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RESEARCH ARTICLE

Variable facial plumage in juvenile Cliff Swallows: A potential offspring recognition cue?

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ABSTRACT

Although the ability to recognize related offspring is essential in the evolution of social behavior, the cues that birds use to identify their own offspring are not fully understood. The Cliff Swallow (*Petrochelidon pyrrhonota*) is a highly social species that nests in large colonies and exhibits a high incidence of both conspecific brood parasitism and extrapair fertilization, behaviors that can potentially lead to parents investing energy and resources in unrelated offspring, which reduces the parents' genetic fitness. Because parents continue to feed offspring after they leave the nest, parents also risk investing in unrelated offspring by misidentifying their own young after mobile, postfledging juveniles form crèches. Cliff Swallows possess a unique system of variable juvenile facial patterns, ranging from almost entirely black to almost entirely white. Interestingly, although these patterns are highly variable and distinctive in juveniles, they disappear upon maturation. We used image analysis to examine facial plumage of nestlings, and microsatellite genotyping to examine genetic relatedness among offspring within nests. We found substantial variation in facial plumage among juveniles and found a significant correlation between facial similarity and relatedness of nestlings. Genetically dissimilar juveniles in the same nest exhibited highly variable faces as measured by median pixel intensity. This variation in facial plumage may serve as a cue to allow birds to avoid misdirected parenting. We found no association between nestling relatedness and weight; this suggests that at least in the developmental period that we examined, parents may have not yet begun to use facial plumage or other cues to differentially provision offspring on the basis of genetic relatedness. If parents are able to use facial markings to distinguish between juveniles, they may do so at later stages of development, such as postfledging, to distinguish young raised in their own nest from others.

Keywords: Cliff Swallow, individual recognition, juvenile plumage, kin recognition

Variación del plumaje facial en juveniles de *Petrochelidon pyrrhonota*: Una potencial señal para el reconocimiento de las crías?

RESUMEN

Mientras que la habilidad de reconocer a las crías emparentadas es esencial en la evolución del comportamiento social, no se comprenden del todo las señales que usan las aves para identificar a sus propias crías. *Petrochelidon pyrrhonota* es una especie altamente social que anida en grandes colonias y que exhibe una alta incidencia tanto de parasitismo coespecífico de nidada como de fertilización extra pareja, comportamientos que pueden potencialmente llevar a que los padres inviertan energía y recursos en crías no emparentadas, reduciendo la adecuación biológica de los padres genéticos. Debido a que los padres continúan alimentando a las crías luego de que dejan el nido, también se arriesgan a invertir en crías no emparentadas si confunden a sus propios hijos una vez que los juveniles se mueven y se agrupan en guarderías luego de emplumar. Los individuos de *P. pyrrhonota* poseen un sistema único de patrones faciales juveniles variables, yendo desde casi completamente negro hasta casi completamente blanco. De modo interesante, mientras que estos patrones son muy variables y distintivos en los juveniles, desaparecen con la maduración. Empleamos análisis de imágenes para examinar el plumaje facial de los pichones y tipificación genotípica microsatelital para examinar el parentesco genético entre crías adentro de los nidos. Encontramos una variación substancial en el plumaje facial entre los juveniles e identificamos una correlación significativa entre la similitud facial y el parentesco de los pichones. Los nidos con juveniles genéticamente disímiles exhibieron caras muy variables, medido como la intensidad mediana del píxel. Esta variación en el plumaje facial puede servir como una señal que permita a las aves evitar realizar tareas de paternidad mal direccionadas. No encontramos una asociación entre el parentesco de los pichones y el peso, sugiriendo que al menos durante el periodo de desarrollo que examinamos, los padres no han comenzado aún a usar el plumaje facial u otras señales para aprovisionar diferencialmente a las crías basados en el parentesco genético. Si los padres son capaces de usar las marcas faciales para distinguir a los juveniles,

podrían hacerlo en estadios de desarrollo más tardíos, como luego del emplumamiento, para distinguir a los jóvenes criados en sus propios nidos de los otros.

Palabras clave: *Petrochelidon pyrrhonota*, plumaje juvenil, reconocimiento de parientes, reconocimiento individual

INTRODUCTION

Because social behavior is often directed toward relatives, the ability to distinguish individuals using traits associated with genetic relatedness can play an important role in taxa characterized by extreme sociality (Beecher 1988, Hepper 1991). In many colonial species, parents continue to feed offspring after they mix during fledging, and the ability to recognize individuals reared in the nest can allow parents to direct feeding behavior to their putative offspring (Davies and Carrick 1962, Burt 1977). In systems with a high likelihood of brood parasitism and/or extrapair paternity (Weatherhead and Boag 1995, Kempenaers et al. 1997, Dunn et al. 2009), contextual cues that normally can be used to identify kin (e.g., nestlings in an individual's nest) are less reliable indicators of kinship, potentially favoring complex recognition systems (Medvin et al. 1992, Neff and Sherman 2002, Hain and Neff 2006). Recognition systems may also be used by juveniles, who can alter begging behavior in response to the presence of nonkin in the nest (Boncoraglio et al. 2009). Kin recognition in mammals has been studied extensively, but little work has been done on the role of kin recognition in the early rearing of birds (reviewed in Mateo 2002).

The Cliff Swallow (*Petrochelidon pyrrhonota*) is a small, highly social passerine that breeds in densely packed colonies of up to 6,000 nests. Intraspecific brood parasitism is particularly common in large colonies, occurring in $\leq 24\%$ of the nests in a given colony (Brown 1984, Brown and Brown 1988a, 1989, 1996). Extrapair copulations are also common (Brown and Brown 1988b), although initial attempts to quantify rates of successful extrapair fertilizations have been inconclusive (Brown and Brown 1996). Throughout the rearing period (~ 21 days), both parents reside in the nest, feeding and tending to offspring (Brown and Brown 1991, 1996). After fledging, but prior to migrating, juvenile Cliff Swallows form crèches and continue to receive food from the adults for 3–5 days (Brown and Brown 1996).

Selection is expected to favor traits that allow parents to recognize their own genetic offspring (Brown and Brown 1989), but these characters have not been identified in birds (Wright 1998, Roldán and Soler 2011). Traits that are under selection to signal individual identity, such as those that allow parents to learn offspring identities and recognize them outside of the nest, are likely to be associated with genetic relatedness as well (Dale et al. 2001). Recent work has identified olfaction as a nonassociative cue that can

allow songbirds to recognize genetically related kin (Krause et al. 2012), but it is unclear whether this cue can be used in parent–offspring recognition. Stoddard and Beecher (1983) found juvenile Cliff Swallow vocalizations to be more similar within nests than between nests, and Beecher et al. (1989) found that adults use vocalizations to recognize offspring within the colony. Although many aspects of vocalizations in passerines are learned from parents and/or peers, some components of song are heritable (Forstmeier et al. 2009), and thus song might serve as a kin recognition cue in Cliff Swallows (Medvin et al. 1992). However, juvenile calls cannot be used as a reliable kin recognition cue for long, if at all, before fledging, because the calls do not become unique until 15 days after hatching and do not crystallize until days 18–21 (Stoddard and Beecher 1983). Consistent with this pattern, Burt (1977) found that adult Tree Swallows (*Tachycineta bicolor*) and Barn Swallows (*Hirundo rustica*) did not discriminate between their own offspring and alien young until after the young had fledged, at which point parents used vocalizations to recognize offspring.

Distinctive juvenile facial patterning in Cliff Swallows was first noted by Stoddard and Beecher (1983) on the basis of scores by human observers. Patterning becomes distinct around day 13 and likely remains fixed for a given individual until the first molt during the winter of their hatch year (Turner and Rose 1989). Coloration of the patterning varies from almost entirely white to near black, with intricately mottled patterns of gray, brown, and/or white (Figure 1). Although conspicuous juvenile coloration is used in lieu of vocalization during begging in nonvocal birds (Lyon et al. 1994), juvenile swallows are very vocal while begging. The high level of plumage variability has led to suggestions that facial patterning in swallows could indicate individual identity (Loesche et al. 1991). Stoddard and Beecher (1983) speculated that facial plumage may be a cue used by Cliff Swallows to recognize offspring. Consistent with this scenario, facial plumage is highly distinctive in juveniles but disappears permanently during the first year of life. It is possible that facial plumage, like vocalization, is used by adults to locate offspring in crèches formed by juveniles after leaving the nest, or that it increases a parent's ability to distinguish between juveniles within these crèches. Plumage variation has rarely been documented so strikingly in juvenile birds (Buckley and Buckley 1970, Dale et al. 2001).

Facial patterning becomes fixed several days earlier than vocalizations, potentially offering the opportunity to allow

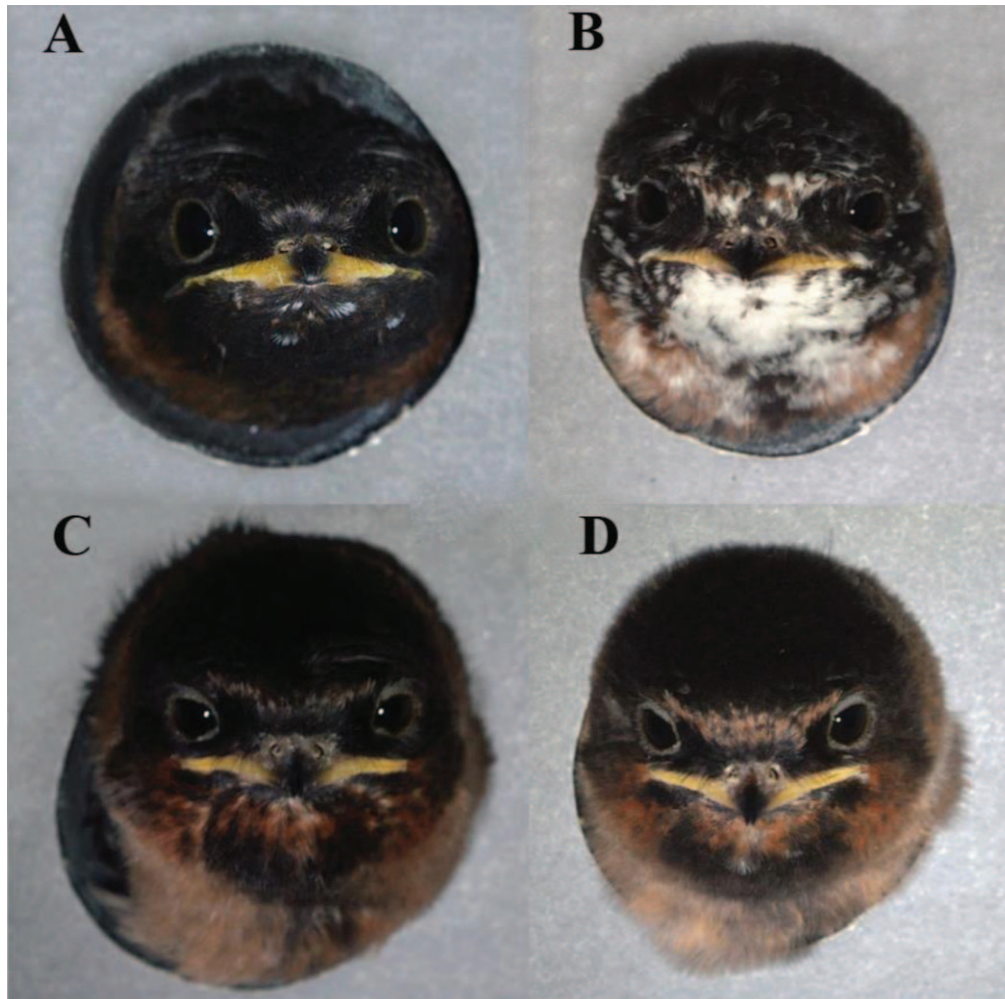


FIGURE 1. Images of juvenile Cliff Swallows' faces at ~17 days of age, illustrating the variation in facial patterns among individuals. (A, B) Individuals with a low relatedness score ($r < 0.25$). (C, D) Individuals with a high relatedness score ($r > 0.5$).

parents to begin distinguishing kin prior to fledging. Common Waxbill (*Estrilda astrild*) chicks suffer reduced in-nest growth when their gape flanges are painted black, which suggests that parents are able to use visual cues to discriminate against outlying phenotypes (Schuetz 2005b). Indeed, that both egg and gape patterns in some parasitic species match those of their host species indicates the importance of visual cues for birds in discriminating between true and alien offspring (Schuetz 2005a, Stoddard and Stevens 2010). Furthermore, although vocalizations in passerine birds are influenced by cultural transmission (Forstmeier et al. 2009), it is unlikely that facial plumage can be influenced by environmental influences or interactions with conspecifics. Thus, although juveniles that are unrelated to their nest parents as a result of extrapair fertilization or brood parasitism may imprint on vocalizations of their nestmates, facial plumage may serve as a more reliable indicator of parentage if it has an underlying genetic basis. Although facial plumage has the potential to

play an important role in kin recognition in birds, no previous study has documented a relationship between genetic relatedness and facial plumage in an avian system.

We examined variation in facial plumage in nestling Cliff Swallows within and between nests within a colony. We quantified genetic relatedness among birds using five variable microsatellite markers and examined whether patterns of relatedness were associated with similarity in facial plumage of juveniles. Because opportunities for misdirected parental care can occur both before and after fledging in this system, associations between relatedness and facial markings may serve as an important cue, allowing parents to recognize their own offspring.

METHODS

Study Site and Species

The field work was conducted during the summer of 2008 in Cannon Falls, Goodhue County, Minnesota

TABLE 1. Results of polymerase chain reactions (PCR) used to quantify genetic relatedness among Cliff Swallows using five variable microsatellite markers (primer sequences were obtained from Tsyusko et al. 2007; PCR conditions are described in the text).

Locus	Primer sequence	Repeat motif	Size (bp)	T(a)	Number of alleles	Observed heterozygosity
Hir7	CTTGCGCAGAAAGTAT GCTCTGGGATCTCTAG	CT	136–144	53.0°C	3	0.043
Hir10	GGACCAGGGGAGTCTT ATTCAGCCAGCCTCTAAT	TTTG	161–173	54.9°C	4	0.656
Hir11	AACACCTGAAAACCTACAC CTTTGAGCAAAATGAGTG	AAAT	167–187	54.9°C	6	0.378
Hir17	ATGCCATGCTTCAGAT CTGTCATGCCTAAGTATCA	TAGA	183–227	53.0°C	14	0.857
Hir20	GAAGTTGGAGAAAGATTAG TTATTGCTCTGGGTATGT	TAGA	225–273	57.5°C	12	0.89

(44°30'25.92''N, 92°54'30.54''W). We studied a large colony of Cliff Swallows located on the underside of a bridge over the Cannon River. Females in this colony began laying eggs in early June, and the whole colony had fledged by late July. Only females develop brood patches, but both adults assist in feeding the young while they are in the nest. Nests had been built on the walls of the bridge where vertical supports met the ceiling. Nests were adjacent to each other in linear fashion across each wall of the bridge, such that each nest shared one or more of its mud walls with immediately neighboring nests.

The colony contained ~300 nests, of which we identified 139 that were synchronous with one another (i.e. young were being reared simultaneously). Of these 139 nests, 26 nests (housing 93 birds) were randomly chosen from a single wall of the colony for genotyping and facial analysis. Nests were monitored after females began laying eggs. When nestlings had reached 16–19 days of age, they were removed from the nests for sampling. Approximately 20 μ L of blood was collected from each individual via venous puncture of the brachial vein. The blood was stored in 600 μ L of cell lysis solution. Pressure was applied to the blood collection site for 2–5 min to ensure that clotting had occurred.

Immediately after blood collection, each nestling's face was photographed with a digital camera (a Fujifilm FinePix S2 Pro, using an AF Micor Nikkor 60-mm lens). Photographs were taken in a shaded box affixed with two stationary lights (Fantasea LED 44) and an illuminated lens ring (Digi-Slave Ultra II). Each nestling was placed in a holding chamber ~50 cm from the lens with a uniform gray background, allowing light readings and the camera angle to be standardized for each photograph (Figure 1). Two or three photographs were taken of each individual, and the photo with the most evenly distributed light (lacking in shadowing) was chosen for analysis. After being photographed, each bird was placed in a mesh bag and weighed with a Pesola spring balance to the nearest 0.5 g, banded with an individually numbered federal leg band, and returned to the nest.

Laboratory Methods

DNA was extracted from each blood sample using a Gentra Puregene kit from Qiagen (Venlo, The Netherlands) for whole blood. Individuals were genotyped using five microsatellite loci, with primer sequences originally developed for Barn Swallows (Tsyusko et al. 2007). Polymerase chain reaction (PCR) amplification was performed in 10- μ L volumes consisting of 10 mM Tris buffer pH 8.4, 50 mM KCl, 0.2 mM unlabeled primer, 0.2 mM fluorescently labeled primer, 1.5 mM MgCl₂, 0.15 mM dNTP, 0.5 units *Taq* DNA polymerase, and ~50 ng DNA template. For all loci, an initial amplification cycle (4 min at 95°C) was followed by 35 cycles of 30 s at 95°C, 30 s at the annealing temperature (Table 1), and 40 s at 72°C, followed by a final 4-min extension at 72°C.

The PCR products were assayed on a 2% agarose gel to confirm amplification and were sent to The Ohio State University Plant-Microbe Genomics Facility for genotyping. Relatedness (r) was estimated for all pairwise combinations of the 93 individuals by using the Queller and Goodnight index (Queller and Goodnight 1989) and the program Kingroup v2 (Konovalov et al. 2004).

To quantify the facial markings of each nestling, the photographs were analyzed using ImageJ 1.43u. Each image was converted to 32-bit grayscale for pixel analysis. Although both the forehead and the throat were variable, the forehead was chosen for analysis because of the ease of photographing it. The region analyzed was defined as a triangle between the top of the beak and the top of both eyes, the area where most of the facial markings were concentrated. Forehead pixel intensity values ranged from 7 (near black) to 255 (white) and were sorted into bins of width 0.969 (default bin size for ImageJ). Total pixel number varied between individuals (mean \pm SD = 52,849.89 \pm 10,648.95); however, given that distance from the camera was standardized, this variation likely reflects variation in the size of individuals' plumage patches and should be minimally affected by the angle of each face from the camera lens. For each individual, a distribution of intensity values for all pixels was computed and a median

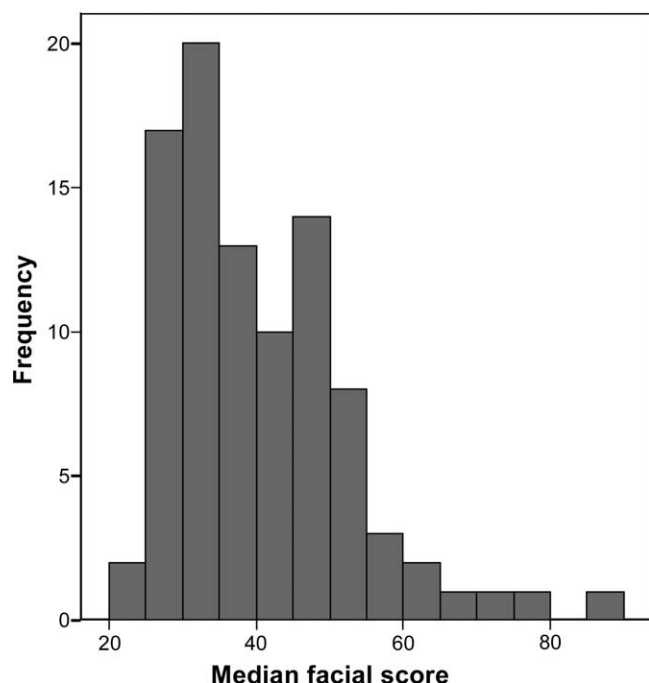


FIGURE 2. Distribution of untransformed forehead median pixel values. Unlike most passerine birds, juvenile Cliff Swallows display considerable individual variation in facial plumage, with median pixel values ranging from 22.5 to 86.4.

pixel value was assigned. Other studies of passerines have found that female selection of mates can be based on the proportion of dark versus light feathers (Hill et al. 1999), which suggests that birds are capable of detecting variation in this trait.

Statistical Analyses

All statistical analyses were performed in PASW Statistics 18.0.0 (SPSS 2009). Because we were interested in whether related nestlings had similar facial plumage, the average of pairwise facial differences between nestlings and the average relatedness as calculated by Kingroup for each nest were used in regression analysis. To test whether variation in offspring weight was associated with variation in facial plumage and/or relatedness, the average of the pairwise weight differences between nestlings within a nest was regressed against both average within-nest facial differences and average within-nest relatedness. Means of pertinent data are presented \pm SE.

RESULTS

Average clutch size for the colony was 3.68 eggs ($n = 139$, range: 2–6). Neither raw median facial scores (recorded as bin size, 40.45 ± 1.27 ; Shapiro-Wilks, $P = 0.02$; Figure 2) nor nestling body mass (23.19 ± 0.26 g; Shapiro-Wilks, P

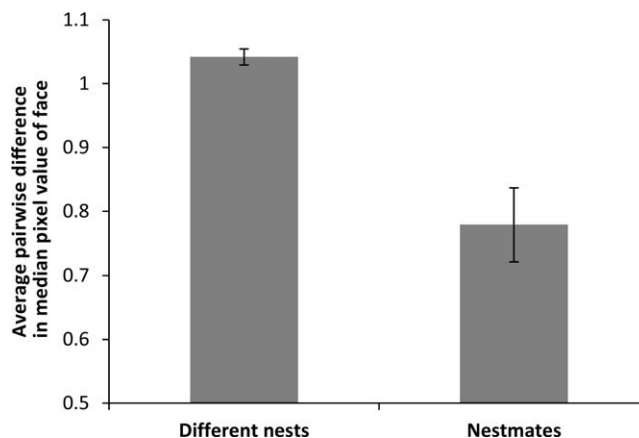


FIGURE 3. Average pairwise difference in median transformed forehead pixel values between nestmates and between birds residing in different nests (\pm SE).

$= 0.005$) was normally distributed, and consequently both were square-root transformed. These transformed distributions did not deviate from normality (Shapiro-Wilks, $P = 0.635$ and $P = 0.372$, respectively) and are used in all subsequent analyses. The average pairwise difference of transformed face values was lower for nestmates than between birds residing in different nests (0.78 for nestmates vs. 1.04 for different nests; Figure 3).

Microsatellite genotypes were highly variable, with observed heterozygosities >0.65 for three of the five loci analyzed (Table 1). The average of all within-nest average relatedness values was 0.436 ± 0.031 . In the absence of inbreeding, nests containing only full siblings are expected to be characterized by an average within-nest relatedness of 0.5 (Queller and Goodnight 1989), and nests characterized by substantially lower relatedness indicate a higher probability of extrapair fertilization and/or brood parasitism. Cliff Swallows exhibit substantial among-colony movement between years, and high levels of inbreeding were not observed at this colony (A. E. Johnson and S. Freedberg personal observation). There was considerable variation in relatedness of juveniles within the same nests, with a standard deviation of 0.276 for all pairwise within-nest relatedness values.

Relatedness and facial similarity were positively correlated across nests: Nestlings in nests with high average relatedness values had median transformed pixel intensity values more similar to those of their nestmates than those in nests with low average relatedness scores ($R = 0.413$, $df = 1$, $P = 0.036$; Figure 4). Average transformed weight difference within a nest did not correlate significantly with average within-nest relatedness ($R = 0.232$, $df = 1$, $P = 0.254$), nor did it correlate significantly with the mean within-nest difference in transformed median pixel values ($R = 0.171$, $df = 1$, $P = 0.404$).

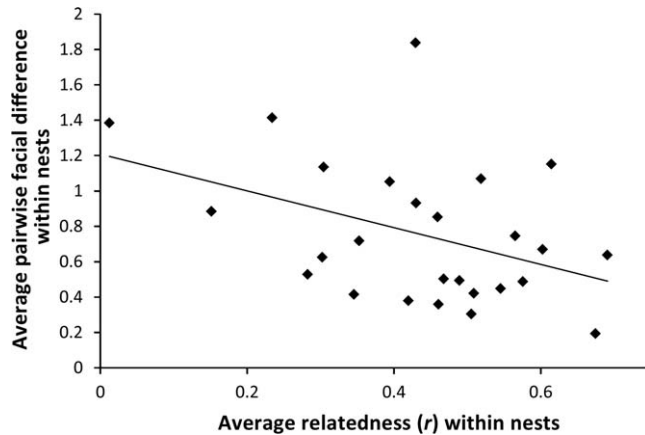


FIGURE 4. Regression of transformed average facial differences against average relatedness within each nest (square root median pixel intensity). Nests with high average relatedness values had more similar facial values ($R = 0.413$, $P = 0.036$).

DISCUSSION

We found that facial plumage in juvenile Cliff Swallows varied with genetic relatedness. Nests with genetically dissimilar juveniles were characterized by significantly higher facial variability than nests containing more closely related nestlings. Because adults in this system can be susceptible to misdirected parental care, either through extrapair young in the nest or by misidentifying juveniles in mobile crèches, facial plumage may reveal general information about genetic relatedness of offspring both within and outside of the nest. Although we did not directly measure parental relatedness, the high variation in relatedness among nestmates suggests that chicks likely varied in relatedness to their nest parents. Although the role of transient juvenile facial plumage in birds has long been speculated, this is the first report of a relationship between facial plumage and genetic relatedness in an avian system.

The most reliable method for kin recognition is self-referent phenotype matching (Beecher 1982, Waldman 1987), in which an individual learns its own “template” and then compares others to this template. Facial patterns in Cliff Swallows are unlikely to be self-referent cues for parents because distinctive patterns are displayed only by juveniles. Once individuals have experienced their first molt in the winter of their hatch year (Turner and Rose 1989), all such variation disappears, and the faces of adults show no noticeable variation in plumage. Some research has shown that individuals can still use a form of phenotype matching through the rejection of odd phenotypes. For example, some birds experiencing interspecific brood parasitism will reject the egg type that is the minority in its nest, regardless of whether this is the parasite’s egg or the host’s (Hauber and Sherman 2001).

Because dissimilar facial plumage was associated with reduced relatedness within nests, adult Cliff Swallows may be able to identify nonkin through detection of outlying facial patterns.

Studies of birds without juvenile plumage variation have suggested that parents do not alter provisioning behavior on the basis of genetic relatedness (reviewed in Kempenaers and Sheldon 1996, Wright 1998). We did not observe a relationship between variation in offspring weight and relatedness or between variation in offspring weight and facial plumage. Although these findings are consistent with adults failing to alter early provisioning on the basis of offspring relatedness, it is possible that differential provisioning had not yet significantly affected offspring weight. Juvenile facial plumage had been present only 3–6 days prior to our sampling, and thus small amounts of differential provisioning based on facial plumage may have not yet produced a detectable difference in body mass. Chicks that are starved for a short time (24–36 hr) still suffer significant weight loss immediately following food deprivation (Negro et al. 1994, Halevy et al. 2000), which suggests that if parents completely starve chicks upon the formation of facial plumage, these chicks would be characterized by significant weight loss at the stage at which we weighed them. Although juveniles in the same nest were of approximately the same age, other factors, such as parasite load and genetics may influence offspring weight, further limiting our ability to detect any effects of provisioning. While fathers are under strong selection to recognize traits that can discriminate kin from nonkin (Kempenaers and Sheldon 1996), offspring may be under countervailing selection to minimize the expression of traits that would enable males to determine their parentage (Beecher 1988). It is also possible that even if fathers use facial cues to discriminate against offspring that resulted from extrapair fertilization, offspring weight is not affected, because female swallows can compensate for reduced feeding behavior of males by overfeeding neglected offspring (Saino and Møller 1995). Studies that directly examine parental provisioning behavior may ultimately reveal whether the relationship between relatedness and juvenile facial plumage reported here allows for differential provisioning decisions in the nest or after fledging.

Juvenile Cliff Swallows form large crèches after fledging, and these crèches contain juveniles from multiple nests and, often, multiple colonies (Brown and Brown 1996). Facial patterning in juveniles may increase an adult’s likelihood of finding those birds in a large crèche by allowing the parents to distinguish between juveniles raised in their nest (known juveniles) from others, rather than by direct kin recognition. Brown and Brown (1996) reported that adults in crèches appeared to distinguish between individual juveniles. However, because crèches may reach sizes of >1,000 juveniles, and because calls

become fully crystallized around the time of fledging, facial patterning may serve as an additional cue to identify fledglings (Thorpe 1958, Stoddard and Beecher 1983, Brown and Brown 1996, Brenowitz et al. 1997). Occasionally, adult Cliff Swallows will approach a juvenile within the crèche with a food bolus and fail to deliver it (A. E. Johnson personal observation, C. R. Brown and M. B. Brown personal communication). It is possible that adults use juvenile vocalizations to identify potential offspring in crèches and then use visual cues to secondarily distinguish between individuals. Buckley and Buckley (1970, 1972) reported variability in color and patterning of plumage and soft tissues (leg and beak) in chicks of colonially nesting Royal Terns (*Thalasseus maximus*). After using vocalizations to locate offspring in crèches, adult Royal Terns reject some birds, which has prompted the researchers to speculate that visual cues act as a second recognition system within the crèche.

Although the relationship between relatedness and variation in facial plumage makes it tempting to speculate about an adaptive relationship between the two, it is possible that swallows do not use facial plumage to distinguish individuals according to genetic relatedness. For instance, parents may use facial plumage to imprint on all offspring that reside in their nest, regardless of their genetic relatedness, and then may use this information to locate nestlings when they fledge to the crèche. Under this scenario, parents invest resources in unrelated offspring because they are incapable of using visual cues to differentiate among offspring. Several systems of interspecific brood parasitism are known in which parents appear not to distinguish between their own genetic offspring and nest parasites, despite extensive morphological divergence between the two (May and Robinson 1985, Davies 1999). Studies that combine molecular data with long-term behavioral observations may further help reveal the adaptive value, if any, of transient facial patterning in passerine birds.

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LITERATURE CITED

- Beecher, M. D. (1982). Signature systems and kin recognition. *American Zoologist* 22:477–490.
- Beecher, M. D. (1988). Kin recognition in birds. *Behavior Genetics* 18:465–482.
- Beecher, M. D., P. Loesche, P. K. Stoddard, and M. B. Medvin (1989). Individual recognition by voice in swallows: Signal or perceptual adaptation? In *The Comparative Psychology of Audition: Perceiving Complex Sounds* (R. J. Dooling and S. H. Hulse, Editors). Erlbaum, Hillsdale, NJ, USA.
- Boncoraglio, G., M. Caprioli, and N. Saino (2009). Fine-tuned modulation of competitive behaviour according to kinship in Barn Swallow nestlings. *Proceedings of the Royal Society of London, Series B* 276:2117–2123.
- Brenowitz, E. A., D. Margoliash, and K. W. Nordeen (1997). An introduction to birdsong and the avian song system. *Journal of Neurobiology* 33:495–500.
- Brown, C. R. (1984). Laying eggs in a neighbor's nest: Benefit and cost of colonial nesting in swallows. *Science* 224:518–519.
- Brown, C. R., and M. B. Brown (1988a). A new form of reproductive parasitism in Cliff Swallows. *Nature* 331:66–68.
- Brown, C. R., and M. B. Brown (1988b). Genetic evidence of multiple parentage in broods of Cliff Swallows. *Behavioral Ecology and Sociobiology* 23:379–387.
- Brown, C. R., and M. B. Brown (1989). Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Animal Behaviour* 37:777–796.
- Brown, C. R., and M. B. Brown (1991). Selection of high-quality host nests by parasitic Cliff Swallows. *Animal Behaviour* 41:457–465.
- Brown, C. R., and M. B. Brown (1996). *Coloniality in the Cliff Swallow*. University of Chicago Press, Chicago, IL, USA.
- Buckley, P. A., and F. G. Buckley (1970). Color variation in the soft parts and down of Royal Tern chicks. *The Auk* 87:1–13.
- Buckley, P. A., and F. G. Buckley (1972). Individual egg and chick recognition by adult Royal Terns (*Sterna maxima maxima*). *Animal Behaviour* 20:457–462.
- Burt, E. H., Jr. (1977). Some factors in the timing of parent-chick recognition in swallows. *Animal Behaviour* 25:231–239.
- Dale, J., D. B. Lank, and H. K. Reeve (2001). Signaling individual identity versus quality: A model and case studies with ruffs, queleas, and House Finches. *American Naturalist* 158:75–86.
- Davies, N. B. (1999). Cuckoos and cowbirds versus hosts: Co-evolutionary lag and equilibrium. *Ostrich* 70:71–79.
- Davies, S. J. J. F., and R. Carrick (1962). On the ability of Crested Terns, *Sterna bergii*, to recognize their own chicks. *Australian Journal of Zoology* 10:171–177.
- Dunn, P. O., J. T. Lifjeld, and L. A. Whittingham (2009). Multiple paternity and offspring quality in Tree Swallows. *Behavioral Ecology and Sociobiology* 63:911–922.
- Forstmeier, W., C. Burger, K. Temnow, and S. Derégnaucourt (2009). The genetic basis of Zebra Finch vocalizations. *Evolution* 63:2114–2130.
- Hain, T. J. A., and B. D. Neff (2006). Promiscuity drives self-referent kin recognition. *Current Biology* 16:1807–1811.
- Halevy, O., A. Geyra, M. Barak, Z. Uni, and D. Sklan (2000). Early posthatch starvation decreases satellite cell proliferation and skeletal muscle growth in chicks. *Journal of Nutrition* 130:858–864.
- Hauber, M. E., and P. W. Sherman (2001). Self-referent phenotype matching: Theoretical considerations and empirical evidence. *Trends in Neurosciences* 24:609–616.
- Hepper, P. G. (1991). *Kin Recognition*. Cambridge University Press, Cambridge, UK.
- Hill, J. A., D. A. Enstrom, E. D. Ketterson, V. Nolan, Jr., and C. Ziegenfuss (1999). Mate choice based on static versus dynamic secondary sexual traits in the Dark-eyed Junco. *Behavioral Ecology* 10:91–96.

- Kempnaers, B., and B. C. Sheldon (1996). Why do male birds not discriminate between their own and extra-pair offspring? *Animal Behaviour* 51:1165–1173.
- Kempnaers, B., G. R. Verheyen, and A. A. Dhondt (1997). Extra-pair paternity in the Blue Tit (*Parus caeruleus*): Female choice, male characteristics, and offspring quality. *Behavioral Ecology* 8:481–492.
- Konovalov, D. A., C. Manning, and M. T. Henshaw (2004). KINGROUP: A program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes* 4:779–782.
- Krause, E. T., O. Krüger, P. Kohlmeier, and B. A. Caspers (2012). Olfactory kin recognition in a songbird. *Biology Letters* 8: 327–329.
- Loesche, P., P. K. Stoddard, B. J. Higgins, and M. D. Beecher (1991). Signature versus perceptual adaptations for individual vocal recognition in swallows. *Behaviour* 118:15–25.
- Lyon, B., J. Eadie, and L. Hamilton (1994). Parental choice selects for ornamental plumage in American Coot chicks. *Nature* 371:240–243.
- Mateo, J. M. (2002). Kin-recognition abilities and nepotism as a function of sociality. *Proceedings of the Royal Society London* 269:721–727.
- May, R. M., and S. K. Robinson (1985). Population dynamics of avian brood parasitism. *American Naturalist* 126:475–494.
- Medvin, M. B., P. K. Stoddard, and M. D. Beecher (1992). Signals for parent-offspring recognition: Strong sib-sib similarity in Cliff Swallows but not Barn Swallows. *Ethology* 90:17–28.
- Neff, B. D., and P. W. Sherman (2002). Decision making and recognition mechanisms. *Proceedings of the Royal Society London* 269:1435–1441.
- Negro, J. J., A. Chastin, and D. M. Bird (1994). Effects of short-term food deprivation on growth of hand-reared American Kestrels. *The Condor* 96:749–760.
- Queller, D. C., and K. F. Goodnight (1989). Estimating relatedness using genetic markers. *Evolution* 43:258–275.
- Roldán, M., and M. Soler (2011). Parental-care parasitism: How do unrelated offspring attain acceptance by foster parents? *Behavioral Ecology* 22:679–691.
- Saino, N., and A. P. Møller (1995). Testosterone-induced depression of male parental behavior in the Barn Swallow: Female compensation and effects on seasonal fitness. *Behavioral Ecology and Sociobiology* 36:151–157.
- Schuetz, J. G. (2005a). Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of defenses against parasitism. *Evolution* 59: 2017–2024.
- Schuetz, J. G. (2005b). Reduced growth but not survival of chicks with altered gape patterns: Implications for the evolution of nestling similarity in a parasitic finch. *Animal Behaviour* 70: 839–848.
- SPSS (2009). PASW Statistics 18 Core System User's Guide. SPSS, Chicago, IL, USA.
- Stoddard, M. C., and M. Stevens (2010). Pattern mimicry of host eggs by the Common Cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society of London, Series B* 277: 1387–1393.
- Stoddard, P. K., and M. D. Beecher (1983). Parental recognition of offspring in the Cliff Swallow. *The Auk* 100:795–799.
- Thorpe, W. H. (1958). The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis* 100:535–570.
- Tsyusko, O. V., M. B. Peters, C. Hagen, T. D. Tuberville, T. A. Mousseau, A. P. Møller, and T. C. Glenn (2007). Microsatellite markers isolated from Barn Swallows (*Hirundo rustica*). *Molecular Ecology Notes* 7:833–835.
- Turner, A., and C. Rose (1989). *A Handbook to the Swallows and Martins of the World*. Christopher Helm, London, UK.
- Waldman, B. (1987). Mechanisms of kin recognition. *Journal of Theoretical Biology* 128:159–185.
- Weatherhead, P. J., and P. T. Boag (1995). Pair and extra-pair mating success relative to male quality in Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* 37:81–91.
- Wright, J. (1998). Paternity and paternal care. In *Sperm Competition and Sexual Selection* (T. R. Birkhead and A. P. Møller, Editors). Academic Press, London, UK. pp. 117–145.