



## Does nesting habitat predict hatch synchrony between brood parasitic brown-headed cowbirds *Molothrus ater* and two host species?

Christopher M. Tonra, Matthew D. Johnson, Sacha K. Heath and Mark E. Hauber

C. M. Tonra ([christopher.tonra@umit.maine.edu](mailto:christopher.tonra@umit.maine.edu)) and M. D. Johnson, Dept of Wildlife, Humboldt State Univ., 1 Harpst St. Arcata, CA 95521, USA. (Present address of C. M. T.: School of Biology and Ecology, 5751 Murray Hall, Univ. of Maine, Orono, ME 04469, USA.) – S. K. Heath, PRBO Conservation Science, 3820 Cypress Dr., #11, Petaluma, CA 94954, USA. – M. E. Hauber, School of Biological Sciences, Univ. of Auckland, 3A Symonds Street, Auckland, PB 92019, New Zealand and Dept of Psychology, Hunter College, CUNY, 695 Park Ave., New York, NY 10065, USA.

Nestling brown-headed cowbirds *Molothrus ater* typically hatch earlier and grow faster than young of the many host species of this generalist obligate brood parasite. However, a cowbird chick also benefits from the presence of some host nest mates as the parasite is provisioned disproportionately more with increasing brood size. Since asynchronous hatching affects both cowbird and host nestlings' growth and survival, mechanisms that optimize the timing of egg-laying by female parasites should be prevalent. Several habitat features might facilitate optimal timing of parasitic egg-laying and we examined whether aspects of host nesting habitat predicted cowbird hatching synchrony. We tested whether synchronous nests were less concealed, closer to perches, and located in areas of higher host density than asynchronous nests using a broad-scale information theoretic approach. There was no support for these predictions regarding song sparrow (*Melospiza melodia*;  $n = 55$ ) or yellow warbler (*Dendroica petechia*;  $n = 67$ ) nests parasitized by brown-headed cowbirds at Mono Lake, USA. For example, the best statistical models for predicting hatching synchrony in yellow warbler nests included nesting-patch width and nest-substrate shrub species. However, these relationships were relatively weak: both synchronous and asynchronous nests were in patches with statistically indistinguishable widths and the two dominant shrub species at our site contained similar proportions of synchronous and asynchronous nests. We conclude that the variability of host nesting habitats does not contribute to a biologically consistent effect on hatching synchrony by this generalist brood parasite.

Hatch asynchrony, or conversely hatch synchrony, in birds refers to the relative timing of when chicks leave their eggs within a clutch. Increased hatching asynchrony impacts the ability of some nestlings to procure resources; specifically, later-hatching young are less able to acquire food compared to earlier-hatching young and often experience higher mortality (Mock and Parker 1997, McMaster and Sealy 1999). Host-parasite hatch synchrony (hereafter: hatch synchrony) is critically relevant for the life history strategies of the generalist obligate brood parasite, the brown-headed cowbird (*Molothrus ater*, hereafter: cowbird) which lays its eggs in other species' nests. Cowbird young typically grow up together with some nestmates (Hauber 2003a). This is in contrast to young of brood parasites that evict their nestmates, including *Cuculus* cuckoos and honeyguides (family Indicatoridae) (Davies 2000).

Accordingly, in natural and experimental broods, earlier hatching by a single cowbird chick reduced both the hatching (Hauber 2003b) and fledging (Hauber 2003a) success of host nestmates. In turn, overall, earlier hatching

imparted fitness benefits for parasite chicks through increased survival (Kilner 2003) and growth rates (Kilner et al. 2004), especially for male hatchlings (Tonra et al. 2008). However, when comparing the survival of parasite chicks across the many host species of the generalist cowbird, Kilner (2003) also found that survival was higher for cowbird chicks in host nests where they were raised together with some (1–2) host young compared to none or many nestmates. Subsequent comparative and experimental tests in eastern phoebes *Sayornis phoebe* confirmed that cowbirds grew faster when sharing the nest with two host young compared to when they were raised alone (Kilner et al. 2004). More chicks in a nest led to greater parental food delivery rates in variety of birds, including both common cowbird hosts and other passerines (Conrad and Robertson 1993, Stoehr et al. 2001, Neuenschwander et al. 2003, Forbes 2007), and cowbirds benefit because they receive disproportionately more food in larger broods (Kilner et al. 2004) as they out-compete the young of smaller hosts for food through more vigorous begging and size differences

(Dearborn 1998, Lichtenstein and Sealy 1998, Hauber 2003b, c).

As a result, cowbirds that hatch too early relative to their host nest mates would reduce the hatching success for nestmates (Hauber 2003b, c) and would monopolize parental feedings (Kilner et al. 2004) to an extent that reduces the number of surviving nest mates and/or the begging intensity of younger, smaller nest mates (Rivers 2007). Conversely, late-hatching cowbirds may be smaller and relatively less vigorous than their nest mates, which may diminish their capacity to monopolize food acquisition and, thus, lead to decreased growth (Lichtenstein 2001). Given these factors, we assumed that for female cowbirds, the optimal breeding strategy would be to time their egg-laying to enable synchronous hatching with hosts.

Several biotic features of cowbird hosts' nesting habitats appear to impact host selection and parasitism rates, presumably through affecting the ability of female cowbirds to locate suitable nests (Lowther 1993). Studies of host nest microhabitat have generally identified three types of variables influencing the likelihood of parasitism in a given nest: perch proximity, concealment, and host density. Support is strongest for the "perch proximity" hypothesis, which predicts that the probability that a nest is parasitized increases with decreasing distance to prominent perches from which cowbirds can scan for nests and/or observe host behavior (Clotfelter 1998, Spautz 1999, Hauber and Russo 2000). Additional studies also found support for the "nest visibility" hypothesis by reporting a negative relationship between the likelihood of nest parasitism and lateral concealment of the nest by vegetation (Spautz 1999, Staab and Morrison 1999). Finally, Tewksbury et al. (1998) found a positive relationship between variability in parasitism rates and breeding densities within three different host species. Generally, at relatively high host densities cowbirds appear to have more opportunities to lay eggs in "appropriate" nests (i.e. of suitable host species, proper nesting stage, etc.; Strausberger and Ashley 1997).

Female brood parasites appear to monitor nesting activity and timing of egg-laying of potential hosts (Sealy et al. 2002). Consequently, if particular features of the hosts' nesting habitats affect the search time and efficiency of cowbirds identifying suitable host nests, the same habitat features may also affect the subsequent timing of egg-laying. Since cowbirds have shorter incubation periods than many hosts (Rahn and Ar 1974, Briskie and Sealy 1990, Hauber 2003a), asynchronous hatching would result if female cowbirds laid their eggs in host nests prior to or early during the incubation period of the host (resulting in early-hatching) or too many days into incubation (resulting in late-hatching).

To understand the impact of biotic aspects of host nest site use upon the competitive ability of cowbird chicks in parasitized broods, we tested the hypothesis that habitat and host community features known to aid nest-searching by female cowbirds also resulted in increased hatch synchrony, defined as hatching on the same day, between host and parasitic young. To this aim, given the patterns discussed above (Clotfelter 1998, Tewksbury et al. 1998, Spautz 1999, Staab and Morrison 1999, Hauber and Russo 2000), we tested specifically the a priori predictions that synchronously hatching nests would be 1) closer to perch sites, 2),

less concealed and 3) located in areas of higher host density than asynchronous nests.

## Methods

### Field work

We conducted this study in 2004 and 2005 in the riparian corridors of three natural tributaries and one anthropogenic watercourse adjoining to Mono Lake (38°1'N, 119°3'W): Lee Vining, Mill, Rush, and Wilson Creeks, respectively, located on the eastern slope of the Sierra Nevada, Mono County, California, USA. Predominant vegetation in the riparian corridors consisted of Woods' rose *Rosa woodsii*, black cottonwood *Populus balsamifera* ssp. *trichocarpa* and willow *Salix* spp. Study plots on these streams were 29.5, 15, 39 and 15 ha respectively and encompassed 2–3 km of stream length each.

Details of the general methods are given in Tonra et al. (2008). In short, we located and monitored song sparrow *Melospiza melodia* and yellow warbler *Dendroica petechia* nests during the 2004 and 2005 breeding seasons (1 May–15 August) using standard methods (Martin and Geupel 1993, Ralph et al. 1993). These two host species represent 93.8 and 90.1% of all parasitized nests in our study in 2004 and 2005, respectively. Other infrequently used hosts were western wood-pewee *Contopus sordidulus*, willow flycatcher *Empidonax traillii*, warbling vireo *Vireo gilvus*, brewers blackbird *Euphagus cyanocephalus*, green-tailed towhee *Pipilo chlorurus*, and spotted towhee *Pipilo maculatus*. Large numbers of red-winged blackbirds *Agelaius phoeniceus* nested on the study plots but no parasitized nests were found in either year of the study. We revisited each nest every 1–4 d to observe nest contents and determine the outcome of each nesting attempt. Nests were monitored in the same fashion in both years with the exception of synchrony estimation. Specifically, in 2005 we visited nests every 1–2 d starting 2 d before the predicted hatch date to ensure accurate determination of hatching sequence. To ascertain hatch synchrony we used either observed hatching sequence, or observed age differences, determined by morphological features of the nestlings (i.e. feather emergence, eye development, size; Baicich and Harrison 1997). Nest checks at the time of hatching were done more frequently to minimize the confounding effects of food availability and/or brood reduction on perceived age differences within the brood. We determined synchrony group membership in 2004 for each cowbird nestling after completion of the field season using field notes which described age differences between cowbird and host young. Field technicians always recorded observations of age and development difference, however they did not visit the nest more often circa hatching (as was done in 2005) as synchrony determination was not yet an objective of the study. As a result, it is possible that the 2004 estimates of synchrony are less precise than those from 2005.

We considered a nest "synchronous" if the first host egg and the first cowbird egg hatched on the same day and we considered a nest "asynchronous" if host or parasite young hatched on different days, or one failed to hatch. As our hypothesis makes the same reduced growth rate prediction

in asynchronous broods, whether due to early (song sparrow: 29% of all nests monitored, yellow warbler: 34%) or late (song sparrow: 24%, yellow warbler: 31%) hatching by the parasite, compared to synchronous broods (song sparrow: 47%, yellow warbler: 35%), we created a combined single asynchrony category. While we do not have quantitative data on baseline hatching asynchrony in unparasitized host nests at our study site, both of these host species typically begin incubation on the day of laying the penultimate egg (Hauber and Pilz 2003) and the vast majority of unparasitized host broods hatched synchronously at Mono Lake (Tonra and Heath unpubl.).

The two nesting species studied here represent two different types of cowbird hosts. Yellow warblers are smaller, have a shorter breeding season, and are frequent cowbird egg rejecters, often burying parasite eggs laid before the first warbler egg (Sealy 1992). Song sparrows are larger and closer in size to cowbirds, have a relatively long breeding season, and are infrequent egg rejecters (Latif et al. 2006).

Only parasitized nests that survived beyond hatching with host eggs present were included in the analysis. This did not bias our results because depredated nests were not influenced by hatching asynchrony since neither host nor parasite survived to hatching. A limited amount of mapping of individually marked adult female cowbirds' space use revealed that each of the study plots were used by several individual parasites, which could reliably be found on defined home-ranges throughout the cowbird breeding season with limited overlap (Tonra unpubl.). Lee Vining Creek, for example, was used regularly by at least 7 female parasites with distinct home ranges in both years of the study. In addition, these efforts revealed that many transient females also occurred on the sites irregularly. Therefore, although an individual female cowbird is physiologically capable of laying as many as 80 eggs within a breeding season (Lowther 1993), we consider our sample to represent the reproductive efforts and egg-laying decisions of many female cowbirds (*sensu* Hauber 2001), and that our data are not skewed by the efforts of few individuals parasitizing the host community in this study.

### Parameter estimates

Nest site vegetation was measured using standard methods (Ralph et al. 1993, Martin et al. 1997, see Supplementary material, Appendix for definitions). All measurements were taken within a 5 m radius centered on the nest, with the exception of: tree data (11.3 m radius), distance to nearest perch, perch species, and perch height. Past research considered perches to be shrubs or trees >2 m in height (Spautz 1999, Hauber and Russo 2000) or trees >8 cm dbh (Averill-Murray et al. 1999). For this study, a perch was defined as any object (all were vegetative with the exception of one telephone poll)  $\geq 5$  m in height upon which a bird could be supported and that was separate from, but within line of sight of, the nest plant. These criteria were chosen because vegetation at the study sites was generally  $\sim 2$  m in height and 5 m represented the typical emergent vegetation (PRBO Conservation Science unpubl. Tonra unpubl.).

To calculate host densities, we first estimated the number of yellow warbler and song sparrow breeding territories using mapping methods described in Robbins (1970) and Ralph et al. (1993). The same biologist visited her/his study plot generally every other day (1 May–15 August) and mapped all territorial activity. For Lee Vining, Mill, Rush, and Wilson Creeks, respectively, territory mapping effort was 402, 235, 484, and 252 h in 2004, and 481, 280, 451, 259 h in 2005. Observations were made of both color-banded and unbanded host individuals as we only color banded hosts in 2005 with 22% of territories having at least one member of the pair color banded for song sparrow, and 17% for yellow warbler. For unbanded individuals, we carefully distinguished individuals from one another by making season-long observations of simultaneous nesting, counter singing, and aggressive interactions. At the end of the field season, daily territory maps were transferred onto a single territory map for each host species at each census plot and number of territories per plot was determined. Final territory maps only included territories for which breeding was confirmed (i.e. nest found, material or food carry, or dependent juveniles observed). For song sparrow and yellow warbler, respectively, we found nests for 67 and 78% of territories in 2004, and 76 and 78% of territories in 2005.

To estimate host density around each nest, we generated a circular buffer in ArcView (ESRI 1999). The buffer radius, 121.71 m, was established by the mean female cowbird home-range size on the study site, determined by averaging the area of minimum convex polygons generated from mapping of individually marked adult female cowbirds (4.63 ha; Tonra unpubl.). The number of song sparrow and yellow warbler territories that were included within the buffer yielded a measure of host density (number of host territories  $\text{ha}^{-1}$ ) for each nest. Although there is some evidence of a positive correlation between host density and hatch synchrony in some brood parasites (Moskat et al. 2006), this is by no means a statistical certainty for all sites and parasite species; therefore including host density in the models was necessary in our analyses.

### Statistical approach

To test the prediction that the best model for predicting synchrony includes distance to cowbird perch, host density, and lateral concealment as independent variables, we used information theoretic model selection approach (Burnham and Anderson 2002). We generated statistical models using logistic regression with the binary response variable as synchronous or asynchronous.

In addition to including the a priori hypothesized habitat variables as described above, we ran stepwise forward and backward logistic regressions with all potentially influential habitat variables in SPSS 11.5 (SPSS 2002) to determine a subset of variables to include in candidate models. In addition to the habitat variables, we included clutch size of host and the number of cowbird eggs in the variable selection routines as possible confounding variables for predicting synchrony. All variables were screened for collinearity and any outliers were removed. We did not include any variables derived from others in models with

Table 1. Model selection results for logistic regression models predicting cowbird hatch synchrony in song sparrow nests at Mono Lake, CA, top ten models presented.

Model <sup>a</sup>	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
host density × year + host density + year + distance to perch	5	75.56	0.00	0.08
YWAR density × year + YWAR density + year + distance to perch	5	75.93	0.36	0.07
host density × year + host density + year + perch height	5	76.26	0.70	0.06
host density × year + host density + year + patch width	5	76.33	0.76	0.06
distance to perch	2	76.47	0.91	0.05
YWAR density × year + YWAR density + year + perch height	5	76.63	1.06	0.05
YWAR density × year + YWAR density + year + patch width	5	76.83	1.26	0.04
host density × year + host density + year	4	76.8	1.30	0.04
YWAR density × year + YWAR density + year	4	77.01	1.44	0.04
host density + distance to perch	3	77.05	1.48	0.04

Note: models ranked by descending corrected Akaike weights (w<sub>i</sub>); k is the number of parameters, AIC<sub>c</sub> is Akaike's information criterion corrected for sample size, and ΔAIC<sub>c</sub> is the change in AIC<sub>c</sub> from the best model. Additive models are indicated by +, multiplicative by ×. <sup>a</sup>YWAR density = density of yellow warbler territories.

the source variables nor any pairs of variables that were multicollinear.

Following variable selection, we generated a posteriori models for each host species. We determined the best model based on corrected Akaike's information criterion (AIC<sub>c</sub>) and the corrected Akaike weight (w<sub>i</sub>) (Burnham and Anderson 2002). Model weights were summed with and without each variable to determine the relative importance of each independent variable.

To determine goodness of fit, we generated a receiver operator characteristic (ROC) curve for the best model, and the area under the curve (AUC) was calculated. This metric provides a measure of model performance independent of classification cut-point. An AUC of 1.0 indicates a perfect fit of the model, while an AUC of 0.5 indicates the model was no better than random chance (Zweig and Campbell 1993, Fielding and Bell 1997, Boyce et al. 2002). When further examining independent variables we used two-sample t-tests to compare means and, when data were non-parametric, Mann-Whitney U-tests to compare.

## Results

We included a total of 55 song sparrow and 67 yellow warbler nests in the analysis. During the two years of the study, similar proportions of song sparrow and yellow warbler nests contained synchronously hatching parasite and host chicks (0.47 and 0.34 respectively; Fisher's exact test, n = 122, p = 0.20). Although multiple parasitism was more prevalent in song sparrow than yellow warbler in our sample, 44 and 27% respectively, the difference was not significant (Fisher's exact test, n = 122, p = 0.058). The proportion of nests parasitized was significantly greater in high density sites (Lee Vining and Rush Creeks) than low

density sites (Mill and Wilson Creek) for all host species' nests monitored in 2004 and 2005 (0.59 and 0.48, respectively; Fisher's exact test, n = 576, p = 0.01).

The best of 41 models for predicting hatch synchrony in song sparrow nests included the variables host density, year, the interaction of host density and year, and distance to cowbird perch (Table 1). However, many of the top models were highly competitive (ΔAIC<sub>c</sub> < 2) and so, based on the corrected Akaike weight, there was only a 9% chance that this specific combination of parameters constituted the best model for predicting hatch synchrony, given the variables and the data. Furthermore, this model was only 1.2 times better than the next best model, which included the territory density of the more common host species (yellow warbler), in the place of the combined host density. Similarly, we found by summing the Akaike weights by variable that models which included year were 1.7 more likely to provide the best fit to the data than models without it. Nests in areas of high host density were more likely to be synchronous in 2004, while the opposite was true in 2005, even though there was no significant difference in the host density between years (Mann-Whitney U-test: Z = -0.59, DF = 53, p = 0.56). No other variable had a positive effect on model weights, and only the coefficient for the interaction of host density and year was significant (Table 2). The area under the ROC curve for the best model was 0.73; therefore regardless of classification cut-point the model was a modest improvement over random chance.

The best of 56 models for predicting hatch synchrony in yellow warbler nests included the variables patch width, nest height, and whether a nest was in *Rosa woodsii* or *Salix* sp. (hereafter rose versus willow), but again several top models were competitive (Table 3). Synchronous nests were more likely to be in larger patches, closer to the ground, and

Table 2. Estimates of parameter coefficients (β) and 95% confidence intervals (95% CI) for the best fitting logistic regression model predicting cowbird hatch synchrony in song sparrow nests and subsequent statistics in Mono County, CA.

Parameter	β	SE	Wald χ <sup>2</sup>	DF	p	95% CI	
constant	2.366	1.926	1.23	1	0.219	-1.409	6.141
distance to perch	1.807	1.184	-1.53	1	0.127	-0.513	4.127
host density	0.079	0.044	1.80	1	0.071	-0.007	0.164
host density × year	0.875	0.412	2.12	1	0.034	0.067	1.684
year	-1.468	0.656	-2.24	1	0.025	-2.754	-0.181

Table 3. Model selection results for logistic regression models predicting cowbird hatch synchrony in yellow warbler nests at Mono Lake, CA, top 10 models presented.

Model	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
nest height+rose vs willow <sup>a</sup> +patch width	4	84.78	0.00	0.11
rose vs willow <sup>a</sup> +patch width	3	85.20	0.42	0.09
patch width	2	85.60	0.82	0.07
patch area+rose vs willow <sup>a</sup>	3	85.81	1.02	0.06
patch width+rose vs willow <sup>a</sup> +distance to edge	4	86.08	1.30	0.06
host clutch size+rose vs willow <sup>a</sup> +patch width	4	86.37	1.58	0.05
patch width+host clutch size	3	86.68	1.80	0.04
patch width+number cowbird eggs	3	86.76	1.97	0.04
rose vs willow <sup>a</sup> +patch area+distance to edge	3	87.04	2.26	0.03
patch width+nest height	3	87.07	2.29	0.03

<sup>a</sup>whether a nest was in *R. woodsii* (rose) or *Salix* sp. (willow).

Note: models ranked by descending corrected Akaike weights (w<sub>i</sub>); k is the number of parameters, AIC<sub>c</sub> is Akaike's information criterion corrected for sample size, and ΔAIC<sub>c</sub> is the change in AIC<sub>c</sub> from the best model.

located in willow. Patch width was the only variable that had a positive effect on model weight, with models including it being two times more likely to provide the best fit to the data than models without it. Although the coefficients for patch width and rose vs willow were significant (Table 4), a paired t-test on patch width, after a log-transformation to normalize the distribution, revealed that synchronous nests were in patches not significantly wider than asynchronous nests (t<sub>65</sub> = 1.97, p = 0.053) and a contingency analysis with rose vs willow and the synchrony category did not reveal significant effects (χ<sup>2</sup> = 1.6, n = 67, p = 0.21).

Neither the coefficient (Table 4), nor the difference in the log-transformed means was significant for the height of nest between synchrony categories (t<sub>65</sub> = 0.21, p = 0.83). The area under the ROC curve for the best model was 0.74. Therefore, regardless of classification cut-point, the model was a modest improvement on random chance. Nevertheless, the number of cowbird eggs per nest was correlated with the variable rose versus willow, with nests in rose significantly less likely to have more than one cowbird egg (χ<sup>2</sup> = 5.69, n = 67, p = 0.017).

## Discussion

Our results did not support the hypothesis that biotic features of hosts' nesting habitat influenced the hatch synchrony of cowbirds with host chicks. The most parsimonious model for predicting hatch synchrony in song sparrow nests included two known variables associated with female cowbirds' use of habitat cues to find host nests and hypothesized to be predictors of hatch synchrony: host density and distance to cowbird perch. Yet, the variable that had the strongest contribution to model weight was year of

observations. This was because the direction of effect of host density on hatch synchrony actually reversed between the two years of the study. This pattern was present despite the lack of significant difference in host density between years and provides no statistical evidence for a consistent relationship of host density with cowbird hatch synchrony. As this study was fully observational on nest use by cowbirds (Clotfelter 1998, Hauber and Russo 2000), unmeasured confounding variables, including individual parasites' behavioral changes in host nest use, or inter-annual differences in cowbird host use owing to the switch in the identity of the local parasite females from year to year are possible explanations for the significant year effect on host-parasite hatch synchrony.

The width of the vegetation patch and the nest plant species (rose versus willow) were the only biotic variables that had a positive effect on model weights in either of the two host species examined in this study, and in both cases only in yellow warbler. Budnick et al. (2002) found a positive relationship between patch width and both the likelihood of cowbird parasitism as well as nest predation in Bell's vireos *Vireo bellii*. Though narrow patches may at first appear more easily "searchable," neither our measures of patch area nor variables measured within the patch (e.g. nest distance to edge, maximum patch height) had positive effects on model weights. Thus, the mechanisms relating patch width and the likelihood of parasitism and hatch synchrony remain to be uncovered.

The results of this study do not imply that nest placement is inconsequential to cowbird productivity. For example, we did not take into account host behavior (Smith 1981, Sealy et al. 2000, Tewksbury et al. 2002, Garamszegi and Aviles 2005), host quality (Hauber 2001), parasite age (White et al. 2007), competition between cowbirds (McClaren and Sealy 2000, Jensen and Cully 2005) and

Table 4. Estimates of parameter coefficients (β) and 95% confidence intervals (95% CI) for the best fitting logistic regression model predicting cowbird hatch synchrony in yellow warbler nests and subsequent statistics in Mono County, CA.

Parameter	β	SE	Wald χ <sup>2</sup>	DF	p	95% CI	
constant	-1.890	0.821	2.30	1	0.021	0.281	3.499
patch width	0.149	0.060	-2.48	1	0.013	-0.267	-0.032
nest height	-0.006	0.004	1.53	1	0.125	-0.002	0.014
rose vs willow <sup>a</sup>	1.519	0.765	-1.99	1	0.047	-3.019	-0.020

<sup>a</sup>whether a nest was in *R. woodsii* (rose) or *Salix* sp. (willow).

rates of nest predation (Hauber 2000), including predation by cowbirds as means of inducing re-nesting of host pairs (Arcese et al. 1996, McClaren and Sealy 2000, Hoover and Robinson 2007). The timing of egg-laying can be perhaps more accurately monitored by a parasite in a forced re-nest attempt, which could reduce the parasite's loss of reproductive investment into eggs that are unlikely to hatch or to produce healthy, competitive cowbird young due to suboptimal timing, relative to the host nesting cycle. Alternatively, the effects of host nest placement on cowbird productivity may be realized at the gross level of nest detection and subsequent parasitism (Clotfelter 1998, Hauber and Russo 2000), rather than at the finer level of well-timed egg-laying events and the resulting variation in hatch synchrony among micro-habitats (examined in our study). Explanations other than habitat-influenced detectability of the nests of hosts and the resulting habitat specific variation in parasitism rate remain to be tested. For example, cowbirds may be selective in choosing host nests based on habitat that maximizes the sex-specific growth and survival probabilities of their offspring (Tonra et al. 2008), thereby minimizing resource loss to eggs with little or no chance of surviving to fledging.

*Acknowledgements* – We thank the many fine PRBO biologists, too numerous to name here, who assisted in collecting field data. Their names can be viewed at <www.prbo.org/easternsierra>. M. A. Colwell and T. L. George were instrumental in the completion and design of this study. D. Banta and D. Marquart generously allowed us to capture birds on their property. Financial support was provided by the Bureau of Land Management, Humboldt State Univ. Foundation, Inyo National Forest, the Marin Rod and Gun Club, the Miller Inst. for Basic Research in Science at UC Berkeley, the Mono Basin Bird Chautauqua Grant, Mono Lake Committee, Mono Market, the New Zealand Marsden Fund, UARC, PRBO bird-a-thon participants, and U.S. Forest Service Region 5 Partners in Flight. We thank G. Ballard and Q. S. Latif for discussions and field work, and three anonymous reviewers who provided comments on an earlier version of this manuscript. This is PRBO contribution no. 1644.

## References

- Arcese, P. et al. 1996. Nest predation by cowbirds and its consequences for passerine demography. – *Proc. Nat. Acad. Sci. USA* 93: 4608–4611.
- Averill-Murray, A. et al. 1999. Cowbird parasitism of Arizona bell's vireos (*Vireo bellii arizonae*) in a desert riparian: implications for cowbird management and riparian restoration. – *Stud. Avian Biol.* 18: 109–120.
- Baicich, P. J. and Harrison, J. O. 1997. A guide to the nests, eggs, and nestlings of North American birds. – Academic Press.
- Boyce, M. S. et al. 2002. Evaluating resource selection functions. – *Ecol. Model.* 157: 281–300.
- Briskie, J. V. and Sealy, S. G. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. – *Auk* 107: 789–794.
- Budnick, J. M. et al. 2002. Effect of habitat characteristics on the probability of parasitism and predation of Bell's vireo nests. – *J. Wildl. Manage.* 66: 232–239.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and inference: a practical information theoretic approach, 2nd ed. – Springer.
- Clotfelter, E. D. 1998. What cues do brown-headed cowbirds use to locate red-winged blackbird host nests? – *Anim. Behav.* 55: 1181–1189.
- Conrad, K. F. and Robertson, R. J. 1993. Patterns of parental provisioning by eastern phoebes. – *Condor* 95: 57–62.
- Davies, N. B. 2000. Cuckoos, cowbirds, and other cheats. – T. and A. D. Poyser.
- Dearborn, C. D. et al. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. – *Condor* 100: 326–334.
- ESRI 1999. ArcView, ver. 3.2. – Environmental Systems Research Inst., Redlands, CA, USA.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – *Environ. Conserv.* 24: 38–49.
- Forbes, S. 2007. Sibling symbiosis in nestling birds. – *Auk* 124: 1–10.
- Garamszegi, L. Z. and Aviles, J. M. 2005. Brood parasitism by brown-headed cowbirds and the expression of sexual characters in their hosts. – *Oecologia* 143: 167–177.
- Hauber, M. E. 2000. Nest predation and cowbird parasitism in song sparrows. – *J. Field Ornithol.* 71: 389–398.
- Hauber, M. E. 2001. Site selection and repeatability in brown-headed cowbird (*Molothrus ater*) parasitism of eastern phoebe (*Sayornis phoebe*) nests. – *Can. J. Zool.* 79: 1518–1523.
- Hauber, M. E. 2003a. Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. – *Behav. Ecol.* 14: 227–235.
- Hauber, M. E. 2003b. Egg-capping is a cost paid by hosts of interspecific brood parasites. – *Auk* 120: 860–865.
- Hauber, M. E. 2003c. Lower begging responsiveness of host vs cowbird nestlings is related to species identity but not to early social experience in parasitized broods. – *J. Comp. Psychol.* 117: 24–30.
- Hauber, M. E. and Russo, S. A. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting song sparrows. – *Wilson Bull.* 112: 150–153.
- Hauber, M. E. and Pilz, K. M. 2003. Yolk testosterone levels are not consistently higher in the eggs of obligate brood parasites than their hosts. – *Am. Midl. Nat.* 149: 354–362.
- Hoover, J. P. and Robinson, S. K. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. – *Proc. Nat. Acad. Sci. USA* 104: 4479–4483.
- Jensen, W. E. and Cully Jr, J. F. 2005. Density-dependent habitat selection by brown-headed cowbirds (*Molothrus ater*) in tallgrass prairie. – *Oecologia* 142: 136–149.
- Kilner, R. M. 2003. How selfish is a cowbird nestling? – *Anim. Behav.* 66: 569–576.
- Kilner, R. M. et al. 2004. Brood parasitic cowbird nestlings use host young to procure resources. – *Science* 305: 877–879.
- Latif, Q. et al. 2006. First evidence of conspecific brood parasitism in song sparrows accompanied by egg ejection and discussion of methods sufficient to document these behaviors. – *Condor* 108: 452–458.
- Lichtenstein, G. 2001. Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick–chick competition or parental discrimination? – *Anim. Behav.* 61: 401–413.
- Lichtenstein, G. and Sealy, S. G. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. – *Proc. R. Soc. B* 265: 249–254.
- Lowther, P. E. 1993. Brown-headed cowbird. – In: Poole, A. and Gill, F. (eds), *The birds of North America*, no. 47. Academy of Natural Sciences and American Ornithologists' Union, pp. 1–24.
- Martin, T. E. and Geupel, G. R. 1993. Nest monitoring plots: methods for locating nests and monitoring success. – *J. Field Ornithol.* 64: 507–519.

- Martin, T. E. et al. 1997. The breeding biology and monitoring database (BBIRD) field protocol. – Univ. of Montana Coop. Unit, unpubl. manual.
- McClaren, C. M. and Sealy, S. G. 2000. Are nest predation and brood parasitism correlated in yellow warblers? A test of the cowbird predation hypothesis. – *Auk* 117: 1056–1060.
- McMaster, D. G. and Sealy, S. G. 1999. Do brown-headed cowbird hatchlings alter adult yellow warbler behavior during the hatching period? – *J. Field Ornithol.* 70: 365–373.
- Mock, D. W. and Parker, G. A. 1997. The evolution of sibling rivalry. – Oxford Univ. Press.
- Moskát, C. et al. 2006. High synchrony of egg laying in common cuckoos (*Cuculus canorus*) and their great reed warbler (*Acrocephalus arundinaceus*) hosts. – *Ethol. Ecol. Evol.* 18: 159–167.
- Neuenschwander, S. et al. 2003. Brood size, sibling competition, and the costs of begging in great tits (*Parus major*). – *Behav. Ecol.* 14: 457–462.
- Rahn, H. and Ar, A. 1974. The avian egg: incubation time and water loss. – *Condor* 76: 147–152.
- Ralph, C. J. et al. 1993. Field methods for monitoring landbirds. – USDA Forest Service Publ.: PSW-GTR 144, Albany, CA.
- Rivers, J. W. 2007. Nestmate size, but not short-term need, influences the begging behavior of a generalist brood parasite. – *Behav. Ecol.* 18: 222–230.
- Robbins, C. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. – *Audubon Field Not.* 24: 722–726.
- Sealy, S. G. 1992. Removal of yellow warbler eggs in association with cowbird parasitism. – *Condor* 94: 40–54.
- Sealy, S. G. et al. 2000. Yellow warbler nest attentiveness before sunrise: antiparasite strategy or onset of incubation? – In: Smith, J. N. M. et al. (eds), *Ecology and management of cowbirds and their hosts: studies in the conservation of North American passerine birds*. Univ. of Texas Press, pp. 169–177.
- Sealy, S. G. et al. 2002. Tactics of obligate brood parasites to secure adequate incubators. – In: Deeming, D. C. (ed.), *Avian incubation: behaviour, environment, and evolution*. Oxford Univ. Press, pp. 254–269.
- Smith, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. – *Condor* 83: 152–161.
- Spautz, H. 1999. Common yellowthroat brood parasitism and nest success vary with host density and site characteristics. – *Stud. Avian Biol.* 18: 218–228.
- SPSS 2002. SPSS for Windows, ver. 11.5. – SPSS Inst., Chicago, IL, USA.
- Staab, C. A. and Morrison, M. L. 1999. Managing riparian vegetation to control cowbirds. – *Stud. Avian Biol.* 18: 18–22.
- Stoehr, A. M. et al. 2001. Parental care in relation to brood size in the house finch. – *J. Field Ornithol.* 72: 412–418.
- Strausberger, B. M. and Ashley, M. V. 1997. Community-wide patterns of parasitism of a host “generalist” brood-parasitic cowbird. – *Oecologia* 112: 254–262.
- Tewksbury, J. J. et al. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. – *Ecology* 79: 2890–2903.
- Tewksbury, J. J. et al. 2002. Parental care of a cowbird host: caught between the costs of egg-removal and nest predation. – *Proc. R. Soc. B* 269: 423–429.
- Tonra, C. M. et al. 2008. Ecological correlates and sex differences in early development of a generalist brood parasite. – *Auk* 125: 205–213.
- White, D. J. et al. 2007. An experimental test of preferences for nest contents in an obligate brood parasite, *Molothrus ater*. – *Behav. Ecol.* 18: 922–928.
- Zweig, M. H. and Campbell, G. 1993. Receiver operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. – *Clin. Med.* 39: 561–577.

Download the Supplementary material as file E5736 from  
<[www.oikos.ekol.lu.se/appendix](http://www.oikos.ekol.lu.se/appendix)>.