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SUNRISE NEST ATTENDANCE AND AGGRESSION BY LEAST BELL'S VIREOS FAIL TO DETER COWBIRD PARASITISM

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ABSTRACT.—We video-recorded three, natural, brood-parasitism events by Brown-headed Cowbirds (*Molothrus ater*) at nests of Least Bell's Vireos (*Vireo bellii pusillus*). All instances occurred near dawn, during both egg-laying and incubation stages of the nesting cycle. In each case, an adult vireo was on the nest when the female cowbird arrived. Both members of each parasitized pair vigorously attacked the intruding cowbird, but in no encounter did a pair of vireos successfully defend its nest from parasitism. Thus, Least Bell's Vireos in our study were unable to prevent a female cowbird from parasitizing their nests once the cowbird had reached the nest. *Received 16 October 2003, accepted 1 April 2004.*

There are several ways in which potential hosts may protect a nest from the detrimental impacts of brood parasitism. Two strategies may prevent a cowbird from laying: nest sitting (rushing to the nest and sitting in it; Hobson and Sealy 1989, Gill and Sealy 1996) and aggression directed at the intruding cowbird (Robertson and Norman 1977, Briskie et al. 1990). The effectiveness of such behaviors in deterring parasitism is unclear. The findings of Sealy et al. (1998) suggest that these behaviors do not thwart parasitism. However, J. M. Budnik (pers. comm.) video-recorded a Brown-headed Cowbird (*Molothrus ater*) laying an egg on the back of a midwestern Bell's Vireo (*Vireo bellii bellii*) that refused to leave the nest, and several times observed vireo pairs preventing cowbirds from laying by physically attacking and driving them away (Budnik 1999, Budnik et al. 2001).

After a nest has been parasitized, the most effective anti-parasite responses by the host are to (1) eject the egg from the nest (Rothstein 1976, Sealy and Bazin 1995), or (2) bury the egg (Clark and Robertson 1981, Sealy 1995). A third strategy is that of abandoning the nest and re-nesting, but the effectiveness of this strategy varies (Graham 1988, Hosoi and Rothstein 2000, Kus 2002).

Nest-attendance behavior by potential hosts during times when cowbirds may lay eggs is an important consideration when examining a host's defense capability (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999). Scott (1991) and Neudorf and Sealy (1994) found that Brown-headed Cowbirds lay near (usually before) sunrise during the laying stage of the nesting cycle. A host that is vigilant near the nest at these times may be able to defend its nest better than a host that is not attending its nest (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999). However, Sealy et al. (2000) found that sunrise nest attendance was a function of the onset of incubation rather than a nest-defense strategy.

Least Bell's Vireo (*V. b. pusillus*) is a federally endangered songbird that is heavily parasitized throughout most of its current range in California (Franzreb 1989; Kus 1999, 2002). Consequently, extensive cowbird-trapping programs have been instituted within the geographic range of this vireo. As Least Bell's Vireo is a recent host, co-occurring with cowbirds only during the last century (Mayfield 1965), it may lack natural defenses against parasitism. Least Bell's Vireos only rarely bury cowbird eggs (BEK unpubl. data), and, like many other small hosts, including the western subspecies of Warbling Vireo (*V. gilvus swainsonii*; S. G. Sealy pers. comm.), Least Bell's Vireos are probably unable to grasp- or puncture-eject cowbird eggs (Rothstein 1975a, Spaw and Rohwer 1987, Rohwer and Spaw 1988). Least Bell's Vireos abandon parasitized nests, but they do so at a much

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lower rate (mean = 29%, n = 207; Kus 1999) than the nominate subspecies, *V. b. bellii* [74%, n = 43 (Parker 1999); 51%, n = 63, (Budnik et al. 2001)], and nest desertion and re-nesting by Least Bell's Vireos is not currently an effective defense against the impacts of parasitism (Kus 2002). Nothing is known about the ability of Least Bell's Vireos to deter parasitism through nest defense.

We video-recorded natural parasitism events of Least Bell's Vireos by Brown-headed Cowbirds to examine this host's ability to defend its nest and to analyze host responses after being parasitized. The specific questions we addressed were (1) when do Brown-headed Cowbirds lay their eggs in Least Bell's Vireo nests with regard to time of day and stage in the nesting cycle, (2) are Least Bell's Vireos attending the nest when cowbirds arrive to lay an egg, (3) how do Least Bell's Vireos interact with cowbirds at the nest, and (4) do Least Bell's Vireos accept or reject a parasitic egg? We addressed these questions to evaluate whether Least Bell's Vireo may be able to adapt to the pressure of brood parasitism.

METHODS

We monitored 129 Least Bell's Vireo nests along the San Luis Rey River in northern San Diego County, California, during the 2000 breeding season as part of a larger, long-term study of vireo demographics. Cowbirds were not trapped within our study site during this season. We placed cameras at 19 nests of 13 different vireo pairs between 28 April and 7 July. These nests were in early stages of the nesting cycle when Brown-headed Cowbirds typically parasitize nests (Lowther 1993, Sealy 1995). Videotapings were made from 1 day before clutch initiation through the midpoint (day 6) of incubation. We extended videotaping through day 6 of incubation to find if parasitism might occur later in the cycle. Cameras were of two types: Fuhrman Microcams and Christensen Sentinel Systems. Lenses were placed within 1 m of nests, camouflaged by surrounding vegetation. The camera was connected by cable to the recorder, which was hidden 10–20 m away from the nest. The field of view for cameras included the nest and 5–50 cm radii around the nest, depending on where we were able to locate the camera lens. We videotaped nest activity continuously in time-lapse mode (20 frames/sec) until either the young fledged, or the nest was depredated or abandoned for other reasons, at which time we moved the camera to another nest.

We reviewed video recordings to determine whether an adult vireo was on or near the nest prior to parasitism, whether vireos defended the nest during parasitism attempts, and whether vireos accepted or rejected cowbird eggs after being parasitized. We noted the duration of each encounter between a female cowbird and the pair of vireos (*sensu* the "laying bout" described in Sealy et al. 1995) as well as the actual time each cowbird spent poised in a laying posture on the nest. We reviewed 2-hr segments (from 1 hr before sunrise to 1 hr after sunrise) for each day a camera was located at a nest, up to the midpoint of incubation, targeting the time of day (Scott 1991, Neudorf and Sealy 1994) and stage of the nesting cycle (Lowther 1993, Sealy 1995) when cowbirds typically parasitize nests. We also noted whether an adult vireo roosted on its nest overnight. If an adult was not on the nest within 1 hr before sunrise, we assumed no adult roosted on the nest, and we recorded the time an adult first visited the nest in the morning relative to time of sunrise. We obtained sunrise times from the U.S. Naval Observatory website.

We considered incubation to begin the day after the last egg was laid, although incubation begins with the penultimate egg (BEK pers. obs.). We chose this chronology to allow us to designate days as either laying days or incubation days. For nests parasitized during laying, we left cowbird eggs in place until clutches were complete (6–10 days after parasitism), and then removed them as authorized by federal and state permits. Means are reported ± SE.

RESULTS

We videotaped three parasitism events by Brown-headed Cowbirds (Table 1). Two events occurred before sunrise, and one took place shortly after sunrise, yielding a mean parasitism-event time of sunrise − 11.0 ± 6.4 min (Table 1). One nest was parasitized on day 4 of incubation, whereas the others were parasitized during laying (Table 1). No nest was abandoned.

In each parasitism event, an adult vireo was

TABLE 1. Characteristics of the nesting stage of videotaped parasitism events at Least Bell's Vireo nests, San Luis Rey River, San Diego County, California, 28 April–7 July 2000.[a]

Date of parasitism	Time of parasitism	Duration of encounter	Time cowbird in nest, laying	Nesting stage when parasitized	Clutch size when parasitized	Completed clutch size (vireo eggs only)
6 May	SR[b] − 21 min	42 sec	23 sec	Day 2 of laying	1	4
15 May	SR − 13 min	35 sec	33 sec	Day 3 of laying	2	4
12 June	SR + 1 min	43 sec	23 sec	Day 4 of incubation	2	2

[a] Parasitism event at a fourth nest was not recorded on tape due to technical difficulties.
[b] SR = sunrise.

still on the nest from the nocturnal roosting/incubation period. Because birds were not marked, we were unable to identify the gender of individuals. Attendant vireos remained on the nest, but were forced off the nest after being pecked repeatedly by the female cowbird. Once ousted from the nest, the vireo attacked the cowbird and was joined by its mate within a few seconds, suggesting the mate was nearby. Although we could not record sound in time-lapse mode, we could see that the vireos were scolding, and we presume that this vocalization is what attracted the second adult vireo. Both vireos scolded, jumped on the cowbird, struck the cowbird while flying by it, tried to pull the cowbird away from the nest, and repeatedly pecked the intruder. One cowbird left the nest on its first attempt, but returned within 6 sec and successfully laid an egg. Encounters between female cowbirds and hosts averaged 40.0 ± 2.5 sec (Table 1). The mean time each cowbird spent on the nest poised in a laying posture was 26.3 ± 3.3 sec (Table 1). No host eggs were removed by cowbirds.

After parasitism, one member of each vireo pair returned to its nest 7–18 sec (n = 3 pairs) after the cowbird left, and resumed normal nest attendance 21–146 sec after parasitism. Upon returning to the nest to brood, the adult inspected the contents prior to sitting in the nest. Pairs parasitized during laying continued laying until completing the typical clutch of four vireo eggs (Brown 1993, Kus 1999). Egg-laying continued at a normal rate of one egg per day, with the exception of one female that did not lay her fourth egg until 5–7 days after her third egg (6–8 days after parasitism). None of the vireo pairs removed the parasitic egg. In the 114 "nest-days" of tapes we reviewed (n = 19 nests), there were no encounters with cowbirds other than the three that resulted in parasitism. Thus, we found no instances in which Least Bell's Vireos prevented a cowbird from parasitizing a nest once the cowbird had reached the nest.

Of the 114 nest-days of tapes, there were only 11 instances in which an adult vireo was not on the nest overnight. Of these 11 cases, 4 occurred before laying began, 6 were during laying, and 1 occurred on day 2 of incubation (Table 2). There were no instances in which an adult did not roost on a nest overnight from day 3 of incubation forward. Linear regression

TABLE 2. Frequency of overnight roosting on the nest and arrival times of non-roosting adult Least Bell's Vireos over the nesting cycle, San Luis Rey River, San Diego County, California, 28 April–7 July 2000.

	Day before lay[a]	Day 1 lay	Day 2 lay	Day 3 lay	Day 4 lay	Day 1 inc[a]	Day 2 inc
Adult on nest overnight/total nests observed	0/4	3/5	11/13	9/10	5/6	15/15	13/14
Mean arrival time of non-roosting adult relative to SR[b] ± SE (min)	+26.0 ± 13.1	+30.0 ± 5.0	+16.5 ± 0.5	+26	+4		−9

[a] lay = laying, inc = incubation
[b] SR = sunrise.

of arrival time (relative to sunrise) versus day of nesting cycle demonstrated that adults that did not roost on the nest overnight arrived at the nest earlier in the day as the nesting cycle progressed ($t = -3.859$, $P = 0.018$; Table 2).

DISCUSSION

Our recordings represent the first video documentation of parasitism by Brown-headed Cowbirds of Least Bell's Vireos. Two of the recorded instances of parasitism occurred during the laying stage of the nesting cycle, as is most often reported in the literature (Lowther 1993, Sealy 1995). The third nest was not parasitized until midway through the incubation stage. Although most parasitism occurs during the laying stage, instances of parasitism during the incubation stage are not uncommon (Lowther 1993, Sealy 1995).

As reported elsewhere (Scott 1991, Neudorf and Sealy 1994), Brown-headed Cowbirds laid their eggs around sunrise. This timing of laying is believed to be an adaptation for laying when host adults do not typically attend nests (Scott 1991); however, Neudorf and Sealy (1994) and Sealy et al. (2000) found that some hosts do attend their nests at sunrise. Clotfelter and Yasukawa (1999) suggested that onset of nocturnal incubation early in the nesting cycle may be a strategy by which Red-winged Blackbirds (*Agelaius phoeniceus*) prevent parasitism. Birds roosting or incubating overnight will be on the nest at dawn, when cowbirds lay and, thus, will be able to defend the nest better than if they were away from the nest during a cowbird visit (Neudorf and Sealy 1994, Clotfelter and Yasukawa 1999).

An adult vireo was roosting at the nest or incubating before each parasitism event we videotaped and an adult roosted overnight on nearly every nest-day we observed. All 11 instances in which an adult did not roost on the nest overnight occurred before or during laying, with the exception of one instance that occurred on day 2 of incubation (Table 2). This pattern, the earlier arrival times of non-roosting adults as the nesting cycle progressed (Table 2), and the vireos' inability to defend their nest when present at the time of a cowbird visit, support the conclusion of Sealy et al. (2000): nest attentiveness is more a function of the onset of incubation than an anti-parasite strategy.

Vireos responded aggressively to the female cowbird in each instance of parasitism. However, sitting in the nest and attacking the cowbird did not prevent parasitism, contrary to observations that midwestern Bell's Vireos escaped parasitism with similar behavior (Budnik 1999, Budnik et al. 2001). We are uncertain as to why defense tactics that were effective in the midwestern subspecies failed to deter parasitism in Least Bell's Vireos.

Least Bell's Vireos quickly accepted cowbird eggs. Possible reasons for acceptance may be (1) lack of recognition of the cowbird egg (Rothstein 1975b, 1990; Sealy 1996; Takasu 1998), or (2) vireos may recognize cowbird eggs as foreign but are unable to eject them. If the latter is the case, nest abandonment is the only response to parasitism available to Least Bell's Vireos. Although nest abandonment was not observed in our sample of videotaped nests, Least Bell's Vireos are known to abandon parasitized nests (Kus 1999), albeit it at a low rate (Kus 2002).

When Least Bell's Vireos accept cowbird eggs, the end result, without human intervention (i.e., removal of cowbird eggs from nests), is the failure to produce vireo young (Kus 1999, 2002). Least Bell's Vireos have never been observed to fledge vireo and cowbird young from the same nest (BEK unpubl. data). We recognize that our sample size is small (such data are extremely difficult to obtain); however, all of the vireos in our study failed to deter parasitism. Given the apparent inability to avert parasitism even when attending the nest at sunrise, and the ineffectiveness of nest abandonment and re-nesting in response to parasitism (Kus 2002), Least Bell's Vireos may lack behavioral defenses sufficient to prevent parasitism or its negative impacts once a female cowbird has reached a vireo nest.

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