HABITAT AS A PREDICTOR OF HATCH SYNCHRONY IN THE BROWN-HEADED COWBIRD

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INTRODUCTION

Offspring of the brown-headed cowbird (*Molothrus ater*), an obligate brood parasite, appear to grow and survive better when sharing the nest with one or two young of their host species. This is due to the combination of a greater feeding rates delivered to nests containing more young and the disproportionately greater success of cowbirds chicks v. host chicks at receiving feeds (Kilner 2003, Kilner et al. 2004). Taking this into consideration, one would expect that a parasitism strategy by female cowbirds that favors the survival of some host young along with their own would in turn have a positive effect on the parasites' fitness. Since more asynchronous hatching decreases both cowbird fledging success (Kilner 2003) and host hatching and fledging success (Hauber 2003a,b), one mechanism that might enhance the survival of host and cowbird young would be optimal timing of egg laying by cowbirds such that the chances of hatching failure or nestling mortality for both host and parasite young are reduced. We hypothesize that features of cowbird habitat that facilitate optimal timing of egg laying will increase hatching synchrony (defined as hatching on the same day) between host and parasitic young and, ultimately, lead to greater cowbird fitness.

Unlike the majority of obligate brood parasites, such as *Cuculus* cuckoos, cowbird nestlings do not generally attack or eject host young (Davies 2000). When comparing the non-predation mortality rates among host species of the generalist brown-headed cowbird, Kilner (2003) found that mortality was lowest for chicks in host nests where they were accompanied by one or two host young, as compared to those that were alone. When experimentally examining this phenomenon in Eastern Phoebes (*Sayornis phoebe*), Kilner et al. (2004) discovered that cowbirds develop faster when sharing the nest with two host young than when they are alone. A greater number of young in a nest increases the overall feeding rate (Conrad and Robertson 1993, Stoehr et al. 2001, Nevenschwander et al. 2003) and cowbirds are able to out-compete host young for feeds through more vigorous begging and larger size (Dearborn 1998, Lichtenstein and Sealy 1999). By exploiting this relationship, the cowbird chick is able to use its nest mates to procure more resources from the host parents. One may postulate from this that in addition to the presence of nest mates, the vigor of those nest mates may also impact the ability of the cowbird to procure resources, in that more vigorous nest mates will attract more feeds to the nest than less vigorous (i.e. late hatching) nest mates.

Hatch synchrony has been shown to impact the ability of nestlings to procure resources; specifically late hatching young are not as capable at acquiring food as earlier-hatching young and often experience higher mortality (Mock and Parker 1997, McMaster and Sealy 1999). In the case of brown-headed cowbirds Hauber (2003a) found that earlier hatching by a single cowbird chick results in decreased hatching and fledging success of host young, to an even greater degree than when conspecifics hatch early. Given these factors, one would expect that cowbirds in more synchronous nests will develop at a greater rate than in those that are more asynchronous as a result of reduction in nest mates and/or begging intensity of nest mates, or decreased competitive ability of late hatching cowbirds (Hauber 2003a, Kilner 2003).

Several features of cowbird habitat have been shown to impact parasitism rate presumably by impacting the ability of female cowbirds to locate nests. Studies of nest micro-habitat have generally identified three habitat variables important for parasitism rate: perch proximity, concealment, and host density. Several researchers have found support for the 'perch proximity' hypothesis which predicts that the probability a nest is parasitized increases with decreasing distance to prominent perches from which cowbirds can scan for nests and/or observe host behavior (e.g. Clotfelter 1998, Spautz 1999, Hauber and Russo 2000). Several studies have found a negative relationship between likelihood of parasitism and lateral concealment of the nest (Staab and Morrison 1999, Spautz 1999). Tewksbury et al. (1998) found a positive relationship between parasitism rate and density of three different host species. At higher host densities it is likely that cowbirds have more opportunities to lay eggs in appropriate (i.e. viable host, proper nesting stage) nests.

Brood parasites are known to monitor nesting activity of hosts prior to laying (reviewed in Sealy et al. 2002). If habitat affects the search time of cowbirds searching for nests one would expect it to also affect the subsequent timing of egg laying. Cowbirds will have limited information regarding nests that are not located relatively early in the host nesting cycle, specifically the point at which incubation was initiated. Since cowbirds have shorter incubation periods than many hosts (Hauber 2003a) they would need to lay their eggs a certain number of days after the initiation of incubation to ensure synchrony. Therefore, asynchrony would result if nests receive eggs at non-optimal times, i.e. too early relative to the incubation period of the host such that the cowbird hatches too early or too late such that the cowbird hatches late. Small size and decreased begging intensity of either the host young or the cowbird, as a result of asynchronous hatching, could result in fewer feeds to the nest and/or fewer feeds to the cowbird. Additionally, total host hatching failure due to asynchrony can reduce resources brought to the cowbird (Kilner et al. 2004) and hatching failure of the cowbird due to asynchrony has obvious fitness costs.

In this study we begin to address these phenomena by asking the question: Is habitat a good predictor of brown-headed cowbird hatch synchrony? We test the hypothesis that synchronous nests will be less concealed, closer to perches, and located in areas of higher host density than asynchronous nests in two host species; song sparrow (*Melospiza melodia*) and yellow warbler (*Dendroica petechia*). This study will lay the groundwork for ultimately asking the question: Does host habitat indirectly influence cowbird fitness?

STUDY SITE

This study was conducted in the riparian corridors of four tributaries to Mono Lake (320,000mE 4,210,000mN): Lee Vining, Mill, Rush, and Wilson Creeks, located on the east slope of the Sierra Nevada, CA, USA. Predominant vegetation in the riparian corridor now consists of wild rose (Rosa woodsii), black cottonwood (Populus trichocarpa) and willow (Salix spp.) (Heath et al. 2003). Heath et al. (2003) provided a detailed description of this study's eight nest searching plots (2 per creek) which have been intensively nest searched and monitored since 2000.

METHODS

During the 2004 breeding season we located and monitored song sparrow and yellow warbler nests on the study plots using standard methods (Martin and Geupel 1993, Ralph et al. 1993). Each nest found was revisited at least every four days to determine outcome/contents. Hatch synchrony was determined by either observed age differences, determined by morphological features (i.e. feather characters, eyes, size) in the nestlings or observed hatching sequence. A nest was considered synchronous if the first host egg and the first cowbird egg hatched on the same day; all nests where either host or parasite hatched before the other or one failed to hatch were considered asynchronous. Based on published incubation periods (10.5 days for cowbird, 13 days for song sparrow, and 11 days for yellow warbler) (summarized in Hauber 2003a) this would assume that optimal laying time, in terms of synchrony, would be day 3 or 4 of incubation for song sparrow and day 1 or 2 for yellow warbler. Only parasitized nests that survived beyond hatching with host eggs present were included in the analysis. We do not believe this biases results since predated nests do not incur the costs/benefits of hatching asynchrony since neither host nor parasite survives to hatching.

Nest site vegetation was measured using standard methods (Ralph et al. 1993, Martin et al. 1997). See Appendix A for a list of characteristics measured. All measurements were taken at the vegetation patch containing the nest and within a 5m radius centered at the nest, with the exception of: tree data (11.3m radius), distance to nearest perch, perch species and perch height. Past research has considered perches to be shrubs or trees >2m in height (Spautz 1999, Hauber and Russo 2000) or trees >8cm dbh (Averill-Murray et al. 1999). For this study, a perch was defined as any object (floral or anthropogenic), within line of sight of the nest patch, upon which a bird could reasonably perch, that was separate from the nest patch and at least 5m in height. Vegetation at the study sites was generally ~2m average height and 5m represented the typical emergent vegetation (PRBO unpublished data, personal observation). These criteria were corroborated by field observations of female cowbirds repeatedly using perches of these dimensions on the study plots; therefore we believe these criteria adequately characterized an elevated position from which a bird could search for activity at nest sites.

In order to calculate host densities, host territories were mapped with standard spot mapping methods (Ralph et al. 1993). ArcView (ESRI inc.1996) was used to generate a circular buffer around each individual nest. The buffer size was determined by the mean female cowbird home-range size on the study site (4.63ha) (Tonra unpublished data). The number of territories for two host species (song sparrow and yellow warbler) that were included within the buffer was counted to generate a measure of host density (number of host territories/ha) for each nest. Although there are several other potential host species on the plot they are very rarely parasitized and comprise <10% of potential host territories (PRBO data), therefore those species were not included in measures of host density.

ANALYSIS

Information theoretic model selection was used to test the prediction that the best model for predicting synchrony would include distance to cowbird perch, host density, and lateral concealment as independent variables (Burnham and Anderson 2002). Models were generated using logistic regression with the binary response variable as synchronous or asynchronous.

In addition to including the *a priori* hypothesized habitat variables, stepwise forward and backward logistic regressions were run in NCSS (Hintz 2001) with all potentially influential habitat variables to determine a subset of variables to include in candidate models. In addition to the habitat variables, I included clutch size and number of cowbird eggs in the variable selection routines as possible confounding variables for predicting synchrony. This resulted in a subset of 7 variables for song sparrow and 8 for yellow warbler.

Following variable selection, I generated 30 *a posteriori* models for each species. Each model was executed in SPSS 11.5 (SPSS Inc. 2002). The best model was determined based on corrected Akaike's Information Criterion (AIC_c) and the corrected Akaike weight (w_i) (Burnham and Anderson 2002). Model averaging was then performed to determine the relative importance of each independent variable.

To determine goodness of fit a Receiver Operator Response (ROC) curve was generated for the best model, and the area under the curve (AUC) was calculated. Regardless 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).

We examined the predictive performance of each model using confusion matrices (Fielding and Bell 1997). Since the purpose of this analysis was to build a model to reveal important ecological variables rather than make future quantitative predictions, I used all data to build the model rather than reserve a subset for model evaluation (see Fielding and Bell 1997). Since, both false positive and false negative classification errors were considered of equal importance, the optimum classification cut-point was determined by the simultaneous maximum of both sensitivity and specificity. The resulting matrix was then used to determine correct classification rate, false negative rate, false positive rate, and kappa. Kappa measured the improvement of the model over random chance, where values of <0.4 are poor, values between 0.4 and 0.75 are good, and values >0.75 are excellent (Fielding and Bell 1997, Boyce et al. 2002).

Lastly, to test the assumption that nestling condition will vary according to synchrony, we examined the hatching and fledging rates of host eggs and young in synchronous vs. asynchronous nests in both species using two sample t-tests. For both species we compared percent eggs to hatch and percent eggs to fledge between the two asynchrony groups. This analysis excluded those nests that failed due to predation. For this reason there was insufficient sample size to perform the same analysis on cowbird eggs.

RESULTS

A total of 28 song sparrow and 37 yellow warbler nests were included in the analysis. . Fifty-four percent of the song sparrow nests were synchronous compared to 30% in yellow warbler (Fig. 1).

SONG SPARROW

The best model for predicting hatch synchrony in song sparrow nests included the variables: host density, distance to nearest cowbird perch, and height of the nearest cowbird perch (Table 1). Neither potential confounding variable for predicting asynchrony (i.e. clutch size, number of cowbird eggs) was chosen by the variable selection routines. The variables selected by the stepwise logistic regression are found in Table 2. Based on the corrected Akaike weight there was a 41% chance that this was the best model for predicting hatch synchrony, given the variables and the data. This model was only 1.13 times better than the next best model which included the above variables and the interaction between perch height and distance to perch. Model averaging demonstrated that host density was by far the most important variable, followed by distance to perch, then perch height (Table 2). Examination of the coefficients of these variables revealed that synchronous nests were found at greater host densities, closer to perches, and had shorter perches nearby than asynchronous nests (Table 3).

The area under the ROC curve for the best model (Fig. 2) was 0.96; therefore regardless of classification cut-point the model was an extreme improvement on random chance. Examination of specificity and sensitivity values resulted in an optimum classification cut-point of 0.56. The resulting confusion matrix and accuracy measures are reported in Table 4.

The mean percentage of song sparrow eggs to hatch in synchronous nests was greater than in asynchronous nests (78.6% and 59.6% respectively) but not significantly so ($n = 28$, $t = -1.55$, $p > 0.10$). This pattern held for mean percentage of eggs to survive to fledging; 65.0% in synchronous nests and 50.8% in asynchronous ($n = 20$, $t = -0.907$, $p > 0.30$).

YELLOW WARBLER

The best model for predicting hatch synchrony in yellow warbler nests included the variables; clump width, distance to edge of clump, and rose vs. willow (Table 5). Neither potential confounding variable for predicting asynchrony (i.e. clutch size, number of cowbird eggs) was chosen by the variable selection routines. The variables selected by the stepwise logistic regression are found in Table 6. Based on the corrected Akaike weight there was a 49% chance that this is the best model for predicting hatch synchrony, given the variables and the data. This model was 1.69 times better than the next best model which did not include rose vs. willow. Model averaging demonstrated that clump width was by far the most important variable, followed by distance to edge of clump and then rose vs. willow (Table6). Examination of the coefficients of these variables revealed that synchronous nests were in larger clumps, closer to the edges of clumps, and were more likely to be in rose than asynchronous nests (Table 7).

The area under the ROC curve for the best model (Fig. 3) was 0.89; therefore regardless of classification cut-point the model was a sizeable improvement on random chance. Examination of specificity and sensitivity values resulted in an optimum classification cut-point of 0.23. The resulting confusion matrix and accuracy measures are reported in Table 8.

The mean percentage of yellow warbler eggs to hatch in synchronous nests was greater than in asynchronous nests (66.7% and 43.9% respectively) but not significantly so ($n = 37$, $t = -1.92$, $p = 0.06$). This pattern held for mean percentage of eggs to survive to fledging; 62.9% in synchronous nests and 28.7% in asynchronous, this difference was significant ($n = 18$, $t = -2.39$, $p < 0.05$).

DISCUSSION

This study demonstrates that habitat variables can be reliable predictors of hatch synchrony in the brown-headed cowbird. Although the predictive variables were completely different between the two host species examined, in both cases highly accurate models were generated. This provides evidence for the idea that habitat can influence the ability of cowbirds to accurately time egg laying. This is especially intriguing, considering that these results could potentially imply that host habitat and nest site use and selection may influence cowbird fitness.

The fact that the variables to predict synchrony were so different for the two host species is not surprising considering the differences in these two hosts' life histories. Song sparrows are a predominantly ground nesting, cryptic species that forages generally in low dense vegetation (Arcese et al. 2002, personal observation, PRBO unpublished data). Yellow warblers by contrast generally nest between 0.5 and 2m high on our study sites and are substantially more conspicuous in their habits (i.e. foraging higher in vegetation, more conspicuous plumage) (Lowther et al. 1999, personal observation, PRBO unpublished data). Since cowbirds rely on observing host behavior to locate nests (Clotfelter 1999) these differences in observability between species could result in different habitat features aiding cowbirds in locating nests promptly.

In addition there was a considerable difference between the hosts in the proportion of nests that were synchronous. This could very likely due to the difference in incubation times. If cowbirds need to confirm that incubation has been initiated, they have more of an opportunity to do so in song sparrow nests. Cowbirds essentially have a buffer of 2-3 days to determine if song sparrows have finished laying, while they only have one day at best for yellow warbler. Therefore the costs of delaying egg laying is much higher in yellow warbler because there is a greater risk of the cowbird hatching late or failing to hatch by waiting too long. In other words, if a cowbird finds a nest with a possible complete clutch it can afford to wait an additional day to confirm this in song sparrow, however it may not be worth the risk to wait the extra day in yellow warbler which may cause more early hatching cowbirds in that species. This is of course only speculation of one potential mechanism for asynchrony in these species.

SONG SPARROW

The song sparrow model included two of the variables hypothesized as predictors of hatch synchrony; host density and distance to cowbird perch. As breeding densities increase territory sizes decrease in many species including song sparrow (Knapton and Krebs 1974). Cowbirds will likely have more opportunities to observe host behavior if such behavior is constrained to a smaller area. For this reason it seems logical that cowbird search time would decrease in high density areas, leading to enhanced oppurtunities for synchronized hatching. However, Spautz (1999) observed a negative relationship between density and parasitism rate in common yellowthroat (*Geothlypis trichas*), possibly due to alarm calling by conspecifics alerting neighbors of a cowbirds presence. In contrast, Clotfelter (1998) found that female cowbirds may use host alarm calls to locate nests in red-winged blackbirds. Such relationships between host behavior and parasitism have not been documented among the song sparrows in the study population however. Alternatively, negative relationships with density may be indicative of a "swamping" of resources (i.e. available nests) for cowbirds (Freeman 1990), given that they are territorial and may have limited number of eggs to lay per season (Hahn et al. 1999, Wolfenden et al. 2003) and may not necessarily be indicative of a hindrance on the searching behavior of cowbirds.

Cowbirds are likely to utilize adult activity as a cue for locating nests (Norman and Robertson 1975, Clotfelter 1999, Robinson and Robinson 2001). Given this one would expect that any habitat feature that increases observability should enhance the ability of cowbirds in locating nests more rapidly, especially for a ground nesting species like the song sparrow which will generally be active in low dense vegetation. Elevated perches are likely to increase visibility of host parents activities while allowing the cowbird to remain still and possibly decrease the chances of being detected. Similar to this study Freeman et al. (1990) found that cowbirds were less successful at synchronizing their egg laying with red-winged blackbirds in marshes that lacked trees as opposed to those with trees. In addition to cowbirds (Hauber and Russo 2000, Budnick et al. 2002), distance to perch sites has also been found to predict parasitism in other brood parasites such as the European Cuckoo (*Cuculus canorus*) (Moskat and Honza 2000). These results suggest that the closer a perch is to the nest the more chances there will be to observe an adult returning to or leaving it, and thereby the information that a cowbird has on the status of a nest will be more accurate.

The negative relationship between height of the nearest perch to a nest and synchrony is a curious one. Budnick et al. (2002) similarly observed a negative relationship between perch height and likelihood of parasitism in Bell's vireo (*Vireo bellii*). It is possible that taller trees may have had larger crowns resulting in decreased visibility compared to relatively short trees. Though such a relationship may have been expressed in the variable canopy cover, canopy cover did not appear in the top models and it was not correlated with perch height ($R^2 = 0.07$). It is also possible that relatively short perches are simply better for observation of adult behavior of understory hosts because it is easier for the cowbird to see through the understory when closer to it. This could indicate that there is some optimal perch height for nest searching, though this would likely vary quite a bit based on the micro habitat around a perch.

YELLOW WARBLER

The width of the vegetation clump a yellow warbler nest was in was by far the best predictor of synchrony. This is contrary to expectations that larger clumps would provide greater concealment and thereby increase cowbird search time. However, Budnick et al. (2002) found a positive relationship between patch width and both the likelihood of parasitism and predation in Bell's vireos. Though it is a possibility that area may more accurately reflect clump size, the product of clump width and clump length was not determined to be important in the variable selection phase of the analysis. Perhaps cowbirds spend more time searching for nests in wide patches and in so doing have relatively little information on the timing of nests in narrower ones.

The negative relationship between distance to the edge of a patch and synchrony is more intuitive. The association between cowbird activity and edges has been well documented (e.g. Cain et al. 2003). In dense patches of vegetation adult activity is much more easily observed at edges, were openings minimize concealment. If cowbirds are using activity as a cue to locate nests it is likely that the activity of adults near the edges of patches will be much more observable than those deep within a patch.

The dichotomy of nests in rose versus willow in this yellow warbler population has been previously documented (Heath et al. *in press*). Nest success is significantly higher in rose, specifically in terms of predation. This study reveals that there may be additional benefits for cowbirds in terms of synchrony, but the variable was not very strong in comparison to others. The rose brambles on the study plots tend to have many emergent willows >5m in height that could be used to observe warblers using the rose (personal observation). However, if concealment were driving this response, one would expect distance to perch to have been a much stronger variable.

FUTURE RESEARCH

This study was a first step in addressing the question: Does habitat have an indirect impact on cowbird fitness. The next step will be to examine the development of cowbird chicks in both synchronous and asynchronous nests. This will be done by measuring the growth rate of all nestling cowbirds in the study as well as the mass at day 7 as a surrogate measure of fledging mass (Kilpatrick 2002). Past research has shown that mass at fledging is correlated with fledgling survival (e.g. Krementz et al. 1989, Caffrey 2000). This will allow us to test the prediction that chicks in synchronous nests will develop faster than those in asynchronous nests. Genetic methods will be used to control for sex as a covariate.

Additionally, Kilner (2003) found that, in terms of reducing mortality, cowbirds fair better in nests of species with slightly longer incubation times, and relatively worse in species that had much longer or the same incubation time. Since with this study we have only looked at a gross categorical measure of synchrony we will begin checking nests every day to determine exact hatch dates for all nestlings. This will enable us to tease out more subtle variation in synchrony such as differences in micro-habitat and development between degrees of asynchrony (i.e. one day asynchronous vs. two or three).

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TABLES AND FIGURES

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

Model	k	-2 log likelihood	AIC	AIC_c	Δ_i	w_i
host dense + bhcodist + bhcoht	4	12.54	20.54	22.28	0.00	0.41
host dense + bhcodist + bhcoht + (bhcodist*bhcoht)	5	9.81	19.81	22.54	0.26	0.36
(bhcodist*bhcoht) + host dense	3	17.66	23.66	24.66	2.38	0.13
(bhcodist*bhcoht) + lat conceal + host dense	4	17.63	25.63	27.37	5.09	0.03
bhcodist + host dense	3	21.09	27.09	28.09	5.81	0.02
bhcodist + host dense + canopy cov	4	18.70	26.70	28.44	6.16	0.02
bhcodist + lat conceal + host dense	4	20.87	28.87	30.61	8.34	0.01
bhcoht + host dense	3	24.56	30.56	31.56	9.29	0.00
(bhcodist*bhcoht)	2	27.39	31.39	31.87	9.59	0.00
host dense + dist to edge	3	25.53	31.53	32.53	10.25	0.00

[a] Abbreviations for model parameters: host dense = host density, bhcodist = distance of nest to nearest perch, bhcoht = height of nearest perch, canopy cov = % canopy cover at the nest, lat conceal = % lateral concealment of the nest, dist to edge = distance of nest to edge of nest patch.

Table 2. Model averaging results showing relative importance of all parameters included in song sparrow model selection of logistic regression models predicting cowbird hatch synchrony.

Evidence for effects of:	Sum w_i with factor:	Sum w_i without factor:	Times better without:	Times better with:
host dense	0.99	0.01	0.01	122.39
bhco dist	0.83	0.17	0.21	4.82
bhcoht	0.79	0.21	0.26	3.83
(bhcodist*bhcoht)	0.53	0.47	0.89	1.12
lat conceal	0.04	0.96	24.61	0.04
canopy cov	0.02	0.98	44.78	0.02
dist to edge	0.00	1.00	385.75	0.00

[a] Abbreviations for model parameters: host dense = host density, bhcodist = distance of nest to nearest perch, bhcoht = height of nearest perch, canopy cov = % canopy cover at the nest, lat conceal = % lateral concealment of the nest, dist to edge = distance of nest to edge of nest patch.

Table 3. Parameter estimates for the best fitting model of cowbird hatch synchrony in song sparrow nests including Wald χ^2 statistic and p-values.

parameter	β	SE	Wald χ^2	df	P
host dense	1.903	0.990	3.694	1	0.055
bhcoht	-3.129	1.811	2.984	1	0.084
bhcodist	-0.660	0.344	3.694	1	0.055
constant	19.275	10.949	3.099	1	0.078

[a] Abbreviations for model parameters: host dense = host density, bhcodist = distance of nest to nearest perch, bhcoht = height of nearest perch.

Table 4. Confusion matrix and resulting evaluation statictics for best fitting model of cowbird hatch synchrony in song sparrow nests.

	Observed	
Predicted	synchronous	asyncronus
synchronous	14	1
asyncronus	1	12
N	28	
Cut Point	0.56	

Measure	Calculation
Prevalence	0.536
Correct Classification Rate (CCR)	0.929
Sensitivity	0.933
Specificity	0.923
False Positive Rate	0.077
False Negative Rate	0.067
Kappa	0.856

Table 5. Model selection results for logistic regression models predicting cowbird hatch synchrony in yellow warbler, top ten models presented.

Model	k	-2 log likelihood	AIC	AIC_c	Δ_i	w_i
clump width + d to e + r vs. w	4	26.57	34.57	35.82	0.00	0.49
clump width + d to e	3	30.15	36.15	36.88	1.06	0.29
bhco ht + d to e + clump width	4	29.95	37.95	39.20	3.38	0.09
clump width	2	37.22	41.22	41.57	5.75	0.03
clump width + max ht	3	35.39	41.39	42.12	6.30	0.02
clump width + lat conceal	3	36.15	42.15	42.88	7.06	0.01
bhco ht + clump width	3	36.43	42.43	43.16	7.34	0.01
clumpwidth + host dense	3	36.77	42.77	43.50	7.68	0.01
clump width + r vs. w	3	36.99	42.99	43.72	7.90	0.01
clump width + bhco dist	3	37.17	43.17	43.89	8.07	0.01

[a] Abbreviations for model parameters: clump width = the width of the nest clump at it's widest point, dist to edge = distance of nest to edge of nest clump, host dense = host density, lat conceal = % lateral concealment of the nest, bhcoht = height of nearest perch, maxht = maximum height of nest clump, r vs. w = rose versus willow.

Table 6. Model averaging results showing relative importance of all parameters included in yellow warbler model selection of logistic regression models predicting cowbird hatch synchrony.

Evidence for effects of:	**Sum wi with factor:**	**Sum wi without factor:**	**Times better without**	**Times better with**
clump width	0.97	0.03	0.03	37.99
d to e	0.89	0.11	0.13	7.70
r vs. w	0.51	0.49	0.98	1.02
lat conceal	0.03	0.97	31.49	0.03
bhcoht	0.12	0.88	7.67	0.13
maxht	0.03	0.97	32.36	0.03
bhcodist	0.01	0.99	68.25	0.01
host dense	0.02	0.98	62.16	0.02

[a] Abbreviations for model parameters: clump width = the width of the nest clump at it's widest point, dist to edge = distance of nest to edge of nest clump, host dense = host density, lat conceal = % lateral concealment of the nest, bhcodist = distance of nest to nearest perch bhcoht = height of nearest perch, maxht = maximum height of nest clump, r vs. w = rose versus willow.

Table 7. Parameter estimates for the best fitting model of cowbird hatch synchrony in yellow warbler nests including Wald χ^2 statistic and p-values.

parameter	**β**	**SE**	**Wald χ^2**	**df**	**P**
clump width	0.471	0.183	6.608	1	0.010
d to e	-0.072	0.033	4.757	1	0.029
r vs. w	2.247	1.341	2.806	1	0.094
constant	19.275	1.258	3.281	1	0.070

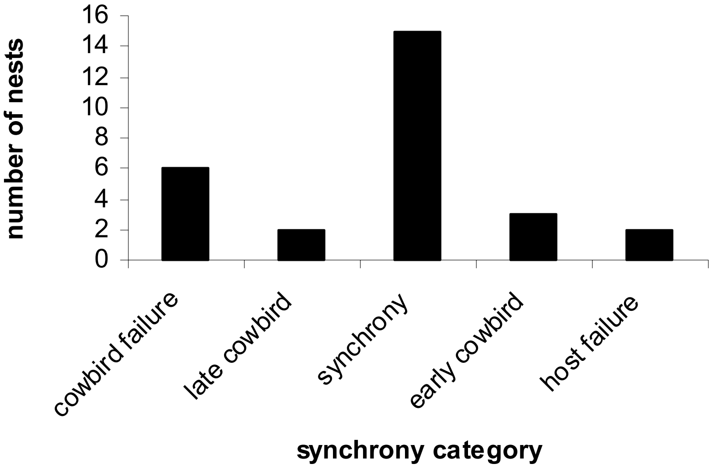
[a] clump width = the width of the nest clump at it's widest point, dist to edge = distance of nest to edge of nest clump, r vs. w = rose versus willow.

Table 8. Confusion matrix and resulting evaluation statictics for best fitting model of cowbird hatch synchrony in yellow warbler nests

	Observed	
Predicted	synchronous	asynchronous
synchronous	10	6
asynchronous	1	20
N	37	
Cut Point	0.23	

Measure	**Calculation**
Prevalence	0.297
Correct Classification Rate (CCR)	0.811
Sensitivity	0.909
Specificity	0.769
False Positive Rate	0.231
False Negative Rate	0.091
Kappa	0.600

a)



b)

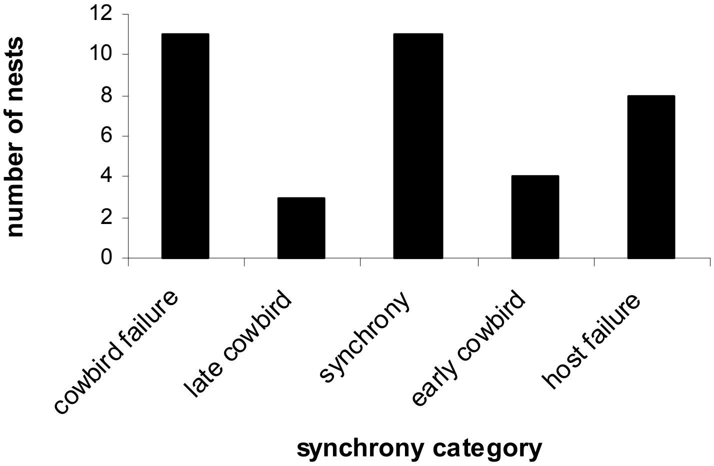


Figure 1. Number of nests in each synchrony category for a) song sparrow (n = 28) and b) yellow warbler (n = 37).

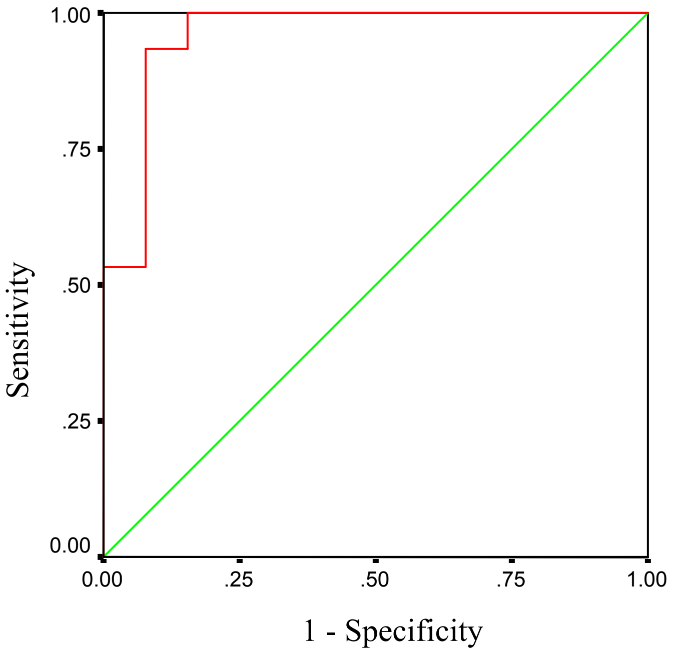


Figure 2. ROC curve for best model fitting model of cowbird hatch synchrony in song sparrow nests.

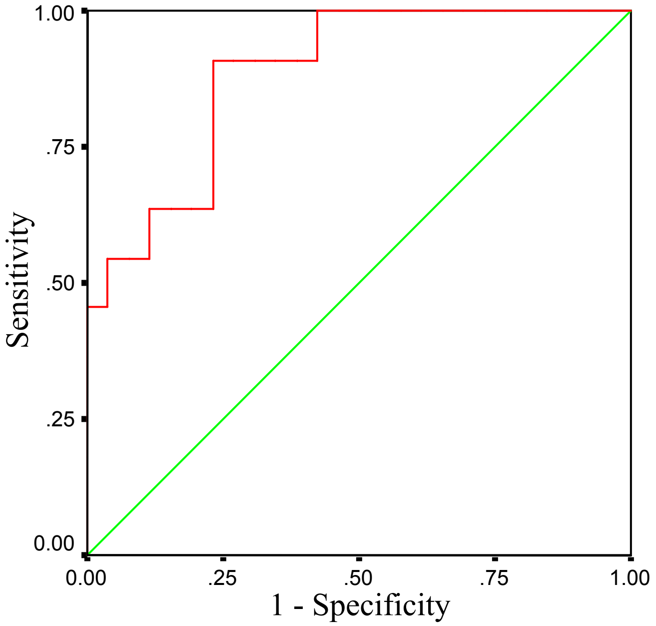


Figure 3. ROC curve for best model fitting model of cowbird hatch synchrony in yellow warbler nests.

APPENDIX A – Nest micro-habitat measurements.

NEST PATCH MEASUREMENTS

- **Patch width** – width of the nest patch at it's widest point.
- **Perpendicular width** – width of nest patch perpendicular to widest point.
- **Maximum patch height**
- **Plant height** – height of the individual plant the nest is in.
- **Height from ground** – measured from the ground to the top of the nest cup.
- **Plant species 1** – primary species the nest is attached to.
- **Plant species 2** – secondary species the nest is attached to.
- **Nest conceal 1** – primary plant species concealing the nest.
- **Nest conceal 2** – secondary plant species concealing the nest.
- **dbh (for nests in trees and shrubs only)** – diameter at breast ht. for trees and at 10cm for shrubs.
- **Distance to edge** – distance to the closest foliage edge from the edge of the nest cup.
- **Conceal above and below** – percent of the nest visible from 1m above and below.
- **Lateral concealment** – the percent of the nest concealed at all four cardinal directions averaged.
- **Compass direction** – orientation of the nest relative to the center of the patch.
- **Canopy cover** – average of four densitometer readings taken at the nest site.
- **Litter depth** – average of 10 measurements taken at the nest site.

NEST SITE MEASUREMENTS

- **Cover data** – percent of a 5m radius centered on the nest covered by shrubs, forbs, logs, litter, bare ground, rock, and water.
- **Tree data** – List of all species within an 11.3m radius centered on the nest, a count of how many fall into each of three dbh categories for each species, and a count of the number of snags. A tree is defined as being at least 8cm dbh and at least 5m in height.
- **Shrub data** – List of all shrub species, low, high, and average heights, number of stems, and relative cover (% of total shrub cover) for each species.
- **Forb data** - List of all forb species, low, high, and average heights, and relative cover (percent of total forb cover) for each species.
- **Width of riparian** – approx. width of riparian vegetation on a line perpendicular to the creek from the nest.

PERCH DATA

- **Distance to nearest perch** – Distance from center of nest patch to nearest object (floral or anthropogenic), upon which a bird could reasonably perch, that is separate from the nest patch, at least 5m in height, and in line of sight of the nest patch.
- **Nearest perch species** – Plant species or type of object.
- **Nearest perch height**
- **Overhead perch** – whether or not there is a perch present at >2m directly above the nest.