

# Nest Site Co-Occupancy and Nest Parasitism of Purple Martins by White-Throated Swifts within Bridges in Sacramento, California

Daniel A. Airola, Conservation Research and Planning, 114 Merritt Way,  
Sacramento, CA 95864 d.airola@sbcglobal.net

Kevin Thomas, 4520 Vega Del Rio Dr, Fair Oaks, CA 95628

Dan Kopp, 8295 La Riviera Drive, Sacramento, CA 95826

Stan Kostka, 28603 Kunde Road, Arlington, WA 98223

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Cavity-nesting birds defend their nest sites from conspecifics and individuals of other species, with established patterns of species dominance (Podulka et al. 2004). Cavity-nesting and nest-site defense enhance the reproductive success and fitness of nesting birds by providing a protected site for nesting and rearing young. These behaviors also discourage interspecific and intraspecific brood parasitism, which reduces the fitness of host nesting pairs (Rothstein and Robinson 1998).

Nest parasitism in birds takes several forms including obligate nest parasites, such as the Brown-headed Cowbird (*Mothothrus atar*) that only reproduce by parasitizing other species, and facultative parasites that attend their own nests but also parasitize other species or individuals of their own species (Payne 1998, Brown and Brown 1989). The mechanisms by which brood parasitism may evolve in bird species are of considerable interest (Hamilton and Orians 1965, Payne 1977, Lyon and Eadie 1991). Novel nesting circumstances that bring different species into close proximity may create new brood parasitism opportunities. When a species with a declining population is involved, co-occupancy of nest sites and brood parasitism also have the potential to detrimentally affect a species' conservation status (Kus 1999).

We document White-throated Swift (*Aeronautes saxatalis*) nest cavity co-occupancy and the first reported cases of swift brood parasitism of the Western Purple Martin (*Progne subis arboricola*) which occurred in overpasses and elevated freeways ("bridges") in Sacramento, California. We describe the circumstances, frequency, and potential effects of cavity co-occupancy and parasitism on this declining martin population.

The White-throated Swift and Purple Martin are both aerial insectivores that forage in open airspace (Brown and Tarof 2013, Ryan and Collins 2000).

The swift typically nests in cliff crevices but has expanded its population and range by colonizing bridges and other human structures (Ryan and Collins 2000). Swifts nest in many bridges within the Sacramento region, including those occupied by martins (Airola in press).

The Western Purple Martin (Baker et al. 2008) uses a variety of cavity-providing substrates in western North America, including tree cavities, nest boxes, niches in cliffs and caves, as well as buildings and other human structures (Brown and Tarof 2013, Airola and Williams 2008). Martins' nesting use of tree holes and buildings in the Central Valley of California was eliminated during the 1960s to 1970s, following the colonization and rapid population increase by the European Starling (*Sturnus vulgaris*; Airola and Grantham 2003, Airola and Williams 2008). The sole remaining Central Valley martin population in Sacramento transitioned to nesting in bridges in the 1960-70s and has declined by 88%, from 173 to 21 pairs during 2004-2019 (Airola and Kopp 2018, Airola in press).

We surveyed the Sacramento Purple Martin population by mapping their use of entrance holes on the undersides of bridges ("weep holes") for nesting and noting nesting behaviors over the nesting season (Airola and Grantham 2003). During our studies, we periodically observed use of the same bridge-chamber entrance holes by martins and White-throated Swifts. These novel observations could have various explanations, including nest site exploration, entry into the wrong hole by a nesting bird, or co-use of the chamber by both species. During 2007-2009, we used a pole-mounted video camera to monitor martin reproduction in Sacramento area bridges (Airola et al. 2008, Airola in press). Here, we report species interactions, co-occupation of nesting chambers by nesting pairs of both species, and occurrence of swift nestlings in Purple Martin nests, a form of brood parasitism.

## STUDY AREA

We conducted studies at 11 bridges that were occupied by nesting Purple Martins in Sacramento, California. Locations and of colony site characteristics are described by Leeman 2003 and Airola (in press). Occupied bridges are generally >70 m long and support a series of internal chambers that are 1.3-m tall, 2.5-m wide, and 3 to 15-m long (Airola and Grantham 2003). The interior of chambers often contained scattered framing and debris left during bridge construction. Each chamber is vented by two 18-cm diameter vertical weep-holes, with one located at each end of the chamber, through which martins and swifts access the chamber to use it for nesting (Kostka et al. 2003).

## METHODS

During 2007-2009, we surveyed White-throated Swift and Purple Martin nest site use as a part of regular monitoring of Sacramento martin colony sites (Airola et al. 2008, Airola and Kopp 2009, 2018). We mapped nest holes used

by both species during at least eight visits annually to bridge sites within the nesting season. For martins, we verified nesting use by observations of diagnostic nesting behaviors (i.e., carrying food to nests, removal of fecal sacs, juvenile begging, or by observing nestlings in nest holes; Airola and Grantham 2003). We could not detect food deliveries by swifts because they carry food within their mouths (Ryan and Collins 2000); and therefore we relied on visual or aural confirmation of the presence of nestlings and frequencies of hole use to indicate nesting use. To determine the extent of co-use of nest holes, we identified and counted the nest sites used by both species over the breeding season at six of the nine to 11 occupied colony sites occupied during 2007-2009. We also observed use of nest holes entrances by both species during trapping of martins at nest sites (Airola et al. 2006).

In 2007-2009, we conducted video monitoring of 92 Purple Martin nest sites (26 to 34/yr), at the following six bridge colony sites (with number of occupied martin nest sites monitored over the period): Arden (21), El Camino (11), I St. (23), S St. (22), 20th St. (5), and Roseville Rd. (10). (See Leeman et al. 2003 and Airola in press for colony locations.) This monitoring sampled 30%, 41%, and 29% respectively of total Sacramento martin nesting population in each of the three years (Airola and Kopp 2009). Generally, we conducted video recording surveys of the interiors of bridge chambers using infrared lighting to avoid alarming adults and young, followed by LED light to maximize visibility. We transferred video imagery to DVD format, and interpreted results by replaying them on a television or computer monitor. We identified nestling martins and their ages based on reference photos (Hill 1999). Swift young were identified based on a variety of obvious features, including head and bill size and shape, the light color of the neck, and wing length relative to body size. Young swifts were identified based on the presence of rectal flanges.

## RESULTS

### *Species Interactions*

We regularly observed aggressive encounters between Purple Martins and White-throated Swifts during hole-use mapping. The larger martins ( $\bar{x}$  mass = 52 grams at Sacramento colonies, Kostka, unpubl. data) were clearly dominant over the smaller swifts ( $\bar{x}$  mass = 33 grams; Ryan and Collins 2000). Most aggressive encounters occurred when swifts attempted to enter chambers when martins were inside. In such circumstances, martins often attacked swifts and drove them away, or occasionally to the ground, although we never observed evidence of injury or mortality. Less frequently, swifts attacked martins entering nest holes and drove them to the ground.

### *Co-Use of Nesting Chambers for Nesting*

Co-occurrence of Purple Martin and White-throated Swift nests in the same cavity are based on observations during hole use mapping, trapping, and video monitoring.

During hole-use mapping, we observed co-use of six (6%) of 96 martin nest sites at the six colonies monitored for both species during 2007-2009. Co-use occurred at four of the six colonies, with co-use occurring at 0-12% of martin nest sites at various colonies. Holes with co-occurrence represented a small, but undetermined, proportion of all the holes used by swifts.

During trapping for banding at the Sutterville colony site in 2007, we observed co-use of a hole where martins had been confirmed nesting. We had covered a martin nest hole entrance with a pole mounted hoop net (Airola et al. 2006, 2008) after a martin had entered the nest hole. A swift repeatedly attempted to enter the netted hole and bounced off the net. When we moved the net aside, the swift flew up into the hole. The intensity of attraction of the swift to this hole in the middle of the nesting season indicates that the nesting chamber was used by both a martin pair and swift pair to access nests in the same bridge chamber.

During video monitoring of nest sites, we observed White-throated Swifts within three (5%) of 66 bridge chambers occupied by Purple Martin nesting pairs in 2007-2009. At one site we observed a swift nest with nestlings and a swift nestling in a martin nest. We observed swift nests with swift nestlings at two other chambers with occupied martin nests. We also observed a single swift nestling in martin nests in two other chambers where we did not observe a swift nest (see *Occurrence of Swift Nestlings in Martin Nests*).

All nest sites observed through video monitoring to be co-used by both species were at the Arden colony. The Arden site contained a total of 56 bridge chambers accessible to martins and swifts (Airola in press). Martins occupied only 9-12 (16-21%) of the available chambers during this period.

#### *Occurrence of Swift Nestlings in Martin Nests*

As described below, we observed three instances of a single swift nestling within different Purple Martin nests during video monitoring of bridge chambers at the Arden colony site during 2007-2008. In two instances, no swift nest was found within either chamber, although visual obstructions within the bridge compartment precluded an exhaustive survey. In the third instance, a swift nest in the compartment contained two swift nestlings of the same size as the single swift nestling in the martin nest.

*Hole D5, 2007.* We first observed a swift nestling in this chamber during the third video survey of the nest site on 30 June. Although a swift nest was not observed within the chamber, it could have been undetected due to the presence of visual obstructions. The lack of a swift nestling in the martin nest

during surveys over the previous two weeks suggests that a swift nest was present and that the swift nestling moved into the martin nest. The site was not monitored after 30 June.

*Hole F2, 2008.* We first observed a swift nestling on 14 June during the second video survey of the nest site, when martin nestlings were 11 days old. The swift nestling was similar in size to the martin young. No swift nestling had been observed in the martin nest when it was monitored six days earlier. The martin nest subsequently failed, and we observed a swift nest in the same chamber on 23 June and 1 July. The swift nest included two young at an age that would have been similar to that of the swift in the martin nest. This information suggests that the swift young may not have hatched in the martin nest, but rather moved to the martin nest after hatching in the swift nest.

*Hole C6, 2008.* We observed a swift nestling in a martin nest on 14 and 23 June, when martins were about 10 and 19 days old, respectively. No swift had been noted on 8 June, however, identification of 4-day-old young present then would have been difficult. No swift nest was observed in this chamber, but visual obstruction could have prevented detection of one. A swift pair was confirmed nesting in this chamber in 2007. Thus, it is uncertain whether this nestling came from an egg that a swift laid in the martin nest or if it wandered to the martin nest from an undetected swift nest.

#### *Effects of Co-Occupancy and Brood Parasitism*

The impact of nesting chamber co-occupancy and possible brood parasitism on the host species can be assessed based on the frequency of occurrence and the potential negative effect on reproduction when it occurs. The worst-case effect would be that each swift in a martin nest reduced the productivity of that nest by one martin young. Under this assumption, and assuming an overall martin productivity during this period of young per nests (Airola in press) occurrence of young swifts in three of 92 video-monitored nests would have reduced productivity by only 2% (i.e., three martin young replaced/[92 nests x 1.64 young/nest]).

#### DISCUSSION

Our findings demonstrate for the first time that Purple Martins and White-throated Swifts co-occupy nesting cavities and that swift nestlings appear to parasitize martins by moving from their natal nests to martin nests. A swift nestling observed within a martin nest on two dates nine days apart (hole C6, 2008) strongly suggests that swift nestlings are cared for by martin adults. Our observations do not allow us, however, to determine if swifts laid eggs in martin nests.

Observation of regular agonistic interactions at nest sites between Purple Martins and White-throated Swifts indicates that some degree of interspecific territoriality reduces the incidence of co-use of the nest chambers by the two

species. The abundance of nesting sites within bridges also likely reduces the need for frequent co-occupancy of nest chambers.

Several factors may facilitate co-occurrence of the species. The large size of individual bridge chambers allows co-occupying pairs to nest relatively far apart. Wooden framing material and other construction debris left within chambers provides visual obstructions between nesting pairs, which may reduce aggression. Finally, martin perch sites at urban colonies, from which they defend nest sites, are often located away from the nest hole entrance (up to 40-95 m away at monitored colonies; Airola in press), which may reduce the effectiveness of martin nest site defense against swifts.

Nest hole mapping indicates that nesting cavity co-use is widespread but infrequent at Sacramento Purple Martin colony sites. The concentration of all video-confirmed co-occurrences at the Arden colony site appears to be anomalous, as we have no causes to which we can attribute this phenomenon.

The overall similarity in the rates of co-occurrence derived from hole use mapping (6%) and video survey of nest cavities (5%) demonstrates that both methods similarly depict this phenomenon. The co-occupancy rate we report from video monitoring should be viewed as a minimum, because visual obstructions within the nesting chambers, as well as the swift's tendency to locate nests in narrow spaces, could have prevented us from observing all nests in these chambers. Assuming that those chambers in which we observed swifts in martin nests where we did not observe a swift nest actually contained a nest, the co-occupancy rate from video monitoring would be 8%.

Two possible explanations exist for the observation of White-throated Swift young in Purple Martin nests: brood parasitism through egg laying by adult swifts in martin nests or wandering by post-hatching swift young from swift nests to martin nests. The presence of a swift nest in the same chamber as a martin nest at one site in the same year suggests that the swift nestling may have moved to the martin nest. The presence of nestlings in two martin nests in chambers where we did not find a swift nest suggests the possibility that swift adults parasitized martin nests through egg-laying. We cannot, however, dismiss the possibility that swift nests were present in these chambers and not observed, especially considering that one site (C6) had a swift nest there the previous year.

Regardless of the mechanism, the occurrence of nestling White-throated Swifts in Purple Martin nests constitutes a form of nest parasitism, which has not been reported previously. Our unique results add to the knowledge of the behavioral plasticity of these ecologically similar aerial insectivores.

The Sacramento Purple Martin population declined by 50% (from 141 to 70 nesting pairs) while we monitored nests in 2006 to 2009 (Airola and Kopp

2009). The martin nesting population has continued to decline since then to only 21 nesting pairs in 2019, a cumulative 88% decline since 2004 (Airola, in press).

Understanding the causes of the martin nesting population decline in Sacramento is critical to enacting effective conservation efforts. Our results indicate that White-throated Swift co-occupancy of bridge nesting chambers used by Purple Martins, and nest parasitism from either swift egg laying or nestlings wandering into martin nests, did not substantially reduce reproduction of the population and thus did not contribute substantially to martin population decline during that period. Largely through elimination of potential factors, the martin population decline is now considered most likely due to a reduction in larger insect prey and resulting low reproduction caused by increased use of neonicotinoid pesticides (Airola et al. 2004, Airola in press).

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