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DEMOGRAPHY OF BELL'S VIREOS IN MISSOURI GRASSLAND-SHRUB HABITATS

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ABSTRACT.—Numbers of Bell's Vireos (*Vireo bellii*) have declined throughout much of the breeding range in recent years, yet little information exists to determine factors that are causing these declines. We studied Bell's Vireos nesting in grassland-shrub habitats at two study areas in central Missouri to determine reproductive performance, survival, and population growth potential. Birds were color banded and observed during the breeding seasons of 1996, 1997, and 1998 to determine seasonal fecundity. We monitored 124 breeding pairs (127 pair years) and 213 nests. Density declined from 1.00 to 0.80 territories per 10 ha at the first site and increased from 1.11 to 1.33 at the second site during the study. Mean nesting success was 31 ± SE of 0.03% overall and ranged from 13 to 42% among years and study areas; 57% of the pairs fledged at least one young. Low annual production was a function of high rates of nest predation (41% of all nests observed, accounting for 44 to 78% of daily nest mortality annually) and nest parasitism by Brown-headed Cowbirds (*Molothrus ater*; 29% of nests observed, 17 to 37% of daily nest mortality annually). Mean seasonal fecundity was 1.60 young fledged per pair per year (range 1.00 to 1.79). Annual survival of adults was 61 ± 0.04% and was higher than previously reported. We used our estimates of seasonal fecundity and annual survival of adults to determine the finite rate of increase (λ) for our study population. Our study areas seemingly comprised sink habitats ($\lambda = 0.85$). Thus, the vireos on our study areas likely were limited by low reproductive success. Population declines also may be caused by habitat loss, which highlights the need for investigation of historical and current rates of loss of grassland-shrub habitat. *Received 23 August 1999, accepted 27 April 2000.*

BELL'S VIREO (*Vireo bellii*) populations have declined significantly throughout much of the species' breeding range during the past 30 years (Sauer et al. 1997). As with many Neotropical migrants, habitat loss and degradation resulting in low productivity on the breeding grounds are thought to be important factors contributing to these declines (e.g. Sherry and Holmes 1993, Brown 1993, Robinson 1996). However, factors limiting population growth for Bell's Vireos have not been assessed in detail across the species' range. Understanding the relative importance of limiting factors for declining species, and when they operate during the annual cycle, are essential for the development of effective conservation plans (Sherry and Holmes 1993).

Most research on this species has focused on the endangered Least Bell's Vireo (*V. b. pusillus*) in the southwestern United States (Goldwasser et al. 1980, Franzreb 1990, Kus 1999). Least Bell's Vireos are limited by loss and degradation of riparian shrub habitats, along with increased brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). This information may be relevant to conservation efforts for two other subspecies of Bell's Vireos, *V. b. medius* and *V. b. arizonae*, which breed in similar riparian habitats in the southern and southwestern United States. However, the fourth subspecies, *V. b. bellii*, occurs in the central United States, where it typically breeds in upland shrub habitats associated with grasslands. Factors that limit populations of Bell's Vireos in riparian habitats in the southern and southwestern United States may differ from those that affect vireos in upland grassland-shrub habitats in the central United States.

Although loss and degradation of habitat likely limit population growth of Bell's Vireos in the central United States, no data on the extent of loss of grassland-shrub habitat are available. Grassland-shrub habitat is considered part of the tallgrass prairie continuum, and approximately 90% of the tallgrass prairie eco-

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system has been destroyed in the United States (Noss et al. 1995). Shrub habitats associated with these grasslands very likely were destroyed in the process. Remaining grassland-shrub habitats used by Bell's Vireos in the central United States often occur as isolated patches in highly fragmented landscapes. Most of these habitats differ from shrub habitats that existed in historic prairies (Schroeder 1981) and likely are distributed across the landscape in different patterns than before (Robinson 1996). Rates of cowbird parasitism and nest predation may be elevated in such landscapes (e.g. Johnson and Temple 1990, Robinson 1992, Robinson et al. 1995).

Little demographic information exists for Bell's Vireos in the central United States, especially in recent years. The published studies of *V. b. bellii* breeding biology and nesting success are based almost entirely on small numbers of nests located non-systematically and produced by unmarked pairs (DuBois 1940, Pitelka and Koestner 1942, Hensley 1950, Mumford 1952, Nolan 1960, Barlow 1962, Overmire 1962, Cink 1977). Extrapolating estimates of seasonal fecundity and other reproductive parameters from randomly located nesting attempts is unsuitable for determining the status of populations (Pease and Grzybowski 1995). Robinson (1992) and Martin (1995) identified a need for studies in which local populations of birds are marked and followed throughout the breeding season at the same time that all nest attempts are monitored. Collecting data in this manner will reduce biases in nesting-success estimates and allow direct examination of annual fecundity and adult survival to improve estimates of demographic parameters.

Consequently, we studied the demography of *V. b. bellii* that nest in grassland-shrub habitats in central Missouri. We determined breeding density, nesting success, seasonal fecundity, causes of nest failure, cowbird parasitism levels, and annual survival of adults and also estimated the finite rate of increase for our study population.

STUDY AREAS AND METHODS

Rocky Fork Lakes Conservation Area.—We studied Bell's Vireos at two areas in central Missouri during the breeding seasons of 1996 to 1998. Research was conducted in the Rocky Fork Lakes Conservation Area (RF), approximately 16 km north of Columbia, in all three years. This 890-ha area is owned and managed by the Missouri Department of Conservation (MDC) and was operated as a stripmine by the Peabody Coal Company before its purchase by MDC in 1979. The 676 ha of RF used in this study consisted of 60% forest or tree-dominated habitats, 22% grassland-shrub habitat, 5% grasslands without shrubs, 9% water, 2% cropland or food plots, 1% roads and buildings, and 1% nonvegetated ground.

Forests contained native and exotic species of trees and forbs. Mature oak-hickory forest also occurred on unmined portions of the area. Grassland-shrub habitats were relatively small and isolated from one another. Management on RF consisted of periodic burning of the larger grassland and grassland-shrub patches and planting of small food plots for wildlife.

RF is bordered by forest fragments, pastures, residential areas, and row crops on three sides. Little grassland-shrub habitat occurs adjacent to RF. Finger Lakes State Park borders the area and also was stripmined. Young forests have since developed on much of the park, and little grassland-shrub habitat occurs there.

Whetstone Creek Conservation Area.—The Whetstone Creek Conservation Area (WC) is about 48 km east of Columbia and was studied in 1997 and 1998. The 2,083-ha area was operated as a cattle ranch before its purchase by MDC in 1976. The southern 923 ha of WC used in this study consisted of 43% grassland-shrub habitat, 37% forest, 13% croplands and food plots, 4% grasslands without shrubs, 1% roads and buildings, 1% woody fencerows or hedgerows, and 1% water. Forests were dominated by oaks and hickories and occurred along tributaries and on steep slopes surrounding Whetstone Creek. Grassland-shrub habitats were relatively large and continuous compared with those at RF. Unlike RF, shrubs grew in long, linear patches.

Management at WC has been intensive. Periodic logging of forest habitats has occurred, and much of the nonforested area was leased for row cropping or cattle grazing. Burning and haying are used to maintain open grassland and grassland-shrub habitats on the rest of the area. Large trees and exotic shrubs have been mechanically removed from grassland-shrub habitats to reduce the number of raptor perches and exotic plants, and large trees and shrubs are periodically removed from fencerows and hedgerows.

WC is surrounded by intensive agriculture on about two-thirds of its border. Large fields are farmed annually on the southern and western borders. A corporate hog farm occurs immediately west of the area, and agriculture, pastures, and forests abut the northern border. The eastern border is surrounded by mature forest interspersed with pastures. The landscape in general is much less forested than that surrounding RF.

Territory mapping and density estimates.—We searched all grassland-shrub habitats in the study areas for territorial vireos starting in early May each year. We conducted searches every few days until the first Bell's Vireo was located, after which we searched daily. Usually, we located males first because of their songs. We used song playbacks to elicit responses from males in potential habitats where males were not already singing. Once located, the pairing status of males was determined and locations mapped every one to two days throughout the breeding season. The presence of pairs or of males defending territories with nests were used to determine the pairing status of males.

We mapped territories as convex polygons and used a portable global positioning system to record coordinates of territory boundaries. We overlaid territories on aerial photos and calculated territory size with a geographic information system. We calculated territory density as the number of male territories per 10 ha of grassland-shrub breeding habitat searched.

Capture and color banding.—We mist netted and color banded male and female vireos to determine seasonal fecundity. We placed two 6-m long mist nets in flight paths to nests during nest building or between shrub patches used for feeding at other times. We also used song playbacks to attract males into mist nets. We netted as many birds as possible before nest building began; however, because nesting began shortly after females arrived, pairs were often captured during nest building. In these cases, we placed nets away from nests to reduce abandonment. The two instances where we believed nests were abandoned because of netting activities were excluded from analyses of number of nesting attempts and nesting success.

All individuals captured received a numbered aluminum leg band and a unique combination of two or three color bands. Males often were the only member of a pair banded because females were difficult to capture. In these instances, we assumed that the same pair stayed together throughout the breeding season because Bell's Vireos usually began to renest quickly after nesting failure. We reasoned that not enough time existed for a new female to arrive and pair with a male when renesting activity began within one or two days after a nest failed. Also, all marked females (n = 32) remained with the same males throughout the breeding season.

Nest monitoring.—We followed pairs throughout the breeding season and monitored each nesting attempt. Active nests were those in which vireo eggs were known to have been laid. Nests were visited every one to three days depending on stage of the nesting cycle. During laying and near the estimated fledging time, we often checked nests daily. We approached nests from different sides on successive checks whenever possible to minimize disturbance to the surrounding vegetation. All nests were low enough for observers to see contents. Numbers of eggs, nestlings, and/or fledglings (both host and cowbird) were recorded at each visit.

A nesting attempt was considered complete when all nestlings fledged (i.e. left the nest), all contents of the nest disappeared, or the adults abandoned the nest. To confirm that young had fledged, we looked and listened for fledglings or for scolding calls of adults. We assumed that the number of fledglings was the number of nestlings seen in the nest on the last visit. A nest was considered successful if it fledged one or more host young. If no fledglings were located, adults did not scold when we were close to the nest site, and parents began to renest within one or two days after estimated fledging time, the nest was considered to have failed.

We considered nests to have failed from predation if all eggs or some or all nestlings (vireo or cowbird) disappeared, or if some vireo eggs disappeared and no evidence of cowbird egg removal had occurred (i.e. no new cowbird eggs were located in or below the nest). Evidence such as egg shells, nestling parts, or destruction of nests and nest plants was recorded. However, because recent studies using video cameras indicate that evidence left by nest predators is not sufficient to determine predator type, we made no attempt to identify nest predators (Thompson et al. 1999).

Nests were considered to have failed from cowbirds if nests were abandoned and cowbird eggs were present in the nest. We documented interactions between vireos and cowbirds that resulted in cowbird eggs being laid on or falling to the ground (Budnik 1999). Therefore, if an abandoned nest contained vireo eggs, and a cowbird egg was found on the ground below the nest, we considered the nest to have failed due to interactions with a cowbird. Because nestling cowbirds usually hatched first and outcompeted host nestlings for food and space, we also considered a nest to have failed from parasitism if the cowbird nestling remained in the nest after all host eggs or nestlings had disappeared. For Mayfield calculations, we counted exposure days until the last vireo egg or nestling disappeared from a nest.

We recorded nests as failed owing to weather or other natural events when nests located near small streams were destroyed in flash floods, or when it appeared that the nest substrate failed to support the mass of the nest (e.g. if all nest contents were present in the nest or on the ground below a leaning nest). In addition, nests in which nestlings died for no apparent reason were considered to have failed from weather or other natural events.

Nests were recorded as abandoned for unknown reasons if a nest was built but no contents were documented. In some of these cases, it is likely that a predator or cowbird removed the first egg, resulting in abandonment before an observer was able to document the egg. In addition, if all nest contents that were recorded during the previous visit were present in subsequent visits, but the nest appeared to be abandoned, the nest was considered abandoned for unknown reasons.

Estimating daily survival and nesting success.—We used Mayfield's exposure method (Mayfield 1975) to estimate daily nest survival for the entire 26-day nesting cycle (14 days incubation,12 days nestling period). Program CONTRAST was used to test for differences in daily nest mortality rates or nesting success (Sauer and Williams 1989). We used analysis of variance to test for seasonal differences in mean clutch size but used a chi-square test of independence to examine seasonal differences in fledging rates because these data were not normally distributed. We considered P-values ≤ 0.10 to be significant to reduce the probability of a type II error.

Hatching rate.—We calculated hatching rates and obtained fresh egg masses to determine if our study birds were producing a high frequency of nonviable eggs. We counted the total number of eggs that hatched and divided it by the total number of eggs that survived the 14-day incubation period to obtain hatching rates (Mayfield 1975), and we report the percentage of nests in which total hatching failure occurred (Rothstein 1973).

Seasonal fecundity.—We calculated season-long fecundity as the mean number of young fledged per pair per year. For population-growth models, the number of female young produced per adult female was used. We assumed the sex ratio at hatching to be 1:1 and divided the total number of young per pair per year by two to obtain the number of female young. We examined within-season patterns of reproductive output and success by dividing the breeding season into early (nest initiations in May), middle (June), and late (July) periods. Nearly all nests monitored in May were first nesting attempts. July nest initiations occurred near the end of cowbird egg-laying period in our area (Burhans et al. 2000). We combined data across years for within-season analyses because of low statistical power associated with small sample sizes in some comparisons.

Survival estimates.—We estimated adult survival rates from banding and resighting data. We also revisited both study areas during May through July of 1999 to obtain an additional year of resighting data. We used program MARK to estimate annual survival for the sexes combined and for each sex individually (White and Burnham 1999). MARK incorporates variable resighting rates into estimates of survival. The final model selected to estimate survival included constant resighting probabilities and survival among years. We tested for differences between estimates for males and females using CONTRAST (Sauer and Williams 1989). We used the combined survival estimate for source-sink assessments discussed below because female survival estimates were based on a relatively small sample size. Because we did not band nestlings or fledglings, and estimates of juvenile survival are lacking for this species, we assumed that juvenile survival was half that of the adult survival estimate (see Temple and Cary 1988, Donovan et al. 1995). In separate analyses, we used chi-square tests to examine differences in return rates and territory fidelity between successfully and unsuccessfully breeding males and females.

Source-sink assessment.—To determine whether our Bell's Vireo population could maintain itself if it were a closed population (no emigration or immigration), we calculated the finite rate of increase (λ):

$$\lambda = P_A + P_J\beta, \tag{1}$$

where P_A is the annual survival rate of adult vireos, P_J is the probability a juvenile female will survive to the next breeding season, and β is the number of juvenile females produced per breeding female (Pulliam 1988). If $\lambda < 1$, the population is declining or is a potential sink; if $\lambda > 1$, the population is increasing or is a potential source of emigrants; and if $\lambda = 1$, the population is considered stable. The number of female young produced per female needed to obtain a stable population was calculated by setting $\lambda = 1$ and solving for β. This variation of the source-sink model may be used to determine if a given study area conceivably could produce a stable or source population with slight increases in reproductive success via habitat improvements or other management actions. We calculated 95% confidence intervals (CI) around λ using the lower and upper CIs for adult survival and seasonal fecundity estimates. These intervals distinguished the best-case and worst-case finite rate of increase expected in our population based on the observed estimates for survival and fecundity.

RESULTS

We observed 124 vireo pairs (127 pair years) over the three-year study period (Table 1). Individual females (n = 115) from those pairs produced 213 active nests ($\bar{x}$ = 1.78 ± SE of 0.10, range 1 to 7 per year) and laid from 1 to 19 eggs per year ($\bar{x}$ = 5.97 ± 0.32; Table 1). Mean territory size at RF (1.18 ± 0.19 ha, range 0.39 to 1.98, n = 9) was larger ($P < 0.001$) than at WC (0.61 ± 0.06 ha, range 0.12 to 2.12 ha, n = 51). Density of male territories was 1.11 per 10 ha of grassland-shrub habitat overall, ranging from 0.80 at RF in 1998 to 1.33 at WC in 1998 (Table 1). During the study, 90% of all territorial males acquired mates.

TABLE 1. Densities and nesting effort of Bell's Vireos in central Missouri, 1996 to 1998.

Study area	Density[a]	No. breeding pairs	No. breeding females	Clutches per female[b]	Eggs per female[b]
			1996		
RF	1.00	15	14	2.29 ± 0.37	7.07 ± 1.17
WC	—	—	—	—	—
			1997		
RF	0.94	13	11	2.64 ± 0.56	8.09 ± 1.57
WC	1.11	38	36	1.83 ± 0.15	6.00 ± 0.57
Total	1.06	51	47	2.02 ± 0.18	6.49 ± 0.58
			1998		
RF	0.80	10	9	1.67 ± 0.29	5.33 ± 0.82
WC	1.33	51	49	1.43 ± 0.11	4.80 ± 0.32
Total	1.19	61	58	1.47 ± 0.10	4.88 ± 0.30
			Years and sites pooled		
Total	1.11	124[c]	115[d]	1.78 ± 0.10	5.97 ± 0.32

[a] Number of territorial males per 10 ha.

[b] Values are $\bar{x}$ ± SE.

[c] Three pairs observed in 1997 also were paired in 1998 at WC (i.e. 127 pair years).

[d] Four females were observed in 1997 and 1998 (i.e. 119 female years).

Mean nesting success for all years and both study areas was 31 ± 0.03%. Because of persistent renesting after nest failures, 57% (71 of 124) of breeding pairs fledged one or more host young (Table 2). We did not detect differences in nesting success between study areas in 1997 ($\chi^2 = 1.10$, df = 1, $P = 0.295$) or 1998 ($\chi^2 = 1.15$, df = 1, $P = 0.282$), nor among years at either study area (RF, $\chi^2 = 1.93$, df = 2, $P = 0.38$; WC, $\chi^2 = 1.33$, df = 1, $P = 0.25$; Table 2). Hatching rate was 88% (316 of 359 eggs that survived to the hatching date) over three years; no nests had total hatching failure. Mean fresh egg mass was 1.47 ± 0.03 g (range 1.15 to 1.85 g, $n = 30$).

Reproductive output and nesting success varied seasonally (Table 3). Mean clutch size declined from May through July ($F = 22.7$, df = 2 and 133, $P < 0.0001$), but nesting success was higher in May and July than in June ($\chi^2 = 6.2$, df = 2, $P = 0.045$). These patterns resulted in fledging rates that peaked in May and de-

TABLE 2. Nesting success and productivity of Bell's Vireos in central Missouri, 1996 to 1998.

Study area	n[a]	Daily nest survival[b]	% Nesting success	% Pairs successful	No. young fledged per pair[b]
			1996		
RF	32	0.923 ± 0.014	0.126	33	1.00 ± 0.41
WC	—	—	—	—	—
			1997		
RF	28	0.943 ± 0.013	0.215	62	1.46 ± 0.43
WC	64	0.958 ± 0.006	0.331	63	1.79 ± 0.25
Total	92	0.954 ± 0.006	0.296	63	1.71 ± 0.22
			1998		
RF	15	0.950 ± 0.015	0.267	40	1.00 ± 0.47
WC	70	0.967 ± 0.005	0.421	59	1.78 ± 0.24
Total	85	0.965 ± 0.005	0.393	56	1.66 ± 0.22
			Years and sites pooled		
Total	209	0.956 ± 0.004	0.308	57	1.60 ± 0.14

[a] Number of nests used for calculating Mayfield estimates.

[b] Values are $\bar{x}$ ± SE.

TABLE 3. Seasonal variation in mean nesting success, clutch size, and number of young fledged per pair by Bell's Vireo in central Missouri, 1996 to 1998 combined.

Month	No. pairs	Clutch size[a,b]	% Nesting success	No. young fledged per pair[b]	Daily mortality from predation[b]	Daily mortality from parasitism[b]
May	74	3.88 ± 0.06 (52)	35.3	1.24 ± 0.19	0.026 ± 0.004	0.011 ± 0.003
June	45	3.71 ± 0.07 (51)	21.2	0.78 ± 0.15	0.030 ± 0.005	0.020 ± 0.005
July	33	3.16 ± 0.09 (31)	39.0	1.03 ± 0.23	0.029 ± 0.007	0.001 ± 0.002

[a] Based on nests for which clutch size was known for certain (n in parentheses).

[b] Values are $\bar{x}$ ± SE.

clined sharply in June but then rebounded partially in July ($\chi^2 = 13.91$, df = 8, $P = 0.087$; Table 3).

Predation consistently was the most frequent cause of nesting mortality, accounting for 61% of all nesting failures, whereas parasitism by Brown-headed Cowbirds was responsible for 28% of nesting failures (Table 4). Predators destroyed 37.5% ($n = 32$) of the active nests in 1996, 36.5% ($n = 96$) in 1997, and 47.1% ($n = 85$) in 1998. Daily nest mortality related to predation did not vary seasonally ($\chi^2 = 0.55$, df = 2, $P = 0.76$; Table 3).

Brown-headed Cowbirds parasitized 43.8% ($n = 32$) of the active nests in 1996, 31.3% ($n = 96$) in 1997, and 21.2% ($n = 85$) in 1998. No vireos fledged from nests that contained cowbird eggs or nestlings. Daily nest mortality from cowbird parasitism peaked in June and was rare in July ($\chi^2 = 20.5$, df = 2, $P < 0.0001$; Table 3). Parasitized nests ($n = 62$) contained a mean of 1.29 ± 0.06 cowbird eggs (range 1 to 3). An additional cowbird egg was found on the ground directly below the nest at 3 of the 62 active nests that contained cowbird eggs. At five other nests, cowbird eggs were found on the ground but not in the nest. Vireos abandoned 58% (36 of 62) of the active nests that were parasitized by cowbirds. Two of the three nests that had both a cowbird egg inside the nest and one below the nest were abandoned. Of the five nests with only cowbird eggs present on the ground, three were abandoned. The remaining two nests also failed when a predator took all of the nest contents (before we determined if vireos abandoned). Vireos incubated cowbird eggs and vireo eggs in 24 nests (39% of nests that contained cowbird eggs).

TABLE 4. Proportion of daily nest mortality attributed to each cause of nesting failure for Bell's Vireos in central Missouri, 1996 to 1998.

Study area	Cause of failure: Predation	Parasitism	Stochastic events	Abandoned/ unknown
		1996		
RF	0.44	0.37	0.12	0.07
WC	—	—	—	—
		1997		
RF	0.52	0.43	0.00	0.05
WC	0.57	0.29	0.07	0.07
Total	0.56	0.33	0.05	0.06
		1998		
RF	0.72	0.18	0.00	0.10
WC	0.78	0.17	0.00	0.05
Total	0.77	0.17	0.00	0.06
		Years and sites pooled		
Total	0.61	0.28	0.04	0.06

Mean fecundity ranged from 1.0 fledgling per pair at RF in 1996 and 1998 to 1.79 fledglings per pair at WC in 1997 (Table 2). Only one pair of vireos successfully raised two broods of their own young in one year. Four other pairs attempted second broods, three after fledging only cowbirds from the first nest.

We banded 102 adults (71 males, 31 females) from 1996 to 1998. Based on resightings in subsequent years (Table 5), the estimated annual survival for the combined sample of adults was 0.61 ± 0.04. The survival estimate for males (0.68 ± 0.05) was significantly higher than that for females (0.43 ± 0.07; $\chi^2 = 7.89$, df = 1, $P = 0.005$), although interpretation of this difference is confounded by the fact that we banded more than twice as many males as females.

Forty of 58 (69%) males that bred successfully one year returned to breed the following year. This did not differ from the 32 of 54 (60%) unsuccessful males that returned ($\chi^2 = 1.14$, df = 1, $P > 0.25$). Thirty-four of the 40 (85%) successful males returned to breed on the same

TABLE 5. Number of Bell's Vireos banded and resighted by year in central Missouri, 1996 to 1999.

Year banded	No. banded	No. resighted 1997	1998	1999
Sexes combined				
1996	7	3	2	2
1997	76	—	49	29
1998	19	—	—	8
Males				
1996	5	3	2	2
1997	50	—	36	24
1998	16	—	—	7
Females				
1996	2	0	0	0
1997	26	—	13	5
1998	3	—	—	1

territory as the previous year, whereas significantly fewer (16 of 32 [50%]) unsuccessful males reoccupied the same territory upon returning ($\chi^2 = 10.26$, df = 1, $P < 0.05$). Fourteen of 27 (52%) females that produced young returned to breed the following year. This did not differ from the 5 of 13 (38%) unsuccessful females that returned ($\chi^2 = 0.63$, df = 1, $P > 0.25$). Eight of the 14 (57%) successful females that returned to breed the following year reoccupied the same territory, whereas only one of five (20%) unsuccessful females did so.

Estimates of λ (using survival = 0.61 for sexes combined) were below 1.0 in each study area. For years and study areas combined, $\lambda = 0.85$ (95% CI = 0.70 to 1.01). To maintain a stable population, vireos would need to produce 2.56 young per breeding pair per year. Alternatively, annual survival rates of 72% and 36% for adult females and juveniles, respectively, would be needed to maintain a stable population given the observed fecundity. The RF study area was consistently a potential sink habitat with ($\lambda = 0.79$, 95% CI = 0.62 to 0.97), ranging from 0.76 in 1996 and 1998 to 0.83 in 1997. The number of breeding pairs at that area declined from 15 to 10 from 1996 to 1998. Although $\lambda = 0.88$ at WC in 1997 and 1998, the 95% confidence interval included 1.0 for all years combined (0.72 to 1.06). The number of breeding pairs at WC increased from 38 in 1997 to 51 in 1998.

We found further evidence that vireo numbers were declining at RF and were more stable at WC during 1999. Based on limited observations, we located 10 territorial males at RF in 1999, only 5 of which were paired. At WC in 1999, more than 50 of 57 territorial males were paired.

DISCUSSION

Bell's Vireos in central Missouri did not produce enough young to compensate for annual mortality during our study. This low reproductive success was the result of high rates of nest predation by unknown predators and nest parasitism by Brown-headed Cowbirds. Predators and cowbirds typically are the main causes of nesting failure for North American songbirds (Martin 1992). Lower nesting success at RF could have resulted in the decline in number and density of breeding pairs during the study. At WC, the 95% confidence limits for λ included 1.0, and the number and density of breeding pairs increased during the study period. Had we used the much lower female survival rate in our calculations of λ, sink status would have been indicated for WC. It is feasible that WC was a sink and still had an increasing population during our study if immigration occurred from unknown source habitats or from recently altered or destroyed grassland-shrub habitats. In any case, it seems likely that only in years with unusually high fecundity and survival would we expect the overall central Missouri population to remain stable if it was a closed population.

The overall nesting success (30%) we measured using the Mayfield (1975) method was similar to the simple nesting success reported by Overmire (1962) and Graber et al. (1985) for Bell's Vireos in Oklahoma (31% based on 61 nests) and Illinois (32%, 15 nests), respectively. Barlow (1962) reported 11% simple nesting success for 35 nests in Kansas. Predators caused most of the nesting failures throughout our study, accounting for 61% of total daily nest mortality (87 of 213 [41%] active nests depredated).

Rates of cowbird parasitism ranged from 21 to 44% annually and accounted for 28% of daily nest mortality. Daily nest mortality from parasitism was consistently lower at WC than at RF. Wood Thrushes (*Hylocichla mustelina*) nesting in adjacent forest fragments at WC experienced higher rates of nest parasitism during the study period (66 to 92%), and multiply parasitized nests were common (M. L. Fink unpubl. data). Hahn and Hatfield (1995) also reported significantly higher parasitism rates in forest than in adjacent old-field and edge habitats. Parasitism rates for individual hosts at a given site may be influenced by the entire assemblage of hosts available to cowbirds (Hahn and Hatfield 1995). Cowbirds were abundant in and around the grassland-shrub habitats at WC and may have focused parasitism in the adjacent forest owing to fewer hosts exhibiting defenses to parasitism in those areas (Rothstein 1975, Hahn and Hatfield 1995). Parasitism rates reported for Bell's Vireos elsewhere ranged from 30% to more than 80% (Nice 1929, Mumford 1952, Barlow 1962, Overmire 1962, Goldwasser et al. 1980, Franzreb 1989, Averill-Murray et al. 1999, Kus 1999); however, because protocols for determining parasitism rates vary, it is difficult to interpret differences among studies (Pease and Grzybowski 1995).

In our study, predators typically destroyed all nest contents, usually resulting in renesting immediately after failure. Pease and Grzybowski (1995) and Schmidt and Whelan (1999) indicated that females might ameliorate effects of nest predation by renesting following failure. Small clutch sizes and short nesting cycles likely reduce energetic costs for Bell's Vireos, allowing them to renest numerous times following failure from nest predation (e.g. Slagsvold 1982, Martin 1995, Schmidt and Whelan 1999). However, the response of pairs to nest parasitism can have opposite effects. Bell's Vireo pairs incubated and cared for cowbird eggs and nestlings in 17% of all nests initiated (39% of parasitized nests). By continuing to care for parasitized nests, adults wasted crucial time and energy that could have been used for future nesting attempts. Therefore, the effect of cowbird parasitism on seasonal fecundity may have been greater than is apparent from our data because parasitism limited the number of nesting attempts within a breeding season (Pease and Gryzbowski 1995, Schmidt and Whelan 1999).

The strong seasonal pattern in fledging production we detected was a function of seasonal variation in cowbird parasitism and clutch size. Fledging productivity was highest in May (although still well below the threshold needed to maintain a stable population) when clutch size was highest and parasitism effects were moderate. The much lower nesting success and fledging productivity in June coincided with the peak of cowbird parasitism. Cowbirds typically cease egg laying in late June or early July in Missouri (Burhans et al. 2000), and the substantial decline in nest mortality from parasitism resulted in high nesting success at that time. However, mean clutch size was almost one egg lower in July than in May, and overall fledgling production was lower than that earlier in the season. Also, despite substantial renesting efforts, the number of vireo pairs attempting to nest in July was low, and their contribution to population growth was limited.

The number of broods raised each year has a strong effect on annual fecundity (Pulliam 1988, Schmidt and Whelan 1999). Only one pair fledged two broods of vireo young during our study. Franzreb (1989) suggested that Bell's Vireos are double brooded, but the frequency of second broods often is limited by high rates of nest failure, as in our study. The number of broods attempted may be limited if food availability is low late in the breeding season (e.g. Holmes et al. 1992). This effect would be heightened for pairs that renest repeatedly.

Estimated annual survival rate of adults for our study population (61%) was at the high end of the range typically reported for small landbirds (40 to 60%; Ricklefs 1973, Martin 1995) and for grassland-shrub nesting species in general (53%; Martin 1995). However, some of this difference could result from the use of different analytical methods to estimate survivorship. Comparable survival estimates for Bell's Vireos elsewhere are lacking, although annual return rates were estimated at 47% (Franzreb 1989, Brown 1993). Survival estimates were much higher for males than for females at our sites. Estimates of female survival could be biased because of the smaller number of individuals banded (Table 5). However, lower female survival also could have been related to higher energy demands associated with higher reproductive effort, higher risks associated with increased foraging time to meet higher energy demands, or late arrival on the wintering grounds (e.g. Ricklefs 1973, Ekman and Askenmo 1986). Alternatively, estimates of survival for females may have been lower because of lower resightability associated with reduced site fidelity between years.

Low annual production of young Bell's Vireos during our study suggested that events on the breeding grounds contributed to the declining population trend for this species. Sherry and Holmes (1993) suggested that populations of many other Neotropical migrant birds also were limited by events on the breeding grounds.

The Bell's Vireo population we studied in central Missouri probably was a sink ($\lambda = 0.85$). These findings, coupled with trend data suggesting a long-term population decline (Sauer et al. 1997), suggest that conservation efforts for this species should be intensified. Low reproductive success resulting from high rates of nest predation and parasitism by Brown-headed Cowbirds seemingly limited population growth in our study. The availability of grassland-shrub breeding habitat throughout the central United States is another likely factor in the decline, because the abundance of a migrant species often is roughly proportional to the total area of suitable habitat available (Sherry and Holmes 1993).

Efforts to quantify the availability and rate of loss of grassland-shrub habitat are needed. In addition, research is needed in other parts of the central United States to determine where (or if) source populations of Bell's Vireos exist. Pulliam (1988) suggested that for some species, only a small fraction of the population might be breeding in source habitats at any given time. Protection of existing source habitats for Bell's Vireos should be a conservation priority.

The identification and manipulation of habitat features that reduce nest predation and brood parasitism represent the best long-term solution for increasing productivity of birds (Martin 1992, Schmidt and Whelan 1999). Management to reduce predation at Bell's Vireo nests will require additional information on the identity of nest predators. Early initiation of conservation efforts to protect and manage for high-quality grassland-shrub habitats for Bell's Vireos in the central United States could prevent expensive and uncertain last-ditch actions such as predator and cowbird removal, or reintroduction of Bell's Vireos.

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