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Central Nests are Heavier and Have Larger Clutches than Peripheral Nests in Cliff Swallow (*Petrochelidon pyrrohonota*) Colonies

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Running title: Within Colony Nest Site Selection and Clutch Size in Cliff Swallows

Predator avoidance is a major factor influencing nest site selection in colonial birds (Robinson 1985; Burger and Gochfield 1988; Lee and Walsh-McGee 1998). Cliff Swallows (*Petrochelidon pyrrohonota*) are common colonial nesting birds in summer in Arkansas (James and Neal 1986). They construct oblong mud nests mainly under bridges and overpasses. Old nests from previous years are frequently enhanced and reused. In some colonies, nests are in multiple horizontal tiers due to high demand for sites (Brown and Brown 1995). Colony selection in these swallows is closely related to the historical nesting success of the colony (Brown *et al*. 2000), but little is known of nest site selection within colonies.

Previous studies have documented snake predation in Cliff Swallow colonies, with nests located near the edge being more vulnerable to predation than those at the center of colonies (Brown and Brown 1987; Brown 1998; Czaplewski *et al*. 2012). Upon arrival at sites, the birds compete intensely for central nests, ostensibly because of increased risk of predation at peripheral nests (Brown and Brown 1995). In this study, we investigated if central nests are more coveted and preferred for reuse than peripheral nests in Cliff Swallow colonies. Since it is widely accepted that high-quality individuals occupy prime sites (Kokko 1999), we predicted that central nests will have higher clutch sizes than peripheral ones. If central nests are preferred for reuse, we predicted that these nests will have a higher mud mass, since old nests are augmented with new additions of mud. Accordingly, we tested two null hypotheses:

1. There is no significant difference in clutch size between central and peripheral nests within a colony, and
2. There is no significant difference in nest mass between central and peripheral regions of a colony.

During 2008, two Cliff Swallow colonies were observed near Fort Smith (Sebastian Co.), Arkansas. Both colonies were accessible by ladder and located on the undersides of small bridges over drainage canals. Nest contents were observed repeatedly throughout the nesting cycle (May-June) by using a dental mirror and flashlight as described in Brown and Brown (1996) and Leasure *et al*. (2010). In winter of 2012, one 33m-long site was used to measure mass of Cliff Swallow nests in various regions of the colony. This nest mass study was repeated in the same site in late summer of 2016 to augment sample size. Old nests were removed completely and the mass measured using a standard Triple-beam balance. The central region of the Cliff Swallow colony was designated arbitrarily as the middle 50% (16.5m) of the length of the colony, and the outer 50% of the region (25%, i.e., 8.25m, on each side) was designated as the peripheral region. Statistical analyses were performed using R (R core team 2016) and Statdisk (www.statdisk.org, Triola 2016).

Our results supported our hypotheses. Average clutch size in central nests (total 79 eggs) was 1.68 ± 1.25, 0-4 (mean ± STD, range) (n = 47 nests); average clutch size in peripheral nests (total 21 eggs) was 0.58 ± 1.13, 0-4 (mean ± STD, range) (n = 36 nests). This difference was significant (Wilcoxon Rank-Sum Test Statistic = 3.68 > Critical Value 1.95, $P < 0.05$). Therefore, clutch size was significantly higher in central compared to peripheral nests, suggesting that central nests are occupied by more robust individuals than peripheral ones. Since we examined nest content repeatedly in May-June, we are certain that the lower egg numbers in peripheral nests was not a result of predation.

In both 2012 and 2016, central nests were significantly heavier than peripheral nests (Fig. 1). In 2012, mass (g) of central nests was 342.98 ± 164.42, 95.5-541.5 (mean ± STD, range) (n = 30 nests); mass of peripheral nests was 234.42 ± 119.94, 76.2-280.9 (mean ± STD, range) (n = 10 nests). This difference was significant ($t = 1.84$, $P < 0.05$). In 2016, central nests weighed 572 ± 179g, 259-1360 (mean ± STD, range) (n = 109 nests), and peripheral nests 511 ± 123, 246-830 (mean ± STD, range) (n = 86 nests). Again, the difference in the masses was statistically significant (t = 2.69, P = 0.003, one-tailed t-test). Nest mass was significantly higher in central compared to peripheral nests, suggesting that central nests are more reused than peripheral nests. Our nest masses data augments the previously reported information from only two nests (578 and 816 g; Emlen 1954). The low masses from 2012 may have been either due to inadequate sample size, or the fact that May 2012 was the third driest and the hottest May on record (National Oceanic and Atmospheric Administration 2017).

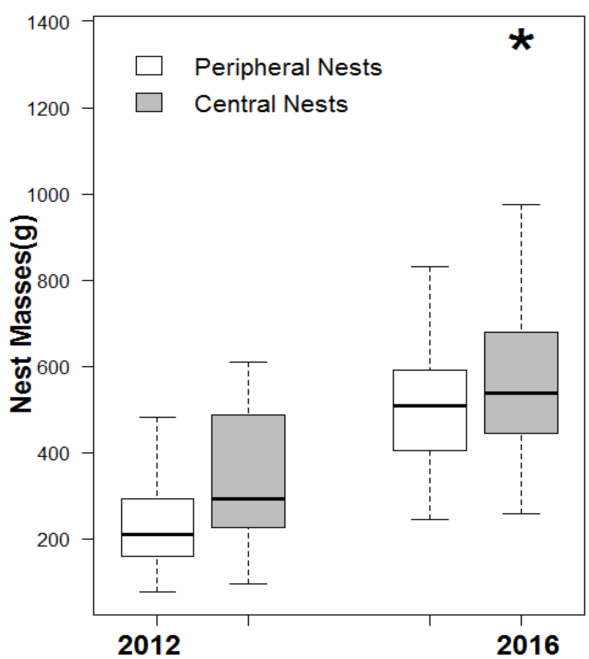

Fig. 1. Box plots comparing masses of central and peripheral nests within a colony for two seasons. The boxes represent the middle half of the data and the horizontal bars within boxes are medians. Except for the box with the outlier (*), the bottom and top whiskers represent minimum and maximum values, respectively.

Two other factors tend to suggest that central nests are preferred over peripheral nests. First, there were more central than peripheral nests in all three years of study. The proportion of central nests among all nests (0.56) was significantly greater than 0.5 in the three years combined (Test Statistic z = 2.36 > Critical z 1.64, p = 0.009; 95% Confidence Interval for the proportion is 0.52-0.63). Second, in 2016, there was just one set of 4 stacked nests at the periphery, compared to eight sets of 2-6 stacked nests in the center, indicating that birds crammed more nests (in multiple tiers) in the central zone than in the edge zones.

This study yields some insights into within-colony nest site selection and nesting success in Cliff Swallows. It suggests that there are advantages in choosing central nests over peripheral nests. Peripheral nests offer greater accessibility to predators, as is evident in Brown's (1998) description of bull snake (*Pituophis catenifer*) predation in a Nebraska colony: the snakes climb embankments on either sides of an overpass to gain access to a colony and start their predation on the extreme peripheral nests, progressively moving towards center. They eventually get satiated and stop predation, thus sparing the more interior nests. Owing to this predation pressure on peripheral nests, it is possible that the central and more coveted nesting sites are taken by more dominant and experienced individuals and/or early spring migrants (Møller 1994; Kokko 1999), forcing less experienced birds to take up more risky peripheral sites (see Petit and Petit 1996). Dominant birds may secure interior nest locations and invest more energy for nest construction, resulting in bigger and sturdier nests, than less dominant individuals. Also, since the cluttered interior nests share some walls, less energy may be required to finish a nest, and the birds can energetically afford augmenting other parts of the mud nests. This may also explain why clutch size is higher in central nests: more experienced, ostensibly robust, individuals allocate more of their energies into egg production than relatively weak and less experienced birds that may be forced to occupy the suboptimal edge nest sites.

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