A new form of reproductive parasitism in cliff swallows

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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 species1-4 and sporadically in many others5,6 and may represent a strategy by which individuals augment their reproductive performance7 or succeed in reproducing when it would otherwise be impossible or too costly8. 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, underneat 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 prey9. Females parasite other individuals’ nests by sneaking into nests momentarily left unattended and laying eggs there10. 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 America11. In Nebraska these birds nest both solitary 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 recognition12. 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.

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-swalllow 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 eggs 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
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) indi-
cated 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. 1a), 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.6,7
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 transmitters 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 trans-
ferers may select superior neighbours as hosts. Potential trans-
ferers 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 interspecific parasitism7,11 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.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.1,14
There may be some cost to transferring eggs. In seven of the
eight cases in which the identity of the transferer was known,
a parasitic egg had been previously added to the transferer’s
own nest either by laying or transfer. This suggests that in
assessing which nearby nests are candidates for an egg transfer,
the transferer may leave its own nest unattended to the degree
that it is more likely to be parasitized itself. Transferers are
probably not simply removing someone else’s parasitic eggs
from their nest, as these birds are unable to recognize eggs.6
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 woodpeckers15,16 and in corvids17 and may prove to be more
common in birds than has previously been supposed.
We thank Cathy Boersma, Carol Brashears, Karen Brown,
Rachel Budelsky, Laurie Doss, Jerri Hoskyn, Laura Jackson,
Deborah Johnson, Kathi Miller, Todd Scarlett, Martin Shaffer,
Lora Sherman for field assistance, John Janovy, Jr and Anthony
Loeber for use of the facilities of the Cedar Point Biological
Station, and Harry Poulsen and Bridget Stutchbury for helpful
comments. This work was supported by the NSF, the National
Geographic Society, Princeton and Yale universities, the Chap-
man Fund of the American Museum of Natural History, the
Bache Fund of the National Academy of Sciences, Sigma Xi,
Alpha Chi and Raymond and Kathryn Brown.

Received 7 October; accepted 11 November 1987.