.00048$). Early nests (late May–early June) were parasitized less frequently (34%, 17/50) than nests initiated later (mid-June–early July) in the breeding season (75%, 21/28) ($G = 12.65$, df = 1, $P < 0.05$). Vireo pairs that nested during the height of the season may have decreased their chances of being parasitized.

Solitary Vireos along the Colorado Front Range accept cowbird eggs, and we found 48.7% of their nests were parasitized. The reproductive success of these parasitized nests is decreased significantly. Some vireo populations in these study areas are unlikely to be replacing themselves, given the observed rates of parasitism. These populations may represent "sinks" that can be maintained only by emigrants from areas exposed to less intense parasitism (Hassel and May 1974, May and Robinson 1985). We found pockets of parasitism where many of the nests were parasitized and other areas where few nests were parasitized. In addition, most sites were near settled areas. Vireo populations nesting in more extensive tracts unbroken by settled areas may escape parasitism entirely and act as net producers of young. Solitary Vireos are more often parasitized in the western United States than in the eastern United States (Friedmann et al. 1977, Rothstein et al. 1980, Friedmann and Kiff 1985), but no studies have reported rates of parasitism as high as we observed. Because the genus *Vireo* appears especially susceptible to parasitism (Southern 1958, Goldwasser 1978, Goldwasser et al. 1980, Rothstein et al. 1980, Cruz et al. 1985, Grzybowski 1985, Grzybowski et al. 1986, Beezley and Reiger 1987, Franzreb 1987), the Solitary Vireo ought to receive special monitoring in the years to come.

We would like to thank the city of Boulder and Boulder County Parks and Open Space for allowing us to study on their property. We also thank D. Bennett for his assistance in the field. C. E. Bock, J. A. Moreno, P. Mason, J. Picman, C. P. Ortega, J. W. Wiley, and an anonymous reviewer offered helpful suggestions for improving the manuscript.

Literature Cited

American Ornithologists' Union. 1983. Check-list of North American birds, 6th ed. Washington, D.C., Am. Ornithol. Union.

Beezley, J. A., & J. R. Reiger. 1987. Least Bell's Vireo management by cowbird trapping. West. Birds 18: 55–61.

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. Natl. Mus. Bull. No. 211.

Cruz, A., T. Manolis, & J. W. Wiley. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Pp. 609–620 *in* Neotropical ornithology (P. A. Buckley et al., Eds.). Am. Ornithol. Union Monograph 36: 607–620.

Franzreb, K. E. 1987. Endangered status and strategies for protection of the Least Bell's Vireo (*Vireo bellii pusillus*) in California. West. Birds 18: 43–49.

Friedmann, H. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88: 239–255.

———, L. F. Kiff. 1985. The parasitic cowbirds and

their hosts. Proc. West. Foundation Vertebr. Zool. 2: 225-302.
———, ———, & S. I. ROTHSTEIN. 1977. A further contribution to the knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. 235: 1-75.
GOLDWASSER, S. 1978. Distribution, reproductive success and impact of brood parasitism by Brown-headed Cowbirds on Least Bell's Vireo. Rep., California Dep. Fish & Game, Project SWY-R10, Job IV-1.5.1.
———, D. GOINES, & S. R. WILBUR. 1980. The Least Bell's Vireo in California: a de facto endangered race. Am. Birds 34: 742-745.
GRZYBOWSKI, J. A. 1985. Population and nesting ecology of the Black-capped Vireo (*Vireo atricapillus*): II. Nesting ecology of the Black-capped Vireo. U.S. Fish Wildl. Serv. Rep.
———, R. B. CLAPP, & J. T. MARSHALL JR. 1986. History and current status of the Black-capped Vireo in Oklahoma. Am. Birds 40: 151-161.
HASSEL, M. P., & R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. J. Anim. Ecol. 43: 567-594.
MAY, R. M., & S. K. ROBINSON. 1985. Population dynamics of avian brood parasitism. Am. Nat. 126: 475-494.
ROTHSTEIN, S. I., J. VERNER, & E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97: 253-267.
SEDGWICK, J. A., & F. L. KNOPF. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90: 253-256.
SOUTHERN, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake region, Michigan, part 2. Jack Pine Warbler 36: 185-207.
WILEY, J. W. 1982. Ecology of avian brood parasitism at an early interfacing of host and parasite populations. Ph.D. dissertation, Coral Gables, Florida, Univ. Miami.

Received 9 May 1988, accepted 26 January 1989.

A Comparison of Two Methods of Estimating Breeding Group Size in Harris' Hawks

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Accurate estimates of the size of social units or breeding groups are central to studies of cooperative breeding in birds and a variety of methods are used in conjunction with color-banding to census group members (Brown 1987). The particular methods used depend largely on how species respond to the presence of humans. Scrub Jays (*Aphelocoma coerulescens*) and Arabian Babblers (*Turdoides squamiceps*), for example, can habituate to the presence of humans; consequently, group sizes can be accurately estimated by simply walking through territories and counting marked individuals (Woolfenden and Fitzpatrick 1984, Carlisle and Zahavi 1986). In other species, group size is estimated by watching the nest and counting individuals from a distance at which birds are not disturbed (e.g. Dow 1977). Some species, however, are extremely wary of humans and remain alarmed when humans are near the nest. Accurate estimates of group size in these species are obtained by observing nests from blinds or other concealed positions (e.g. Ridpath 1972, Craig 1980, Koenig and Mumme 1987).

The Harris' Hawk (*Parabuteo unicinctus*) breeds in groups of >2 throughout its range in the southwestern United States (Mader 1975a, Griffin 1976, Bednarz 1987). Interest in the Harris' Hawk increased dramatically after Mader (1975a) reported helpers at nests (e.g. Griffin 1976, Whaley 1979). Recent studies have focused on the cooperative breeding behavior of this species (Mader 1979, Bednarz 1987, Bednarz and Ligon 1988, Dawson 1988).

Harris' Hawks are extremely wary of humans near the nest and respond to humans by soaring over the nest and giving alarm-calls (Mader 1975b, Whaley 1979), or by fleeing the nest area altogether (Bednarz 1986). Estimates of the size of breeding groups of Harris' Hawks generally are made by counting the number of hawks seen while walking through the nest area, or during visits to the nest for other purposes (Mader 1975b, Whaley 1979, Bednarz 1987). An assumption of this method is that all group members respond to human intruders in such a way that they can be observed and counted. The validity of this assumption has never been established.

We studied breeding Harris' Hawks in Arizona and used two methods to estimate group size at each nest. We compared estimates obtained by counting hawks while visiting the nest with estimates made while observing social behavior from a blind at the nest. We also recorded the behavioral responses of Harris' Hawks to a human approaching the nest.

We studied Harris' Hawks in Pinal County, Arizona, for 3 seasons (January to August, 1984-1986). Vegetation in the study area is in the Paloverde-cacti-mixed scrub series of the Sonoran Desert (Turner and Brown 1982). We banded 362 Harris' Hawks with unique combinations of 3 colored leg bands and a