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A new form of reproductive parasitism in cliff swallows

Charles R. Brown & Mary Bomberger Brown

Department of Biology, Yale University, PO Box 6666, New Haven, Connecticut 06511, USA

A common reproductive strategy among some egg-laying animals, especially birds, is to lay an egg in another individual's nest and thereby parasitize the reproductive effort of others of either the same species or a different species. Intraspecific parasitism is now known to occur regularly in some species[1–4] and sporadically in many others[5,6], and may represent a strategy by which individuals augment their reproductive performance[2] or succeed in reproducing when it would otherwise be impossible or too costly[5]. We have discovered that colonial cliff swallows (*Hirundo pyrrhonota*) not only lay eggs in other individuals' nests, but also physically transfer eggs between nests after the eggs are laid. Egg transfers can occur at any time after an egg is laid and before it hatches, and may represent a strategy by which an individual distributes its eggs in several nests to ensure some surviving offspring in the event of nesting failures. Sneaky transfer of eggs between nests represents a previously unknown form of reproductive parasitism in birds.

Cliff swallows build gourd-shaped nests out of mud pellets which are fastened in dense colonies underneath overhanging rock ledges on the sides of cliffs and canyons and, more recently, underneath bridges and in highway culverts throughout much of western North America. Breeding within a colony is highly synchronous and colonies allow cliff swallows to gain information from each other on the whereabouts of flying insect prey[7]. Females parasitize other individuals' nests by sneaking into nests momentarily left unattended and laying eggs there[2]. At our study site near Ogallala in Keith County, Nebraska, cliff swallows arrive in early May each year and remain until mid August, when they migrate to their wintering range in southern South America[8]. In Nebraska these birds nest both solitarily and in colonies ranging from 2 to 3,500 nests in size (mean colony size = 355 nests, s.d. = 561, $n = 276$ colonies).

While studying cliff swallows from 1982–1987, three sorts of evidence for transfers of eggs between nests were found: (1) direct observations of birds transferring eggs, (2) movement of marked eggs between nests, and (3) appearance in nests, after incubation began, of eggs that hatched at the same time as the rest of the clutch.

Upon their arrival in the spring, cliff swallows at selected colonies were captured in mist nets and their white forehead patches were painted in unique colour combinations for individual recognition[2]. Between 50 and 80% of the nest owners in samples of 45–75 nests in each colony were individually marked. We watched nests continuously for ~75% of the daylight hours, beginning before egg laying and continuing during part of incubation at each colony. Samples of nests in six colonies that ranged in total size from 125 to 1,100 nests were observed.

We observed two definite and three probable instances of cliff swallows carrying eggs to other nests. In two instances a bird left its own nest with an intact egg between its mandibles and flew to a neighbouring nest. In one case the owner of the neighbouring nest was not present and the intruder entered, deposited the egg in the nest, and returned to its own nest. In the second case one owner of the neighbouring nest was present; a fight ensued when the intruder entered with the egg. The intruder was evicted from the nest within 10 s, but the egg remained in the nest. In the three remaining instances, a cliff swallow emerged from its own nest carrying an egg between its mandibles, but we lost sight of the bird when it flew towards the opposite end of the colony. We are certain that these birds did not drop the eggs because the entire colony was located over water and we did not see or hear any splashes. In each case the bird either transferred the egg to another nest unseen by us, or carried the egg away from the colony. Three of the five perpetrators of transfers were females, and the sex of the remaining two individuals was unknown. The five transfers directly observed occurred in colonies of 750 and 1,100 nests, the two largest colonies which were intensively watched.

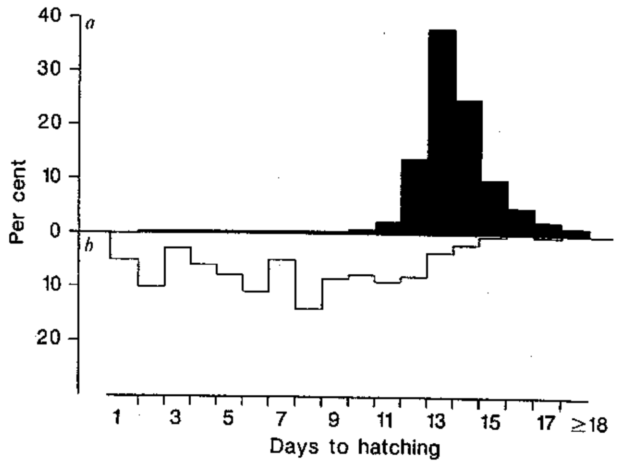

Fig. 1 *a*, Percentage occurrence of time periods from the laying of the last egg until the hatching of the first egg for whole cliff swallow clutches ($n = 3{,}370$). *b*, Percentage occurrence of time periods from appearance of an egg added to a clutch by transfer, until hatching of the first egg in the clutch ($n = 357$).

We also recorded the transfer of numbered eggs. Each nest's number was written in several places on the outside of each egg in a clutch with a Sharpie magic marker. All clutches marked were in stages of incubation and appeared to be complete. We marked a total 204 eggs from 50 nests in three colonies of 90, 120 and 1,100 nests. After marking we returned every second day and checked the contents of each marked nest and all neighbouring unmarked nests. Within two days of numbering, three of the 50 nests (6%) had acquired an intact numbered egg from a neighbouring nest. The clutches from which these transferred eggs came had decreased by one marked egg in two cases and by two marked eggs in the other.

An indirect measure of the frequency of egg transfers is how often eggs appear in nests during incubation yet still hatch in synchrony with the clutch to which they were added. As all cliff-swallow eggs presumably require a reasonably constant period of incubation (12–14 days), any parasitic egg that appears after a host starts incubation, yet still hatches with the host's own eggs, must have been incubated elsewhere for some period of time before being transferred. We used appearance of eggs in a nest three or more days after the clutch size there had stopped increasing and incubation had presumably started, as evidence of a transfer. These eggs were in fact likely to have been physically transferred, because in 25 actual observed cases of parasitic egg laying, no eggs were laid in a host's nest more than two days after the host had completed laying (unpublished data).

The contents of 5,077 nests in 46 colonies were checked every (or every second) day during this study, beginning before eggs were laid and continuing until clutches hatched. One or more transferred eggs appeared in 306 of 4,821 nests (6.3%). This percentage occurrence of transferred eggs agreed closely with that obtained by marking eggs (6%). The time elapsing between the arrival of a transferred egg in a nest and the start of hatching in that nest varied between 1 and 17 days (mean = 7.33, s.d. = 3.58), a considerably shorter interval than the normal clutch incubation period (mean = 13.58, s.d. = 1.85) (Fig. 1). These 306 nests had 384 eggs transferred to them; 70 nests had multiple transfers (2–5 eggs) occurring either simultaneously or sequentially. Of the 384 transferred eggs, 42 (10.9%) definitely did not produce fledged offspring because the nests containing them failed; 166 eggs (43.2%) hatched in synchrony with the host's clutch and definitely produced fledged offspring; and the fate of 176 eggs (45.9%) was unclear. Among the transferred eggs detected by direct observation and egg numbering ($n = 5$), one egg definitely produced offspring, while the fate of the remaining four was uncertain.

Of the 273 nests containing transferred eggs which produced some nestlings, in 271 (99.3%) all viable eggs including the

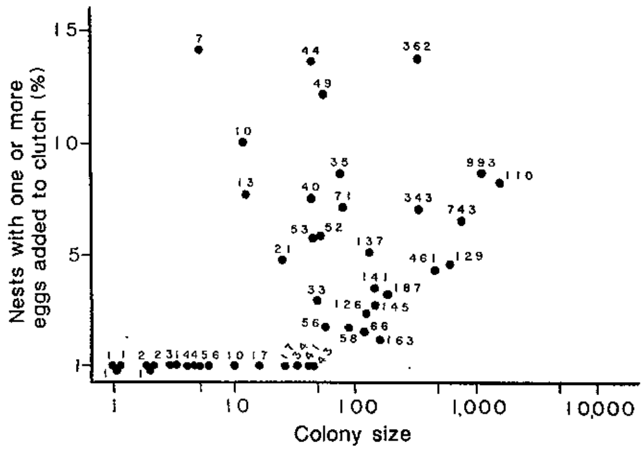

Fig. 2 Percentage nests containing one or more eggs added to a clutch by transfer versus cliff swallow colony size (number of active nests). Sample size is shown for each colony. When all colonies were considered, percentage nests with one or more eggs added increased significantly with colony size ($r_s = 0.60$, $P < 0.001$). When only colonies with more that 10 nests were considered, there was no significant correlation between percentage nests with one or more eggs added and colony size (Spearman rank correlation coefficient, $r_s = 0.21$, $P = 0.25$).

transfers hatched within 24-36 h of each other. The remaining two nests contained an egg (probably the transfer) that hatched 10 days after the others. Thus, the interval between the time a transferred egg appeared in a nest and hatching (Fig. 1) indicated how long the egg had been incubated elsewhere before being transferred. Cliff swallows transferred eggs to other nests virtually any time after laying, even one and two days before an egg was due to hatch (Fig. 1). The birds directly seen to transfer eggs were still laying in their own nests and had not begun incubation. A small percentage of entire clutches (Fig. 1*a*), had shorter than expected incubation periods. These clutches did not meet our criterion for classification as egg transfers because all the eggs appeared in a normal sequence. Because of the short incubation periods, however, they probably did represent egg transfers, perhaps transfers of entire clutches.

A large cliff-swallow colony potentially might contain more suitable nests to which to transfer an egg, and therefore the incidence of transfers might increase with colony size. Colony size affected the incidence of nests with at least one transferred egg (Fig. 2), but only when small colonies, ≤10 nests in size, were included. In 14 colonies with 10 or fewer nests, only one transfer was detected ($n = 48$ nests). When only colonies with more than 10 nests were considered, colony size did not affect percentage occurrence of transferred eggs (Fig. 2). This result is perhaps not surprising as many of the interactions among cliff swallows within a colony involve only close neighbours[2,7]. Of the five cases in which the perpetrator of the transfer was known and the nest to which it transferred an egg was also known, three occurred between nests that were adjacent to each other (15 cm apart) in the colony. In the other two cases, five nests (52 cm) and 22 nests (112 cm), respectively, separated the perpetrators' and hosts' nests.

Transfer of eggs may be a sophisticated behavioural strategy involving subtle assessment of potential host individuals by potential transferrers and removal of some of the host's eggs in advance. Of the 306 nests known to have an egg transferred to them, 33 failed (10.8%). This is less than half of the total nest failure rate for cliff-swallow nests in our study population as a whole (1,102 of 4,708 nests failed, 23.4%), suggesting that transferrers may select superior neighbours as hosts. Potential transferrers might remove a host's egg in advance of adding one, as is known for other intraspecific (ref. 9; H. W. Power, personal communication) and some interspecific[10,11] parasites and for cliff swallows when laying eggs in hosts' nests (unpublished data). This is suggested by the fact that disappearance of a single egg from the host's nest occurred within the 1-4 day period immediately preceding the appearance of the transferred egg, for 125 of the 377 transferred eggs (33.2%) for which past nest histories were known. Instances of single eggs disappearing from clutches are often caused by intruding cliff swallows that toss out eggs[2,12]. The percentage of host nests suffering single-egg losses before a transfer (33.2%) is over three times that of cliff-swallow nests in our study population as a whole (479 of 4,899 nests with single-egg losses, 9.8%).

How might an individual benefit by transferring eggs? As many transfers occur after the perpetrator has ceased laying (Fig. 1), reproductive output probably cannot be supplemented by transferring eggs. After incubation starts an individual cannot lay more eggs in its own nest to replace those transferred elsewhere. Instead, transfer of eggs might increase the chances of fledging at least some offspring in a risky environment. In their ancestral nesting habitat—rocky cliffs and canyons—cliff swallows are often affected by inclement weather and rock slides which can destroy many nests (unpublished data). Spreading a clutch of eggs around more than one nest could insure against nesting failure[13,14].

There may be some cost to transferring eggs. In seven of the eight cases in which the identity of the transferrer was known, a parasitic egg had been previously added to the transferrer's own nest either by laying or transfer. This suggests that in assessing which nearby nests are candidates for an egg transfer, a transferrer may leave its own nest unattended to the degree that it is more likely to be parasitized itself. Transferrers are probably not simply removing someone else's parasitic eggs from their nest, as these birds are unable to recognize eggs[2].

Our estimate that about 6% of cliff-swallow nests contain transferred eggs is undoubtedly an underestimate. Eggs that are transferred during laying would resemble, in nest-check data, parasitic eggs laid in a nest and go undetected using our criterion (Fig. 1). Colour-marked birds did in fact transfer some eggs during laying. Estimating the true frequency of egg transfers and parasitic egg laying in cliff-swallow colonies may have to await the development of DNA-fingerprinting techniques for precise assignment of parentage. Incredible though egg transfer in cliff swallows may seem, it has in fact been reported (rarely) in woodpeckers[15,16] and in corvids[17] and may prove to be more common in birds than has previously been supposed.

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