



Research

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A plumage patch signalling nest occupancy is shaped by social environment

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The cliff swallow (*Petrochelidon pyrrhonota*) is a colonial bird that nests in groups of different sizes. Adult cliff swallows have a prominent white forehead patch that we hypothesize functions as a signal of nest occupancy to mitigate costly nest intrusions, especially in crowded nesting colonies. To test this hypothesis, we measured variation in forehead patch area and brightness relative to sex, colony size and date of collection for 241 preserved specimens collected over 43 years. Additionally, we experimentally tested signal function by darkening the foreheads of nesting birds and observing intraspecific interactions. Consistent with a signalling role, we found that females had larger patches than males, patch area increased with colony size, and nests of birds with darkened forehead patches attracted significantly more visits from transient cliff swallows than did nests with no darkened owners. These results suggest that variation in social environment, both in space and time, as well as intersexual differences in incubation behaviour shape the evolution of this conspicuous plumage patch.

1. Introduction

Among animals, a signal is an action or feature of an individual that has evolved to influence the behaviour of a second individual receiver [1]. By definition, signals must be suitable for the environments involved in the signalling exchange [2]. A major aim in behavioural ecology is to understand the selective pressures that drive the evolution and maintenance of signals [3,4].

The social environment in which signalling occurs can affect signal transmission, efficacy and its costs and benefits; therefore, the form that a signal takes may evolve in response to these pressures. For example, the cocktail-party effect hypothesis [5] posits that in a crowded social environment, visual signals may be best suited for communication, as opposed to auditory or olfactory signals, because visual cues may be less subject to signal competition associated with sociality—such as overlapping calls and noise [6,7]. Visual signals may be observable to many more individuals and from longer distances. Thus, the form and elaboration of visual signals may evolve with social living and be particularly sensitive to group size.

Cliff swallows (*Petrochelidon pyrrhonota*) are migratory, aerial insectivores widely distributed across western North America during their breeding season. They nest colonially in gourd-shaped mud nests positioned close to each other (usually touching others) along bridges, road culverts, building eaves and cliff faces. Nesting colonies can range in size from 1 to 6000 nests [8], and the propensity of an individual bird to select certain colony sizes has a heritable basis [9]. Swallows often intrude on nests to steal nesting

material, destroy eggs, deposit parasitic eggs, engage in extra-pair copulations (if the male is missing but the female is present) and possibly assess the nest as a later nesting site [10,11]. Both sexes incubate the eggs and defend the nest from these intrusion outcomes, which are more likely at unattended nests [10]. When present, members of the nesting pair will physically repel intruders. Therefore, intruders typically avoid occupied nests, and any trait signalling owner presence may reduce the potential reproductive, energetic and material cost of intrusions, as well as reduce the potential cost of defence itself.

In most North American populations of cliff swallows, adult birds have a patch of whitish plumage directly above their beaks. When occupants are in their nests, which are often shaded underneath an overhang, the white patch is the most easily visible aspect of the bird (figure 1A). We hypothesize that the white forehead patch in cliff swallows serves as a signal of occupancy to mitigate nest intrusions. Thus, we predicted that more prominent patches (i.e. brighter, larger) should enhance signal function and be associated with birds that (i) nest in larger colonies which have potentially greater numbers of intruding neighbours, or that (ii) spend more time in the nest. We also predicted that reducing the white patch by blackening it should result in more intrusions at those birds' nests because the nest would appear unattended. To test these predictions, we measured forehead patches of cliff swallows collected in the same study area over 43 years from colonies of different sizes and altered forehead patches of nesting birds. The collection provided a unique opportunity to investigate how trends in signal evolution may have changed over time. It also allowed study of how a rare climactic event (that caused intense selection on other morphological traits [12,13]) may have affected forehead patches.

2. Methods

(a) Specimen collection

We studied specimens preserved as skins collected from a population of cliff swallows in southwestern Nebraska near the Cedar Point Biological Station (41.210° N, -101.648° W) that has been the subject of ongoing field research since 1982. Skins were acquired opportunistically from 1982 to 2024 from mortalities including: road collisions, mist-netting incidents, predation and from other miscellaneous events [14–16]. The sex, colony location, date of collection and associated colony size were recorded at the time of collection for each specimen, and measurements from a given skin appear once in the dataset (only in its year of collection). Colony size was defined as the maximum number of active nests (at least one egg laid) in a given breeding season [17]. We excluded specimens collected owing to weather-related mortalities, given that weather events selected a non-random subset of individuals with respect to morphology [12]. We did not measure birds collected after the beginning of the moult period (15 July) to avoid confounding effects on patch shape and colour [18], and we accounted for feather wear earlier in the summer by including day of the year in our analyses.

To account for variation in patch size owing to allometry, we made use of previously collected measurements of the endocranial volume [16]. Ninety-two specimens in the current study were matched by ID to head volume calculated from three lateral measurements of the skull, as described in Wagnon & Brown [16].

(b) Measuring the forehead patch

Each specimen was clamped in place adjacent to a ruler balanced in the same plane of focus as the forehead patch (figure 1B–D). The specimen-ruler set-up was photographed using a digital camera (Cyber-shot, Sony) mounted above the set-up under a focused light source to reduce shadow. Each photo was processed in Fiji [19], using colour thresholding to select the white forehead patch, and the pixel count was then converted to area (mm^2) by scaling to a ruler in each image. In cases where the colour thresholding was not effective in isolating the patch, we outlined and selected the area of the patch manually using a touchscreen computer monitor. This was necessary in cases where the outline of the patch was clearly visible to the researcher but dust or stuffing material from the preserving process confounded the thresholding process. Specimens with obscured, damaged or qualitatively dirty forehead patches were excluded from the analyses. All measurements were collected by a single researcher (H.R.R.).

To measure the total spectral reflectance of the white forehead patch, herein referred to as brightness, we used an OceanOptics Inc. (Dunedin, FL, USA) Flame-S spectrometer (UV-VIS-NIR), light source (PX-2 Pulsed Xenon Light Source) and bifurcated optical fibre cable with a reflectance probe (UV/SR-VIS high OH content fibre, 400 μm core). Measurements were taken relative to a white standard (Certified Reflectance Standard, Labsphere) and spectra (300–700 nm) were collected at five points across the white forehead patch. Measurements were taken in a darkened room, and the tip of the probe was wrapped in black tape to limit potential interference from other light sources. The sheath around the probe ensured measurements were taken at a constant distance from the reflective surface (9.0 mm).

We processed the reflectance spectra using the R package 'pavo' smoothing the spectra with the procspec function and 'smooth' option with a span of 0.2 to limit noise [20,21]. We calculated brightness of each measure as the mean relative reflectance (%) from 300 to 700 nm (B2, [22]) and then calculated the median value of the replicate measures for estimation of brightness for each specimen.

(c) Field observations

We studied a 25-nest cliff swallow colony in a concrete road culvert in Keith Co., Nebraska (41.209° N, -101.635° W) from 2 to 6 July 2025. Residents were captured in a mist-net at one end of the culvert and forehead patches were completely darkened

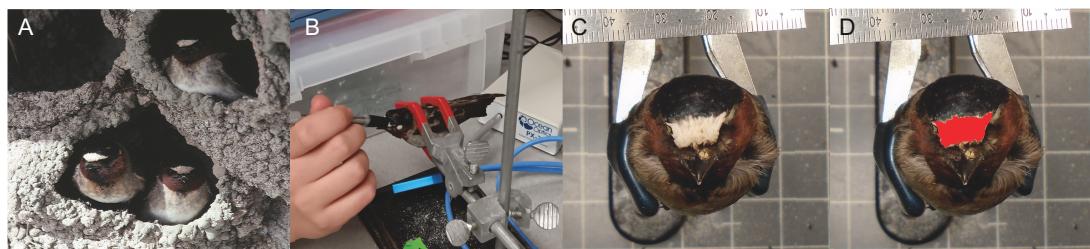


Figure 1. Forehead patch morphology and measurement. (A) Cliff swallows perched in nests (C.R.B.). (B) Apparatus used for reflectance spectrophotometry measurements. (C) Example of forehead patch on a specimen. (D) Example of patch area selection for measurement.

Table 1. ANCOVA table for area of the patch. (Final model was area~log(colony size) + year + sex + date + year². Non-significant interactions were removed (electronic supplementary material, tables S1–S6); final model includes all fixed effects and a polynomial interaction with area. Significant p-values for model terms in bold.)

parameter	β	s.e.	d.f.	F-value	Pr(>F)
(intercept)	89 790	17 380	1	26.68	<0.0001
log _e (colony size)	1.10	0.47	1	5.51	0.02
year	-89.52	17.36	1	26.58	<0.0001
sex:M	-4.84	1.18	1	16.73	0.0001
date	-0.048	0.037	1	1.72	0.19
year ²	0.022	0.0043	1	26.51	<0.0001
residuals	8.94		235		

with a black Sharpie marker (electronic supplementary material, figure S1a,b). Whether nests had an owner with a darkened forehead was determined by repeated observations of birds at nests, resulting in 11 nests with at least one darkened owner and 14 with no darkened owner seen. Birds were primarily incubating during the observations. Sexes were unknown because cliff swallows are sexually monomorphic, and patch manipulation did not allow individual identity to be known. In past studies using distinctly marked birds, we found that owners typically flew straight to their nests and went inside. By contrast, transient cliff swallows often flew through the culvert, hovering briefly at (and sometimes landing on the entrances of) a nest before continuing through to exit the other end (electronic supplementary material, figure S1c). A single observer (C.R.B.) counted transients' visits at each nest during 1 h observation periods. Most owners were inside their nests during these observations, and their extent of visibility to the human observer was not recorded. Nests failing during the study (owners abandoned nest) were excluded from analysis after failure.

(d) Statistical analysis

Area and brightness of the patch were not significantly correlated (Pearson's product-moment correlation, $t = -1.44$, $p = 0.15$), so we considered each measure separately in our analyses. Repeatability, as defined by Lessells & Boag [23], was calculated for a sample of 49 specimens measured 18 months apart and then verified using a scale for intraclass correlation coefficient (ICC) and the ICC package in R [23–25]. The measurements of area and brightness were significantly repeatable across the 18 month interval with higher repeatability for area ($r = 0.74$, 95% confidence interval (CI) [0.60, 0.84]; electronic supplementary material, table S13) compared with the brightness measure ($r = 0.30$, 95% CI [0.21, 0.42]; electronic supplementary material, table S15). The lower repeatability of brightness may reflect the relatively low variance between the biological samples and inherent noise in the brightness measures, and we thus interpret these results with some caution.

For brightness and area of the patch, we fitted separate models with fixed effects of colony size, year of collection, date of collection and sex. We also added a squared interaction term for year (year*year, written as year² in the models), because exploratory plots of the data showed a nonlinear relationship with year. We first fitted models with all possible two-way interactions, and a three-way interaction term, and refined these by backward stepwise elimination of non-significant ($p > 0.05$) interaction terms [26]. All fixed effects of biological interest were retained in the final models, regardless of significance [26,27]. For area of the patch, models were fitted using the 'lm' function in the base 'stats' package in R [28]. Normality was confirmed using quartile-quartile plots and Shapiro-Wilk tests for model fit. Previous studies in this system log-transformed colony size owing to the distribution of this type of data [29], and we performed the same transformation. Parametric results are included in the final analysis (table 1; electronic supplementary material, tables S1–S6), but we also fitted non-parametric regression [30] to confirm robustness, which yielded comparable results. Brightness measures are constrained between 0 and 1 non-inclusive, which violates the assumptions of standard parametric analyses. Therefore, we fitted beta regression models using the betareg function in the 'betareg' package in R [31]. To account for the potential non-independence of birds sampled in the same year, we also fitted mixed effects models that include year as a categorical, random variable (electronic supplementary material, table S1a). In both the brightness and area analyses, the mixed models yielded similar fits to the data

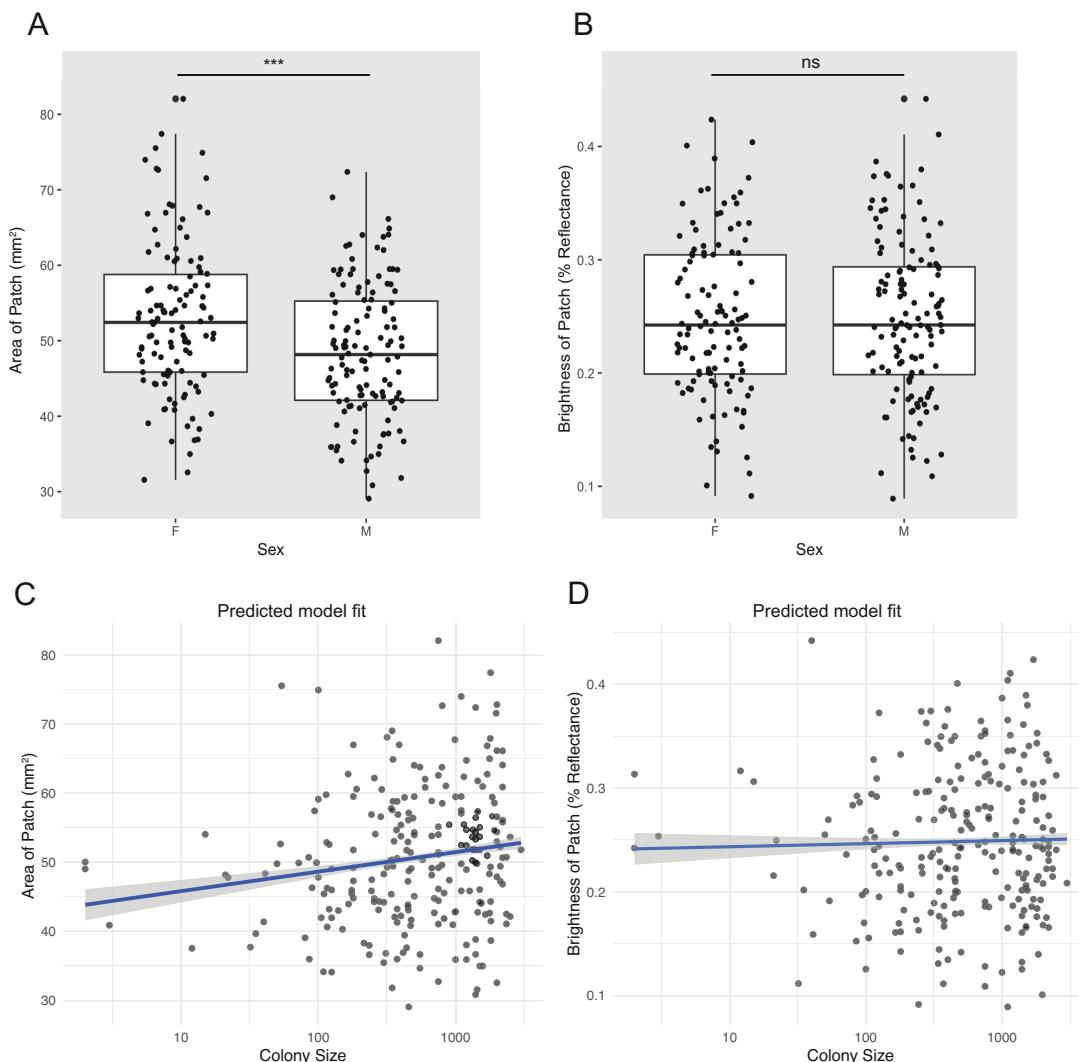


Figure 2. Plots of differences in area and brightness for sex and colony size. (A) Boxplot of patch area for females and males. Females exhibited significantly larger patches than those of males (table 1). (B) Boxplot of patch brightness for females and males. Female and male patches did not differ significantly in brightness (table 2). (C) Predicted model fit, relating patch area and colony size, plotted over raw data. Larger patches were associated with larger colony sizes (table 1). (D) Predicted model fit, relating patch brightness and colony size, plotted over raw data. Patch brightness did not vary significantly with colony size (table 2).

and were associated with the same significant effects as in the original analysis, indicating that the relationship among data sampled in the same year is unlikely to confound the patterns we observed (electronic supplementary material, table S2a).

The inflection point of the polynomial trend in patch area with year (approx. 1996) corresponded to a mass mortality event that led to a reduction of at least 53% of the cliff swallow population and led to selection on skeletal traits and wing and tail length [12,32]. Therefore, we tested for selection on forehead patch size in this event by calculating a selection differential [33]. For this calculation we grouped the data from the 14 year period available before the weather event (1982–1995) as the combined survivors and non-survivors, and the birds collected in the 14 years after the event as the survivors (1997–2010). No birds dying in 1996 were included in selection analyses. Significance testing was carried out as in Endler [33].

In the field experiment, counts of transients' visits to nests were analysed with PROC MIXED in SAS. Transient traffic through the culvert varied at different times and dates, so each 1 h observation period was designated as a random effect (session), along with the nest identification number (nest).

3. Results

(a) Area of patch

The area of the forehead patch differed significantly between the sexes, with colony size, and with a polynomial interaction of year (table 1; figures 2A,C and 3A). Birds with larger patches were associated with larger colonies (table 1; figure 2C). The size of the patch fluctuated over the study period, with an inflection in direction of trends in approximately 1996. Patches before 1996 were larger, and patches after 1996 trended smaller (table 1; figure 3A). There was no significant effect of date (day of the year) of collection on patch area (table 1; electronic supplementary material, figure S2). Female patches ($\text{mean} \pm \text{s.e.}, 53.01 \pm 0.95 \text{ mm}^2, n = 114$) were significantly larger than male patches ($48.44 \pm 0.80 \text{ mm}^2, n = 127$) (table 1; figure 2A). The female-biased difference in patch size is unlikely to be owing to differences in head size between sexes; head volume and area of the patch were uncorrelated (Pearson's $r = 0.16, p = 0.14, n = 92$).

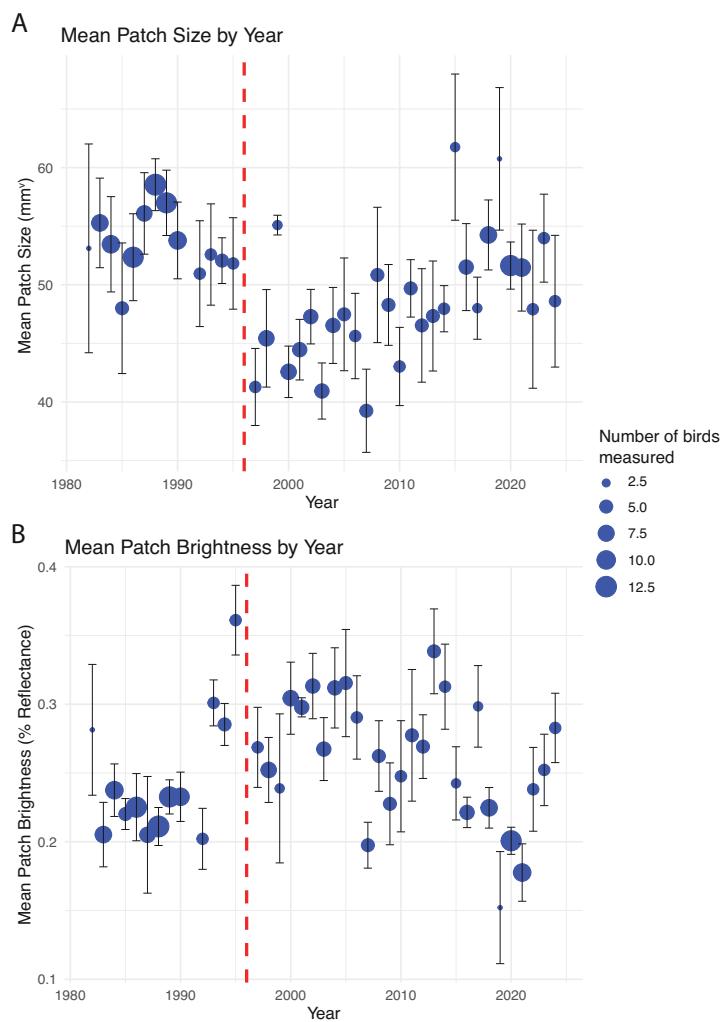


Figure 3. Changes in cliff swallow forehead patch area (A) and brightness (B) across time. Each point represents the mean value for the sampled individuals of the year, and the size of the point corresponds to how many birds were analysed (2–13). Error bars reflect standard error from the average patch measurement per year. Red vertical dashed line indicates the year 1996, used as a cut-off for calculation of the selection differential for patch area and when the severe weather occurred.

Table 2. ANCOVA table for patch brightness. (Final model of patch brightness: forehead brightness~ $\log(\text{colony size}) + \text{year} + \text{sex} + \text{date} + \text{year}^2$. Non-significant interactions were removed (electronic supplementary material, tables S7–S12); final model includes all fixed effects and a polynomial interaction with year. Significant p-values for model terms in bold.)

parameter	estimate	s.e.	d.f.	F-value	Pr(>F)
(intercept)	-4006	687.0	1	34.01	<0.0001
$\log_e(\text{colony size})$	-9.54	0.0184	1	0.27	0.60
year	4.00	0.6862	1	33.97	<0.0001
sex:M	-0.013	0.0461	1	0.08	0.78
date	-0.0032	0.0014	1	4.99	0.03
year^2	-0.0010	0.00017	1	33.94	<0.0001
residuals			234		

(b) Brightness of patch

The brightness of the forehead patch was significantly negatively associated with the date on which the bird was collected (table 2; electronic supplementary material, figure S3). There was no significant effect of sex or colony size (table 2) on patch brightness (table 2; figure 2B,D). There was a significant polynomial interaction with the collection year of the bird (table 2; figure 3B).

(c) Selection event in 1996

Specimens collected in the years following the 1996 mortality event tended to have smaller forehead patches than specimens collected before 1996 (figure 3A). A comparison of birds collected in the 14 years before and the 14 years after the event indicate

that there was significant directional selection for smaller patches ($i = -0.91$, $t_{165} = -6.27$, $p < 0.0001$) and a significant reduction in the variance of patch size ($j = -0.32$, $F_{93,72} = 1.47$, $p = 0.045$) following the mortality event (figure 3A).

(d) Signal function of patch

Nests with at least one owner with a darkened forehead patch were over seven times more likely to have transients visit them (mean 2.90 visits h^{-1} , s.e. = 0.22, $n = 74$ hourly watches) than were nests without an owner with a darkened forehead (mean 0.37 visits h^{-1} , s.e. = 0.064, $n = 95$ hourly watches). Nest status (darkened, non-darkened) significantly affected visits by transients ($F_{1,135} = 52.0$, $p < 0.0001$) while controlling for the random effect of nest ($Z = 2.22$, $p = 0.0131$) and session ($Z = 1.67$, $p = 0.0472$).

4. Discussion

Our results support the hypothesis that the white forehead patch is a social signal in cliff swallows, a species with varying levels of sociality and a heritable propensity for group size. Cliff swallows inhabiting larger colonies, on average, have larger patches than birds from smaller colonies. In larger colonies where there are more neighbours and perhaps more importantly, more transient birds investigating nests [11,34], opportunities for nest intrusions increase, and the forehead patch may be favoured as a signal of presence in the nest. A white plumage signal is conspicuous to intruders [35,36] and prominent signals can deter nest intrusion [37], as our experimental field study illustrates. These advantages may link patch sizes with colony-size preference [9].

Female cliff swallows on average, have larger forehead patches than males, which is a rare example of a songbird exhibiting a female-biased plumage ornament. Selection for crypsis, especially during nesting, is thought to be a major driver of the evolution of reduced female plumage colour ornamentation [38]. Female-biased ornamentation is observed in shorebirds [39], and expansion of female ornaments can occur in other taxa as a result of competition and varying levels of reproductive capacity. However, for cliff swallows it is unlikely that the dimorphism in patch size is the result of sexual selection. Cliff swallows form socially monogamous breeding pairs that only associate in the nest, and the Nebraska population exhibits a near equal sex ratio [12,17,18]. We suggest that patch size sexual dimorphism in cliff swallows is the product of stronger selection on females for the mitigation of costly nest intrusions. Our observations suggest that females spend more time in the nest incubating eggs than males (C. R. Brown, unpublished data, 1983–1987) and thus may be subject to a greater frequency of nest intrusions and experience a greater benefit of a plumage patch signalling occupancy than do males.

The 1996 weather mortality event caused a significant shift in patch size. Birds with large patches were selected against during the event, but over time, selection may have relaxed and the mean patch size in more recent years is similar to the sizes prior to the event. This 1996 mortality event caused intense natural selection on migratory arrival time, wing and tail asymmetry, and body size [12,32]. The reasons for selection against birds with bigger patches during the weather event are unclear; however, possibly we witnessed correlated selection between patch size and arrival times, given that earlier-arriving birds were also selected against [32]. If so, this could suggest a condition-dependent aspect to larger patches, with better condition birds arriving first. We do not know if patch size varies with arrival time. However, patch size was not related to head size, a trait that was under selection in the weather event [16], so correlated selection with morphology may be unlikely. Finally, we note that brightness of the patch also varied over time, with a shift towards brighter patches in the early 1990s (figure 3B). This may indicate there was some other selective event in those years, although we are unaware of any major weather anomalies during that time.

The plumage colours of birds are most often investigated for their functions in mate choice, antagonistic contests and crypsis [40]. Here we offer evidence of long-term morphological change and behavioural responses that indicate another, seldom considered, function of a plumage patch as a signal of occupancy.

Ethics. No special permissions were required for access to field sites; the 2025 observations were done under IACUC permit TU-0047R3 from the University of Tulsa.

Data accessibility. The primary datasets references and the supporting code and materials referenced in this manuscript are available from the Dryad Digital Repository [41]. Additional and exported figures, graphs and tables in support of this article have been uploaded as the electronic supplementary material, available online [42].

Declaration of AI use. AI (ChatGPT, version 4) was used as a search engine to edit code assisting in replicating graphs in R that were originally visualized in SAS. This appears in the manuscript in figure 2C,D (access date: 9 September 2024) and in figure 3A,B (access date: 18 December 2024). The prompts and outputs are disclosed in the electronic supplementary material. The decision to represent the information graphically in this style, the analysis and the data collection associated with the plot was not influenced or checked by AI in any capacity. The resulting code was edited and checked against outside sources.

Authors' contributions. H.R.R.: conceptualization, data curation, formal analysis, investigation, methodology, software, supervision, validation, visualization, writing—original draft, writing—review and editing; M.B.T.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—review and editing; C.R.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Bradbury JW, Vehrencamp SL. 2011 *Principles of animal communication*, 2nd edn. Sunderland, MA: Sinauer Associates.
2. Searcy WA, Nowicki S. 2010 *The evolution of animal communication: reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press. (doi:[10.1515/9781400835720](https://doi.org/10.1515/9781400835720))
3. Endler JA. 1992 Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153. (doi:[10.1086/285308](https://doi.org/10.1086/285308))
4. Johnstone RA. 1997 The evolution of animal signals. In *Behavioural ecology: an evolutionary approach* (eds JR Krebs, NB Davies), pp. 155–178. Malden, MA: Blackwell Publishing.
5. Smith WJ. 1997 *The behavior of communicating: an ethological approach*. Cambridge, MA: Harvard University Press.
6. Brumm H. 2006 Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *J. Comp. Physiol. A* **192**, 1279–1285. (doi:[10.1007/s00359-006-0158-x](https://doi.org/10.1007/s00359-006-0158-x))
7. Planqué R, Slabbekoorn H. 2008 Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology* **114**, 262–271. (doi:[10.1111/j.1439-0310.2007.01461.x](https://doi.org/10.1111/j.1439-0310.2007.01461.x))
8. Brown CR, Brown MB, Roche EA. 2013 Spatial and temporal unpredictability of colony size in cliff swallows across 30 years. *Ecol. Monogr.* **83**, 511–530. (doi:[10.1890/12-2001.1](https://doi.org/10.1890/12-2001.1))
9. Brown CR, Brown MB. 2000 Heritable basis for choice of group size in a colonial bird. *Proc. Natl Acad. Sci. USA* **97**, 14825–14830. (doi:[10.1073/pnas.97.26.14825](https://doi.org/10.1073/pnas.97.26.14825))
10. Brown CR, Bomberger Brown M. 1989 Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. *Anim. Behav.* **37**, 777–796. (doi:[10.1016/0003-3472\(89\)90063-8](https://doi.org/10.1016/0003-3472(89)90063-8))
11. Brown CR. 1998 *Swallow summer*. Lincoln, NE: University of Nebraska Press.
12. Brown CR, Brown MB. 1998 Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* **52**, 1461–1475. (doi:[10.1111/j.1558-5646.1998.tb02027.x](https://doi.org/10.1111/j.1558-5646.1998.tb02027.x))
13. Brown MB, Brown CR. 2011 Intense natural selection on morphology of cliff swallows (*Petrochelidon pyrrhonota*) a decade later: did the population move between adaptive peaks? *Auk* **128**, 69–77. (doi:[10.1525/auk.2011.10219](https://doi.org/10.1525/auk.2011.10219))
14. Brown CR, Bomberger Brown M. 2013 Where has all the road kill gone? *Curr. Biol.* **23**, R233–4. (doi:[10.1016/j.cub.2013.02.023](https://doi.org/10.1016/j.cub.2013.02.023))
15. Wagnon GS, Pletcher OM, Brown CR. 2022 Change in beak overhangs of cliff swallows over 40 years: partly a response to parasites? *PLoS ONE* **17**, e0263422. (doi:[10.1371/journal.pone.0263422](https://doi.org/10.1371/journal.pone.0263422))
16. Wagnon GS, Brown CR. 2020 Smaller brained cliff swallows are more likely to die during harsh weather. *Biol. Lett.* **16**, 20200264. (doi:[10.1098/rsbl.2020.0264](https://doi.org/10.1098/rsbl.2020.0264))
17. Brown CR, Brown MB. 1996 *Coloniality in the cliff swallow: the effect of group size on social behavior*. Chicago, IL: University of Chicago Press.
18. Brown CR, Brown MB, Pyle P, Patten MA. 2020 Cliff swallow (*Petrochelidon pyrrhonota*), version 1.0. In *Birds of the world* (ed. PG Rodewald). Ithaca, NY: Cornell Lab of Ornithology. (doi:[10.2173/bow](https://doi.org/10.2173/bow))
19. Schindelin J *et al.* 2012 Fiji: an open-source platform for biological-image analysis. *Nat. Methods* **9**, 676–682. (doi:[10.1038/nmeth.2019](https://doi.org/10.1038/nmeth.2019))
20. Chappell DR, Boggs CL, Speiser DL. 2023 Two sides of the same wing: ventral scales enhance dorsal wing color in the butterfly *Speyeria mormonia*. *J. Exp. Biol.* **226**, b246396. (doi:[10.1242/jeb.246396](https://doi.org/10.1242/jeb.246396))
21. Maia R, Eliason CM, Bitton P, Doucet SM, Shawkey MD. 2013 pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**, 906–913. (doi:[10.1111/2041-210x.12069](https://doi.org/10.1111/2041-210x.12069))
22. Montgomerie R. 2006 Analyzing colors. In *Bird coloration: volume 1: mechanisms and measurements* (eds GE Hill, KJ McGraw), pp. 90–147. Cambridge, MA: Harvard University Press. (doi:[10.2307/j.ctv22jnscm.6](https://doi.org/10.2307/j.ctv22jnscm.6))
23. Lessells CM, Boag PT. 1987 Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121. (doi:[10.2307/4087240](https://doi.org/10.2307/4087240))
24. Koo TK, Li MY. 2016 A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163. (doi:[10.1016/j.jcm.2016.02.012](https://doi.org/10.1016/j.jcm.2016.02.012))
25. Wolak ME, Fairbairn DJ, Paulsen YR. 2012 Guidelines for estimating repeatability. *Methods Ecol. Evol.* **3**, 129–137. (doi:[10.1111/j.2041-210x.2011.00125.x](https://doi.org/10.1111/j.2041-210x.2011.00125.x))
26. Engqvist L. 2005 The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**, 967–971. (doi:[10.1016/j.anbehav.2005.01.016](https://doi.org/10.1016/j.anbehav.2005.01.016))
27. Brown CR, Brown MB, Hannebaum SL, Wagnon GS, Pletcher OM, Page CE, West AC, O'Brien VA. 2024 Social foraging and the associated benefits of group-living in cliff swallows decrease over 40 years. *Ecol. Monogr.* **94**, e1602. (doi:[10.1002/ecm.1602](https://doi.org/10.1002/ecm.1602))
28. R Core Team. 2024 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
29. Brown CR, Roche EA, Bomberger Brown M. 2014 Variation in age composition among colony sizes in cliff swallows. *J. Field Ornithol.* **85**, 289–300. (doi:[10.1111/jfof.12068](https://doi.org/10.1111/jfof.12068))
30. Mangiafico S. 2016 *Summary and analysis of extension program evaluation in R* (version 1.22.2, revised 2025). New Brunswick, NJ: Rutgers Cooperative Extension. See <http://rcompanion.org/handbook/>.
31. Cribari-Neto F, Zeileis A. 2010 Beta regression in R. *J. Stat. Softw.* **34**, 1–24. (doi:[10.18637/jss.v034.i02](https://doi.org/10.18637/jss.v034.i02))
32. Brown CR, Bomberger Brown M. 2000 Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behav. Ecol. Sociobiol.* **47**, 339–345. (doi:[10.1007/s002650050674](https://doi.org/10.1007/s002650050674))
33. Endler JA. 1986 *Natural selection in the wild*. Princeton, NJ: Princeton University Press.
34. Brown CR, Brown MB. 2004 Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology* **85**, 1619–1626. (doi:[10.1890/03-0206](https://doi.org/10.1890/03-0206))
35. Dale S, Slagsvold T. 1996 Plumage coloration and conspicuousness in birds: experiments with the pied flycatcher. *Auk* **113**, 849–857. (doi:[10.2307/4088863](https://doi.org/10.2307/4088863))

36. Moulton CE, Brady RS, Belthoff JR. 2004 Territory defense of nesting burrowing owls: responses to simulated conspecific intrusion. *J. Field Ornithol.* **75**, 288–295. (doi:[10.1648/0273-8570-75.3.288](https://doi.org/10.1648/0273-8570-75.3.288))
37. Davidson GL, Clayton NS, Thornton A. 2014 Salient eyes deter conspecific nest intruders in wild jackdaws (*Corvus monedula*). *Biol. Lett.* **10**, 20131077. (doi:[10.1098/rsbl.2013.1077](https://doi.org/10.1098/rsbl.2013.1077))
38. Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life history and sexual selection on male and female plumage colouration. *Nature* **527**, 367–370. (doi:[10.1038/nature15509](https://doi.org/10.1038/nature15509))
39. Székely T *et al.* 2024 The causes and implications of sex role diversity in shorebird breeding systems. *Ibis* **166**, 357–385. (doi:[10.1111/ibi.13277](https://doi.org/10.1111/ibi.13277))
40. Hill GE, McGraw KJ (eds). 2006 *Bird coloration: volume 2: function and evolution*. Cambridge, MA: Harvard University Press. (doi:[10.2307/j.ctv22jnr8k](https://doi.org/10.2307/j.ctv22jnr8k))
41. Reeb HR, Toomey MB, Brown CR. Data from: A plumage patch signalling nest occupancy is shaped by social environment. Dryad Digital Repository. (doi:[10.5061/dryad.37pvmcvz1](https://doi.org/10.5061/dryad.37pvmcvz1))
42. Reeb HR, Toomey MB, Brown CR. 2025 Supplementary material from: A plumage patch signaling nest occupancy is shaped by social environment. Figshare. (doi:[10.6084/m9.figshare.c.8194836](https://doi.org/10.6084/m9.figshare.c.8194836))