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Short communication

# Predator density influences nest attendance of Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*

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Nest attendance behaviour in birds is a function of the careful balance between the risk of nest predation and the needs of the parents and nestlings. This attendance must be carefully regulated, as increased parental activity at the nest increases nest predation risk. We tested the long-standing hypothesis that nest predation risk influences parental behaviour by evaluating the influence of local Marsh Wren *Cistothorus palustris* density on the off-bout frequency of Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*. Marsh Wren density was negatively correlated with Yellow-headed Blackbird off-bout frequency during the morning (05:00–10:00 h) and evening (16:00–21:00 h), suggesting that Yellow-headed Blackbirds alter their nest attendance behaviour in response to a perceived increased risk of nest predation. We suggest that Yellow-headed Blackbirds are sensitive to nest predation risk and alter their behaviour accordingly to increase overall fitness, although future research is needed to evaluate the influence of Marsh Wren nest predation on the reproductive success of Yellow-headed Blackbirds.

**Keywords:** behaviour, Marsh Wren, parental activity, predation, Yellow-headed Blackbird.

Nest predation is a major factor limiting reproductive success in birds (Martin 1988). Factors such as predator search intensity, nest partitioning and habitat quality can all drive variation in nest predation rates (Martin 1988, Martin & Joron 2003). A study by Skutch (1949) suggested that the risk of nest predation increases with an increase in the rate at which parents visit the nest to feed their young. Other more recent studies have confirmed this correlation (Conway & Martin 2000, Martin *et al.* 2000, Muchai & du Plessis 2005), emphasizing the need to understand the influence of nest predation risk on parental behaviour in birds.

In addition to feeding nestlings, adult birds must manage time spent away from the nest according to the risks of nest predation, their needs and the needs of their clutch, and the degree to which they balance these factors varies greatly both within and among species (Conway & Martin 2000). Frequent off-bouts can increase the risk of predation and prolonged absences can cause eggs to cool or heat excessively, depending on ambient temperatures, which can affect embryonic development (Feast *et al.* 1998, Olson *et al.* 2006). This suggests that in the presence of predators, birds should minimize parental activity around the nest during the incubation period to decrease the risk of nest predation and ultimately increase overall fitness (Martin *et al.* 2000).

The Yellow-headed Blackbird *Xanthocephalus xanthocephalus* is a common species of marsh bird in semi-permanent wetlands throughout the Upper Midwest, USA. These colony-nesting birds build compact, open-cup nests over water and defend them from potential nest predators. Another marsh bird, the Marsh Wren *Cistothorus palustris*, is known to destroy eggs and depredate unattended nests of Yellow-headed Blackbirds and Red-winged Blackbirds *Agelaius phoeniceus* (Leonard & Picman 1986), as well as other species such as Sora *Porzana carolina* (Grieves & Forbes 2012), Tree Swallow *Tachycineta bicolor* (Quinn & Holroyd 1989) and Yellow Warbler *Dendroica petechial* (Belles-Isles & Picman 1986). Picman (1984) suggested that Marsh Wren predation evolved to reduce inter-specific competition, rather than to provide additional food sources. This predation can account for a considerable amount of nest failure in blackbirds (Bump 1986). In response to this predation, Yellow-headed Blackbirds aggressively respond to both the visible and the audible presence of Marsh Wrens (Neudorf *et al.* 2011). Nest location and

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territories of the two species are also spatially segregated, and previous research has shown the separation is probably due to negative interactions between the species (Leonard & Picman 1986).

In this study, we tested the hypothesis that parental activity is influenced by nest predation risk, using Yellow-headed Blackbirds and Marsh Wrens as our study system. Specifically, we evaluated the off-bout frequency of Yellow-headed Blackbirds as a function of Marsh Wren density and predicted that Yellow-headed Blackbird off-bouts would decrease with increased local Marsh Wren density. As each off-bout represents significant nest activity that can attract a nest predator and leaves the nest unprotected by an adult, Yellow-headed Blackbirds should limit off-bouts when predator density, and therefore predation risk, is highest.

## METHODS

We conducted our study at Big Wall Lake, a shallow-lake marsh of approximately 364 ha located in Wright County in north-central Iowa, USA (42.6228°N, 93.6497°W). We focused our efforts on the southern two-thirds of the lake because of ease of access and because this area contained habitat characteristics most preferred by our study species. This portion of the lake is characterized by an equal mixture of open water approximately 2 m in depth and emergent vegetation consisting of cattail *Typha* spp., both Softstem Bulrush *Schoenoplectus tabernaemontani* and River Bulrush *Schoenoplectus fluviatilis*, American Lotus *Nelumbo lutea* and Arrowhead *Sagittaria latifolia*. The northern third of the lake is completely covered with emergent vegetation, which is less suitable for our study species. Prior to fieldwork, we established a 100-m point grid over the study site ($n$ = 165 points). At each point within the grid, we conducted point-count surveys for Marsh Wrens and Yellow-headed Blackbirds from 18 May to 10 July 2015. Each point was surveyed once early in the survey season (18 May–15 June) and once late in the survey season (16 June–10 July). Point counts were of 5 min duration following a 1-min acclimation period, and were conducted from 30 min before to 3 h after sunrise. We recorded all visual and auditory detections of our two study species, and recorded the distance (m) to each bird within a 50-m radius of the survey point. Any birds > 50 m from the survey point were recorded, but distance was recorded as '> 50 m'. We alternated points at which we conducted surveys within the point grid so that points immediately adjacent to one another were not surveyed consecutively. We avoided double-counting birds at survey points by carefully noting the location of each bird detected at each survey point. We recorded wind speed (km/h), ambient temperature (°C), and cloud cover (%) at each survey point prior to starting the survey. We did not conduct surveys during periods of high winds (> 20 km/h) or precipitation.

In addition to point counts, we located Yellow-headed Blackbird nests by canoe between 13 May and 17 July 2015, which is the primary breeding season for this species in Iowa (Kent & Dinsmore 1996). Nests were located by first observing the activity and behaviour of adult females, specifically looking for times at which females appeared to be near or entering a nest. We then systematically searched the general area in which the female was last observed by traversing short transects no more than 5 m apart until a nest was found or until observers were confident there was no nest in the area. Most of these targeted searches lasted no longer than 15 min. Once a nest was located, we recorded the Universal Transverse Mercator (UTM) location of all active nests, which we defined as a nest containing at least one egg or chick, or newly constructed, using a Garmin GPS unit. We aged eggs in the nest using the flotation method and aged chicks based on the eruption of different feather tracts (Holcomb & Twiest 1971). After initial discovery, we checked nests every 3–4 days until fledging or nest failure. We measured the water depth (cm) at each nest as well as the height of the nest (cm) from the water surface. We also measured the distance (m) from the nest to the nearest patch of open water *post hoc* in ArcGIS using georeferenced aerial photographs of Big Wall Lake.

To evaluate the influence of Marsh Wren and Yellow-headed Blackbird density on the number of off-bouts of Yellow-headed Blackbirds, we used distance data to estimate density and interpolate a density surface for each species across our study area on Big Wall Lake (Thomas *et al.* 2010). Using the 'Distance' package in Program R (R Core Team 2016), we estimated density (birds/ha) and detection probability for the Marsh Wren and Yellow-headed Blackbird throughout our study area. We grouped data for each species into various distance bins *post hoc* (Buckland *et al.* 2001). For Marsh Wren, we used the following distance bins: 0–10, 10–15, 15–20, 20–25, 25–30, 30–35, 35–45 and 45–50 m. The bins used for Yellow-headed Blackbird were: 0–5, 5–10, 10–20, 20–30, 30–40 and 40–50 m. We modelled detection probability as a function of wind speed, ambient temperature and cloud cover, as well as constant detection. We considered detection functions and expansion factors for the model with constant detection probability according to Thomas *et al.* (2010). For models with covariates on detection probability, we considered only those detection functions and expansion factors described by Marques *et al.* (2007). We evaluated models using Akaike's information criterion (AIC; Akaike 1973) and considered the model with the lowest AIC value to be the best supported. We also considered models within two AIC units of the top model ($\Delta$AIC $\leq$ 2) to have strong support (Burnham & Anderson 2002).

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Once we determined the best supported models and corresponding detection functions for each species, we used the package 'dsm' in R (R Core Team 2016) to interpolate a density surface across our study area for each species using a generalized additive model described by Miller *et al.* (2013). We assessed the variance of our density surface for each species using the method described by Williams *et al.* (2011). Next, we converted the interpolated surface to a raster file and overlaid point locations for each Yellow-headed Blackbird nest. We then extracted density values for both Marsh Wren and Yellow-headed Blackbird for each individual nest to use as covariates in our analysis of Yellow-headed Blackbird off-bouts.

Between 13 May and 8 July 2015, we measured nest temperatures (°C) in 52 Yellow-headed Blackbird nests located on Big Wall Lake using Thermocron iButton temperature data loggers (Model #DS1921G; OnSolution Pty Ltd, Baulkam Hills, Australia). We measured nest temperature only on nests during the incubation stage. Data loggers were programmed to record nest temperature at 5-min intervals 24 h/day for a total of 2048 readings. We used superglue to attach each data logger to the head of a 2-inch (*c.* 5.08 cm) galvanized nail and stuck that into the floor of the nest just under the eggs. We then replaced the eggs directly on the data loggers. We recorded nest temperature in each nest for a maximum of 5 days and removed the data logger at this time, or when the nest succeeded or failed. Ambient temperatures (°C) and precipitation (cm) were recorded nearby (approximately 25 km) at the Clarion Airport AWOS (Automated Weather Observing System) sensor. Because Yellow-headed Blackbirds were likely to be on the nest at night (21:00–05:00 h), resulting in a stable nest temperature relative to ambient temperature, we summarized night-time nest temperatures for 50 nights for each nest to determine the average standard deviation in nest temperature. We found the average standard deviation in night-time nest temperature to be 1.24 °C and considered this the natural variation in nest temperature during incubation. Using this number, we then identified an off-bout as any incidence of a drop of at least 1.5 °C until the temperature increased again by at least 1.5 °C, similar to methods used by Walters *et al.* (2016). We counted the number of off-bouts during four periods of the day: morning (05:00–10:00), day (10:00–16:00), evening (16:00–21:00) and night (21:00–05:00). As few off-bouts occurred during the

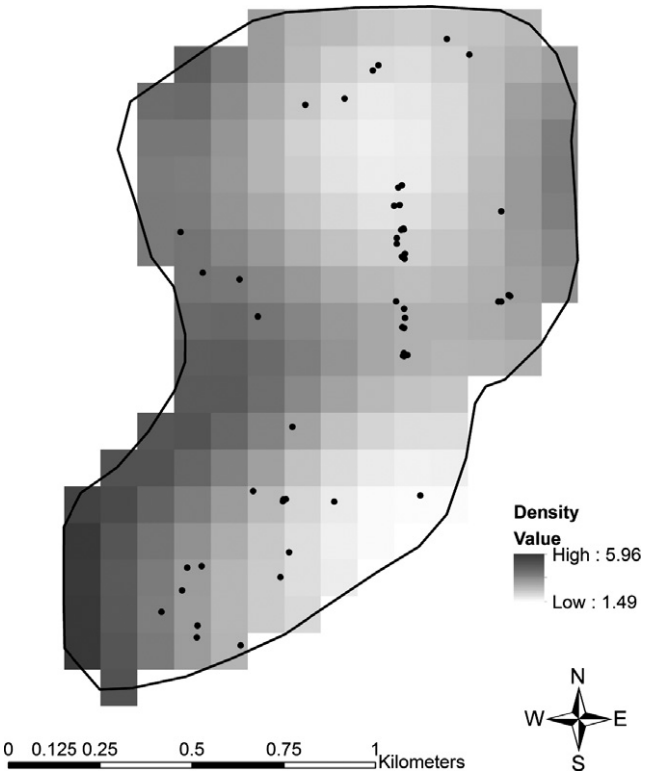


**Figure 1.** Interpolated density of Marsh Wrens within our study area in relation to nests on which nest temperature was monitored. The solid black line represents the outline of the study area and the black dots represent locations of individual Yellow-headed Blackbird nests.

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night, we only analysed off-bouts for the morning, day and evening time periods. Therefore, each nest was represented only once in the dataset for each time period. We used the average number of off-bouts by nest for each time period as the response variable in our models.

The number of off-bouts during each of the three time periods mentioned above was right-skewed with excess zeroes. Therefore, we analysed these data as a function of Marsh Wren density, Yellow-headed Blackbird density, ambient temperature (°C), precipitation (cm) and Julian Day using generalized linear models with a Poisson distribution in Program R (R Core Team 2016). We also evaluated the quadratic effect of Julian Day and the interaction of Marsh Wren density and Yellow-headed Blackbird density on the number of off-bouts during each of the three time periods. We included the log-transformed number of hours the temperature sensor was in the nest during each of the three time periods as an offset to account for differences in the number of off-bouts driven by differences in the length of data collection. We evaluated models for each time period separately, but evaluated the same seven models for each time period. We assessed the fit of the top model for each time period using a Chi-square goodness-of-fit test. We evaluated models using AIC adjusted for small sample sizes (AICc) and considered all models within two AICc units of the top model ($\Delta$AICc $\leq$ 2) to have strong support (Burnham & Anderson 2002). We considered covariate effects in top models to be significant if their respective 95% confidence intervals (CI) did not include zero.

## RESULTS

We analysed the number of off-bouts from 52 Yellow-headed Blackbird nests, which varied by nest and time period. Although it is challenging to attribute a specific cause to nest abandonment or failure without physical evidence, we observed no nest abandonment or failure as a direct result of the addition of a temperature data logger to the nest. The average number of off-bouts (±sd) was 9.82 (±4.87) during the morning time period, 10.09 (±5.67) during the day period and 8.84 (±5.17) during the evening period. Marsh Wren density, which includes both males and females, averaged 2.69 birds/ha (Fig. 1) and Yellow-headed Blackbird density averaged 5.66 birds/ha. Ambient temperature averaged 14.42, 20.95 and 21.76 °C for the morning, day and evening periods, respectively. Nest temperatures averaged 23.09, 25.11 and 25.13 °C for the morning, day and evening periods, respectively. Chi-square goodness-of-fit tests on the top model for each time period suggested a good fit ($P > 0.05$).

Marsh Wren density was included in the best supported models for off-bouts during two of the three time periods and was included in a competing model for the remaining time period (Table 1). It was the sole variable in the top model during the morning and evening time periods and in a competitive model ($\Delta$AICc = 1.87) for the day time period (Table 1). Additionally, Marsh Wren density was included as an interaction with Yellow-headed Blackbird density in a competing model for both the day time period ($\Delta$AICc = 1.16) and evening time period ($\Delta$AICc = 1.12; Table 1). Marsh Wren density had a significant negative effect on off-bouts in the morning ($\beta = -0.19$, 95% CI: −0.33 to −0.04) and evening ($\beta = -0.21$, 95% CI: −0.37 to −0.06; Fig. 2) but did not significantly influence off-bouts during the day. Yellow-headed Blackbird density did not impact off-bout frequency. Likewise, the interaction of Marsh Wren density and Yellow-headed Blackbird density on off-bouts/h was not significant for any time period.

**Table 1.** Model selection results for covariate effects on the average number of off-bouts/h by Yellow-headed Blackbirds during the morning (05:00–10:00), day (10:00–16:00) and evening (16:00–21:00) time periods at Big Wall Lake in Iowa, 2015.

| Covariate | AICc | ΔAICc | *k* | $w_i$ | *cum* $w_i$ |
|---|---|---|---|---|---|
| Morning | | | | | |
| MAWR dens | 333.53 | 0.00 | 2 | 0.53 | 0.53 |
| MAWR dens*YHBL dens | 334.69 | 1.16 | 4 | 0.30 | 0.83 |
| YHBL dens | 335.71 | 2.18 | 2 | 0.18 | 1.00 |
| Julian Day$^2$ | 371.74 | 38.21 | 2 | 0.00 | 1.00 |
| Julian Day | 372.58 | 39.05 | 2 | 0.00 | 1.00 |
| Precipitation (cm) | 375.47 | 41.94 | 2 | 0.00 | 1.00 |
| Temperature (°C) | 375.68 | 42.15 | 2 | 0.00 | 1.00 |
| Day | | | | | |
| YHBL dens | 361.80 | 0.00 | 2 | 0.64 | 0.64 |
| MAWR dens | 363.67 | 1.87 | 2 | 0.25 | 0.89 |
| MAWR dens*YHBL dens | 365.29 | 3.49 | 4 | 0.11 | 1.00 |
| Julian Day$^2$ | 398.84 | 37.04 | 2 | 0.00 | 1.00 |
| Julian Day | 400.42 | 38.63 | 2 | 0.00 | 1.00 |
| Precipitation (cm) | 413.31 | 51.52 | 2 | 0.00 | 1.00 |
| Temperature (°C) | 413.37 | 51.57 | 2 | 0.00 | 1.00 |
| Evening | | | | | |
| MAWR dens | 363.13 | 0.00 | 2 | 0.57 | 0.57 |
| MAWR dens*YHBL dens | 364.25 | 1.12 | 4 | 0.32 | 0.89 |
| YHBL dens | 366.42 | 3.30 | 2 | 0.11 | 1.00 |
| Julian Day$^2$ | 401.23 | 38.11 | 2 | 0.00 | 1.00 |
| Julian Day | 401.49 | 38.36 | 2 | 0.00 | 1.00 |
| Temperature (°C) | 403.42 | 40.29 | 2 | 0.00 | 1.00 |
| Precipitation (cm) | 403.84 | 40.72 | 2 | 0.00 | 1.00 |

'MAWR dens' represents Marsh Wren density, 'YHBL dens' represents Yellow-headed Blackbird density, and 'Julian Day$^2$' represents the quadratic effect of Julian Day. '*k*' represents the number of parameters in the model, '$w_i$' represents the individual model weight, and '*cum* $w_i$' represents the cumulative model weight.

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## DISCUSSION

Our results suggest that Yellow-headed Blackbirds alter their nesting behaviour in response to Marsh Wren density. Previous studies have shown that Marsh Wrens act as significant nest predators of both Yellow-headed Blackbirds (Bump 1986, Leonard & Picman 1986) and other species (Belles-Isles & Picman 1986, Quinn & Holroyd 1989). Additionally, Yellow-headed Blackbirds respond aggressively to Marsh Wren presence (Neudorf *et al.* 2011) and these species are spatially segregated in their nesting habitats (Leonard & Picman 1986). We found that Marsh Wren density was a significant predictor of Yellow-headed Blackbird off-bout frequency. Blackbirds exhibited significantly fewer off-bouts in areas of high Marsh Wren density during the morning and evening time periods but not during the day. This suggests an adaptive ability of Yellow-headed Blackbirds to alter nest attendance strategy in response to predation risk, as demonstrated in previous research on other species (Conway & Martin 2000, Massaro *et al.* 2008), and suggests that Yellow-headed Blackbird parental behaviour is plastic to increase overall fitness in the presence of an aggressive nest predator. Our study did not examine off-bout frequency in the absence of Marsh Wrens, which could be valuable in further establishing the adaptive response of Yellow-headed Blackbirds to nest predation risk. Although our study does indicate that decreased off-bout frequency could reduce the risk of nest predation and increase overall fitness of the parents, further research is needed to evaluate the impact of Marsh Wren density on Yellow-headed Blackbird reproductive success (e.g. nest survival) and on survival of the parents.

Although Yellow-headed Blackbird density was the sole variable in the best model for daytime off-bout frequency, the effect of blackbird density on off-bouts was not significant. This suggests blackbirds alter nest attendance behaviour in response to Marsh Wren presence regardless of conspecific density. Yellow-headed Blackbirds are a colonial nesting species, a behaviour that has evolved, in part, as an anti-predator behaviour during the nesting period (Horn 1968, Picman *et al.* 2002). However, our results show that Yellow-headed Blackbirds will alter nesting behaviour in response to nesting threats, which suggests that blackbird colonies may not confer additional protection from Marsh Wrens, or that this added protection is not as large as previously assumed. Colonial nesting in this species may have evolved as a function of other advantages such as exploitation of food resources, although further research is needed in this area (Horn 1968).

It is important to recognize other factors that could have influenced Yellow-headed Blackbird off-bout

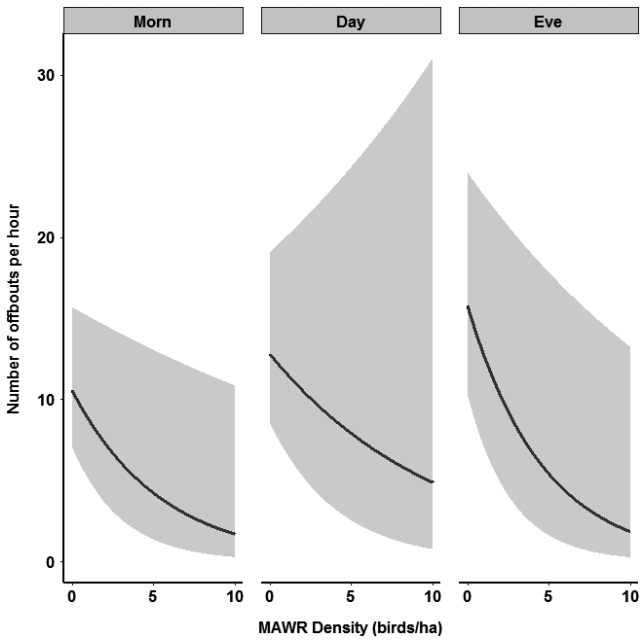


**Figure 2.** Predicted number of off-bouts/h as a function of Marsh Wren density for the morning (Morn), day (Day) and evening (Eve) time periods at Big Wall Lake in Iowa, 2015. The solid line, which was created using the linear equation from the model that included Marsh Wren density as the single covariate for each time period, shows the point estimates, and the grey envelope represents the 95% confidence interval.

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frequency which were not considered in our study. For instance, female nutritional state and food availability could influence nest attendance behaviour such that females with greater access to food resources spend less time off the nest (Chalfoun & Martin 2007). Because Marsh Wrens and Yellow-headed Blackbirds exploit similar food resources (Picman 1984), it is possible that Yellow-headed Blackbird off-bout frequency could be low in areas of high Marsh Wren density due to abundant food. This further emphasizes the need to evaluate the impact of Marsh Wren density on reproductive success and adult survival. Additionally, differences in nesting substrate and microhabitat characteristics at the nest-site can influence nest attendance (Conway & Martin 2000), although we contend that these differences were minimal at our study site because all nests were located in similar habitat. While ambient temperature has been shown by several studies to drive nest attendance in several bird species (Conway & Martin 2000, Walters *et al.* 2016), our study demonstrated a stronger influence of predation risk on nest attendance behaviour, a factor that could be controlled if needed through actions such as predator removal in order to increase reproductive output of birds, particularly those of conservation concern.

Although intriguing, our results could have been strengthened by our use of a control data logger to monitor ambient temperature rather than the nearby AWOS sensor. Although the AWOS sensor provides precise temperature readings, its location (approximately 25 km away) limits detection of small temperature fluctuations in the marsh that a control logger could have effectively captured. Such a control allows for greater precision in calculating on- and off-bouts, as in Walters *et al.* (2016). However, our results still demonstrate the efficacy of temperature data loggers for monitoring parental activity at nests, and illustrate how such data can be used to investigate changes in nest attendance behaviour in response to various threats to the nest. We suggest future studies utilize this technology to measure parental activity at nests, particularly if changes in parental activity and subsequent impacts on reproductive success are suspected in the study system, as this information could lead to a better understanding of predator impacts on lifetime reproductive output in birds.

It has been long known that Marsh Wrens depredate nests of many bird species. Our study is the first, however, to document changes in nest attendance behaviour in a species targeted by this aggressive nest predator. This finding, coupled with the already existing knowledge that these two species segregate breeding territories in co-occupied marshes (Leonard & Picman 1986, Harms & Dinsmore 2016), demonstrates behavioural plasticity of blackbirds as a function of the potential threat of Marsh Wrens to their nests. Behavioural plasticity in response to the threat of nest predation has been demonstrated by other species of songbirds with different types of predators (e.g. mammalian; Fontaine & Martin 2006) and by some species specifically in response to predation risk by other egg-puncturing species such as House Wren *Troglodytes aedon* (White & Kennedy 1997, Ghalambor & Martin 2000). Our study provides more evidence of the significance of nest predation in shaping reproductive strategies, even for a colonial-nesting species assumed to benefit from the added protection of other conspecifics near the nest.

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