BROOD PARASITISM AND EGG TRANSFER IN CAVE SWALLOWS (*PETROCHELIDON FULVA*) AND CLIFF SWALLOWS (*P. PYRRHONOTA*) IN SOUTH TEXAS

Heath B. Weaver[1] and Charles R. Brown[2]

Department of Biological Sciences, University of Tulsa, Tulsa, Oklahoma 74104, USA

Abstract.—We studied the frequency of intraspecific brood parasitism and physical transfer of eggs between nests in colonially nesting Cave Swallows (*Petrochelidon fulva*) and Cliff Swallows (*P. pyrrhonota*) in south Texas in 2001. Although the eggs of the two species look similar, frequency of brood parasitism in each species was unaffected by presence of the other species, which suggests that the parasitism we observed was largely by conspecifics. We detected brood parasitism in 4.6–5.0% of Cave Swallow nests and in 10.7–11.9% of Cliff Swallow nests. Brood parasitism was not significantly related to colony size in either species, to eventual success of the host nest, or to overall colony nesting success (a measure of environmental risk). We detected evidence of physical transfer of eggs in 0.7–2.0% of nests of these species. Cliff Swallows parasitized nests more often than Cave Swallows, but the frequencies of brood parasitism and egg transfer in the two species in south Texas appeared broadly comparable to those reported for Cliff Swallows in Nebraska, despite geographic differences in habitat, seasonality, breeding phenology, and levels of sociality between the populations. *Received 28 January 2003, accepted 12 May 2004.*

Resumen.—Estudiamos la frecuencia de parasitismo de nidada intraespecífico y de transferencia física de huevos en las golondrinas *Petrochelidon fulva* y *P. pyrrhonota* en el sur de Texas en 2001. A pesar de que los huevos de ambas especies son similares, la frecuencia de parasitismo en cada especie no se vió afectada por la presencia de la otra especie, lo que sugiere que en gran medida el parasitismo observado fue ocasionado por individuos coespecíficos. Detectamos parasitismo de nidada en un 4.6–5.0% de los nidos de *P. fulva* y en un 10.7–11.9% de los nidos de *P. pyrrhonota.* El parasitismo de nidada no se correlacionó con el tamaño de la colonia, con el éxito eventual del nido hospedero, ni con el éxito de nidificación general de la colonia (una medida de riesgo ambiental) en ninguna de las dos especies. *P. pyrrhonota* parasitó nidos con mayor frecuencia que *P. fulva*, pero la frecuencia de parasitismo de nidada y de transferencia de huevos en las dos especies en el sur de Texas parecen ser comparables con las frecuencias reportadas para *P. pyrrhonota* en Nebraska, a pesar de las diferencias geográficas en el hábitat, en la estacionalidad, en la fenología de nidificación y en los niveles de estructura social entre las poblaciones.

An alternative reproductive tactic in some animals is to lay eggs in nests of conspecifics and parasitize the parental effort of the hosts. Brood parasitism among conspecifics is now known for scores of bird species and some insects (Yom-Tov 1980, Andersson 1984, Rohwer and Freeman 1989, Rothstein and Robinson 1998) and, across taxa, appears to be associated especially with high fecundity (Arnold and Owens 2002). However, ecological conditions favoring parasitic laying have been investigated for only a few species, such as swallows (Brown 1984, Møller 1987, Brown and Brown 1989), bee-eaters (Emlen and Wrege 1986), coots and moorhens (Gibbons 1986, Lyon 1993, McRae 1998), starlings (Evans 1988, Romagnano et al. 1990), weavers (Jackson 1993, 1998), and waterfowl (Andersson and Eriksson 1982, Semel et al. 1988, Lank et al. 1989, Sorenson 1998, Andersson and Åhlund 2000). From those studies, it is clear that the frequency of parasitic laying varies among individuals both within and between populations of the same species.

One potential ecological determinant of conspecific brood parasitism is population density. When suitable hosts occur in high density and close proximity, such as in breeding colonies, parasitism may be a viable alternative

[1]Present address: 630 North 80th West, no. 3, Logan, Utah 84321, USA.

[2]Address correspondence to this author. E-mail: charles-brown@utulsa.edu

reproductive strategy (Eadie and Fryxell 1992). Various workers have shown that in some species, conspecific brood parasitism increases with colony size or is more prevalent in larger colonies (Brown 1984, Møller 1987, Brown and Brown 1996, Lyon and Everding 1996, Hill et al. 1997), though in other species, colony size or coloniality *per se* has no effect (Hoogland and Sherman 1976, Lank et al. 1989, Rohwer and Freeman 1989, Davis 1998).

Colonial Cliff Swallows (*Petrochelidon pyrrhonota*) show a relatively high incidence of conspecific brood parasitism (Brown and Brown 1989, 1996). In that species, brood parasitism increases with colony size and appears to be a successful reproductive strategy of high-quality individuals (Brown and Brown 1998) that involves accurate assessment of the best host nests to parasitize (Brown and Brown 1991). However, some Cliff Swallow populations have been reported to have a much lower incidence of brood parasitism (Smyth et al. 1993). Better understanding of the ecological conditions that do or do not promote brood parasitism requires comparative data, collected in similar ways, on other populations and closely related species.

The present study examines patterns of brood parasitism in a congener of the Cliff Swallow, the Cave Swallow (*P. fulva*), and also reports information on brood parasitism in Cliff Swallows from an area (south Texas) where that species has been little studied. We provide the first known reports of brood parasitism (including physical transfer of eggs between nests) in Cave Swallows, and we investigate how brood parasitism in both *Petrochelidon* swallows varies with colony size.

METHODS

Study animals.—Cave and Cliff swallows are morphologically, behaviorally, and ecologically similar. Both are colonial breeders. Cave Swallows nest in colonies that can range from <5 to ≥1,500 nests (Selander and Baker 1957, West 1995), and Cliff Swallows in colonies from 2 to 3,700 nests (Brown and Brown 1996). Both are highly social—feeding, nest-building, and mobbing predators in large groups; they also spend the winter in large roosts (Brown and Brown 1995, Komar 1997). They feed on flying insects caught at relatively high altitudes over open areas. Both species build mud nests that they attach to a wall or ceiling of a nesting site. Cliff Swallows consistently build an enclosed gourd-shaped nest throughout their range;

but in Cave Swallows, nest architecture varies widely between populations (Kirchman et al. 2000). Some Cave Swallow nests resemble those of Barn Swallows (*Hirundo rustica*) in shape, whereas others look more like incomplete Cliff Swallow nests with the makings of an enclosed entrance tube. In our Texas study area, Cave Swallows generally build half-cup nests with flared rims, but variation exists even within the same colony. The breeding season for both species at our study site extends from at least late March to late August, during which time two broods are apparently attempted by many individuals.

The Cave Swallow has undergone a dramatic range expansion and nesting-site shift in Texas within the last 30 years. Previously, Cave Swallows were limited to nesting in natural caverns and sinkholes in the Edwards Plateau, where they attached their nests to cavern walls or ceilings in the twilight zones (Selander and Baker 1957). The species is still restricted to such nesting sites in southeastern New Mexico (West 1988, 1995). In the early 1970s, however, Cave Swallows began using highway culverts and bridges as nesting sites (Martin 1974, Palmer 1988), and in so doing expanded into areas well to the north, east, and south of their historical range in Texas (including our study area).

Cliff Swallows historically nested on the sides of steep cliffs and canyons, where nests are attached to a vertical wall underneath a horizontal overhang. They still commonly use cliffs in some areas, though not in our Texas study area. Like Cave Swallows, Cliff Swallows have adapted to artificial structures, often nesting in culverts and under the eaves of buildings and bridges. In areas where Cliff and Cave swallows co-occur, Cliff Swallows are generally more likely to use the bigger, more exposed highway bridges, but the two species often nest side-by-side at the same site.

Study site.—Our study site was centered at the Rob and Bessie Welder Wildlife Foundation, near Sinton, Texas (28°06′N, 97°22′W), and included portions of San Patricio, Refugio, Bee, and Live Oak counties. Cave Swallows in the study area nested exclusively in highway culverts and on bridges. We selected colonies for study largely on the basis of proximity to the Welder Wildlife Foundation and ease of getting to the nests. The topography was mostly flat coastal plain, with some rolling hills near Beeville. Most culverts contained dry streambeds, though a few would retain standing water for up to a week after a rain. At many colonies, trees such as live oak (*Quercus* sp.), elm (*Ulmus* sp.), and mesquite (*Prosopis* sp.) grew on both sides of the culvert. Most colonies were at least 3 km from the next nearest one.

Detecting brood parasitism and egg transfer.—Brood parasitism was detected by the appearance of >1 egg in a nest per day during laying. We numbered nests with chalk marks on the substrate and observed nest contents with a flashlight and dental mirror. We conducted nest checks at each colony every other day for

the entire 2001 nesting season (from mid-April to early August). We did not check nests in rainy weather or before 0800 hours (to avoid disruption of normal egg laying patterns) and did not spend longer than 1.5 h per visit at any colony (Brown and Brown 1996). We scored a brood parasitism whenever we found more than one egg added to a nest per elapsed 24-h period between nest checks (usually 48 h). Because birds do not lay more than one egg per day, appearance of multiple eggs per day is a reliable method of detecting brood parasitism and has been used in various studies (Brown 1984, Emlen and Wrege 1986, Brown and Brown 1989). However, some parasitic eggs can be overlooked, especially when the parasitism occurs just before the host itself begins laying or just after it ceases laying, and thus our frequency estimates are conservative. We could not identify specific eggs as the parasitic ones. Once determining the hatching date for a nest, we did not check the nest again until the nestlings were 10 days old, at which time the number of nestlings surviving was recorded (Brown and Brown 1996). A nest was considered successful if at least one nestling survived to day 10. Data on nest success were recorded only for Cave Swallows.

We scored nests as having an egg physically transferred into them using the criteria of Brown and Brown (1988). If a nest gained an egg three or more days after the clutch there had stopped increasing and incubation had presumably started, yet all eggs hatched together, we inferred an egg transfer (Brown and Brown 1988). Such cases were confirmed to result from egg transfer in the Nebraska study by direct observation of birds moving eggs. However, because we did not directly observe swallows moving eggs in the Texas study area (we did not watch for it), we did not include cases of egg transfer in our quantitative analyses of brood parasitism. The observed cases of egg transfer or parasitism by laying are unlikely to have represented observational error (miscounting or not seeing eggs). We always rechecked a nest if the egg count was unusual in any way, compared with previous counts, and the more open nests of Cave Swallows were relatively easy to see into.

Designating first- and second-wave nestings.—Both Cave and Cliff swallows in our study area nested essentially throughout the summer, and in many cases the same individuals presumably nested at least twice. At most colonies, that resulted in two temporally distinct "waves" of reproductive activity, consisting in most cases of a first clutch laid in a nest, followed by a second clutch (and rarely a third) in the same nest. In general, there was about a six-week span between the peak period of laying during the first wave and that during the second wave. However, because birds were not marked, we could not be certain that the same individuals that had nested earlier were in fact attempting second broods, and thus we refer to those as only the first and second waves.

Usually, the first breeding attempt in a given nest was designated as part of the first wave for that colony, and the second nesting attempt in that nest as part of the second wave. In a few cases, however, the first egg laid in a nest coincided with the second wave of egg laying. Because those clutches were likely laid by late-arriving (perhaps younger) birds laying for the first time, or by birds laying for the second time in a new nest, they were functionally distinct from the first clutches laid at the beginning of the breeding season. Late clutches were assigned to the second wave if they met the criterion of being a statistical outlier in the first wave. We used the quartiles method to detect outliers (Zar 1999) and designated dates as outliers through analysis of boxplots (Schlotzhauer and Littell 1997), repeating the method until no outliers remained in the first-wave category. Because of the difference in clutch initiation dates between waves, the fact that some of the same individuals may have been represented in both waves, and the possibility that the second wave consisted of some birds that differed qualitatively (younger, less experienced) from those in the first wave, we performed all analyses separately for each wave.

Designating colony size.—Colony size was defined as maximum number of nests at a site to have contained one egg (Brown and Brown 1996). Swallows in Nebraska have never been seen to lay eggs in inactive nests (C. and M. Brown pers. obs.), so we believe that the presence of eggs is an accurate reflection of whether a nest was used. We checked all nests at all colonies, so we had an exact colony size for each site. Colony size was designated separately for each wave of nesting. Colony size tended to be smaller during the second wave at most sites, owing in part to falling of nests from the substrate but also because some nests did not receive a second clutch. Consequently, colony sizes for first- and second-wave nestings at the same site usually differ in our analyses.

Some colonies in our study area contained nests of both Cave and Cliff swallows. In the 17 colonies we studied, Cliff Swallows represented ~11% of colony size on average, varying from 0 to ~40% across the different sites. Nests of both species were often interspersed (sometimes touching). In other cases, each species occupied separate sections of a culvert or placed their nests in rows or clusters abutting each other. Regardless of nest placement, both species at a site interacted and behaved as a single colony. During alarm responses, both species flew together, circling and calling near the entrance to a colony. They synchronized their activities, such that after a disturbance, both species would return to a colony site at the same time. One definition of a colony is that individuals interact in the mobbing of predators or in foraging (Brown and Brown 1996, 2001). Thus, in many ways, the two species form functional mixed-species colonies. However, because parasitism appeared to occur only between conspecifics (see below), our measure of

colony size in the analyses was the number of active conspecific nests.

RESULTS

Congeneric or conspecific brood parasitism?— Because the eggs of *Petrochelidon* swallows look similar, it is not possible to visually identify eggs as belonging unambiguously to either a Cave or Cliff swallow. Thus, we first examined whether there was evidence of congeneric parasitism of either species. Among the six Cave Swallow colonies that contained no active Cliff Swallow nests during the first wave, 4.0% of nests ($n = 74$) had brood parasitism, compared to 4.7% of nests ($n = 578$) in the 11 colonies that also contained active Cliff Swallow nests; the difference was not significant ($\chi^2 = 0.06$, df = 1, $P = 0.81$). During the second wave, 6.1% of Cave Swallow nests ($n = 65$) in colonies without Cliff Swallows were brood-parasitized, compared with 4.9% ($n = 535$) in colonies with Cliff Swallows; that difference also was not significant ($\chi^2 = 0.20$, df = 1, $P = 0.65$). We could not do a similar analysis for parasitism in Cliff Swallows because there were no Cliff Swallow colonies without any Cave Swallow nests. However, for the first wave, the percentage of Cliff Swallow nests with brood parasitism at a site was unaffected by the number of active Cave Swallow nests present ($r_s = 0.38$, $P = 0.25$, $n = 11$ colonies); the result was similar for the second wave ($r_s = 0.46$, $P = 0.15$, $n = 11$). Thus, there was no evidence that presence of the other species materially affected frequency of brood parasitism in either species. For that reason (and because all parasitic individuals identified among Cliff Swallows in Nebraska were residents of a colony, not floaters who might have entered the site from the outside; Brown and Brown 1989), we make the explicit assumption in the remaining analyses that the cases of parasitism observed were by conspecifics.

Brood parasitism in relation to colony size.— Overall percentage of Cave Swallow nests with brood parasitism, combined across all colonies, was 4.6% during the first wave ($n = 651$ nests) and 5.0% during the second wave ($n = 598$). Overall percentage of Cliff Swallow nests with brood parasitism, combined across all colonies, was 11.9% during the first wave ($n = 202$ nests) and 10.7% during the second wave ($n = 149$). Cliff Swallows showed a significantly higher percentage of nests parasitized than did Cave

Swallows during both the first ($\chi^2 = 13.8$, df = 1, $P < 0.001$) and second wave ($\chi^2 = 6.8$, df = 1, $P = 0.009$). Those estimates (and those for egg transfer, below) are underestimates, because nest checks alone overlook some cases.

Incidence of brood parasitism per colony varied from 0 to 25% of nests in Cave Swallows and from 0 to 50% in Cliff Swallows. In neither species was the percentage of nests with brood parasitism related significantly to colony size (of conspecifics) in either the first or second wave of nesting (Fig. 1). However, in Cliff Swallows, correlation coefficients for both first and second waves were positive and much larger than in Cave Swallows, and that for the first wave in Cliff Swallows approached significance (Fig. 1).

In both species, there was considerable variation in frequency of brood parasitism, especially among colonies of 10 nests and smaller, with some of those sites having no brood parasitism and others showing the highest frequencies (Fig. 1). Because some of that apparent variation merely reflects the small number of nests in the smaller colonies (a single nest parasitized in a small colony affects the percentage more strongly than does a single nest in a large colony), we examined whether colony size affected frequency of brood parasitism for colonies of >10 nests. For neither species in either wave was the correlation between parasitism and colony size significant when analysis was restricted to colonies of >10 nests ($P > 0.08$ for all).

Brood parasitism in relation to nesting success.— Frequency of brood parasitism was unrelated to nest success at a colony site. We found no significant correlation between the percentage of nests at a site with brood parasitism and the percentage of nests there that were successful in producing at least one young (Fig. 2). However, it was apparent that the colonies with the highest frequencies of brood parasitism tended to be among the more successful ones.

There was no relationship between whether a nest was parasitized and its eventual success at producing young to day 10. Of 23 Cave Swallow nests during the first wave that were parasitized and their success known, all 23 (100.0%) were successful. Of 400 Cave Swallow nests during the first wave for which no evidence of parasitism was detected, 381 (95.3%) were successful. The difference was not significant ($\chi^2 = 1.1$, df = 1, $P = 0.29$). Of 25 Cave Swallow nests during the second wave that were parasitized, 22 (88.0%)
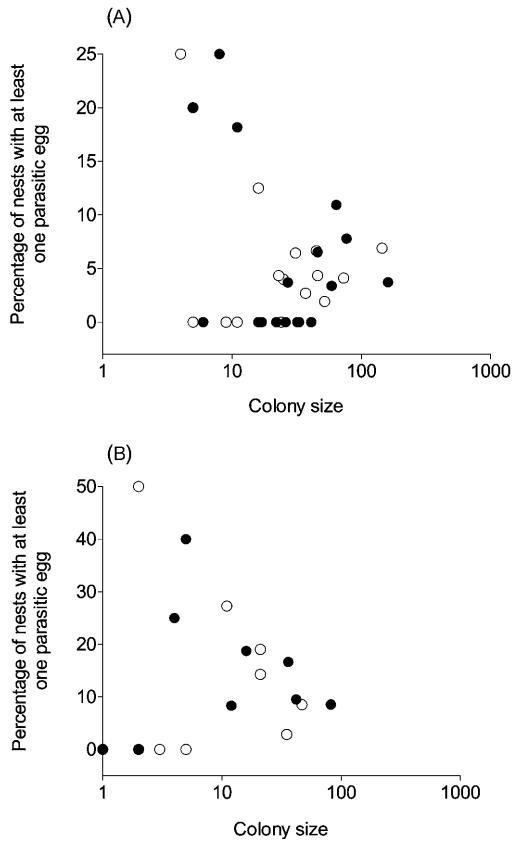
(A)

(B)

FIG. 1. Percentage of nests with at least one parasitic egg in relation to colony size (number of active conspecific nests) for (A) Cave and (B) Cliff swallows in south Texas during first-wave (●) and second-wave (○) nestings. Percentage of nests with parasitic eggs did not vary significantly with colony size in Cave Swallows for either first-wave ($r_s = 0.00$, $P = 0.997$, $n = 17$ colonies) or second-wave nestings ($r_s = 0.01$, $P = 0.97$, $n = 17$ colonies), nor did it vary significantly with colony size in Cliff Swallows during either first-wave ($r_s = 0.56$, $P = 0.08$, $n = 11$ colonies) or second-wave nestings ($r_s = 0.45$, $P = 0.17$, $n = 11$ colonies). Sample sizes (number of nests) for each colony, in order of ascending colony size, were: for Cave Swallows, first wave, 5, 6, 8, 11, 16, 17, 22, 26, 27, 32, 41, 33, 46, 64, 59, 77, and 161; and second wave, 4, 5, 5, 10, 11, 16, 23, 24, 25, 31, 45, 46, 31, 52, 46, 73, and 145; and for Cliff Swallows, first wave, 1, 1, 1, 4, 2, 16, 5, 12, 36, 42, and 82; and second wave, 1, 1, 2, 3, 2, 5, 21, 11, 21, 35, and 47.
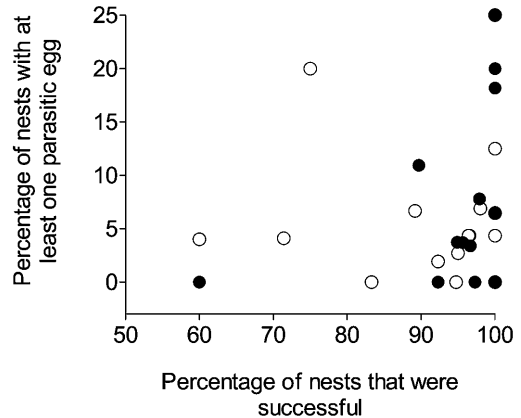

FIG. 2. Percentage of Cave Swallow nests with at least one parasitic egg in relation to percentage of nests at a colony site that were successful (one or more nestling surviving to day 10) during the first wave (●) and second wave (○) of nesting. Percentage of nests with parasitic eggs did not vary significantly with percentage of successful nests at a site during either the first ($r_s = 0.07$, $P = 0.79$, $n = 17$ colonies) or second wave ($r_s = 0.16$, $P = 0.53$, $n = 17$).

Swallow nests (1.1%) with egg transfer during the first wave ($n = 651$ nests) and 6 nests (1.0%) with egg transfer during the second wave ($n = 598$). For Cliff Swallows, there were 4 nests with egg transfer (2.0%) during the first wave ($n = 202$) and 1 (0.7%) during the second wave ($n = 149$). Half of the egg transfers to Cave Swallow nests occurred in the single largest colony during each wave, with the remaining ones distributed among colonies of all sizes (including one in a colony of five nests). The five transfers to Cliff Swallow nests occurred in colonies ranging in size from 16 to 82 nests.

DISCUSSION

The present study provides the first documentation of intraspecific brood parasitism (and egg transfer) in Cave Swallows. Overall frequency of brood parasitism in Cave Swallows, however, was less than half that seen in Cliff Swallows occupying the same colony sites at the same time. That result, together with the relatively high frequency of brood parasitism found in Cliff Swallows in Nebraska (Brown and Brown 1989, 1996), seems to indicate that Cliff Swallows are inherently more likely to parasitize nests than their closely related congener.

were successful, compared with 92.6% ($n = 378$) of nests for which no evidence of parasitism was detected. That difference also was not significant ($\chi^2 = 0.7$, df = 1, $P = 0.40$).

Egg transfer.—We detected a total of 7 Cave

The reason for that difference is unclear, but may be related in part to the Cliff Swallow's greater degree of coloniality. Because nesting near conspecifics theoretically affords greater opportunities for brood parasitism, selection may have more strongly favored brood parasitism as a reproductive strategy in Cliff Swallows. The largest colony size known in Cliff Swallows (3,700 nests; Brown and Brown 1996) is >2× that reported for Cave Swallows (1,500 nests; Selander and Baker 1957). In addition, the much closer nest spacing in Cliff Swallows than in Cave Swallows may make parasitism easier, in part because it allows better assessment of neighbors for suitability as hosts and observation of when they leave their nest unattended.

However, in our Texas study area, we found no significant relationship between frequency of brood parasitism and colony size in either species. In Cliff Swallows, that may have resulted, in part, from the relatively small number of colonies (11); the pattern among Cliff Swallows resembled that seen in the Nebraska population (Brown and Brown 1996) and approached statistical significance. Lack of a colony-size effect in Cave Swallows may have primarily reflected that species' lower overall incidence of parasitism. Although the colony-size range in our study area was smaller than that in Nebraska (our largest colony was only 243 total nests of both species combined), strong colony-size effects over the same range of colony sizes were detected in Nebraska for Cliff Swallows (Brown 1984, Brown and Brown 1989). Absence of very large colonies of either species in Texas, therefore, probably cannot explain our results.

In Cliff Swallows in Nebraska, brood parasitism is practiced by high-quality individuals that apparently accurately assess both individual host nests and overall certainty of reproduction at a site (Brown and Brown 1989, 1991, 1996, 1998). Colony sites that are ultimately more likely to have nest failure have higher frequencies of brood parasitism. That seems to be because individuals are more likely to parasitize nests in such situations, and when they do, they preferentially parasitize nests that are more likely to eventually fledge young, perhaps because those nests have lower infestations of blood-sucking cimicid bugs and fleas (Brown and Brown 1991). We could not determine if parasitic Cliff Swallows in south Texas show the same patterns, because we did not have data on reproductive success of Cliff Swallows. For Cave Swallows, however, we found that the frequency of brood parasitism was not related to overall colony reproductive success. That may be because Cave Swallows have not been as strongly selected to assess potential reproductive uncertainty at a site. Cave Swallows historically used caverns, which, because of their enclosed nature, may be safer and more secure nesting sites, on average, than the sides of cliffs and canyons where Cliff Swallows nest. Cliffs are subject to falling overhangs, crumbling dirt, and severe wind and rain storms that can destroy many nests (Brown and Brown 1996). Cave Swallows may also be less likely to parasitize nests because they suffer from fewer ectoparasites than Cliff Swallows, in which parasitism often seems to be an attempt to place eggs into other nests in a colony that are relatively uninfested (Brown and Brown 1991). We found that Cave Swallows, unlike in Cliff Swallows in Nebraska, did not preferentially parasitize nests that were more likely to fledge young—meaning that when they do parasitize nests, Cave Swallows seem unable to accurately assess the best conspecifics to parasitize.

We found evidence that both *Petrochelidon* swallows in the south Texas study area parasitized nests by physically transferring eggs between nests. Although apparently occurring occasionally in a few other species (Truslow 1967, Blomme 1983, Trost and Webb 1986), only in Cliff Swallows in Nebraska is that behavior known to be regular (Brown and Brown 1988). At least 6% of nests there were found to contain eggs transferred into them. Egg transfer was apparently less frequent in Texas than in Nebraska (though it is never a common behavior), which complicates quantitative comparison between the two areas. Perhaps the lower frequency in Texas (if real) may be brought about by the greater nest spacing there, especially among Cave Swallows. Cliff Swallows in Nebraska transfer eggs only to nests that are nearby, and larger distances between neighboring nests may discourage birds from engaging in such risky behavior (i.e. the egg may break or be dropped during flight).

Although our analyses of the frequency of brood parasitism in these two species in relation to the number of the other species present did not suggest any congeneric parasitism, we cannot rule out the possibility that it at least

occasionally occurs. The two species' nests are sometimes in proximity in the same culverts, their nest shapes and positions on the substrate are similar, and there was strong temporal overlap between laying dates of the two species in both waves. However, even if congeneric parasitism occurs, it does not change our conclusions about the relative frequency of brood parasitism in relation to colony size or to the Nebraska population. Congeneric parasitism would mean that observed levels of parasitism in either species are overestimates of conspecific parasitism, supporting the conclusion that intraspecific brood parasitism is on average less frequent (in either species) in Texas than in Nebraska.

Our results demonstrate that intraspecific brood parasitism and egg transfer occur in two *Petrochelidon* swallows and (for Cliff Swallows) in a geographic region from where it was previously unknown. Cliff Swallows occupying the Texas and Nebraska study areas experience considerable differences in climate, degree of seasonality, breeding phenology, average colony size, and possibly other environmental characteristics (e.g. ectoparasitism). Yet both populations exhibit relatively high frequencies of intraspecific brood parasitism, especially for passerines. The conditions that promote brood parasitism generally in these swallows thus apply across very different habitats. Brood parasitism is behaviorally complex, involving for example the moving of eggs between nests without dropping or breaking them, and the present study indicates that this behavior (including egg transfer) is not restricted to a single population. If brood parasitism in these swallows is largely a supplemental reproductive strategy used by high-quality birds, as annual survival analyses indicate (Brown and Brown 1998), the present study and those from Nebraska (Brown and Brown 1989) and California (Smyth et al. 1993) suggest that such individuals are present in a wide variety of populations and habitats.

LITERATURE CITED

ANDERSSON, M. 1984. Brood parasitism within species. Pages 195–228 *in* Producers and Scroungers: Strategies of Exploitation and Parasitism (C. J. Barnard, Ed.). Croom Helm, London.

ANDERSSON, M., AND M. ÅHLUND. 2000. Host–parasite relatedness shown by protein fingerprinting in a brood parasitic bird. Proceedings of the National Academy of Sciences USA 97:13188–13193.

ANDERSSON, M., AND M. O. G. ERIKSSON. 1982. Nest parasitism in goldeneyes *Bucephala clangula*: Some evolutionary aspects. American Naturalist 120:1–16.

ARNOLD, K. E., AND I. P. F. OWENS. 2002. Extra-pair paternity and egg dumping in birds: Life history, parental care and the risk of retaliation. Proceedings of the Royal Society of London, Series B 269:1263–1269.

BLOMME, C. 1983. Egg-carrying behaviour observed in Northern Flicker. Ontario Field Biologist 37: 34–35.

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. 1988. A new form of reproductive parasitism in Cliff Swallows. Nature 331:66–68.

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. 1995. Cliff Swallow (*Hirundo pyrrhonota*). *In* The Birds of North America, no. 149 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

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.

BROWN, C. R., AND M. B. BROWN. 1998. Fitness components associated with alternative reproductive tactics in Cliff Swallows. Behavioral Ecology 9:158–171.

BROWN, C. R., AND M. B. BROWN. 2001. Avian coloniality: Progress and problems. Current Ornithology 16:1–82.

DAVIS, J. A. 1998. Intraspecific brood parasitism in Purple Martins. Bulletin of the Oklahoma Ornithological Society 31:29–33.

EADIE, J. M., AND J. M. FRYXELL. 1992. Density dependence, frequency dependence, and alternative nesting strategies in goldeneyes. American Naturalist 140:621–641.

EMLEN, S. T., AND P. H. WREGE. 1986. Forced copulations and intra-specific parasitism: Two costs of social living in the White-fronted Bee-eater. Ethology 71:2–29.

EVANS, P. G. H. 1988. Intraspecific nest parasitism in the European Starling *Sturnus vulgaris*. Animal Behaviour 36:1282–1294.

GIBBONS, D. W. 1986. Brood parasitism and cooperative nesting in the Moorhen, *Gallinula chloropus*. Behavioral Ecology and Sociobiology 19: 221–232.

HILL, W. L., K. J. JONES, C. L. HARDENBERGH, AND M. BROWNE. 1997. Nest distance mediates the costs of coloniality in Eared Grebes. Colonial Waterbirds 20:470–477.

HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecological Monographs 46:33–58.

JACKSON, W. M. 1993. Causes of conspecific nest parasitism in the Northern Masked Weaver. Behavioral Ecology and Sociobiology 32: 119–126.

JACKSON, W. M. 1998. Egg discrimination and egg-color variability in the Northern Masked Weaver. Pages 407–416 *in* Parasitic Birds and Their Hosts: Studies in Coevolution (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford.

KIRCHMAN, J. J., L. A. WHITTINGHAM, AND F. H. SHELDON. 2000. Relationships among Cave Swallow populations (*Petrochelidon fulva*) determined by comparisons of microsatellite and cytochrome *b* data. Molecular Phylogenetics and Evolution 14:107–121.

KOMAR, O. 1997. Communal roosting behavior of the Cave Swallow in El Salvador. Wilson Bulletin 109:332–337.

LANK, D. B., E. G. COOCH, R. F. ROCKWELL, AND F. COOKE. 1989. Environmental and demographic correlates of intraspecific nest parasitism in Lesser Snow Geese *Chen caerulescens caerulescens*. Journal of Animal Ecology 58:29–45.

LYON, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American Coots. Animal Behaviour 46:911–928.

LYON, B. E., AND S. EVERDING. 1996. High frequency of conspecific brood parasitism in a colonial waterbird, the Eared Grebe *Podiceps nigricollis*. Journal of Avian Biology 27:238–244.

MARTIN, R. F. 1974. Syntopic culvert nesting of Cave and Barn swallows in Texas. Auk 91:776–782.

MCRAE, S. B. 1998. Relative reproductive success of female Moorhens using conditional strategies of brood parasitism and parental care. Behavioral Ecology 9:93–100.

MØLLER, A. P. 1987. Intraspecific nest parasitism and anti-parasite behaviour in swallows, *Hirundo rustica*. Animal Behaviour 35:247–254.

PALMER, P. C. 1988. Cave Swallow range continues to expand. American Birds 42:174–176.

ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology 67:239–253.

ROMAGNANO, L. C., A. S. HOFFENBERG, AND H. W. POWER. 1990. Intraspecific brood parasitism in the European Starling. Wilson Bulletin 102: 279–291.

ROTHSTEIN, S. I., AND S. K. ROBINSON, EDS. 1998. Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford.

SCHLOTZHAUER, S. D., AND R. C. LITTELL. 1997. SAS System for Elementary Statistical Analysis, 2nd ed. SAS Institute, Cary, North Carolina.

SELANDER, R. K., AND J. K. BAKER. 1957. The Cave Swallow in Texas. Condor 59:345–363.

SEMEL, B., P. W. SHERMAN, AND S. M. BYERS. 1988. Effects of brood parasitism and nest-box placement on Wood Duck breeding ecology. Condor 90:920–930.

SMYTH, A. P., B. K. ORR, AND R. C. FLEISCHER. 1993. Electrophoretic variants of egg white transferrin indicate a low rate of intraspecific brood parasitism in colonial Cliff Swallows in the Sierra Nevada, California. Behavioral Ecology and Sociobiology 32:79–84.

SORENSON, M. D. 1998. Patterns of parasitic egg laying and typical nesting in Redhead and Canvasback ducks. Pages 357–375 *in* Parasitic Birds and Their Hosts: Studies in Coevolution (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford.

TROST, C. H., AND C. L. WEBB. 1986. Egg moving by two species of corvid. Animal Behaviour 34: 294–295.

TRUSLOW, F. K. 1967. Egg-carrying by the Pileated Woodpecker. Living Bird 6:227–236.

WEST, S. 1988. Status of the Cave Swallow (*Hirundo fulva*) in New Mexico. New Mexico Ornithological Society Bulletin 16:26–30.

WEST, S. 1995. Cave Swallow (*Hirundo fulva*). *In* The Birds of North America, no. 141 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. Biological Reviews 55:93–108.

ZAR, J. H. 1999. Biostatistical Analysis, 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.

Associate Editor: S. G. Sealy