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NUMBER OF CLOSE SPATIAL AND TEMPORAL NEIGHBORS DECREASES THE PROBABILITY OF NEST FAILURE AND SHINY COWBIRD PARASITISM IN COLONIAL YELLOW-WINGED BLACKBIRDS

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Abstract. We investigated whether the synchrony and proximity of nests of Yellow-winged Blackbirds (*Agelaius thilius*) provided protection against nest predation or brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*). We analyzed the effect of the temporal aggregation of nests on the daily probability per nest of predation, desertion, egg punctures, and parasitism throughout the breeding season. The probabilities of nest predation and nest desertion increased through the breeding season. The temporal aggregation of nests was negatively associated with the probability of nest desertion, egg punctures, and parasitism, but there was no association with the probability of nest predation. We also analyzed the effect of the number of close neighbor nests on the daily probability per nest of predation, desertion, egg punctures, and brood parasitism. The spatial aggregation of nests was negatively associated with the probability of nest failure and brood parasitism, but there was no association with the probability of egg punctures. We discuss whether dilution effect or group defense, two mechanisms proposed to explain the antipredatory advantages of colonial nesting, are likely to apply to our system.

Key words: Agelaius thilius*, brood parasitism, colonial nesting,* Molothrus bonariensis*, nest failure, Shiny Cowbird, Yellow-winged Blackbird.*

El Número de Vecinos Espaciales y Temporales Disminuye la Probabilidad de Pérdida del Nido y de Parasitismo por *Molothrus bonariensis* en Colonias de *Agelaius thilius*

Resumen. Se investigó si la sincronía y la proximidad de nidos del *Agelaius thilius* proveyó protección ante la depredación del nido y el parasitismo de cría por *Molothrus bonariensis.* Se analizó el efecto de la agregación temporal de nidos sobre la probabilidad diaria por nido de depredación, abandono, picaduras y parasitismo a lo largo de la temporada reproductiva. Las probabilidades de predación y abandono del nido aumentaron a medida que avanzó la temporada reproductiva. La agregación temporal de nidos estuvo negativamente asociada con la probabilidad de abandono, picaduras y parasitismo pero no se observó asociación de ésta con la probabilidad de predación. También se analizó el efecto del número de nidos vecinos cercanos sobre la probabilidad de pérdida del nido y de parasitismo de cría. La agregación espacial de nidos estuvo asociada negativamente con la probabilidad de pérdida del nido y de parasitismo de cría pero no se observó una asociación de ésta con la probabilidad de picadura de huevos. Se discute si el efecto de dilución o la defensa grupal, dos mecanismos propuestos para explicar los beneficios antipredatorios de la nidificación colonial, son probables de ocurrir en este sistema.

INTRODUCTION

Avian species living in temperate zones reproduce seasonally and synchronize their breeding activities with conspecifics, partially in response to the availability of common resources to feed their young (Lack 1968). In addition, some species also aggregate spatially to form colonies of breeding pairs nesting at relatively short distances when compared to the total area of suitable nesting places. The advantages that have been invoked to explain these aggregations include enhanced ability to find food, obtain extra-pair copulations, gain information from successful reproductive conspecifics, and decrease the risk of nest predation (Wittenberger and Hunt 1985, Brown and Brown 1996, Danchin and Wagner 1997).

Most studies on avian reproductive success find that nest predation is the most important source of nest mortality (Ricklefs 1969, Martin

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1993). This general pattern holds for blackbirds such as Red-winged Blackbirds (*Agelaius phoeniceus*; Searcy and Yasukawa 1995, Beletsky 1996, Beletsky and Orians 1996), Yellow-hooded Blackbirds (*Agelaius icterocephalus*; Wiley and Wiley 1980), Yellow-rumped Caciques (*Cacicus cela*; Robinson 1985) and Yellow-winged Blackbirds, (*Agelaius thilius*; Massoni and Reboreda 1998).

Among the proposed advantages of aggregated nesting against predation are an enhanced detection of predators, the efficacy of group mobbing, and the dilution effect (Wittenberger and Hunt 1985, Brown and Brown 1996). Evidence for the last two mechanisms has been found within blackbirds. The synchrony of nesting attempts has been found to increase nesting success for two species of blackbirds by reducing the individual probability of predation by either group defense, dilution effect, or both (Robertson 1973, Robinson 1985, Westneat 1992, Beletsky and Orians 1996).

The effects of breeding synchrony and spatial aggregation on brood parasitism rates have not been investigated to the same extent. Egg laying synchrony, but not spatial aggregation, diminishes the proportion of nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) in Yellow Warblers, (*Dendroica petechia*; Clark and Robertson 1979). Similarly, Martínez et al. (1996) demonstrated the advantages of synchrony and spatial aggregation of breeding Magpies (*Pica pica*) against parasitism by Great Spotted Cuckoos (*Clamator glandarius*). These studies have stressed the advantages against brood parasites derived from synchronous breeding by non-colonial species, but detailed data on both the temporal and spatial aggregation of colonial hosts and their effect on the probability of parasitism are sparse. For example, data from Red-winged Blackbirds show that rates of brood parasitism by Brown-headed Cowbirds are lower in nests placed in high-density nesting areas (Friedmann 1963, Robertson and Norman 1977, Freeman et al. 1990). Likewise, Wiley and Wiley (1980) concluded that temporal aggregation diminishes the likelihood of brood parasitism by Shiny Cowbirds in colonial Yellow-hooded Blackbird populations, but no spatial analysis of the data was carried out.

The only study in which the effect of spatial and temporal nesting aggregation on nest success and brood parasitism was examined in detail was by Clotfelter and Yasukawa (1999). These authors found that in Red-winged Blackbirds, individual parasitized nests were less synchronous with their nearest neighbors and farther from the nearest simultaneously active nest than unparasitized nests, but they did not find any effect of nest aggregation on nesting success. Thus far, except for the work of Clotfelter and Yasukawa (1999), there has been a lack of detailed information on the effect of active neighbors, i.e., both temporal and spatial aggregation, on a host's daily probability of parasitism and nest predation.

The Yellow-winged Blackbird is a suitable species in which to analyze the influence of temporal and spatial aggregation on predation and parasitism rates. They are colonial breeders nesting in marshy areas and using only a small portion of the seemingly suitable and available vegetation to build their nests (Orians 1980). Yellow-winged Blackbirds are socially monogamous, and nest construction and incubation are performed primarily by the females (Orians 1980). Both sexes share equally the feeding of the chicks (Massoni and Reboreda, unpubl. data). The main causes of nest failure in Yellow-winged Blackbirds are nest predation and nest desertion after egg punctures inflicted by parasitic Shiny Cowbirds (*Molothrus bonariensis*). This brood parasite severely reduced the nesting success of Yellow-winged Blackbirds from 17% at unparasitized nests to only 3% at parasitized nests (Massoni and Reboreda 1998).

The purpose of this study was to determine whether the increased synchrony and proximity of Yellow-winged Blackbird nests resulted in lower probabilities of nest failure (i.e., nest predation or nest desertion) and Shiny Cowbird parasitism.

METHODS

STUDY AREA

The study was conducted near the town of General Lavalle in the province of Buenos Aires, Argentina (36°25′S, 56°55′W) from early October to late December 1994. The study area is within the so-called ‘‘flooding pampas’’, a flat region no higher than 4 m above sea level. The area includes marshes and humid grasslands with scattered patches of native woodland in the higher areas. The climate is temperate subhumid with mean monthly temperatures of 23°C in January (summer) and 13°C in July (winter). The average annual rainfall in this area is about 1000 mm (Soriano 1991).

DATA COLLECTION

We conducted intensive nest surveys in flat, low, and marshy areas close to an artificial drainage canal (Canal 2). We found a total of 213 active Yellow-winged Blackbird nests: 81 during construction, 42 during egg laying, 80 during incubation, and 10 after the chicks had hatched. All nests were built in cattails (*Typha* sp.), the dominant species of the marshes. Most of the nests were found clumped in two large colonies separated by less than 2 km. The first group (78 nests) was built within an area of 120 × 50 m and the second group (120 nests) spread over an area of 300 × 40 m. In both colonies egg laying started by mid-October and nest activity ended by late December. The two groups also showed similar rates of parasitism, predation, desertion, and nesting success and therefore were analyzed together. There were two other small colonies of six and nine nests, respectively, located within the study area. Egg laying in these colonies started by mid-October and nest activity ended in late October, after all the nests suffered heavy egg losses due to punctures by Shiny Cowbirds and a 100% incidence of parasitism. These two groups were not included in the analysis.

We recorded the spatial position of each nest as x and y coordinates (with a precision of 1 m) on a 10 × 10 m grid over the entire nesting area. Nests were marked with flagging tape placed at 2 m from the nest and visited daily until they either produced fledglings or failed. For each nest we recorded the starting date (laying of the first blackbird egg) and ending date, the dates of parasitism, egg-punctures, and egg losses, and whether the nest was deserted, depredated, or fledged host or cowbird chicks. For those nests found during egg laying, the starting date was estimated from the number of eggs present in the nest, while in nests found during the incubation and nestling stages, the starting date was estimated indirectly by backdating. In Yellow-winged Blackbirds the most frequent clutch size is three eggs; incubation lasts 12–13 days and starts after the laying of the second egg (Massoni and Reboreda 1998). In each visit we recorded the number of host and parasite eggs and the occurrence of egg cracks or punctures. We considered as parasitized those clutches that had cowbird eggs or nestlings at any stage of the host nesting cycle. Nests were considered deserted if the eggs were cold to the touch for two consecutive days and no Yellow-winged Blackbirds tended the nest whereas they were considered depredated if all the eggs or chicks disappeared between two consecutive visits.

TEMPORAL ANALYSIS

We considered the date of the first Yellow-winged Blackbird egg laid as the starting day of the breeding season. To estimate the actual availability of host nests we used the nest-day, equal to one day of nest activity, as our unit of measure (Mayfield 1975). For example, one nest active for four days would be equivalent to four nest-days, as would two nests active for two days each, or four nests active for one day each. We divided the breeding season into five-day periods, and for each period we determined the number of nest-days, the number of events of egg puncture and parasitism, and the number of nests depredated or deserted. We calculated the probability per day of egg punctures, parasitism, nest depredation, or desertion as the number of cases observed during each period over the number of nest-days per period. Because egg punctures and parasitism only occur during the egg stages (i.e., laying or incubation), and because most cases of predation and desertion also occurred during those periods (Massoni and Reboreda 1998), we restricted our analysis to nests in the egg laying and incubation stages.

SPATIAL ANALYSIS

We analyzed the effect of spatially synchronous nesting on the probability of predation, desertion, egg punctures and parasitism. For each nest we recorded the number of close neighbors during each day of the laying and incubation stages. We considered as close neighbors those nests that were in the laying or incubation stages and that were within a 5-m radius of the focal nest. For each failed nest we considered the number of neighbors surrounding the nest on the day that predation or desertion occurred. For each successful nest we considered the average number of neighbors per day during the laying and incubation stages. Similarly, for nests with egg punctures or parasitism, we considered the number of neighbors surrounding each nest on the day egg punctures or parasitic eggs appeared. For nests without egg punctures or that were not parasitized we used the average number of neighbors per day during the laying and incubation stages or until the nest failed.

We considered close neighbors those nests that were within a radius of 5 m of the focal nest because a previous analysis showed that if we considered a shorter radius (1 or 2 m), the majority of focal nests did not have close neighbors, while if we considered a longer radius (10 m) there were very few nests without close neighbors. With the criteria we chose, approximately 50% of the nests did not have close neighbors, while the other 50% had between one and four close neighbors.

Westneat (1992) defined temporal neighbors as those nests where laying started within two days of the focal nest's starting date. Martínez et al. (1996) used the same definition because they considered it to give a quantitative measure of the number of nests that were available to the parasite. We chose to extend the definition of active neighbors to include all Yellow-winged Blackbird nests that were in laying and incubation stages because (a) egg-punctures by Shiny Cowbirds occur throughout the laying and incubation stages (Massoni and Reboreda 1999); (b) most parasitism occurs during the first six days after the start of laying, but there are parasitic events later on in the incubation period; and (c) most cases of nest desertion and predation occur throughout the laying and incubation stages (Massoni and Reboreda 1998).

STATISTICAL ANALYSIS

We used Spearman rank correlations to analyze the association between nest availability through the breeding season and the daily probability per nest of predation, desertion, egg punctures, and parasitism. We used logistic regressions to analyze the effect of the number of close neighbor nests (independent variable) on the daily probability per nest of predation, desertion, egg punctures, and brood parasitism (dependent variable). Statistical tests were performed using StatView 5.0 (SAS Institute Inc. 1998).

RESULTS

EFFECT OF SYNCHRONY AND PROXIMITY ON THE PROBABILITY OF NEST FAILURE

There was a positive correlation between time of the breeding season and the probability per day of nest predation ($r_s = 0.77$, $P < 0.01$, Fig. 1A) or desertion ($r_s = 0.85$, $P < 0.01$, Fig. 1A).

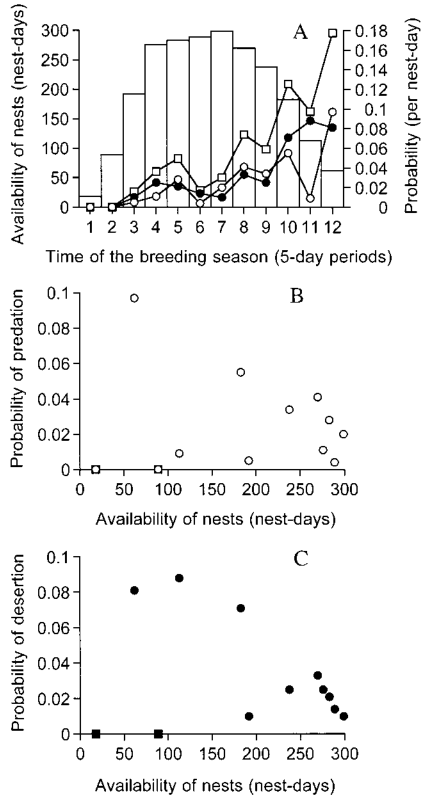

FIGURE 1. (A) Seasonal patterns of Yellow-winged Blackbird nest availability and nest failure in Argentina. Bars show nest availability (expressed as nest-days) through the breeding season. Each bar corresponds to a 5-day period (days 1–5, 6–10, etc.). The starting day of the breeding season corresponds to the date of the first Yellow-winged Blackbird egg laid. The lines show the daily probability per nest of predation (white dots), desertion (black dots) and nest failure (white squares). (B) Daily probability of predation as a function of nest availability per 5-day period. (C) Daily probability per nest of desertion as a function of nest availability per 5-day period. In B and C, the squares show the probability of predation for nests that were available during the first 10 days of the colony.

The correlation between time of the breeding season and the probability per day of nest failure (desertion and predation combined) was also highly significant ($r_s = 0.93$, $P < 0.001$, Fig. 1A). We observed the same correlation when we repeated the analysis and included nests that were in the nestling stage. Again, there was a positive correlation between time of the breeding season and the probability per day of nest failure either by predation or desertion ($r_s = 0.88$, $P < 0.001$ for nest predation; $r_s = 0.52$, P

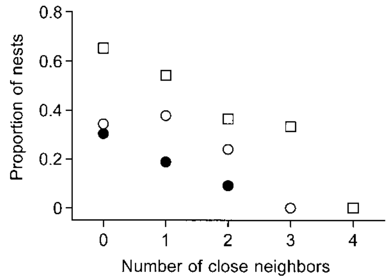

FIGURE 2. Proportion of Yellow-winged Blackbird nests that were depredated (white dots), deserted (black dots) or failed (white squares) as a function of the number of close neighbors.

= 0.07 for nest desertion; $r_s = 0.94$, $P < 0.001$ for nest failure). Because there was an increase in nest predation and nest desertion as the breeding season progressed and there were few nests both at the beginning and at the end of the breeding season, there was no correlation between the number of nests available at a given time and the probability per day that a nest was depredated ($r_s = 0.11$, $P > 0.7$, Fig. 1B) or deserted ($r_s = -0.09$, $P > 0.7$, Fig. 1C).

The lack of correlation between the number of nests available and the probability per day of nest predation or desertion could have been confounded by the absence of predators during the first stages of the colony. Predators could spend some time before detecting that a colony has started or move into the colony only when the density of nesting birds is high. Therefore, we repeated the analysis excluding the nests available during the first 10 days of the colony (squares in Fig. 1B and 1C). During this period none of the nests was either depredated or deserted. There was a negative correlation between nest availability and the probability per day that a nest was deserted ($r_s = -0.77$, $P < 0.05$) or that failed ($r_s = -0.69$, $P < 0.05$) but there was no significant correlation with nest predation ($r_s = -0.41$, $P > 0.05$).

Proximity among Yellow-winged Blackbird nests was associated with a reduced probability of nest failure. There was a negative relationship between the number of close neighbors during a nest's laying and incubation stages and the overall probability of nest failure (logistic regression: $\chi^2 = 7.6$, $P < 0.01$, Fig. 2). The probabilities of predation and nest desertion tended to decrease with the number of neighbors but the effect was not significant (logistic regressions: $\chi^2 = 2.6$, $P = 0.11$ for nest predation and $\chi^2 = 3.1$, $P = 0.08$ for nest desertion, Fig. 2).

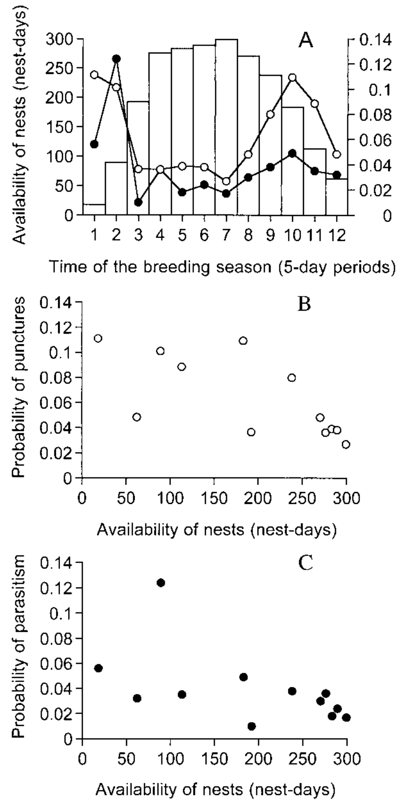

FIGURE 3. (A) Seasonal patterns of Yellow-winged Blackbird nest availability and daily probability per nest of punctures and parasitism. Bars show the nest availability (expressed as nest-days) per 5-day period. The starting day of the breeding season corresponds to the date of the first Yellow-winged Blackbird egg laid. The lines show the daily probability per nest of punctures (white dots), and parasitism (black dots). (B) Daily probability per nest of puncture as a function of nest availability per 5-day period. (C) Daily probability per nest of parasitism as a function of nest availability per 5-day period.

EFFECT OF SYNCHRONY AND PROXIMITY ON THE PROBABILITY OF PARASITISM

Nest availability showed a bell-shaped distribution over time whereas the probabilities of puncture and parasitism followed a U-shaped distribution with higher probabilities at the beginning and at the end of the breeding season (Fig. 3A). As a result, there was a negative correlation between the number of available nests at a given time (their temporal aggregation) and the probability per day that a nest suffered egg punctures

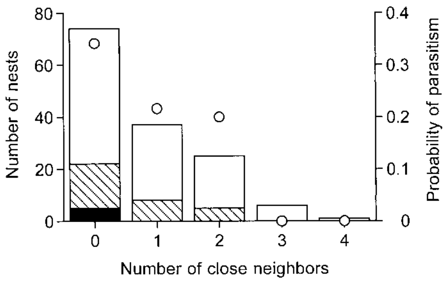

FIGURE 4. Probability of nest parasitism as a function of the number of close neighbors for Yellow-winged Blackbirds in Argentina. Bars show the number of nests with 0, 1, 2, 3, and 4 close neighbors. The black, striped, and white portions of the bars indicate the number of nests with multiple parasitism, single parasitism and unparasitized respectively. The white dots indicate the average number of parasitic events per nest.

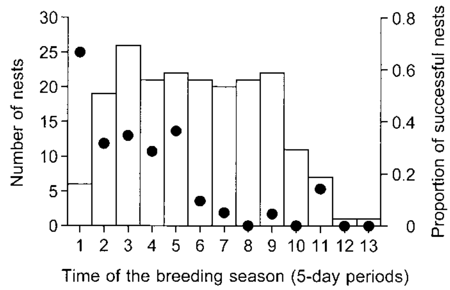

FIGURE 5. Timing of breeding compared with nesting success for Yellow-winged Blackbirds in Argentina. The bars indicate the number of nest attempts (in 5-day periods) through the breeding season. The dots indicate the proportion of those nests that fledged chicks.

(r_s = −0.80, $P < 0.01$, Fig. 3B) or parasitism (r_s = −0.64, $P < 0.05$, Fig. 3C).

Proximity among Yellow-winged Blackbird nests was also associated with a decrease in the likelihood of Shiny Cowbird parasitism. There was a negative association between the number of close neighbors and the probability of parasitism (logistic regression: $\chi^2 = 6.1$, $P < 0.01$, Fig. 4). Nests without close neighbors were the only ones with multiple parasitism, whereas nests that had three or four neighbors were never parasitized. There was no association between the number of close neighbors and the probability of egg punctures (logistic regression: $\chi^2 = 0.01$, $P > 0.9$).

TIMING OF BREEDING SEASON AND NESTING SUCCESS

There was a negative association between timing of the breeding season and nesting success. Yellow-winged Blackbirds that started laying early in the breeding season enjoyed a higher nesting success than late breeders (logistic regression: $\chi^2 = 27.7$, $P < 0.001$, Fig. 5).

DISCUSSION

Our results show that (1) there was a seasonal increase in the daily probability of nest predation and nest desertion; (2) the temporal and spatial aggregation of Yellow-winged Blackbird nests were negatively associated with the probability of nest failure, and (3) both temporal and spatial aggregation of nests were negatively associated with the probability of brood parasitism, yet only the temporal aggregation was negatively associated with the probability of egg punctures by Shiny Cowbirds. These results indicate that Yellow-winged Blackbirds derived indirect benefits from both synchronous and aggregated nesting.

NEST PREDATION, NEST DESERTION, AND SYNCHRONOUS NESTING ATTEMPTS

The daily probability that a nest would be depredated increased as the season progressed but was not significantly affected by the temporal aggregation of nests in the colony. Several authors have proposed that colonial nesting affords antipredatory advantages such as enhanced detection of predators (Brown and Brown 1996), group defense (Wiklund and Andersson 1994), or a dilution effect (Wittenberger and Hunt 1985, Westneat 1992). However, the effectiveness of temporal and spatial aggregation depends on the array of predators faced. Potential predators of Yellow-winged Blackbirds in our study area include small rodents and snakes, the Guira Cuckoo (*Guira guira*), and raptors such as Southern Caracara (*Caracara plancus*), Chimango Caracara (*Milvago chimango*), Long-winged Harrier (*Circus buffoni*), and large mammals such as skunks (*Conepatus* sp.) and thick-tailed opossums (*Lutreolina crassicaudata*). We have repeatedly witnessed, as well as elicited, Yellow-winged Blackbird collective mobbing during our visits to the marshes. Such behavior may regularly deter animals up to only slightly larger than the blackbirds (Beletsky 1996) and we doubt that group mobbing is useful against large predators.

The daily probability that a nest would be deserted increased as the breeding season progressed and was affected by the temporal availability of nests. Previous studies have shown that Yellow-winged Blackbirds desert their nests in response to high egg losses as a result of egg punctures inflicted by Shiny Cowbirds (Massoni and Reboreda 1998). The daily likelihood of egg punctures was negatively associated with the total number of available nests (temporal aggregation, see below), affecting an important proportion of the early and late nests of the season. The daily probability of nest desertion, however, did not show the same U-shaped pattern as the daily probability of egg puncture, but increased throughout the season. High temperatures and reduced availability of water in the marshes as the season progressed were common in our seasonal, temperate study area. Yellow-winged Blackbirds do not reject Shiny Cowbird eggs, either because they do not recognize them or because they risk additional damage to their own eggs by trying to reject them (Massoni and Reboreda 1998). In either case, the occurrence of nests with damaged clutches, along with worsening weather conditions, might prompt Yellow-winged Blackbirds to abandon such nests quickly, as the investment required to raise a damaged brood with a high possibility of raising a cowbird chick would not be worthwhile. Yellow-winged Blackbirds, like other blackbirds (Ortega and Cruz 1991, Peer and Bollinger 1997) could also be more likely to desert the nest when they have fewer neighbors.

Yellow-winged Blackbirds surrounded by high numbers of close neighbors showed a reduced daily probability of overall nest failure. We do not have a clear explanation for this effect as the probability of egg puncture did not vary with the number of close neighbors that surrounded the nest (see below) and, as we mentioned above, Yellow-winged Blackbirds do not appear to be capable of deterring the most common nest predators.

Yellow-winged Blackbirds that started laying early in the breeding season enjoyed a higher nesting success than late breeders did. Most bird species show a seasonal decline in reproductive success (Perrins 1970, Daan et al. 1989) as a consequence of differences in quality between early and late breeders, a seasonal variation in the environment, or both (Hochachka 1990, Verhulst et al. 1995). In our case, the seasonal decrease in nesting success appears to be the result of a seasonal increase in nest predation and desertion, although we cannot exclude the possibility of differences in quality between early and late breeders.

EFFECT OF TEMPORAL AND SPATIAL AGGREGATION ON PARASITISM AND PUNCTURE RATES

The considerations for the interactions between predators and prey apply equally well to the interaction between cowbirds and nests (Wiley and Wiley 1980). These authors found that synchronous nesting by colonial Yellow-hooded Blackbirds diminished the probability of parasitism by Shiny Cowbirds. A similar result was found by Clotfelter and Yasukawa (1999) studying Red-winged Blackbirds and Brown-headed Cowbirds. They found that parasitized nests were farther from their nearest simultaneously active nests than were unparasitized nests.

Shiny Cowbirds puncture Yellow-winged Blackbirds' eggs before they parasitize the nests, and there is a strong correlation between the puncture of the host's eggs and parasitism (Massoni and Reboreda 1998). These parasites, however, also puncture eggs at nests they do not parasitize; their decision to parasitize depends on the stage of incubation of the host egg, as determined from the punctured egg (Massoni and Reboreda 1999). Therefore, both egg punctures and parasitic events have to be considered among the costs of Shiny Cowbird visits to Yellow-winged Blackbird nests.

Our results show that both temporal and spatial aggregation of Yellow-winged Blackbird nests reduced their vulnerability to Shiny Cowbird parasitism. Temporal aggregation of nests was inversely correlated with the daily probability of both parasitism and punctures. Similarly, the number of close active neighbors also diminished the likelihood of parasitism, albeit not the probability of puncture events. We cannot explain why the probability of egg puncture was unaffected by the spatial clumping of nests. It could be argued that egg punctures can be done in seconds, and that high numbers of communally mobbing neighbors might cause visiting Shiny Cowbirds to reduce their likelihood of parasitism.

Despite the Shiny Cowbird's rapid egg laying (Wiley and Wiley 1980), the spatial and temporal clumping of nests at least indirectly protects Yellow-winged Blackbird nests. This effect could be achieved either by parasite dilution (Clark and Robertson 1979) or enhanced efficacy of group defense (Clark and Robertson 1979, Freeman et al 1990). Martínez et al. (1996) reported a similar effect of synchronous breeding in Magpies parasitized by the Great Spotted Cuckoo. Based on the cuckoo's inability to respond to the sudden availability of eggs and the infrequent observation in Magpies of group defense, Martínez et al. (1996) concluded that parasite dilution explained the protective effect of synchronous breeding. We believe ours is a different scenario, although with the available data we are unable to rule out a dilution effect. Yellow-winged Blackbirds, unlike Magpies, are colonial breeders, sometimes placing their nests less than 1 m apart. In addition, group mobbing performed by both sexes is commonly seen in our study area and there is a significant spatial effect of nest aggregation on the daily probability of brood parasitism.

Some authors suggest that predators (or brood parasites) could be attracted to large colonies of their prey or host (Wiley and Wiley 1980, Wittenberger and Hunt 1985, Szep and Barta 1992), and studies by Brown and Brown (1996) on Cliff Swallows have demonstrated that more predators are attracted to larger breeding colonies. Our data, however, provide indirect evidence of the benefits of colonial nesting in this marsh-dwelling species. Yellow-winged Blackbirds profit by nesting temporally and spatially close to each other because it results in lower probabilities of nest failure and brood parasitism by Shiny Cowbirds.

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