LOW INCIDENCE OF COWBIRD PARASITISM ON SWAINSON'S THRUSHES IN CENTRAL COASTAL CALIFORNIA

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ABSTRACT: We found a low incidence of Brown-headed Cowbird (*Molothrus ater*) parasitism (4%; 9/224 nests) of Swainson's Thrush (*Catharus ustulatus*) in central coastal California despite the high rates (33%) reported here for Wilson's Warbler (*Wilsonia pusilla*). Both species nested primarily in blackberry shrubs and ferns in similar proportions and at similar heights. Thrush nests were significantly better concealed than warbler nests. In both the thrush and warbler, however, concealment of parasitized and unparasitized nests did not differ. The number of potential cowbird perches was not significantly greater at warbler nests or at parasitized nests of either species. No cowbirds fledged from thrush nests; in thrush nests cowbird nestlings observed were last seen at ages of 4 to 7 days, whereas thrush nestlings fledged. At our study sites Swainson's Thrushes fed nestlings a variety of fruit; this partially frugivorous diet may not be suitable for cowbird nestlings, leading to their death. Parasitism significantly reduced the thrushes' clutch size, number of nestlings, and number of fledglings. In four thrush nests experimentally parasitized with real cowbird eggs we observed no rejection response, suggesting that ejection of cowbird eggs is not responsible for the low rate of parasitism observed at our sites. It is unclear why Swainson's Thrushes are parasitized infrequently at our sites, but we suggest that nest concealment may be partly responsible. We did not study behavioral differences between Swainson's Thrush and Wilson's Warbler, but such differences may contribute to the observed difference in parasitism rates.

Swainson's Thrush (*Catharus ustulatus*) breeds in northern forests across Canada from Newfoundland to Alaska, in the eastern United States it breeds along the Canadian border in New England and the Midwest, and in the West it breeds in the Rocky Mountains and along the Pacific slope south to southern California (Evans Mack and Yong 2000). The range of the Brown-headed Cowbird (*Molothrus ater*) overlaps the range of Swainson's Thrush widely, but the cowbird is not found in far northern Canada or Alaska (Lowther 1993). Over much of the thrush's range its populations are stable (Rich et al. 2004). However, the subspecies we studied, *C. u. oedicus*, is endemic to California, where it is listed as a species of special concern by the California Department of Fish and Game (W. D. Shuford pers. comm.). This subspecies breeds along the west slope of the Sierra Nevada and along the coast from at least Marin and Lake counties south to San Diego County (M. A. Ramos in Phillips 1991, Evans Mack and Yong 2000). Brown-headed Cowbird parasitism has been named in part as a likely cause of population decline for Swainson's Thrush along the central and southern California coast (Garrett and Dunn 1981, Evans Mack and Yong 2000), though little is known about the breeding biology of Swainson's Thrush. The few nest studies that do exist have found a low incidence of parasitism (0 to 8%, summarized by Evans Mack and Yong 2000). It should be noted that two

parasitism estimates were from nest-record databases (Western Foundation of Vertebrate Zoology and Cornell Nest Record Program) without any reference to cowbird presence or density, four were from unpublished reports (three were single- or two-year reports from our study sites in Marin County, California), and only two estimates were from published studies, one of which found no parasitism in Alaska, where there are no breeding cowbirds (Rogers 1994).

Parasitism rates within species often vary geographically, temporally, and by landscape within a region (Lowther 1993, Donovan et al. 1995, Robinson et al. 1995). Of the other *Catharus* thrushes, only the Veery (*C. fuscesens*) and the Hermit Thrush (*C. guttatus*) have breeding ranges that overlap the Brown-headed Cowbird's (Lowther et al. 2001, Rimmer et al. 2001). The Veery has an observed parasitism rate of 19 to 87% (Moskoff 1995), and the Hermit Thrush has an observed parasitism rate that ranges from 1.5% west of the Rocky Mountains to 21.7% in Michigan (Jones and Donovan 1996). The closely related Wood Thrush (*Hylochichla mustelina*) has its highest parasitism rates in the Midwest (from 10 to 100%, depending on landscape) and lowest rates in the East (Roth et al. 1996).

Host species may have an observed parasitism rate lower than the actual rate if they are able to eject cowbird eggs (Rothstein 1975, Rich and Rothstein 1985, Sealy 1996). J. Smith (in Evans Mack and Yong 2000) reported one instance of a Swainson's Thrush ejecting a cowbird egg. Other factors that explain low brood-parasitism rates in other species include the parasite's selectivity for hosts (Soler et al. 1995, Hahn et al. 1999), avoidance of hosts that are known to eject (Sealy and Bazin 1995, Peer et al. 2002), nest defense or host vigilance (Briskie et al. 1990, Strausberger and Burhans 2001, Davis et al. 2002), host conspicuousness around the nest (Uyehara and Narins 1995, Banks and Martin 2001), asynchrony of breeding seasons (Peer and Bollinger 1997, Underwood et al. 2004), and nest-site characteristics that might make a nest more difficult to find (Briskie et al. 1990, Clarke et al. 2001). Among nest-site characteristics, two hypotheses have frequently been invoked as influencing parasitism rates: the nest-exposure hypothesis (greater nest concealment reduces parasitism rates; Martin 1993, Burhans 1997) and the perch-proximity hypothesis (trees and/or snags near the nest facilitate nest-searching by cowbirds by providing them with perches from which they view nest-building or other nesting activities; Clotfelter 1998, Hauber and Russo 2000).

Here we present data showing a low incidence of observed cowbird parasitism on Swainson's Thrush and contrast that with high rates reported for Wilson's Warbler (*Wilsonia pusilla*) at the same sites (Michaud et al. 2004). In Marin County, these host species have been sympatric with the cowbird since about 1930, when cowbirds moved in (Laymon 1987, Rothstein 1994). Both host species and cowbirds overlap in nesting habitat (Roberson 1993, Shuford 1993, Farmer 1999) and timing of nest initiation (Swainson's Thrush, 7 May–14 July, J. D. White unpubl. data; Wilson's Warbler, 17 April–10 July, Michaud et al. 2004; Brown-headed Cowbird laying dates, mid April–mid July, Trail and Baptista 1993). We compare the thrush's and the warbler's nest placement. We also compare concealment and the number of potential cowbird perches around nests of each species, distinguishing

parasitized and unparasitized nests to evaluate support for the nest-exposure and perch-proximity hypotheses. We measure the effect of parasitism on Swainson's Thrush clutch size and numbers of nestlings and fledglings, and we present outcomes for parasitized nests. In addition, we report results of experimental parasitism of four thrush nests.

METHODS

As part of an ongoing multi-species monitoring project, we studied Wilson's Warblers and Swainson's Thrushes along Redwood Creek (37° 51′ N, 122° 34′ W, Golden Gate National Recreation Area [GGNRA] and Mt. Tamalpais State Park) and Lagunitas Creek (38° 02′ N, 122° 45′ W, GGNRA) in Marin County, California. From 2000 to 2002 Swainson's Thrushes were the focal species of a dissertation project, resulting in larger sample sizes of nests during those years (Table 1). We used Wilson's Warbler data from the same sites (presented by Michaud et al. 2004) for comparison with Swainson's Thrush data; we also summarized some Wilson's Warbler data not presented by those authors (e.g., nest concealment; see below).

Along each creek we established two nest-searching plots from 4 to 7 ha in size and at least 500 m apart. We searched for and monitored all nests following a standardized protocol (Martin and Geupel 1993). We checked nests every 2 to 4 days and within 2 days prior to the estimated date of fledging. After the young fledged or a nest failed, we measured nest-site characteristics and vegetation surrounding the nest (Martin et al. 1997). The primary cause of nest failure for both thrushes and warblers is predation (Evans Mack and Yong 2000, Michaud et al. 2004), and both species may renest up to three (Swainson's Thrush) or four (Wilson's Warbler) times after nest failure (J. D. White unpubl. data, Ammon and Gilbert 1999). For both species, we estimated percent concealment from 1 m above the nest (by standing or leaning over the nest) and from 1 m on the side from four cardinal directions by visually estimating how much of the nest was covered by leaves or stems (Martin et al. 1997). We averaged the four side-concealment measurements to obtain one estimate for each nest. We also examined whether minimum side concealment differed by comparing minimum concealment from any side. We counted the number of trees, snags (>1.4 m tall), and natural stumps

Table 1 Number and Percentage of Parasitized Swainson's Thrush Nests by Year, Marin Co., California, 1997–2003

Year	Parasitized nests	Total nests	Percentage
1997	1	14	7.1
1998	2	20	9.1
1999	1	16	6.3
2000	0	36	0
2001	1	72	1.4
2002	2	55	3.6
2003	2	11	18.2
All years	9	224	4.0

(<1.4 m tall) within an 11.3-m radius of Swainson's Thrush and Wilson's Warbler nests; trees were sorted into three size classes based on stem diameter (8–23, 23–38, and >38 cm diameter at breast height). We assumed that if the number of trees, snags, and stumps within a set of sites was similar then the number of branches and therefore potential cowbird perches was also similar. Sample sizes for different measurements vary because some measurements were logistically difficult to take (e.g., if a nest fell out of the shrub/nest substrate we did not measure concealment).

We used Swainson's Thrush nests monitored from 1997 to 2003 to determine cowbird-parasitism rates and outcomes of parasitized nests. At each nest, the number of fledglings was based on the number of nestlings at the last nest check prior to the estimated date of fledging. Michaud et al. (2004) reported parallel data for Wilson's Warblers at these sites.

In 2002 and 2003 we experimentally parasitized four thrush nests in four different territories (i.e., different females) with real cowbird eggs; no thrush eggs were removed. We gathered the cowbird eggs from inactive Wilson's Warbler nests on the study sites. We placed cowbird eggs in nests during egg laying; we parasitized three nests that contained three thrush eggs (each had a completed clutch of four thrush eggs), and we parasitized one nest on the day the first thrush egg was laid (completed clutch was three thrush eggs). We watched nests from a distance of approximately 30 m for 45–60 min after artificial parasitism and checked the nest after this observation to confirm that the egg remained (Sealy 1996). We removed parasitic eggs after at least two days because most ejectors remove parasitic eggs within 24 hours (Rothstein 1975, Rich and Rothstein 1985, Sealy 1996).

STATISTICAL ANALYSIS

Using Kruskal–Wallis tests (nonparametric one-way analyses of variance; procedure NPAR1WAY, SAS Institute 1999), we tested for differences between Swainson's Thrush and Wilson's Warbler nests in concealment and tree density by size classes, in number of nearby snags and stumps, and between parasitized and unparasitized nests. We used a sequential Bonferroni adjustment for joint significance for concealment (9 tests) and tree density (15 tests) (Rice 1989). We also used Kruskal–Wallis tests to examine differences between parasitized and unparasitized thrush nests in clutch size and in numbers of nestlings and fledglings, and we used a sequential Bonferroni adjustment for joint significance (3 tests). We used nonparametric tests because residuals were not distributed normally. All results are reported as mean ± standard error (SE).

RESULTS

Only 9 of 224 (4%) thrush nests were parasitized by the Brown-headed Cowbird from 1997 to 2003 (Table 1). Each parasitized thrush nest contained one cowbird egg, but none fledged cowbirds. Four of the nine parasitized nests failed during the egg stage. The cowbird eggs failed to hatch or, in two nests, cowbird nestlings were never observed. In the remaining three nests, the cowbird eggs hatched but the cowbird nestlings disappeared,

whereas the thrush nestlings remained. In the first of these nests, the cowbird nestling was last seen at an age of 7 days, and the nest fledged one thrush. In the second, the cowbird was last seen at an age of 4 days, and three thrush nestlings fledged. In the third, the cowbird nestling was last seen at an age of 7 days, and the nest fledged two thrushes.

Cowbird parasitism significantly reduced the thrush's mean clutch size by 1.23 eggs ($\chi^2_1 = 16.8$, $P < 0.0001$) and significantly reduced the mean number of both nestlings and fledglings by 0.9 after Bonferroni adjustment (nestlings, $\chi^2_1 = 5.1$, $P < 0.05$; fledglings, $\chi^2_1 = 4.1$, $P < 0.05$, Table 2). In two of the nine cases of parasitism, we observed a Swainson's Thrush egg outside of the nest: in one instance the thrush egg was left on the edge of the nest: in the other the egg was on the ground approximately 1 m from the nest. Thrush eggs found outside the nest were not included in clutch-size estimates for parasitized nests.

At the nests parasitized experimentally, all females returned to incubate after we inserted cowbird eggs. The cowbird eggs remained after 45–60 min of observation and as long as 2 days (2 nests) and 3 days (2 nests) before we removed them. In three cases we removed cowbird eggs after clutch completion, and in one case we removed the cowbird egg the day of clutch completion.

Both Swainson's Thrushes and Wilson's Warblers nested in the shrub layer and used similar nest substrates at similar proportions and at similar heights (Table 3). Swainson's Thrush nests ($n = 221$) were significantly more concealed from above ($\chi^2_1 = 31.2$, $P < 0.0001$) and the side (mean side concealment, $\chi^2_1 = 14.5$, $P < 0.0001$; minimum side concealment, $\chi^2_1 = 10.5$, $P > 0.0010$) than Wilson's Warbler nests ($n = 114$) after Bonferroni adjustment (Figure 1). In parasitized ($n = 9$) and unparasitized ($n = 211$) thrush nests concealment from above or the side did not differ (above, $\chi^2_1 = 4.5$, $P < 0.05$; mean side, $\chi^2_1 = 0.8$, $P > 0.25$; minimum side, $\chi^2_1 = 0.3$, $P > 0.60$) after Bonferroni adjustment (Figure 1). Concealment from above or the side of parasitized ($n = 30$) and unparasitized ($n = 83$) warbler nests did not differ either (above, $\chi^2_1 = 0.6$, $P > 0.40$; mean side, $\chi^2_1 = 2.4$, $P > 0.10$; minimum side, $\chi^2_1 = 1.4$, $P > 0.20$, Figure 1).

There were more large trees surrounding Swainson's Thrush nests ($n = 236$) than around Wilson's Warbler nests ($n = 122$; $\chi^2_1 = 11.3$, $P < 0.001$), but there was no difference in the mean number of other potential perches (Figure 2). The mean number of potential perches around parasitized and

Table 2 Clutch Size, Number of Nestlings, and Number of Fledgings in Parasitized and Unparasitized Swainson's Thrush Nests, Marin Co., California, 1997–2003

	Unparasitized nests[a]	*n*	Parasitized nests[a]	*n*
Clutch size	3.5 ± 0.05	184	2.2 ± 0.28	9
Number of nestlings	3.1 ± 0.07	134	2.2 ± 0.37	5
Number of fledglings	3.1 ± 0.10	73	2.2 ± 0.37	5

[a]Mean ± standard error.

Table 3 Heights and Substrates of Swainson's Thrush and Wilson's Warbler Nests, Marin Co., California, 1997–2003

	Swainson's Thrush	Wilson's Warbler[a]
n	234	90
Nest height[b]	61.1 ± 2.6 cm	50.4 ± 2.5 cm
Nest substrate		
Blackberry	46%	68%
Thimbleberry	15%	—
Fern	12%	18%

[a]Data from Michaud et al. (2004).

[b]Mean ± standard error.

unparasitized thrush nests did not differ significantly (Figure 2). The mean number of potential perches around parasitized (n = 30) and unparasitized (n = 82) warbler nests did not differ significantly after Bonferroni adjustment ($\chi^2_1 = 4.7$, $P < 0.05$, Figure 2).

DISCUSSION

The observed parasitism frequency of 4% for this population of Swainson's Thrushes is similar to that reported for the species elsewhere (Evans Mack and Yong 2000). Our low parasitism frequency is surprising given the 33% observed parasitism on the sympatric Wilson's Warblers (Michaud et al. 2004) and the relatively high rates reported for other *Catharus* thrushes (Moskoff 1995, Jones and Donovan 1996) and the Wood Thrush (Roth et al. 1996). Once a nest was parasitized, the intensity of parasitism for the Swainson's Thrush and Wilson's Warbler was similar, with 1 cowbird egg per thrush nest compared to an average of 1.2 ± 0.07 cowbird eggs per warbler nest (Michaud et al. 2004).

At our study sites both Swainson's Thrushes and Wilson's Warblers nested in shrubs, and both species used the same nest substrates in similar proportions (Table 3). Swainson's Thrushes tended to nest slightly higher (~10 cm) than Wilson's Warblers (Table 3). Therefore, nest placement may not be different enough to explain the difference in parasitism rates between these species (Briskie et al. 1990). Nest initiation of both species was largely synchronous with the cowbird's egg laying, so nesting asynchrony does not explain the difference. Nest concealment, however, did differ, particularly from above the nest, and may contribute to the difference in observed parasitism. When the number of potential perches around the hosts' nests differed the difference was in a direction opposite of that expected under the perch-proximity hypothesis (Figure 2).

No cowbird nestlings fledged from thrush nests. It seems unlikely, however, that partial predation could explain cowbird nestling losses because no thrush nestlings disappeared. We suggest that cowbird nestling mortality may be due to the partially frugivorous diet of Swainson's Thrush nestlings. Western populations of the Swainson's Thrush are more frugivorous than eastern populations; Beal (1907) reported that diets of adults in California

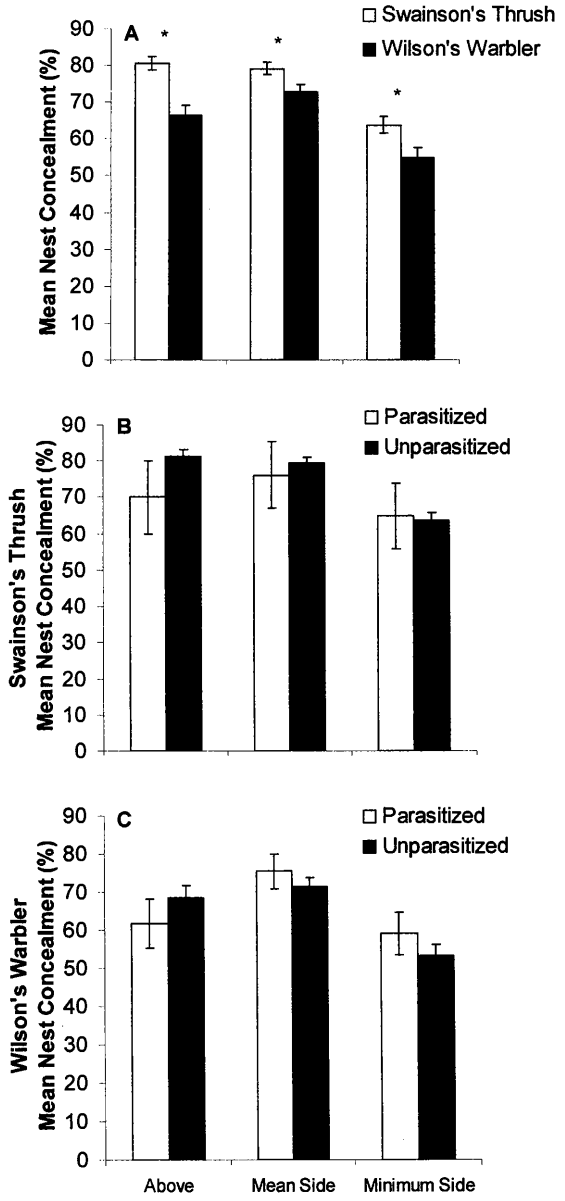

Figure 1. Mean percent concealment from above, and mean and minimum side concealment from four sides, of Swainson's Thrush and Wilson's Warbler nests (A). Mean concealment of parasitized and unparasitized Swainson's Thrush (B) and Wilson's Warbler nests (C), Marin Co., California, 1997–2002. Bars show standard error of mean and minimum percent concealment. Asterisks indicate a significant difference between means after Bonferroni adjustment.

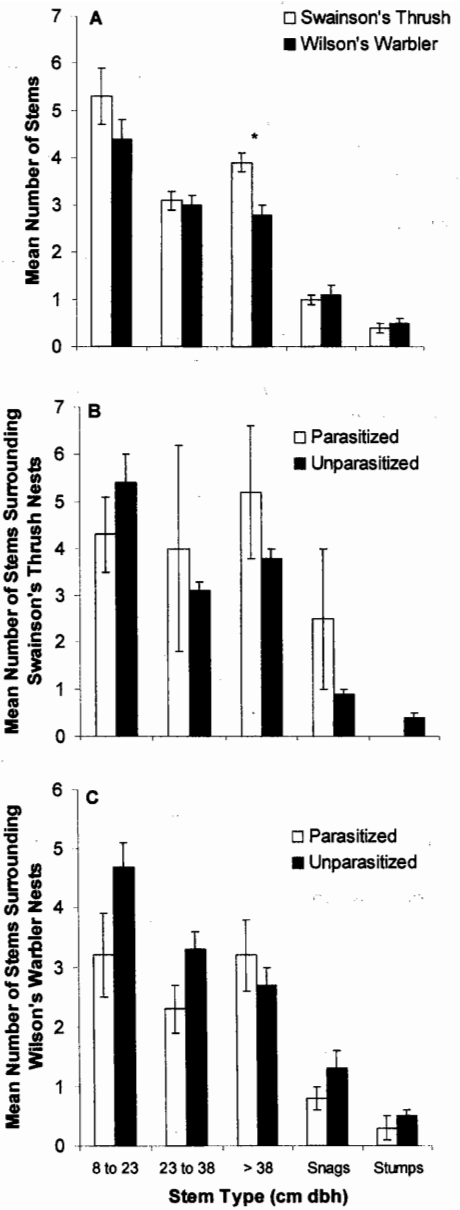

Figure 2. Mean (± standard error) number of stems surrounding Swainson's Thrush and Wilson's Warbler nests (A) and surrounding parasitized and unparasitized Swainson's Thrush (B) and Wilson's Warbler nests (C), Marin Co., California, 1997–2002. Asterisks indicate a significant difference between means after Bonferroni adjustment.

comprise 52% animal and 48% vegetable matter. Although in the thrushes and related families altricial young must be fed insects early in the nestling cycle—for example, before nestling days 3 and 7 for the Cedar Waxwing (*Bombycilla cedrorum*) and Northern Mockingbird (*Mimus polyglottos*), respectively—they may be fed some fruit thereafter (Putnam 1949, Breitwisch et al. 1984). We have observed adults feeding Swainson's Thrush nestlings Red Elderberries (*Sambucus racemosa*), Twinberries (*Lonicera involucrata*), Thimbleberries (*Rubus parviflorus*), and Dogwood berries (*Cornus sericea*). A diet with a fruit component may not be suitable for cowbird nestlings, possibly leading to mortality, as is presumed with cowbird nestlings in Cedar Waxwing nests (Young 1963, Rothstein 1976) and cowbird nestlings fed the granivorous diet of some nestling finches (Middleton 1977, 1991, Kozlovic et al. 1996). Loss of cowbird young early in the nestling period may contribute to a low frequency of observed parasitism when nests are found late in the nestling period.

Our sample of naturally (9) and experimentally (4) parasitized nests was small, but we have no reason to believe that Swainson's Thrushes eject cowbird eggs. If low observed parasitism rates were due to rapid ejection of parasitic eggs then we would expect our experimental eggs to have been ejected immediately or within the first 24 hours of parasitism (Rothstein 1975, Rich and Rothstein 1985). However, experimental parasitic eggs remained in the nest for 2 or 3 days before we removed them. Furthermore, in none of the 13 naturally or experimentally parasitized nests did we observe desertion, which can be an antiparasite response (Hosoi and Rothstein 2000, Strausberger and Burhans 2001). This apparent lack of a rejection response (ejection or desertion) to parasitic eggs is not surprising considering that cowbird parasitism is relatively new to the population we studied and likely to the entire subspecies *Catharus ustulatus oedicus* (Hosoi and Rothstein 2000). Under the evolutionary-lag hypothesis, this thrush may not yet exhibit rejection behavior because the recombinants necessary for the behavior have not yet arisen (Rothstein 1975). Additionally, if parasitic pressure is low it may not elicit antiparasite defenses in the host (Hosoi and Rothstein 2000, Davis et al. 2002). We conclude that Swainson's Thrush accepts cowbird eggs.

Further study is required to determine whether low parasitism frequencies on Swainson's Thrush nests are due to cowbird selectivity, to thrush behavior at the nest, or to some other factor. Currently, there are no data on Swainson's Thrush nest defense or response to cowbirds, nest attendance, or influence of other thrush behavior (e.g., singing rates) on parasitism frequencies. Further study is necessary to quantify the thrush's nestling diet and to establish the effect of a partially frugivorous nestling diet on cowbird nestlings to determine whether difference between the thrush and cowbird in nestling mortality is due to diet. As natural parasitism on Swainson's Thrushes is so infrequent, this could be accomplished by cross-fostering cowbird nestlings into thrush nests and monitoring their health and fate (Mason 1986, Peer and Bollinger 1997).

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