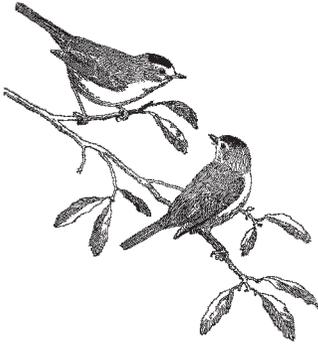




FRONTISPIECE. Cliff Swallow (*Petrochelidon pyrrhonota*) exhibiting typical vigilance at its nest in a southwestern Nebraska breeding colony (see Roche and Brown, pages 685–695). Individuals vary in the extent to which they are vigilant, and these individual differences may reflect different personality types. Photograph by Charles R. Brown.



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## AMONG-INDIVIDUAL VARIATION IN VIGILANCE AT THE NEST IN COLONIAL CLIFF SWALLOWS

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**ABSTRACT.**—Enhanced vigilance against predation is often an advantage of living in groups, but most studies have not examined individual-specific variation in the propensity to be vigilant among the animals within a group. We studied vigilance at the nest in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska in 2011 and 2012, and asked whether differences among individuals were consistent over time, whether vigilance varied among different colonies, and whether there were positive or negative fitness consequences of different levels of vigilance. We found significant among-individual variation in extent of vigilance and some variation among different colony sites. Vigilance also varied with date and nesting stage, but other phenotypic characteristics of a bird had no effect on vigilance. Differences among individuals in vigilance were not strongly related to their reproductive success that season, but more vigilant individuals were more likely to attempt intrusions into their neighbors' nests. Vigilance at the nest may be partly directed at monitoring conspecifics' activities in neighboring nests. This study is among the few that have investigated individual variation in vigilance behavior, a possible index of personality for Cliff Swallows, and the first to measure variation in vigilance for a colonial bird while breeding. *Received 31 December 2012. Accepted 2 March 2013.*

**Key words:** coloniality, personality, *Petrochelidon pyrrhonota*, reproductive success, social behavior, vigilance.

One major challenge facing most animals is allocating time between predator-directed vigilance and mutually incompatible activities such as foraging, courting, or caring for offspring. Many studies have examined correlates associated with individual vigilance, finding that investment in vigilance often varies with age, sex, dominance, reproductive stage, distance to cover, position in a group, predation pressure, and, perhaps most commonly, group size (reviewed in Elgar 1989, Carter et al. 2009). Because the probability of detecting a predator is generally greater in larger

animal groups (Pulliam 1973; Hoogland 1979, 1981; Hart and Lendrem 1984; Brown and Brown 1987; Roberts 1996), it is widely believed that sociality often affords the twin advantages to an individual of reducing both predation risk and the investment it must personally make in being vigilant.

The extent to which a given individual within a group experiences the benefit of being able to allocate less time to vigilance depends largely on context. However, it is well known that certain individuals are routinely more vigilant than others (Jennings and Evans 1980, Inglis and Lazarus 1981, Lima 1987, Elgar 1989), and this implies that vigilance-related advantages apply unequally to animals within a group. Theoretical studies

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TABLE 1. Observation effort for vigilance studies of Cliff Swallows at four colonies, showing the total number of swallows observed ( $n$ ), the total number of focal observations of individuals conducted at each colony, the colony-specific mean and standard deviation (SD) of the number of focal observations conducted per individual, and colony size (number of nests).

Colony site	Year	$n$	Focal observations	Mean (SD)	Colony size
Aqueduct	2012	10	23	2.3 (0.8)	20
CR1	2012	39	169	4.4 (1.1)	165
CR1	2011	41	188	4.5 (1.5)	170
Junkyard	2012	26	118	4.4 (1.5)	1,575

have examined how variation in vigilance among individuals within groups influences the link between group size and predator detection (Bednekoff and Lima 2002, Michelena and Deneubourg 2011, Beauchamp et al. 2012). Behavioral differences among animals that are consistent over time are recognized as animal “personalities” (Réale et al. 2000, Dingemanse et al. 2002, Carere et al. 2005, Réale and Dingemanse 2010), and individual personality traits such as aggressiveness or boldness may be correlated and make up a “behavioral syndrome” (Sih et al. 2004a, b; Bell and Sih 2007).

Empirical studies of individual variation in vigilance behavior are relatively scarce. For example, many studies on vigilance have been done with unmarked animals, often in large foraging flocks where an individual may be difficult to re-locate, or have specifically excluded multiple observations of the same individual for statistical simplicity (Carter et al. 2009). An exception was a study of lizards, in which individuals varied consistently enough in their response to the risk of predation to suggest that anti-predator behavior could be a distinctive personality trait (Lopez et al. 2005), and perhaps part of a wider behavioral syndrome (Sih et al. 2004a, b; Bell and Sih 2007). Thus, could some of the variation in vigilance among individuals be related to personality, independent of extrinsic factors affecting vigilance?

As in many species that live in groups, anti-predator advantages are important in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*). Colony-level vigilance (as reflected in distances at which incoming predators are detected) increases in larger Cliff Swallow colonies (Wilkinson and English-Loeb 1982, Brown and Brown 1987), and enhanced predator avoidance may be one reason these birds form colonies (Brown and Brown 1996). However, despite extensive long-term work on the

benefits of coloniality in Cliff Swallows, we know nothing about individual differences in vigilance allocation or the variability in potential vigilance-related advantages for birds in different colonies.

In this study, we examine whether individual differences in vigilance among nesting Cliff Swallows were consistent over time. Our objectives were to identify: (1) whether individual vigilance levels varied among colonies representing very different social environments; (2) whether there were positive or negative fitness consequences of different levels of vigilance; (3) whether vigilance levels were associated with trespassing behavior; and (4) if individual Cliff Swallows formed breeding pairs assortatively with respect to propensity to be vigilant. Consistent individual differences in vigilance would suggest that this behavior could be useful in defining personality types (Réale et al. 2000, Dingemanse et al. 2002, Carere et al. 2005, Réale and Dingemanse 2010), and systematic differences among birds in colonies of different sizes might suggest some degree of phenotypic sorting into groups (Brown et al. 1990; Brown and Brown 2000, 2001; Spottiswoode 2007, 2009) based on personality traits. Unlike in most studies of vigilance, which have been conducted in flocking species in the non-breeding season or away from breeding sites, we were able to study how Cliff Swallows allocate vigilance at their nest while breeding and thus to directly determine how reproductive success varies among individuals who exhibit different levels of vigilance.

## METHODS

*Study Area.*—Cliff Swallows have been studied since 1982 near the Cedar Point Biological Station (41° 13' N, 101° 39' W) in Keith County, southwestern Nebraska, USA, along the North and South Platte rivers; the study area also includes portions of Deuel, Garden, and Lincoln counties.

In this area the birds nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs. The breeding season lasts from early May to mid-July. The study area contains about 220 colony sites (i.e., physical structures on which colonies may form), with about a third not used in a given year. Colony size varies widely; in southwestern Nebraska it ranges from 2–6,000 nests (mean  $\pm$  SE,  $404 \pm 13$ ,  $n = 2,318$  colonies), with some birds nesting solitarily. The study site is described in detail by Brown and Brown (1996).

**Field Methods.**—In 2011 and 2012, we captured Cliff Swallows in mist nets at selected colonies as they exited from their nests; see Brown (1998) for capture methods. For individual recognition at a distance, we used permanent, non-toxic Sharpie® markers to apply unique 3- and 4-color stripe combinations to the birds' white forehead patches, which are highly visible when Cliff Swallows are present at their nests (Brown and Brown 1996). We color-marked and observed a total of 116 Cliff Swallows at four colonies; at one site, Cliff Swallows were observed in both years (although not the same individuals), and we considered these two separate colonies (Table 1).

Following marking, we observed each colony to determine at which nests the marked swallows were residents. We created schematic maps of each colony and assigned marked swallows to their nests by watching for repeated nest visits, indications of nest defense, and eventual egg-laying. Once nest assignment was complete, we marked focal nests by painting numbers on the nests' mud exteriors to facilitate observation.

Behavioral observations were conducted primarily by two observers in 2011 and three in 2012. We rotated among the color-marked birds, selecting one at a time to watch as a focal animal. We typically watched a given bird only once per day, and selected individuals for each day's observations based only on how many previous times a bird had been observed. We tried to accumulate an equivalent number of focal-animal watches for all color-marked birds, and had at least 4 for most individuals (mean = 4.2, SD = 1.4). In 2011, observations were conducted from initial nest construction at a colony through egg-laying but were terminated when eggs hatched, while in 2012 we conducted observations until nestlings fledged.

Observers sat as close to nests as possible (typically 2–3 meters from the entrance of the colony) without noticeably influencing the behavior

of the birds and conducted 15-min focal observations on color-marked individuals using binoculars. During a focal observation, we recorded the behavior exhibited by the bird during every 15-sec interval, not watching any other bird during that time. This included noting whether the individual was present at the nest entrance, out of sight inside the nest, absent from the colony, interacting with neighbors, or nest-building. Vigilance was defined as a bird being visible in the tubular entrance of its nest, peering out. Birds out of sight inside the nest were considered not vigilant. Sitting in the nest entrance precluded incubating eggs or brooding young, given the gourd-shaped architecture of a typical cliff swallow nest. Any focal individual that left its nest and attempted to enter a neighboring nest (a trespass attempt, as described by Brown and Brown [1996]) was so noted.

We conducted nest checks beginning, prior to, and during, nest initiation at the nests of the focal individuals, using a dental mirror and flashlight inserted through the nest's tubular mud neck. Nests were checked at 2–4 day intervals throughout the nesting season to monitor laying times, hatching dates, and nestling presence. At 17 days after the estimated hatching date, the number of nestlings surviving in each nest was determined, and we used this metric as a relative estimate of annual reproductive success for each color-marked bird. Although Cliff Swallows typically fledge at 23–26 days (Brown and Brown 1995), premature fledging can occur if mirrors are inserted into nests after nestlings reach 17 days of age.

The colonies used in this study were fumigated to remove ectoparasites approximately once a week, as described by Brown and Brown (1996). Cliff Swallow colonies of different sizes vary widely in the numbers of blood-sucking swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) infesting the nests, and bugs represent a major source of nesting failure that tends to increase with colony size and swamps the effects of other independent variables (Brown and Brown 1996). Fumigation eliminated ectoparasitism as a confounding factor on reproductive success, although because parasite load has been implicated as a potential cause of individual variation in behavior (Barber and Dingemans 2010, Kortet et al. 2010), we acknowledge that we possibly affected among-individual variation in vigilance by fumigating nests. Under these conditions, we would expect any

individual variation we detect to be a conservative measure.

*Statistical Analyses.*—We scored vigilance for each bird by tabulating the total number of 15-sec increments during which a swallow was observed being vigilant for each 15-min focal observation period. If a swallow was observed doing more than one activity within a 15-sec interval, we weighted that interval by the number of different activities that individual was engaged in. We log transformed these values to use as a response variable in linear mixed regression models (LN [vigilance + 1]). We considered these values an index of an individual's propensity to be vigilant.

We used linear mixed models to assess whether there was significant variation among individuals by including the identity of each individual as an intercept-only random effect (ID). The unique intercept differences between individuals can be interpreted as among-individual differences in behavior (Betini and Norris 2012, Dingemanse and Dochtermann 2013). Similarly, as each individual was associated with a specific colony, we included colony as an intercept-only random effect (Colony). Statistical support for a random effect of colony would indicate some of the residual variance in vigilance behavior was also explained by among-colony differences (Dingemanse and Dochtermann 2013). As multiple 15-min observation periods were conducted on any given day, we controlled for among-day differences in behavior by also including a random effect of Julian date (Date).

Although we were primarily interested in whether there were differences in vigilance behavior among individuals (i.e., support for ID) and colonies (i.e., support for Colony), we also controlled for other environmental and demographic factors that could influence Cliff Swallow behavior. To do this, we built a full model consisting of all covariates we believed might be important (treated as fixed effects; Table 2) and, beginning with the full model, used a process of backward selection in which we sequentially removed each covariate. We evaluated each model with its Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) and accepted the removal of a covariate if its deletion resulted in a lower  $AIC_c$  value (Burnham and Anderson 2002). We conducted statistical analyses using program R (R Development Core Team 2012), fit general linear mixed models using package "lme4" (Bates et al. 2012), and calculated  $AIC_c$  using the package "AICcmodavg" (Mazerolle 2012).

For linear models of vigilance, we used an (exact) restricted log likelihood ratio test (RLRT) to test whether the variance of a random effect deviated from 0; the RLRT test was fit using the exactRLRT function in the RLRsim package (Sheipl et al. 2008) on the top model that controlled for all relevant fixed effects. We used the RLRT test to investigate whether there was support for significant differences between individuals (i.e., support for the random effect of ID; *sensu* Betini and Norris [2012]). To determine the extent of variation in vigilance explained by the individual, colony, and date, we also calculated repeatabilities for our top model following Dingemanse and Dochtermann (2013; and see Lessells and Boag [1987], Nakagawa and Schielzeth [2010]).

To examine the relationship of vigilance to reproductive success, we extracted conditional modes of the ID random effect from the linear mixed model for use as vigilance scores (Boon et al. 2007, Martin and Réale 2008, Betini and Norris 2012). These conditional modes (or BLUPs, best linear unbiased predictors) predict the random effect term independent of other potentially confounding terms in the linear mixed model (Pinhero and Bates 2000). We hereafter refer to these values as an individual swallow's relative vigilance score. We examined the relationship between reproductive success and vigilance scores using a correlation.

We were similarly interested in whether an individual Cliff Swallow's propensity to trespass might be associated with its vigilance level. We used a Wilcoxon rank-sum test to compare the vigilance scores (represented by the BLUPs) for individuals that had been observed trespassing at least once ( $n = 18$  individuals) to those individuals that had never been observed trespassing ( $n = 98$  individuals).

To assess whether assortative mating by vigilance was occurring, we conducted a two-tailed random permutation test (coded in program R) to compare the difference in mean relative vigilance score (as measured by the vigilance BLUP) within a mated pair ( $n = 13$  mated pairs) to the difference in mean relative vigilance score within randomly paired individuals that were not part of a mated pair in which behavioral observations were made on both individuals ( $n = 4,005$  remaining permutations). The difference in the means between these two groups was taken (e.g.,  $T_{\text{obs}} = \bar{x}_{\text{matediff}} - \bar{x}_{\text{randiff}}$ ). The within-pair differences in vigilance scores for the two groups

TABLE 2. Covariates included in linear mixed-effects models to explain vigilance in Cliff Swallows.

Covariate	Effect	Type	Definition
Age	Fixed	Continuous	Relative age of the focal bird, taken as observation year minus banding year + 1 for birds banded as adults; observation year minus banding year for birds banded as juveniles.
Experience	Fixed	Categorical	Whether or not the focal bird was known to have nested at its colony site in a previous year (only known for birds first banded in a previous year).
Absence	Fixed	Continuous	Total amount of time a swallow was absent during a 15-min focal observation (LN + 1 transformed).
Stage	Fixed	Categorical	Whether the nest of a focal bird had eggs or nestlings on a given date.
Sex	Fixed	Categorical	Sex of the focal bird.
Mass	Fixed	Continuous	Body mass of the focal bird relative to other birds caught at the same site on the same date and of the same sex. <sup>a</sup>
Colony	Random ( <i>intercept</i> )	Categorical	Colony where bird was resident.
Date	Random ( <i>intercept</i> )	Categorical	Julian date on which an observation occurred.
ID	Random ( <i>intercept</i> )	Categorical	Focal individual (ID = band number)

<sup>a</sup> Mass was standardized using the mean body mass of all birds of the same sex caught at the same colony on the same day (i.e.,  $mass_{standardized} = (mass_{individual} - mass_{mean})/mass_{SD}$ ).

were pooled ( $n = 4,018$ ) and a sample of 13 was randomly drawn from the pooled group without replacement, and the mean of this sample was taken. The mean of the random sample was subtracted from the mean of the group without the sampled individuals, and the process was repeated over 10,000 iterations.  $P$ -values were generated by summing the permuted absolute value of the differences  $\geq$  the absolute value of  $T_{obs}$  and taking the mean (Roche et al. 2008).

## RESULTS

We found support for individual differences (the ID random effect) in vigilance after controlling for other environmental covariates associated with behavioral variation (Table 3). The random effect of ID used in our linear mixed models for vigilance behavior was significant using an (exact) restricted log-likelihood test (RLRT = 7.42,  $P = 0.003$  based on 116 individuals and 10,000 simulated values). However, the associated biological repeatability score for among-individual variance, which is a measure of how much of the variation in vigilance behavior is accounted for by the individual (i.e., ID), and thus how different individuals were from each other across the study area, was low (Repeatability =  $V_{ID}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual}) = 0.067$ ; Table 3). On a given day and within a given colony, the repeatability of an individual's behavior was slightly higher (Repeatability =

$V_{ID}/(V_{ID} + V_{Residual}) = 0.089$ ). The amount of vigilance behavior a Cliff Swallow displayed was also explained in part by the amount of time an individual was present at its nest (i.e., those more frequently absent were less vigilant when they were present; Table 3) and stage of reproduction (i.e., birds were more vigilant when incubating eggs than when raising nestlings; Table 3). Age, body mass, sex, and experience had no effect on vigilance, as these covariates were eliminated from the final model based on AIC<sub>c</sub> scores.

We found some evidence of among-colony differences in vigilance of Cliff Swallows using the (exact) restricted log-likelihood test (RLRT = 2.192,  $P = 0.036$  based on 116 individuals and 10,000 simulated values), but biological within-colony repeatability, in this case how different the behavior at different colonies was across the study area, was similarly low (Repeatability =  $V_{Colony}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual}) = 0.029$ ). The colony that was associated with the least amount of vigilance behavior was CR1 in 2012 (BLUP =  $-0.186 \pm 0.106$  SE) and the site with the most vigilance behavior was CR1 in 2011 (BLUP =  $0.136 \pm 0.129$  SE). However, the differences in the (transformed) raw vigilance scores among colonies were not obviously related in any way to colony size (Fig. 1).

The number of nestlings surviving to day 17 in nests of the more vigilant birds (i.e., individuals with higher relative vigilance scores) was slightly

TABLE 3. Regression coefficient estimates and standard errors (SE) for fixed effects and variance estimates for random effects from the top linear mixed model (selected via backwards selection and minimum AIC<sub>c</sub> value) used to explain variation in vigilance among Cliff Swallows. We calculated the “true biological repeatability” of our sample following Dingemanse and Dochtermann (2013). For example, the repeatability of the random effect of individual was calculated as:  $V_{ID}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$  where “ $V_{ID}$ ” is the phenotypic variance attributed to the individual and  $(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$  is the cumulative phenotypic variance of the sample explained by the random effects.

Regression coefficient:		
	Random effects variance	Repeatability
ID (intercept) <sup>a</sup>	0.083	0.067
Colony (intercept) <sup>b</sup>	0.035	0.029
Date (intercept)	0.298	0.242
Residual	0.814	0.662
Fixed effects estimates		
Stage (egg)	1.568 (0.169 SE)	-
Stage (chick)	1.220 (0.205 SE)	-
Absence	-0.125 (0.033 SE)	-

<sup>a</sup> RLRT = 7.42,  $P = 0.003$  based on 116 individuals and 10,000 simulated values.  
<sup>b</sup> RLRT = 2.192,  $P = 0.036$  based on 116 individuals and 10,000 simulated values.

lower than that for the less vigilant individuals, although the relationship was not statistically significant at the  $P = 0.05$  level ( $r_s = -0.16$ ,  $P = 0.08$ ,  $n = 116$  birds, Fig. 2).

There was an association between vigilance and the probability of trespassing into a neighboring Cliff Swallow’s nest: the mean ( $\pm$  SE) relative vigilance score for birds ( $n = 18$ ) seen to trespass

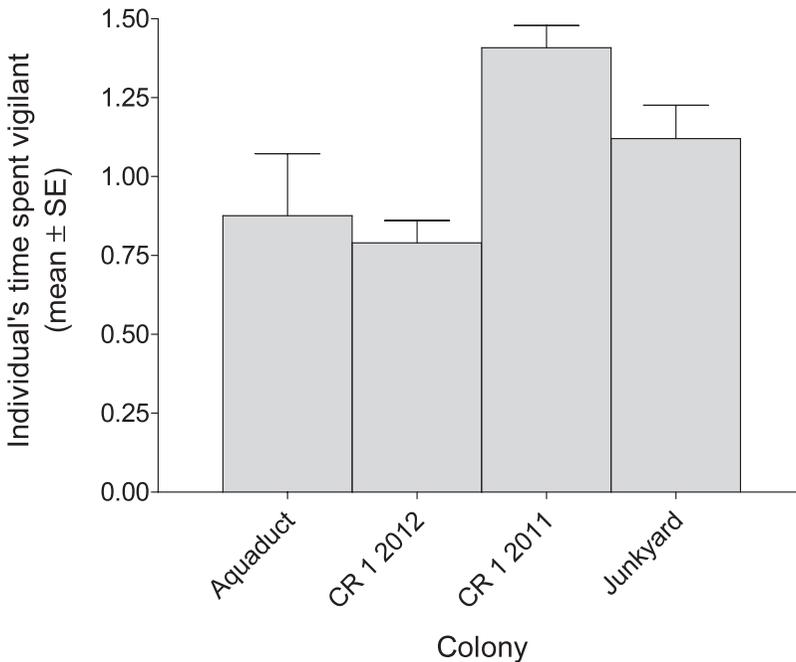


FIG. 1. The frequency with which an individual Cliff Swallow was vigilant at the nest (the natural log-transformed amount of time the bird was vigilant during a 15-min focal observation period) in relation to the colony in which it was resident. Means ( $\pm$  SE) for all birds at a site are shown; sample size (number of individuals observed) and colony size for each site are given in Table 1.

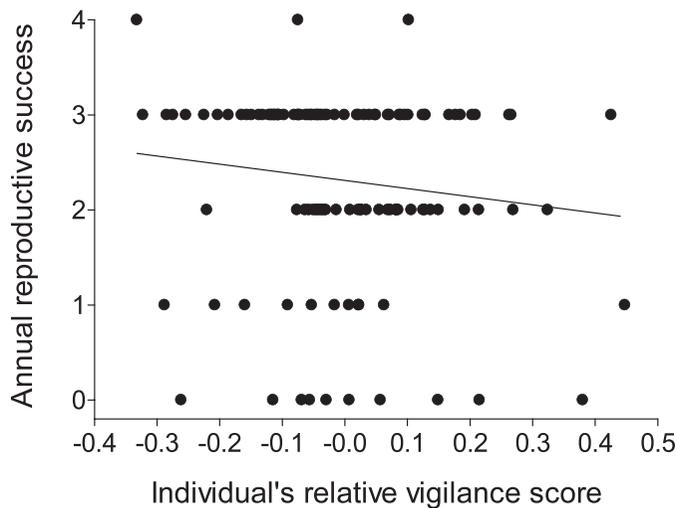


FIG. 2. Annual reproductive success (number of nestlings surviving to 17 days of age) of Cliff Swallows in relation to an individual's relative vigilance score. Higher scores indicate increased vigilance. Vigilance scores are represented by the conditional modes (BLUPs, best unbiased linear predictors), which described the random effect of individual, independent of other fixed effects in the top linear model (Pinheiro and Bates 2000). Reproductive success declined with vigilance score but was not significant ( $r_s = -0.16$ ,  $P = 0.08$ ,  $n = 116$  birds). Line indicates best-fit least-squares regression.

elsewhere at least once ( $0.105 \pm 0.038$ ) was over 5 times that of the scores for individuals ( $n = 98$ ) never seen to trespass ( $-0.020 \pm 0.014$ ), and the difference was significant (Wilcoxon test,  $Z = 3.03$ ,  $P = 0.002$ ).

There was some suggestion that vigilance of Cliff Swallows in mated pairs was more similar than vigilance among randomly generated pairs, although our sample size of mated pairs was small ( $n = 13$ ) and the trend not significant at the  $P = 0.05$  level (two-tailed permutation test,  $P = 0.10$ ).

## DISCUSSION

Our study revealed significant among-individual and among-colony variation in nest-site vigilance exhibited by Cliff Swallows. Vigilance varied with date and nesting stage, but other phenotypic characteristics of a bird (e.g., sex, age, and experience at a site) had no effect on vigilance. Differences among individuals in vigilance were not significantly related to their reproductive success that season, but more vigilant individuals were significantly more likely to attempt intrusions into their neighbors' nests. This study is among the few that have investigated individual variation in vigilance behavior (Carter et al. 2009, Rieucan et al. 2010, Couchoux and Cresswell 2012), and the first to measure variation in vigilance for a colonial bird.

Behavioral syndromes consisting of a constellation of co-occurring personality traits are now well known in many species (Sih et al. 2004a, b; Dingemanse and Wolf 2010). In other species in which significant among-individual differences in anti-predator behavior have been demonstrated, it was suggested that these differences reflect a "shy-bold" continuum in personality types (Lopez et al. 2005). Although our data support the existence of a personality based on vigilance, it remains unclear whether this vigilance is the same as boldness. For example, more vigilant Cliff Swallows were also more likely to trespass at neighboring nests, indicating that the vigilant personality type may be more likely to take risks (i.e., evidence of boldness) and is also more aggressive. Trespass attempts often end in violent fights in which the trespasser is repelled when a neighbor is present in the nest that is invaded (Brown and Brown 1996). Because they presumably can better monitor what is occurring in or near the colony than can birds that are out of sight in the nest, more vigilant individuals probably have better information to judge whether a disturbance to the colony merits vacating the nest. If a bird remains at the colony in the face of imminent threat from a terrestrial predator such as a snake, it could be considered bold, especially since snakes do prey on adult Cliff Swallows in

their nests (Brown and Brown 1996). However, an individual fleeing its nest in the presence of an aerially hunting raptor approaching the colony could also be considered bold, in that it enhances its risk of being attacked as it exits the site. Thus, context is important in knowing whether a given behavior could be considered bold versus shy.

As in most studies of vigilance, we could not rule out that some of the vigilance exhibited by Cliff Swallows at their nest was directed at conspecifics instead of at potential predators. Vigilance in many species may also reflect social interactions with group members, such as in competition for mates or looking for food (Burger and Gochfeld 1988, Beauchamp 2001, Robinette and Ha 2001, Carter et al. 2009). In Common Redshanks (*Tringa totanus*), individuals have been observed to adjust their vigilance level depending on the riskiness of the situation with varying degrees of plasticity (Couchoux and Cresswell 2012). The fact that high levels of vigilance in Cliff Swallows frequently led to trespass attempts supports the view that birds scanning at their nest may be monitoring their neighbors, looking for a nest to intrude upon. However, the vigilant birds at their entrances were also the first ones to give alarm calls if a predator managed to enter the colony undetected by swallows flying overhead, and the vigilant birds were the first ones to exit (C. R. Brown, pers. obs.). Being vigilant was presumably beneficial in allowing a bird to be among the first wave of residents flying out of the colony.

We found a weak association between individual vigilance and reproductive success in Cliff Swallows. The more vigilant swallows tended to rear fewer nestlings to approximate fledging age (Fig. 2). The lack of statistical significance of this relationship may have reflected in part our relatively small sample size ( $n = 116$  individuals) for demographic studies, meaning that we could detect only rather large changes in reproductive success associated with vigilance. Additionally, our use of fumigated nests for this study might have diminished variability in observed reproductive success and reduced our ability to detect a link between vigilance and fitness.

Vigilance-related fitness trade-offs have been previously documented in Gray Partridges (*Perdix perdix*; Watson et al. 2007). For this species, increased vigilance levels were associated with lower winter survival even when flock size was

controlled, suggesting vigilance behavior had long-term costs perhaps as a result of increased starvation risk (Watson et al. 2007). If, as our data suggest, vigilance in Cliff Swallows is associated with a fitness cost such as diminished annual reproductive success, it may be because the more vigilant individuals are more likely to leave their nests unattended while trespassing elsewhere, potentially making their own nests more vulnerable to interference from neighboring conspecifics that may destroy eggs (Brown and Brown 1988, 1996). Also, the more vigilant individuals might have more inconsistent incubation and poorer provisioning of young: perching at the nest entrance precludes incubating eggs or foraging for food for nestlings, and in Cliff Swallows both parents incubate and feed the young. This effect could be potentially exaggerated if swallows are more likely to mate assortatively based on proclivity to be vigilant (and trespass), which our data suggest.

Behaviors such as aggression and boldness have been linked to degree of sociality in some birds (Verbeek et al. 1999, Fox et al. 2009, Kurvers et al. 2009, David et al. 2011), and the same may be true, at least in part, for vigilance in our study. The social environment as represented by the colony site was associated with the level of vigilance a Cliff Swallow exhibited, although there was a relatively small difference in individual vigilance among colonies. This result is somewhat surprising given that the colony sizes (and thus the social environments) of the Cliff Swallow colonies we studied were quite different, with these colonies varying in size by almost two orders of magnitude. One colony, Aquaduct, was small, and birds there rarely interacted in general and by trespassing in particular, perhaps because the nests were far apart (making it more difficult to perhaps impossible for swallows to see what their neighbors were doing). In contrast, Junkyard was a massive colony where nests occurred in high density, with most nests physically touching four or more adjacent ones. If vigilance at the nest is directed primarily at predators, we might expect the most vigilance among birds at Aquaduct and the least at Junkyard, following the group-size effect so pervasive among most studies on flocking animals.

That we did not see these predicted differences may reflect the fact that vigilance at one site (the small colony) was directed primarily at predators and at the other (the large colony) primarily at the

many neighboring conspecifics, including for the gathering of information about foraging success (Brown 1986). Such behavior would not be unprecedented. Results from a study on vigilance in eastern grey kangaroos (*Macropus giganteus*) suggested that the increased vigilance towards conspecifics exhibited by some individuals in larger group sizes could offset the reduction in anti-predator vigilance exhibited by others (Carter et al. 2009). Higher levels of conspecific-directed vigilance in larger groups may often obscure the predicted vigilance-group-size relationship in general (Beauchamp 2001).

Could Cliff Swallows sort among colony sizes based on vigilance and shy-bold personality types? While other evidence suggests that these birds are non-randomly distributed among different colony sizes (Brown and Brown 1996, 2000; Brown et al. 2005), results of this study do not indicate a simple relationship between vigilance and colony size. Experimental manipulation would be necessary to determine if the small (but significant) differences in vigilance between colonies are a result of phenotypic sorting of some sort, or a result of the colony environment and how it affects the behavior of the swallows. For example, inherently more vigilant individuals might settle in smaller colonies, or small colonies may cause the birds who settle there (for other reasons) to be more vigilant. When group size was experimentally manipulated for wild-caught Scaly-breasted Munias (*Lonchura punctulata*), rank individual differences in vigilance were retained, and individuals appeared to respond to increasing group size equivalently (Rieucou et al. 2010). Clearly, a similar mechanism could be at play for Cliff Swallows, with average vigilance levels a product of context (Couchoux and Cresswell 2012). The relatively small number of colonies we studied (four) dictates caution in making conclusions about vigilance behavior and colony size, but the fact that there were so few differences in vigilance behavior over the wide colony-size range indicates that extension of these laborious observations to additional colonies likely would not change our conclusions.

Cliff Swallows have expanded their range in much of North America since the 1960s in response to construction of bridges and culverts (Brown and Brown 1995), and in many areas these birds have adopted locally novel nesting substrates such as buildings of particular types or circular metal drainage tubes. Who are the

individuals that are the first to find these new sites? Are they substantially different from those swallows that have continued to nest on cliff faces or that show higher fidelity to established colony sites? Perhaps they differ in vigilance, aggressiveness, or an as yet unmeasured exploratory personality. Continued study of the behavioral profiles that allow some individuals, but not others, to successfully transition from one breeding environment to another would contribute to our understanding of why animal personalities persist and also have implications for conservation of species that have proved to be less environmentally flexible.

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#### LITERATURE CITED

- BARBER, I. AND N. J. DINGEMANSE. 2010. Parasitism and the evolutionary ecology of animal personality. *Philosophical Transactions of the Royal Society B* 365:4077–4088.
- BATES, D., M. MAECHLER, AND B. BOLKER. 2012. lme4: linear mixed-effects models using Eigen and R syntax. R package version 0.999999-0. CRAN.R-project.org/package=lme4.
- BEAUCHAMP, G. 2001. Should vigilance always decrease with group size? *Behavioral Ecology and Sociobiology* 51:47–52.
- BEAUCHAMP, G., P. ALEXANDER, AND R. JOVANI. 2012. Consistent waves of collective vigilance in groups using public information about predation risk. *Behavioral Ecology* 23:368–374.
- BEDNEKOFF, P. A. AND S. L. LIMA. 2002. Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *Journal of Avian Biology* 33:143–149.
- BELL, A. M. AND A. SIH. 2007. Exposure to predation generates personality in three-spined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters* 10:828–834.
- BETINI, G. S. AND D. R. NORRIS. 2012. The relationship between personality and plasticity in Tree Swallow aggression and the consequences for reproductive success. *Animal Behaviour* 83:137–143.
- BOON, A. K., D. RÉALE, AND S. BOUTIN. 2007. The interaction between personality, offspring fitness, and

- food abundance in North American red squirrels. *Ecology Letters* 10:1094–1104.
- BROWN, C. R. 1986. Cliff Swallow colonies as information centers. *Science* 234:83–85.
- BROWN, C. R. 1998. Swallow summer. University of Nebraska Press, Lincoln, Nebraska, USA.
- BROWN, C. R. AND M. B. BROWN. 1987. Group-living in Cliff Swallows as an advantage in avoiding predators. *Behavioral Ecology and Sociobiology* 21:97–107.
- BROWN, C. R. AND M. B. BROWN. 1988. The costs and benefits of egg destruction by conspecifics in colonial Cliff Swallows. *Auk* 105:737–748.
- BROWN, C. R. AND M. B. BROWN. 1995. Cliff Swallow (*Hirundo pyrrhonota*). The birds of North America. Number 149.
- BROWN, C. R. AND M. B. BROWN. 1996. Coloniality in the Cliff Swallow: The effect of group size on social behavior. University of Chicago Press, Chicago, Illinois, USA.
- BROWN, C. R. AND M. B. BROWN. 2000. Heritable basis for choice of group size in a colonial bird. *Proceedings of the National Academy of Sciences USA* 97:14825–14830.
- BROWN, C. R. AND M. B. BROWN. 2001. Avian coloniality: progress and problems. *Current Ornithology* 16:1–82.
- BROWN, C. R., M. B. BROWN, S. A. RAOUF, L. C. SMITH, AND J. C. WINGFIELD. 2005. Steroid hormone levels are related to choice of colony size in Cliff Swallows. *Ecology* 86:2904–2915.
- BROWN, C. R., B. J. STUTCHBURY, AND P. D. WALSH. 1990. Choice of colony size in birds. *Trends in Ecology and Evolution* 5:398–403.
- BURGER, J. AND M. GOCHFELD. 1988. Effects of group size and sex on vigilance in Ostriches (*Struthio camelus*): antipredator strategy or mate competition? *Ostrich* 59:14–20.
- BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multi-model inference. Second Edition. Springer, New York, USA.
- CARERE, C., P. J. DRENT, L. PRIVITERA, J. M. KOOLHAAS, AND T. G. G. GROOTHUIS. 2005. Personalities in Great Tits, *Parus major*: stability and consistency. *Animal Behaviour* 70:795–805.
- CARTER, A. J., O. PAYS, AND A. W. GOLDIZEN. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. *Behavioral Ecology and Sociobiology* 64:237–245.
- COUCHOUX, C. AND W. CRESSWELL. 2012. Personality constraints versus flexible antipredation behaviors: how important is boldness in risk management of Redshanks (*Tringa totanus*) foraging in a natural system? *Behavioral Ecology* 23:290–301.
- DAVID, M., Y. AUCLAIR, AND R. CÉZILLY. 2011. Personality predicts social dominance in female Zebra Finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour* 81:219–224.
- DINGEMANSE, N. J., C. BOTH, P. J. DRENT, K. VAN OERS, AND A. J. VAN NOORDWIJK. 2002. Repeatability and heritability of exploratory behaviour in Great Tits from the wild. *Animal Behaviour* 64:929–937.
- DINGEMANSE, N. J. AND M. WOLF. 2010. Recent models for adaptive personality difference: a review. *Philosophical Transactions of the Royal Society B* 365:3947–3958.
- DINGEMANSE, N. J. AND N. A. DOCHTERMANN. 2013. Quantifying individual variation in behavior: mixed-effect modeling approaches. *Journal of Animal Ecology* 82:39–54.
- ELGAR, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* 64:13–33.
- FOX, R. A., L. D. LADAGE, T. C. ROTH, II, AND V. V. PRAVOSUDOV. 2009. Behavioral profile predicts dominance status in Mountain Chickadees, *Poecile gambeli*. *Animal Behaviour* 77:1441–1448.
- HART, A. AND D. W. LENDREM. 1984. Vigilance and scanning patterns in birds. *Animal Behaviour* 32:1216–1224.
- HOOGLAND, J. L. 1979. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Animal Behaviour* 27:394–407.
- HOOGLAND, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252–272.
- INGLIS, I. R. AND J. LAZARUS. 1981. Vigilance and flock size in Brent Geese: the edge effect. *Zeitschrift für Tierpsychologie* 57:193–200.
- JENNINGS, T. AND S. M. EVANS. 1980. Influence of position in the flock and flock size on vigilance in the Starling, *Sturnus vulgaris*. *Animal Behaviour* 28:634–635.
- KORTET, R., A. V. HEDRICK, AND A. VAINIKKA. 2010. Parasitism, predation and the evolution of animal personalities. *Ecology Letters* 12:1449–1458.
- KURVERS, R. H. J. M., B. EIKELINKAMP, K. VAN OERS, B. VAN LITH, S. E. VAN WIEREN, R. C. YDENBERG, AND H. H. T. PRINS. 2009. Personality differences explain leadership in Barnacle Geese. *Animal Behavior* 78:447–453.
- LESSELS, C. M. AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116–121.
- LIMA, S. L. 1987. Distance to cover, visual obstructions, and vigilance in House Sparrows. *Behaviour* 102:231–238.
- LOPEZ, P., D. HAWLENA, V. POLO, L. AMO, AND J. MARTIN. 2005. Sources of individual shy-bold variations in antipredator behavior of male Iberian rock lizards. *Animal Behaviour* 69:1–9.
- MARTIN, J. G. AND D. RÉALE. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 75:309–318.
- MAZEROLLE, M. J. 2012. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.26. CRAN.R-project.org/package=AICcmodavg
- MICHELENA, P. AND J.-L. DENEUBOURG. 2011. How group size affects vigilance dynamics and time allocation patterns: the key role of imitation and tempo. *PLoS One* 6:e18631.

- NAKAGAWA, S. AND H. SCHIELZETH. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85:935–956.
- PINHEIRO, J. C. AND D. M. BATES. 2000. Mixed-effects models in S and S-PLUS. Springer, New York, USA.
- PULLIAM, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:419–422.
- RÉALE, D. AND N. J. DINGEMANSE. 2010. Personality and individual social specialization. Pages 417–441 in *Social behaviour: genes, ecology and evolution* (T. Székely, A. J. Moore, and J. Komdeur, Editors), Cambridge University Press, Cambridge, United Kingdom.
- RÉALE, D., B. Y. GALLANT, M. LEBLANC, AND M. FESTA-BIANCHET. 2000. Consistency of temperament in bighorn ewes and correlates with behavior and life history. *Animal Behaviour* 60:589–597.
- R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RIEUCAU, G., J. MORAND-FERRON, AND L. A. GIRALDEAU. 2010. Group size effect in Nutmeg Mannikin: between-individuals behavioral differences but same plasticity. *Behavioral Ecology* 21: 684–689.
- ROBERTS, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* 62:447–452.
- ROBINETTE, R. L. AND J. C. HA. 2001. Social and ecological factors influencing vigilance by Northwestern Crows, *Corvus caurinus*. *Animal Behaviour* 62:447–452.
- ROCHE, E. A., T. W. ARNOLD, AND F. J. CUTHBERT. 2008. Relative fitness of wild and captive-reared Piping Plovers: does egg salvage contribute to recovery of the endangered Great Lakes population? *Biological Conservation* 141:3079–3088.
- SHEIPL, F., S. GREVEN, AND H. KUECHENHOFF. 2008. Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Computational Statistics and Data Analysis* 52:3283–3299.
- SIH, A., A. BELL, AND J. C. JOHNSON. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19:372–378.
- SIH, A., A. M. BELL, J. C. JOHNSON, AND R. E. ZIEMBA. 2004b. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79:241–277.
- SPOTTISWOODE, C. N. 2007. Phenotypic sorting in morphology and reproductive investment among Sociable Weaver colonies. *Oecologia* 154:589–600.
- SPOTTISWOODE, C. N. 2009. Fine-scale life-history variation in Sociable Weavers in relation to colony size. *Journal of Animal Ecology* 78:504–512.
- VERBEEK, M. E. M., P. DE GOEDE, P. J. DRENT, AND P. R. WIEPKEMA. 1999. Individual behavioural characteristics and dominance in aviary groups of Great Tits. *Behaviour* 136:23–48.
- WATSON, M., N. J. AEBISCHER, AND W. CRESSWELL. 2007. Vigilance and fitness in Grey Partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology* 76:211–221.
- WILKINSON, G. S. AND G. M. ENGLISH-LOEB. 1982. Predation and coloniality in Cliff Swallows (*Petrochelidon pyrrhonota*). *Auk* 99:459–467.