# Sexually dimorphic leading-edge serrations evolved in silent swallows

Running title: **leading-edge serrations in silent swallows**

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Number of table 1

Number of figures 2

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**Abstract**

Leading-edge serrations are specialized feather structures, mitigating acoustic noise during foraging flight in owls, and have been extensively studied and applied to man-made noise-reducing structures. Similar structures occur in other avian species, such as swallows, although the ecological functions of the serrations in these species remain unclear. I conducted macroevolutionary analyses of hirundines (subfamily: Hirundininae), in which leading-edge serrations evolved multiple times, to examine their evolution in relation to vocal activity. I found that silent hirundines showed a higher probability of possessing leading-edge serrations, indicating that leading-edge serrations of swallows serve some functions associated with acoustics as in owls. I also found that silent vocal activity accompanied loss of song, a well-known acoustic sexual signal, but not with sexual plumage dimorphism, indicating that not sexual selection in general but sexual selection on acoustic traits matters. These findings explain sexually dimorphic leading-edge serrations, a unique characteristic in these diurnal visually-foraging birds: stealth males rather than noisy males would be favored. Although leading-edge serrations in hirundines would serve acoustic functions like nocturnal birds such as owls, they might serve a unique sexual function.

**Keywords:** aeroacoustics, leading-edge comb, sexual plumage dimorphism, vocalization

Leading-edge serrations, also known as leading-edge comb, are curved hooklets on the leading edge of the primary feathers in owls (reviewed in Wagner et al. 2017; Jaworski & Peake 2020; Terrill & Schultz 2023). This structure has intensively been studied and shown to reduce noise in flight and thus can be adaptive to improve their hearing during foraging flights and to avoid detection by prey (e.g., Rao et al. 2017; reviewed in Wagner et al. 2017; Clark et al. 2020), which is now applied to man-made structure to reduce acoustic noise (e.g., pantograph of Japanese Shinkansen trains: reviewed in Wagner et al. 2017). However, owls are not the only animals that possess leading-edge serrations (Clark et al. 2020); similar structures, albeit somewhat smaller and less curved, can be found in other avian groups, including frogmouths (family: Podargidae) and swallows (family: Hirundinidae), and the function of the serrations in these birds remains unknown (reviewed in Clark et al. 2020).

In swallows (family: Hirundinidae), leading-edge serrations are known to have evolved independently at least twice, once in rough-winged swallows (genus: *Stelgidopteryx*) and the other in saw-wings (genus: *Psalidoprocne*), evident from their English names (Turner & Rose 1994). Similar to other species with leading-edge serrations (see above), these structures might serve to mitigate flight noise. However, different from the majority of owls and frogmouths, swallows are diurnal, visually-foraging birds, and, furthermore, they possess sexually dimorphic leading-edge serrations, in which males, but not females, possess serrations (reviewed in Turner & Rose 1994). This suggests that they might serve somewhat different functions than sexually monomorphic leading-edge serrations found in mainly nocturnal, acoustic predators (i.e., owls and frogmouths; e.g., see Roulin et al. 2013). In fact, although its function has not been shown, several hypotheses are proposed to explain the evolution of this sexually dimorphic structure (reviewed in Lunk 1962); for example, a clasping structure for copulation, to prevent slipping from females (Steinbacher 1931) and a means for generating non-vocal sound production during courtship or territorial chases

(Lunk 1962; de Jong 2020). It is also unclear, if leading-edge serrations are adaptive, why only a few swallows possess leading-edge serrations (Steinbacher 1931; Lunk 1962), which sharply contrasts with owls in which virtually all owl species possess some forms of leading-edge serrations (e.g., Le Piane & Clark 2022).

Here, I studied ecological correlates of leading-edge serrations in swallows and martins (subfamily: Hirundininae). Because leading-edge serrations evolved at least two times (see above), phylogenetic comparative approaches can be used to find out ecological factors promoting the evolution of leading-edge serrations. Of several hypotheses proposed, the most promising hypothesis is that, as in owls, leading-edge serrations serve a function to reduce noise in flight (see above). Then, I can predict that vocal activity would be negatively linked to the evolution of leading-edge serrations. This is because reducing acoustic noise cannot make sense when birds continue to vocalize. I also studied whether leading-edge serrations and its ecological correlates are associated with proxies of sexual selection to clarify the possible role of sexual selection on the evolution of sexually dimorphic leading-edge serrations in hirundines.

## Methods

### Data collection

As before (e.g., Hasegawa & Arai 2020a,b), information on morphological traits (i.e., wing length) and migratory habits (i.e., migrant or not) was obtained from Hasegawa & Arai (2020b), which was derived from Turner & Rose (1994). I also collected data concerning the presence/absence of song, which is usually sung by males, based on the descriptions in the “voice” category of each species (i.e., whether or not “song” is noted in the species) in Turner & Rose (1994). Further details are available elsewhere (Hasegawa 2023). Likewise, I collected data concerning the vocal activities (silent or not). Species with “silent”, “quiet” or similar expression noted in the “voice” category was regarded as silent species and other species were regarded as non-silent species

(unless data was unavailable).

As before (e.g., Hasegawa & Arai 2022), sexual dimorphism in overall plumage characteristics as a proxy of sexual selection was obtained from Turner & Rose (1994). Concerning a proxy of extrapair mating opportunities (frequent/rare), I used incubation type (female-only versus biparental incubation) from a previous study (Hasegawa & Arai 2020b), sourced mainly from Turner & Rose (1994). Incubation type was tightly linked to extrapair paternity both within and between species in this clade (Magrath & Elgar 1997; Hasegawa & Arai 2020b). The dataset used can be found in Table S1.

**Statistics**

A Bayesian phylogenetic mixed model using a binomial error distribution was used to examine the presence/absence of leading-edge serrations. As in previous studies (e.g., Hasegawa & Arai 2020a,b; Hasegawa 2023), potential confounding factors, body size [measured via log(wing length)] and migratory habit, were included alongside vocal activity in the model. To account for phylogenetic uncertainty, I fit the models to each tree and applied a multimodel inference (e.g., Garamszegi & Mundry 2014), using 1000 alternative trees for swallows from birdtree.org (see Jetz et al. 2012, 2014; also see Sheldon et al. 2005 for an original phylogeny on swallows). 1000 trees are sufficient to control for phylogenetic uncertainty (Rubolini et al. 2015). The residual variance was set at 1, in accordance with recommendations for categorical dependent variables (de Villemereuil et al. 2013). I derived the mean coefficients, 95% credible intervals (CIs) based on the highest posterior density, and Markov chain Monte Carlo (MCMC)-based P-values, together with the phylogenetic signal (de Villemereuil & Nakagawa 2014). All analyses were conducted in R ver. 4.1.0 (R Core Team 2021) using the “MCMCglmm” function in the “MCMCglmm” package (ver. 2.29; Hadfield 2010). I ran the analysis for 140,000 iterations, with a burn-in period of 60,000 and a thinning interval of 80 for each

tree. The reproducibility of the MCMC simulation was assessed by calculating the Brooks–Gelman–Rubin statistic (Rhat), which must be <1.2 for all parameters (Kass et al. 1998), by repeating the analyses three times.

A discrete module in BayesTraits (Pagel & Meade 2006) was used to examine evolutionary transitions among states with vocal activities (silent or not) and the presence/absence of leading-edge serrations. I ran for 1,010,000 iterations with a burn-in period of 10,000 and a thinning interval of 1000 (note that the phylogenetic tree was randomly chosen from 1000 trees in each iteration). I denoted means as the representatives of each transition rate. The reproducibility of the MCMC simulation was assessed using the Brooks–Gelman–Rubin statistic (Rhat), which must be <1.2 for all parameters (Kass et al. 1998), by repeating the analyses three times. Bayes factor was calculated via the stepping stone sampler in BayesTraits, comparing the marginal likelihood of a dependent model that assumed correlated evolution of the two traits (i.e., leading-edge serrations and vocal activity) to that of an independent model assuming independent evolution. Bayes factors of >2, 5–10, and >10 indicate positive, strong, and very strong evidence of correlated evolution, respectively (Kass & Raftery 1995; BayesTraits Manual Ver. 3).

## Results

### Leading-edge serrations and silent vocal activity

Probability of possessing leading-edge serrations was significantly explained by the vocal activity of swallows (Table 1): after controlling for phylogeny, hirundines with relatively silent vocal activities showed a higher probability of possessing leading-edge serrations (Fig. 1). Two covariates, body size measured as log(wing length) and migratory habits (migrant or not) were non-significant (Table 1).

When examining evolutionary transitions among states (i.e., presence/absence of leading-edge serrations and silent/non-silent vocal activities), I found strong support

156 for correlated evolution between these two state variables (n = 69, Bayes Factor = 8.49).
157 Leading-edge serrations evolved from the state with silent vocal activities, but virtually
158 did not evolve from the state with non-silent vocal activities (Fig. 2), though the results
159 should be carefully treated as leading-edge serrations evolved only a few times (Fig. 1).
160

161 **Silent vocal activity and proxies of sexual selection**

162 Silent species were less likely to have song (Bayesian phylogenetic mixed model with a
163 binomial error distribution: Coefficient = -3.09, 95% CI = -5.23, -1.08, $P_{MCMC}$ = 0.001,
164 phylogenetic signal = 0.24). In contrast, silent vocal activity had no detectable
165 relationship with sexual plumage dimorphism/monomorphism, a well-known proxy of
166 sexual selection (Bayesian phylogenetic mixed model with a binomial error distribution:
167 Coefficient = -0.04, 95% CI = -2.17, 2.08, $P_{MCMC}$ = 0.97, phylogenetic signal = 0.38).
168 Likewise, silent vocal activity had no detectable relationship with another proxy of
169 sexual selection in this clade, opportunity for extrapair matings measured as incubation
170 type, although the sample size for this analysis was reduced to 41 (Bayesian
171 phylogenetic mixed model with a binomial error distribution: Coefficient = -0.62, 95%
172 CI = -3.47, 2.15, $P_{MCMC}$ = 0.66, phylogenetic signal = 0.40). When silent vocal activity
173 was replaced by each of these variables, the presence of leading-edge serrations was not
174 significantly explained by these variables (i.e., song: $P_{MCMC}$ = 0.10; sexual plumage
175 dimorphism: $P_{MCMC}$ = 0.87; incubation type: $P_{MCMC}$ = 0.08, though this time migratory
176 species had higher probability of possessing leading-edge serrations than others, $P_{MCMC}$
177 < 0.01, perhaps because two non-migratory *Psalidoprocne* species with leading-edge
178 serrations were excluded from dataset due to the missing data, n = 41; details not
179 shown).
180

181 **Discussion**

182 The main finding of the current study is that leading-edge serrations evolved from

183 relatively silent hirundines, supporting that leading-edge serrations serve a function
184 associated with acoustics. Silent vocal activity evolved in a limited number of branches,
185 mostly in relatively young ones (Fig. 1), explaining the limited occurrence of
186 leading-edge serrations in hirundines. Although the current study does not clarify the
187 exact acoustic function, they may reduce noise in flight as found in owls and in artificial
188 wing models (e.g., Rao et al. 2017; see Introduction).

189 I also found that silent vocal activity had no detectable association with proxies
190 of sexual selection, i.e., sexual plumage dimorphism and opportunity for extra-pair
191 matings, and thus silent vocal activities would not result from weak (or intense) sexual
192 selection in general. Rather, silent vocal activity was associated with the absence of
193 male song, a conspicuous acoustic sexual signal (see Hasegawa 2023 for ancestral
194 character reconstruction of song in hirundines), indicating selection favors silent males
195 in these species. As selection sometimes favors muting in acoustic species accompanied
196 with deformed sound-producing structures in males (e.g., Hawaiian crickets; Pascoal et
197 al. 2014), selection for silent males might favor deformed leading-edges in males, which
198 engage in courtship in flight and territorial chases. Although this explanation assumes
199 viability cost of conspicuous sounds, possibly due to predation and other interspecific
200 interactions (e.g., competition over nest sites), silent flight activity might be directly
201 sexually selected. For example, it could aid in avoiding male aggression or female
202 evasions to succeed within-pair reproduction or extra-pair mating (e.g., see Hasselquist
203 & Bensch 1991 for an example of such "silent sneaking" in birds). In fact, this
204 explanation is more likely than the predator avoidance explanation (see above), because
205 even without leading-edge serrations, flight noise is inaudible from a distance (Wagner
206 et al. 2017). Leading-edge serrations would be functional only in a close-range, as in
207 intraspecific interaction. Of course, I cannot exclude the possibility that, as in owls (see
208 Introduction), hirundines use leading-edge serrations to reduce noise in foraging flight,
209 but this hypothesis alone cannot explain sexual dimorphism in leading-edge serrations,

and thus insufficient to explain the overall pattern of macroevolution of leading-edge serrations in hirundines. Serrations are thought to mitigate flight noise just before landing, which is corresponding to the final portion of hunting in owls (Wagner et al 2017; Clark et al. 2017) but this does not align with aerial foraging in hirundines (Turner & Rose 1994).

An alternative explanation of the observed pattern is that leading-edge serrations are used for non-vocal sound production during courtship or territorial chases (Lunk 1962; de Jong 2020). Silent vocal activity might be a pre-condition for the evolution of non-vocal acoustic communication. Although this is a fascinating idea, there is no evidence that leading-edge serrations can produce non-vocal sounds and thus is an unlikely explanation on the basis of an enormous amount of evidence that serrations reduce, rather than increase, acoustic noise (see Introduction). It is, however, possible that leading-edge serrations are a device to reduce noise to increase the detectability of seemingly non-vocal, subtle sounds reported in swallows with leading-edge serrations (i.e., genus: *Stelgidopteryx* and *Psalidoprocne*: Turner & Rose 1994; de Jong 2020), though we still need to identify the mechanisms of the possible non-vocal sounds.

In summary, I demonstrated here that leading-edge serrations co-evolved with silent vocal activities. The current study is the first macroevolutionary analyses of sexually dimorphic leading-edge serrations. Since silent vocal activities are linked to the loss of song, a well-known acoustic sexual signal, changing direction or target of sexual selection (and its relative importance to viability selection: see below) would explain sexually dimorphic expression of leading-edge serrations, which remains to be demonstrated using manipulative experiments (e.g., removal of serrations). Thus, in hirundines, a diurnal visually-oriented foragers, sexual selection might be involved in the evolution of leading-edge serrations, different from acoustic foragers like owls and other nocturnal birds, in which sexually monomorphic leading-edge serrations would

provide viability advantage for capturing prey. For swallows that are hyperaerial birds, flight costs associated with leading-edge serrations (sensu Le Piane & Clark 2022; also see Rao et al. 2017 for reduced lift:drag ratio in serrated wings) might prevent females from evolutionarily maintaining male-like serrations, which is likely the case but should be tested in future.

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**Author contributions:** I performed data analysis and wrote the manuscript alone.

**Availability of data and materials:** The data sets supporting this article are uploaded as Table S1, which is also available from osf.io.

**Conflict of interest:** I have no competing interests.

**Animal welfare note:** This comparative study does not include any treatments of animals, as all the information was gathered from bodies of literature.

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**Table 1** Multivariable Bayesian phylogenetic mixed model with a binary error distribution predicting the presence/absence of leading-edge serrations in relation to vocal activities and covariates (n = 69) in swallows and martins (Aves: Hirundininae).

| Variables | Coefficient [95% CI] | $P_{MCMC}$ |
|---|---|---|
| Intercept | 36.35 [-60.36, 138.33] | 0.45 |
| log(wing length) | -9.44 [-31.45, 11.49] | 0.36 |
| Migration (non-migrant = 0, migrant = 1) | 1.40 [-2.67, 5.60] | 0.48 |
| Vocal activity (non-silent = 0, silent =1) | **4.79 [0.88, 8.96]** | **<0.01** |
| | Mean phylogenetic signal = 0.51 | |

Model-averaged coefficients and 95% credible intervals (CIs) are shown.

Bold indicates significant variables (i.e., $P_{MCMC} < 0.05$).

Figure legends

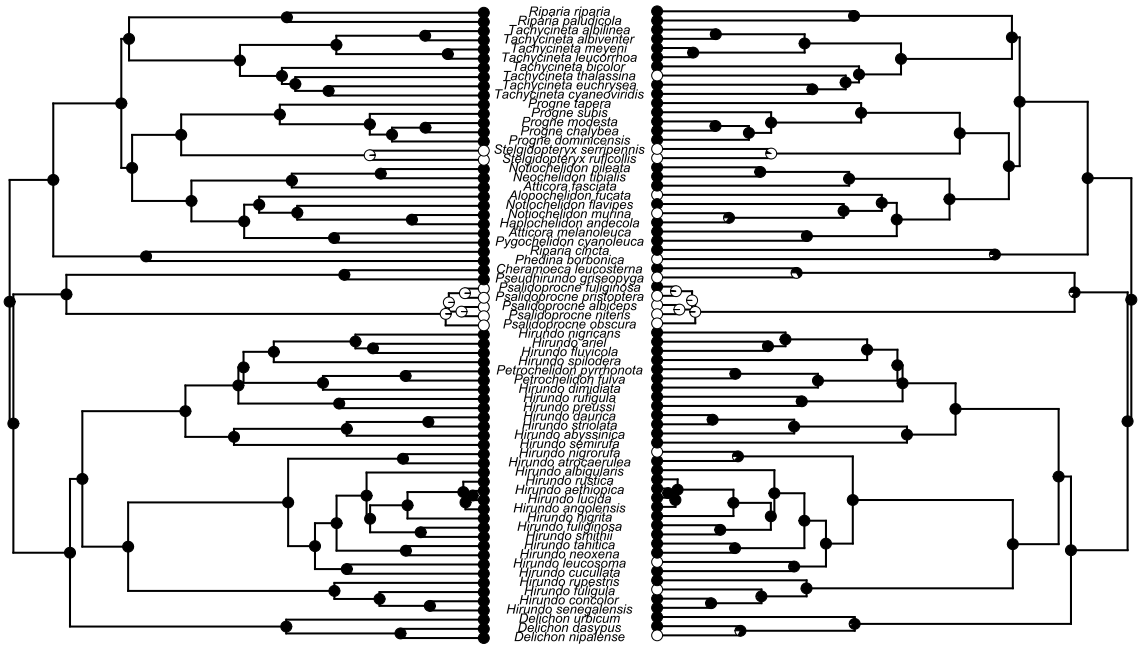


**Fig. 1** An example of ancestral character reconstruction of the leading-edge serrations (left) and of silent vocal activity (right) in swallows and martins (Aves: Hirundininae). Left side: presence and absence of leading-edge serrations are indicated by white and black circles, respectively; silent and non-silent vocal activity are indicated by white and black circles, respectively. The proportions of white and black at the nodes indicate the probability of the ancestral state. Here, I used the functions “ace” in the R package “ape” (with model = “ER”, i.e., an equal-rates model; Paradis et al. 2005) and “plotTree” in the R package “phytools” (Revell 2012) for ancestral character reconstruction.

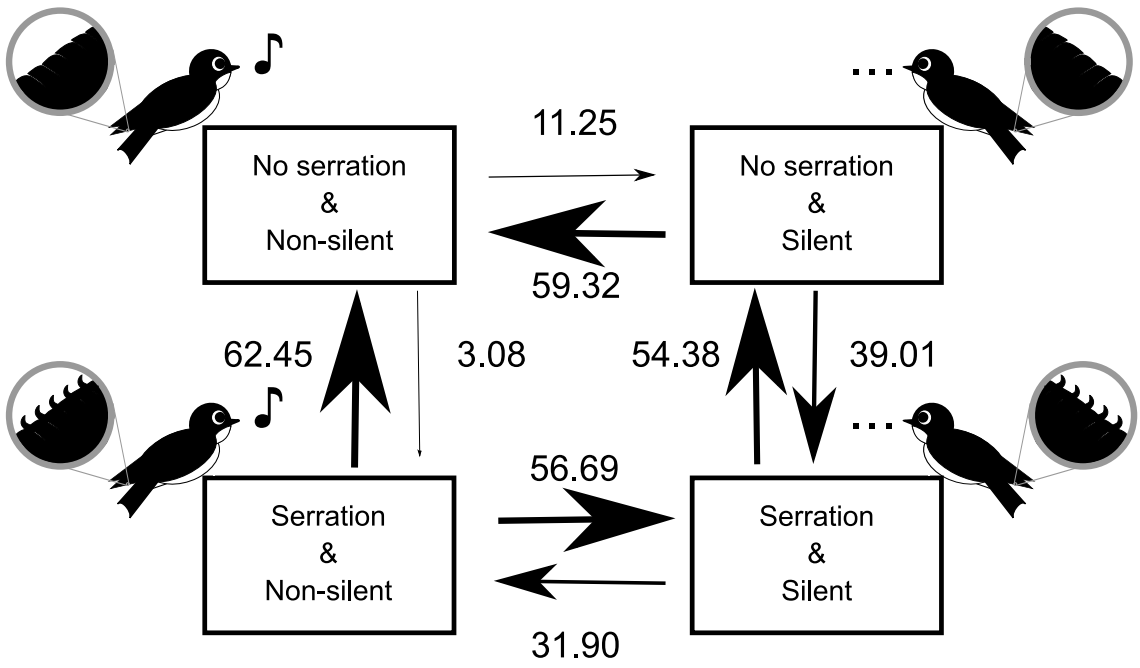


**Fig. 2** The most likely evolutionary transitions between states with the presence/absence of leading-edge serrations and the silent/non-silent vocal activity (see illustrations beside each state) in swallows and martins (Aves: Hirundininae). Numbers next to arrows, represented by arrow size, indicate transition rates between pairs of states. Leading-edge serrations of swallows are illustrated by referring to fig. 6 in de Jong (2020).

393 **Table S1** Dataset of the current study (n = 69).

| Scientific Name | Serrations | Wing length | Migratory habit | Silent/non-silent vocalization | Presence/absence of song | Sexual plumage dimorphism | Incubation type† |
|---|---|---|---|---|---|---|---|
| *Neochelidon tibialis* | 0 | 85 | 0 | 0 | 0 | 0 | NA |
| *Alopochelidon fucata* | 0 | 100 | 1 | 1 | 0 | 0 | NA |
| *Stelgidopteryx ruficollis* | 1 | 109 | 1 | 1 | 0 | 0 | 1 |
| *Stelgidopteryx serripennis* | 1 | 110 | 1 | 1 | 0 | 0 | 1 |
| *Tachycineta bicolor* | 0 | 119 | 1 | 0 | 1 | 1 | 1 |
| *Tachycineta albilinea* | 0 | 97 | 0 | 0 | 1 | 0 | NA |
| *Tachycineta albiventer* | 0 | 104 | 1 | 0 | 1 | 0 | NA |
| *Tachycineta thalassina* | 0 | 122 | 1 | 1 | 0 | 1 | 1 |
| *Tachycineta leucorrhoa* | 0 | 115 | 1 | 0 | 1 | 0 | 1 |
| *Tachycineta meyeni* | 0 | 110 | 1 | 0 | 1 | 0 | 2 |
| *Tachycineta cyaneoviridis* | 0 | 115 | 0 | 0 | 0 | 1 | 1 |
| *Tachycineta euchrysea* | 0 | 106 | 0 | 0 | 0 | 1 | NA |
| *Notiochelidon murina* | 0 | 111 | 0 | 1 | 1 | 0 | NA |
| *Notiochelidon flavipes* | 0 | 90 | 0 | 0 | 0 | 0 | 2 |
| *Notiochelidon pileata* | 0 | 95 | 0 | 0 | 1 | 0 | NA |
| *Pygochelidon cyanoleuca* | 0 | 94 | 1 | 0 | 1 | 0 | 2 |
| *Atticora fasciata* | 0 | 101 | 0 | 0 | 1 | 0 | NA |
| *Atticora melanoleuca* | 0 | 93 | 0 | 0 | 0 | 0 | NA |
| *Progne tapera* | 0 | 130 | 1 | 0 | 1 | 0 | 1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Progne subis* | 0 | 145 | 1 | 0 | 1 | 1 | 1 |
| *Progne chalybea* | 0 | 131 | 1 | 0 | 1 | 1 | 1 |
| *Progne dominicensis* | 0 | 143 | 1 | 0 | 1 | 1 | NA |
| *Progne modesta* | 0 | 125 | 1 | 0 | 1 | 1 | NA |
| *Riparia paludicola* | 0 | 104 | 0 | 0 | 1 | 0 | 2 |
| *Riparia riparia* | 0 | 107 | 1 | 0 | 1 | 0 | 2 |
| *Riparia cincta* | 0 | 130 | 1 | 0 | 1 | 0 | NA |
| *Psalidoprocne fuliginosa* | 1 | 104 | 0 | 0 | 1 | 0 | NA |
| *Psalidoprocne albiceps* | 1 | 102 | 1 | 1 | 0 | 1 | 2 |
| *Psalidoprocne pristoptera* | 1 | 106 | 1 | 1 | 1 | 0 | 1 |
| *Psalidoprocne obscura* | 1 | 96 | 0 | 1 | 1 | 1 | NA |
| *Psalidoprocne nitens* | 1 | 93 | 0 | 1 | 0 | 0 | NA |
| *Cheramoeca leucosterna* | 0 | 102 | 0 | 0 | 1 | 0 | NA |
| *Pseudhirundo griseopyga* | 0 | 97 | 0 | 1 | 1 | 0 | NA |
| *Phedina borbonica* | 0 | 116 | 0 | 1 | 1 | 0 | 1 |
| *Hirundo rupestris* | 0 | 130 | 1 | 0 | 1 | 0 | 1 |
| *Hirundo fuligula* | 0 | 129 | 0 | 1 | 1 | 0 | 2 |
| *Hirundo concolor* | 0 | 106 | 0 | 0 | 1 | 0 | 2 |
| *Hirundo rustica* | 0 | 124 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo lucida* | 0 | 111 | 0 | 0 | 1 | 0 | NA |
| *Hirundo angolensis* | 0 | 119 | 0 | 0 | 1 | 0 | NA |
| *Hirundo tahitica* | 0 | 105 | 0 | 0 | 1 | 0 | 1 |
| *Hirundo neoxena* | 0 | 112 | 0 | 0 | 1 | 0 | 1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Hirundo albigularis* | 0 | 128 | 1 | 0 | 1 | 1 | NA |
| *Hirundo aethiopica* | 0 | 106 | 0 | 0 | 1 | 0 | 1 |
| *Hirundo smithii* | 0 | 110 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo nigrita* | 0 | 106 | 0 | 0 | 1 | 0 | 1 |
| *Hirundo leucosoma* | 0 | 99 | 0 | 1 | 0 | 0 | NA |
| *Hirundo dimidiata* | 0 | 102 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo atrocaerulea* | 0 | 113 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo nigrorufa* | 0 | 112 | 1 | 1 | 1 | 1 | NA |
| *Hirundo cucullata* | 0 | 125 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo abyssinica* | 0 | 106 | 1 | 0 | 1 | 1 | 1 |
| *Hirundo semirufa* | 0 | 132 | 1 | 0 | 1 | 0 | 1 |
| *Hirundo senegalensis* | 0 | 144 | 0 | 0 | 1 | 0 | NA |
| *Hirundo daurica* | 0 | 124 | 1 | 0 | 1 | 0 | 2 |
| *Hirundo striolata* | 0 | 124 | 0 | 0 | 1 | 0 | NA |
| *Hirundo preussi* | 0 | 95 | 0 | 0 | 1 | 0 | NA |
| *Hirundo rufigula* | 0 | 97 | 1 | 0 | 1 | 0 | 2 |
| *Hirundo spilodera* | 0 | 111 | 1 | 0 | 0 | 0 | 2 |
| *Hirundo fuliginosa* | 0 | 88 | 0 | 0 | 1 | 1 | NA |
| *Petrochelidon pyrrhonota* | 0 | 109 | 1 | 0 | 1 | 0 | 2 |
| *Haplochelidon andecola* | 0 | 115 | 0 | 0 | 1 | 0 | NA |
| *Petrochelidon fulva* | 0 | 102 | 1 | 0 | 1 | 0 | 2 |
| *Hirundo fluvicola* | 0 | 91 | 1 | 0 | 1 | 0 | 2 |
| *Hirundo ariel* | 0 | 91 | 1 | 0 | 1 | 0 | 2 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Hirundo nigricans* | 0 | 107 | 1 | 0 | 1 | 0 | NA |
| *Delichon urbicum* | 0 | 110 | 1 | 0 | 1 | 0 | 2 |
| *Delichon dasypus* | 0 | 108 | 1 | 0 | 1 | 0 | 2 |
| Delichon nipalense | 0 | 95 | 0 | 1 | 0 | 0 | 2 |

394 †Female-only incubation is denoted as 1 and biparental incubation is denoted as 2.

395 NA indicates data "Not Available."

396 See text for detailed information.