

FIRST EVIDENCE OF CONSPECIFIC BROOD PARASITISM AND EGG EJECTION IN SONG SPARROWS, WITH COMMENTS ON METHODS SUFFICIENT TO DOCUMENT THESE BEHAVIORS

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Abstract. Conspecific brood parasitism occurs in many songbird species but has not been reported in Song Sparrows (*Melospiza melodia*). In three separate study areas where breeding Song Sparrows experience heavy nest predation pressure and Brown-headed Cowbird (*Molothrus ater*) parasitism, we observed six instances in which newly laid eggs were attributable to female Song Sparrows other than the nest owners. We also recorded the ejection of a sparrow egg from each of two videotaped nests. In a fourth study area without cowbird parasitism, genetic analysis of parentage revealed no conspecific brood parasitism. Given that egg ejection can accompany conspecific parasitism in Song Sparrows, we suggest that daily nest checks are insufficient to document the frequency of this tactic in some species in the absence of egg marking, videotaping, or genetic analyses. Since standard nest monitoring techniques may fail to detect conspecific brood parasitism, this behavior could be more prevalent than currently thought.

Key words: breeding strategies, intraspecific brood parasitism, egg ejection, *Melospiza melodia*, nest monitoring, Song Sparrow, video surveillance.

Primera Evidencia de Parasitismo Coespecífico de Cría y Eyección de Huevos en *Melospiza melodia*, con Comentarios sobre Métodos Adecuados para Documentar estos Comportamientos

Resumen. El parasitismo coespecífico de cría ocurre en muchas especies de aves canoras, pero no ha sido reportado en *Melospiza melodia*. En tres áreas de estudio separadas, donde *M. melodia* está expuesta a una fuerte presión de depredación y parasitismo por *Molothrus ater*, observamos seis instancias en las que los huevos recién puestos fueron atribuibles a otras hembras de *M. melodia* en vez que a la propia hembra del nido. También registramos la eyección del nido de un huevo de *M. melodia* en cada uno de

los dos nidos grabados en video. En un cuarto sitio de estudio sin parasitismo por parte de *M. ater*, un análisis genético de paternidad reveló la ausencia de parasitismo coespecífico de cría. Dado que la eyección de huevos puede acompañar al parasitismo coespecífico en *M. melodia*, sugerimos que el seguimiento diario de nidos es insuficiente para documentar la frecuencia de esta táctica en algunas especies si no se realiza la marcación de huevos, grabaciones en video o análisis genéticos. Puesto que las técnicas estándar de monitoreo pueden fallar en detectar el parasitismo de cría coespecífico, este comportamiento podría ser más frecuente de lo que se piensa en la actualidad.

Conspecific brood parasitism is the laying of eggs in a nest of the same species without investment in nest building, incubation, or care for hatchlings (Yom-Tov 1980). Conspecific brood parasitism has been observed in at least 234 bird species (Yom-Tov 2001). Documenting which species and individuals engage in this form of facultative parasitism provides basic information for determining the ecological context, in particular the role of nest predation, necessary for the maintenance of flexible breeding strategies and tactics (Lyon 2003). Knowledge of conspecific brood parasitism is also critical in reconstructing the evolutionary history of parasitism through comparative analyses (Sorenson 1991, 1992, Cichon 1996). Although conspecific brood parasitism has been reported in an increasing number of species (Yom-Tov 1980, Yom-Tov 2001), it has been documented in disproportionately few altricial taxa. Whether the relative rarity of conspecific brood parasitism in altricial taxa is real or an artifact of observational methods remains to be seen.

We can detect conspecific nest parasitism using four methods (1–4, Table 1). A less reliable fifth method employs observations of asynchronous hatching, asynchronous fledging, skipped days of laying, egg appearance following clutch completion, or unusually large clutch sizes (Yom-Tov 1980), but these require large deviations from the norm. Methods 1 and 5 are very common in ecological and behavioral studies, and thus are often used to document conspecific brood parasitism (Bower and

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TABLE 1. Benefits and limitations of alternative methods for documenting conspecific brood parasitism.

Method	Benefits	Limitations
1. Nest checks at regular intervals	Can detect multiple eggs laid in a day if full clutch is counted and clutch completion, clutch initiation dates, and timing of laying are known.	(A) Nest must be monitored during the laying period. (B) Nest must be checked twice during the laying period, or clutch initiation and clutch completion dates must be known to detect parasitism. (C) If parasitic egg is laid on the day following clutch completion or the day before clutch initiation, parasitism cannot be detected. (D) Egg ejection may mask parasitism. (E) Parasitic species cannot be identified. (F) Egg ejecter species cannot be identified. (G) Time of day of laying must be known in relation to timing of nest checks.
2. Daily marking of eggs	Avoids limitation (B) from Method 1, although monitoring the nest over the entire laying period maximizes likelihood of parasitism detection. Also avoids limitation (G).	(A), (C), (E), and (F) still hold as for Method 1. Ejection of an egg before marking would mask parasitism. (H) Requires daily nest visitations during laying, adding labor and increasing disturbance, which could attract potential nest predators and parasites.
3. Genetic analysis of parentage	Detects parasitism despite ejection of host eggs. No need for monitoring during the laying period. Avoids limitations (A), (B), (C), and (G) from Method 1.	Egg ejection or predation of parasitic eggs or young prior to sampling will prevent detection of parasitism. Limitation (F) as for Method 1. (I) Labor intensive and relatively expensive, though less so than Method 4.
4. Continuous direct observations or video monitoring	Parasite and ejecter species and timing of laying can be determined, avoiding (D), (E), and (G) for Method 1. Also avoids limitations (A), (B), and (C).	Camera angle must allow counting of eggs, or camera must record agonistic interaction between host and parasite. Limitation (I) from Method 3.

Ingold 2004). However, not all methods are equally effective to conclusively document parasitism in a species, especially in cases where either hosts or parasites eject, remove, or carry eggs within the context of parasitism (Brown and Brown 1988).

Conspecific brood parasitism and egg ejection by the host have not been documented in the Song Sparrow (*Melospiza melodia*), despite intensive observations of several focal populations (Nice 1943, Sealy 1994; O'Connor et al., in press) across the species' wide geographic range in North America (Bent 1968, Smith and Myers-Smith 1998) using Methods 1, 2, and 3. In contrast, parasitic egg ejection by the host (Rothstein 1975), though not nestling discrimination (Nice 1937), has been documented in Song Sparrows in the context of Brown-headed Cowbird (*Molothrus ater*) parasitism, although it is not prevalent across most populations (Arcese et al. 2002). Here, we report video-documented (Method 4) events of conspecific brood parasitism and egg ejection in Song Sparrow populations of eastern and western North America. Additionally,

we report three cases of conspecific parasitism in these populations using regular nest checks (Method 1) and egg marking (Method 2). Finally, we give an example in which molecular genetic analysis (Method 3) was used to document the absence of conspecific parasitic nestlings in a salt marsh Song Sparrow population.

METHODS

EASTERN SIERRA NEVADA, CALIFORNIA STUDY SITES

We found and monitored nests of two Song Sparrow populations in 2000–2004 as part of a riparian bird monitoring program at two sites east of the Sierra Nevada: North Lake, Inyo County (2840 m, 37°13'N, 118°37'W), and tributaries of Mono Lake, Mono County (2020 m, 38°04'N, 119°10'W). These populations are under heavy nest predation pressure (41% of nests depredated) and heterospecific brood parasitism by Brown-headed Cowbirds (65% of nests parasitized). All predation and parasitism rates are

based on a sample of nests in which we observed at least one host egg or young.

Following guidelines in Martin and Geupel (1993), we located and monitored nests every two to four days from early May to mid-August. At each nest check, we counted and recorded the number of eggs or nestlings. We used careful observation of egg size, color, and shape, and nestlings after hatching to distinguish between Brown-headed Cowbird and Song Sparrow eggs (Baicich and Harrison 1997, Ehrlich et al. 1988). We reviewed the data for any nest checked at least twice during building and laying to find nests in which more than one sparrow egg was laid in 24 hr, or more eggs were laid than the number of days between checks (Method 1); these were considered cases of conspecific brood parasitism.

In 2003, we deployed a video camera (Method 4) at a Song Sparrow nest at Mono Lake during the laying period. The camera was approximately two feet above the nest aimed at the nest cup so that all nest contents were visible. The infrared video camera, with a wireless connection to a time-lapse VCR, recorded the nest 24 hours a day (King et al. 2001). We also checked the nest every one to four days as described above.

ITHACA, NEW YORK STUDY SITE

Conspecific parasitism of Song Sparrow nests was observed opportunistically during a study of Brown-headed Cowbird parasitism at the Cornell Experimental Ponds near Ithaca, New York (42°50'N, 76°46'E) in 1998–1999 (Hauber and Russo 2000). Only nests that survived to clutch completion and for which egg counts were recorded daily during the laying period are included in this report. Song Sparrows suffered moderate rates of nest predation (28% of nests depredated) and medium levels of cowbird parasitism (39% of nests parasitized) at this site (Hauber 2000).

In 1998, VHS video cameras (Method 4) were opportunistically set up between 05:00 and 05:30 EST to record cowbird parasitism ($n = 3$) during the laying stage. Separately, four nests were checked twice on each of seven observed laying days. First checks were carried out on average at 05:38 ± 2.4 min (SE) and second checks were performed at 07:54 ± 11.9 min. On these days, all seven eggs were laid between the first and second checks, thus the timing of camera setup was appropriate to document laying behavior. Video cameras were in plain view of each focal nest, at a distance of ca. 5 m. Nest contents were examined before and after video-recording. To document the individual and species identity of eggs laid in Song Sparrow nests, eggs were marked and photographed with a digital camera; no eggs that survived to hatching were misidentified (Hauber and Russo 2000). In 1999, eggs in a subset of Song Sparrow nests ($n = 14$) were individually marked daily during the laying period with a black felt pen (Method 2) to record the identities of old and new eggs.

MARIN COUNTY, CALIFORNIA STUDY SITE

From 2000 to 2002, nests were monitored and blood samples of adults and nestlings were collected as part

of an intensive study of salt marsh Song Sparrow (*M. m. samuelis*) behavioral ecology at China Camp State Park (38°00'N, 122°29'W). Sparrows were marked with unique combinations of colored leg bands, and frequent behavioral observations verified the identity of social parents attending nests. Nest predation was high; Mayfield-corrected nest failure (Hazler 2004) was 76% and nest predation was the predominant cause of nest failure. Cowbird parasitism was extremely rare (no cowbird chicks detected) in the study area (Grenier 2004).

We obtained genotypes at 10 nuclear microsatellite loci: MME 1–3, 7, 8, and 12 (Jeffery et al. 2001); GF 2.35 and GF 07 (Petren 1998); ESCU 1 (Hanotte et al. 1994); and PSAP 335 (M. Leonard, Dalhousie University, pers. comm.), following standard DNA extraction and amplification protocols (Grenier 2004). Genotypes were scored by hand with positive controls in every run. Questionable data were checked with an iterative process of rerunning both laboratory and scoring procedures prior to any analyses. Overall, we ran 30% of samples to check the accuracy of genotypes, and the number of replicate runs was usually two to five, with a maximum of 27. We used CERVUS v. 2.0 (Marshall et al. 1998) to analyze genetic parentage. Similar to analyses of Song Sparrow parentage on Mandarte Island (O'Connor et al., in press), we repeatedly reanalyzed genotypes that mismatched putative parents to reduce error. Data from the eight autosomal loci conformed to Hardy-Weinberg equilibrium, and the null-allele frequency estimates were low (≤ 0.03). Observed heterozygosity was high (0.873), and the total exclusionary power for female parents (i.e., the exclusionary power assuming the identity of neither parent was known) was 0.994 (Grenier 2004). If the genotypes of offspring and putative mother matched at all loci, we considered the female to be the true genetic mother.

RESULTS

EASTERN SIERRA NEVADA OBSERVATIONS

Video case. We observed conspecific brood parasitism of our video-recorded Mono Lake nest. On 11 July 2003 during a nest check we recorded two Song Sparrow eggs and two cowbird eggs. At 15:00 PST during the 12 July nest check we counted three sparrow eggs and three cowbird eggs. The camera at this nest recorded the following: At 05:00 PST on 13 July there were six eggs. At 05:22 PST, the nesting female was incubating when a second Song Sparrow entered the nest. We have identified cowbird invaders using video from other nests, so we are confident that the invader at this nest was a Song Sparrow. The nesting female attempted to fight off the invader, jumping onto the invader's back and flapping her wings furiously while the invader laid an egg. It is difficult to discern how and to what extent the host used her bill and feet against the invader, but it is clear the exchange was agonistic. At the end of the event there was clearly a seventh egg in the nest. Although we were able to accurately count the eggs, the image was not detailed enough to distinguish between Song Sparrow and Brown-headed Cowbird

eggs. At 06:06 PST on 15 July the camera recorded the nesting female grasping an egg with her bill and removing it from the nest, leaving six eggs in the nest.

We checked the nest five hours later on 15 July and recorded two "bluish" eggs and four "whitish" eggs. Because no cowbirds were recorded visiting the nest between the checks on 12 July and 15 July, we concluded that one of the four "whitish" eggs was actually that of the parasitic Song Sparrow. We revisited the nest after reviewing the video (within two days following 17 July) and noted that one of the "whitish" eggs was bluer than the cowbird eggs, albeit lighter than the host eggs, confirming the presence of a parasitic Song Sparrow egg, as well as indicating that the host had removed one of her own eggs. We recorded no cowbird visitations between the 13 July and 15 July nest checks, so host egg ejection was not prompted by cowbird-caused egg damage.

Nest monitoring cases. Of the 14 nests at Mono Lake and four nests at North Lake in which conspecific parasitism could have been documented (i.e., those checked twice during the laying period), there was one nest at each site which apparently had two sparrow eggs laid in one day, suggesting parasitism (Method 1). The Mono Lake nest was found with two sparrow eggs at 08:55 PST on 1 June 2001. At 10:20 PST on 3 June there were five sparrow eggs in the nest. The North Lake nest was observed fully built with no sparrow eggs at 12:15 PST on 8 June 2003. At 13:15 PST on 12 June the nest contained five sparrow eggs.

ITHACA, NEW YORK OBSERVATIONS

Video case. On 8 May 1998 at 05:30 EST a video camera was set up at a Song Sparrow nest on the ground of a bank of an empty artificial pond (Hauber and Russo 2000). The nest cup had a clear entrance, so the camera was placed to focus on the entrance of the nest with a 0.5 m radius field of view. At the time of camera setup the nest contained three sparrow eggs. At the end of the videotaping session at 07:30 EST the nest contained four Song Sparrow eggs, and a fifth sparrow egg was on the ground 0.1 m from the nest's entrance. There were no holes or pierce marks on any of the eggs. The video revealed that a Song Sparrow entered the nest at 06:05 EST and remained until 06:09 EST. At 06:21 EST a Song Sparrow entered the nest and exited at 06:23 EST with an egg in its beak. The egg fell as the bird flew away from the nest and remained outside the nest cup at the end of videotaping. No other birds approached the nest during the videotaping period. Although the identity of each Song Sparrow visiting the nest could not be established, this observation reveals the appearance of two new eggs during a period of two hours and the removal of an egg from the nest cup by grasp ejection. Videotaping on four additional mornings at two additional nests yielded no further footage of conspecific brood parasitism.

Egg marking and nest monitoring cases. In 1998–1999 there were no cases of two or more Song Sparrow eggs appearing inside a nest cup within a 24-hr period in nests ($n = 27$) that were monitored at least twice during the laying period (Method 1).

In 1999, at one of the nests with eggs marked daily (Method 2), a previously marked egg disappeared on each of two different days, with the second instance occurring two days after the first. Each of these observations was accompanied by the appearance of two unmarked Song Sparrow eggs. Thus, on each of these days, there was an overall increase in clutch size of only one egg when in fact two eggs were laid. There were no instances of new, unmarked Song Sparrow eggs appearing in the absence of marked egg disappearance at this or any of the other 13 nests.

MARIN COUNTY GENETIC RESULTS

We analyzed the parentage of 176 offspring from 73 nests with known social mothers and fathers. We obtained genotypes from all loci for all offspring and all putative parents; thus, the genetic data were complete. All offspring matched the genotype of the female observed providing parental care at the nest. Therefore, we observed no cases of conspecific brood parasitism at this site (Method 3).

DISCUSSION

Our observations reveal that conspecific brood parasitism occurs in Song Sparrows in both eastern and western parts of their distribution (Bent 1968, Arcese et al. 2002), although not in all populations (see also O'Connor et al., in press). Furthermore, we provide the first documentation of egg ejection by a Song Sparrow host in the context of conspecific brood parasitism. Our results highlight the importance of nest monitoring, video surveillance, and genetics (Gronstol et al. 2006) as sufficient and necessary methods to enable the detection of conspecific brood parasitism, egg ejection, and presence of conspecific parasite nestlings.

Although not definitive, the indirect observations (limitation G, Method 1, Table 1) of conspecific brood parasitism from the eastern Sierra suggest the more definitive video case (Method 4) was not a unique event at these sites. For both indirect observations, it is possible that an egg was laid by the natal female after the first nest check on the same day. However, our video data (laying observed prior to 08:00 in Tompkins County and at 05:22 at Mono Lake), as well as observational and empirical data from elsewhere (Nice 1943, $n = 3$ from McMaster et al. 2004, $n = 1$ from Mono Lake and $n = 6$ from Tompkins County, this study) suggest that Song Sparrows lay their eggs early in the morning (before 09:00). Therefore, we are fairly confident that our indirect observations from the eastern Sierra reflect multiple eggs laid in the same day, and thus represent additional cases of conspecific parasitism.

Because of the limited sample sizes of nests observed simultaneously with different methodologies at each study site, we have not reported rates of conspecific brood parasitism for our study populations. For studies with sufficient sample sizes, Frederick and Shields (1986) derived corrections for estimating conspecific brood parasitism rates that would compensate for the inherent underestimation of these rates when using daily checks. However,

these corrections would not be useful for Song Sparrows because our observations show that two of the method's assumptions are violated. We have observed that: (i) more than one parasitic egg can be laid in one nest, and (ii) that eggs can be removed, albeit by the host rather than the parasite.

Therefore, researchers intending to document parasitism in particular populations or for particular species should carefully consider the methods they will use (Table 1). Due to its unreliability, we would not consider using Method 5 for any systematic attempt to document parasitism, and therefore did not include it in Table 1. All conspecific brood parasitism events detected by methods other than 1 involved egg ejection, and would not have been detected if only Method 1 had been employed. Therefore, for a species in which egg ejection occurs, Methods 2, 3, or 4 are more effective in detecting conspecific brood parasitism. Method 2 differs from Method 1 in that if previously laid eggs are removed, the former has the ability to detect the appearance of two or more newly laid eggs in a particular day. Method 3 can provide evidence for conspecific parasitism despite the occurrence of egg ejection of host eggs, although this method will fail to detect parasitism if hosts always succeed at ejecting parasite eggs. In addition, genetic misidentification, errors in scoring genotypes, and limited genetic diversity within populations, especially when coupled with siblings parasitizing each other or when quasi parasitism occurs, may limit the statistical power of this methodology (Andersson and Ahlund 2001, Blomqvist et al. 2002). Method 4 is a straightforward means of documenting both the occurrence of egg ejection and the identity of the parasite and egg ejector (Soler et al. 2002). However, in contrast to Method 3, Method 4 cannot be used to detect parasitism in nests found after clutch completion. Therefore, we suggest a combination of Methods 3 and 4 to maximize the probability of detecting conspecific brood parasitism.

If conspecific brood parasitism is accompanied by egg ejection or partial predation by heterospecific parasites more frequently in altricial than in precocial species (Sealy 1994, Arcese et al. 1996), exclusive use of Method 1 will be less likely to detect parasitism in the former, creating a bias in favor of detection in precocial species. This bias may confound the effects of phylogenetic, developmental, or life-history factors (e.g., precocial vs. altricial: Lyon and Eadie 1991, anseriforms vs. galliforms: Geffen and Yom-Tov 2001, cavity vs. open-cup nesting taxa: Bower and Ingold 2004), affecting conclusions about selection regimes and evolutionary histories of conspecific brood parasitism (Yom-Tov 2001).

Our observation of a host apparently removing her own egg suggests an inability to correctly identify parasitic eggs. Recognition and rejection of parasitic eggs are only occasionally observed in both host and nonhost species of obligate heterospecific brood parasites (Peer and Sealy 2001, 2004, Lahti and Lahti 2003). However, adaptations to manipulate clutch sizes, either by laying fewer eggs (Lyon 1998, Power et al. 1989), or by removing eggs for incubation efficiency (Peer and Bollinger 2000), may

also influence detection of conspecific parasitism, so evidence for these adaptations should motivate workers to employ several methods to document conspecific parasitism.

In the last two decades, conspecific brood parasitism has been documented in disproportionately more altricial than precocial species, reducing the discrepancy between the number of precocial and altricial species that exhibit conspecific parasitism (13 altricial and 40 precocial in Yom-Tov 1980, 91 altricial and 124 precocial [semiprecocial excluded] in Yom-Tov 2001; $G = 5.8$, $P < 0.02$, Sokal and Rohlf 1995). Therefore, documenting egg ejection and measuring its frequency of occurrence may be an important part of evaluating the evolutionary history of conspecific brood parasitism.

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