

Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows

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Abstract. Colonial cliff swallows, *Hirundo pyrrhonota*, in southwestern Nebraska commonly brood-parasitize (lay eggs in) nests of neighbouring conspecifics. At least 22%, and perhaps as many as 43%, of all nests were estimated to contain one or more parasitic eggs. Colour-marked parasites maintained nests of their own in addition to parasitizing the nests of others. Parasitism usually occurred among close neighbours when nests were left unattended momentarily. Parasites' and hosts' first laying dates tended to be synchronized. Parasitism often occurred early in a host's laying period or 1-3 days prior to the host's start of egg laying. Hosts rejected any eggs added more than 4 days before they began laying. Hosts laid smaller clutches than normal, either as a direct response to being parasitized or because parasites preferentially selected hosts that were to lay small clutches for other reasons. Parasitic egg laying appeared successful, with only about a quarter of parasitic eggs known not to survive. On an annual basis, colour-marked parasites laid more total eggs and fledged more total young than did colour-marked hosts. Parasites, however, were also parasitized themselves, and thus being a parasite was costly. There was little evidence that parasites routinely removed host eggs. Parasitism tended not to occur in extremely small colonies and among solitary nesters, but there was no relationship between incidence of parasitism and colony size for colonies with more than 10 nests. Intraspecific brood parasitism probably serves to minimize risk in uncertain environments by distributing eggs in several nests to ensure that at least one offspring will survive to independence. Incidence of brood parasitism in a colony increased with uncertainty of reproduction.

Brood parasitism is a common reproductive strategy in some egg-laying animals. Until recently, almost all research was directed toward interspecific brood parasitism and the coevolution between hosts and parasites of different species (e.g. Weller 1959; Hamilton & Orians 1965; Payne 1967, 1973, 1977a, b; Smith 1968; Rothstein 1975a, b). There is increasing evidence, however, that individuals may often parasitize the reproductive efforts of conspecifics, enabling an animal to either supplement its reproductive output or breed when reproduction would otherwise be impossible or too costly (Yom-Tov 1980; Andersson 1984). Intraspecific brood parasitism is known to occur regularly in wood ducks (*Aix sponsa*, Morse & Wight 1969; Heusmann et al. 1980; Semel & Sherman 1986), snow geese (*Chen caerulescens*, Cooke & Mirsky 1972), starlings (*Sturnus vulgaris*, Yom-Tov et al. 1974; Power et al. 1981, personal communication; Feare 1983), goldeneyes (*Bucephala clangula*, Andersson & Eriksson 1982), cliff swallows (*Hirundo pyrrhonota*, Brown 1984), white-fronted bee-eaters (*Merops bullockoides*, Emlen & Wrege 1986), moorhens (*Gallinula chloropus*, Gibbons 1986), European

barn swallows (*H. rustica*, Møller 1987), and sporadically, or rarely, in many other species (see Yom-Tov 1980). The frequency at which intraspecific brood parasitism occurs in some of these species suggests that it may be an alternative reproductive strategy used by substantial numbers of individuals within a population.

The dynamics of intraspecific brood parasitism are still poorly understood. This deficiency arises in part because of the difficulty in detecting parasitism among conspecifics. Unless an individual is actually observed to lay an egg in another individual's nest, precise identification of the parasitic individual is usually impossible. Techniques such as protein electrophoresis (Gowaty & Karlin 1984; Westneat et al. 1987), checking the sequence of egg laying in nests (Brown 1984; Emlen & Wrege 1986), or comparison of egg marking patterns (Gibbons 1986; Møller 1987) allow one to infer whether parasitism might have occurred at a given nest but (for different reasons) seldom allow confident assignment of parentage. Electrophoresis is too expensive and time-intensive to use on a large scale. Although Gibbons (1986) and Møller (1987)

assumed that differences in egg markings among eggs in a clutch can be used to infer parasitism, no one has shown quantitatively that each female always lays eggs that look similar. Host individuals may often be overlooked with all of these techniques, resulting in gross underestimation of the frequency of brood parasitism. As a result, previous researchers have focused mainly on documenting the presence of intraspecific brood parasitism. The costs and benefits of this phenomenon have not been thoroughly explored at the empirical level.

Intraspecific brood parasitism occurs commonly in colonial cliff swallows. In a preliminary report it was estimated that up to 24% of the nests in some colonies contained at least one parasitic egg laid by a conspecific (Brown 1984). Intraspecific brood parasitism is perhaps more common in cliff swallows than in any other species that has been studied in natural nesting densities. However, little is understood about the evolution of brood parasitism in cliff swallows and the selective consequences of parasitism to host and parasitic individuals. The goal of this paper is to describe intraspecific brood parasitism and to examine its costs and benefits and possible evolution in colonial cliff swallows. Unlike previous studies, we rely heavily on direct observations of colour-marked birds parasitizing nests and thus we have unique information on the identities and status of individuals that engage in intraspecific parasitism.

We recently discovered that cliff swallows practise a bizarre form of intraspecific brood parasitism not previously known. These birds physically transfer eggs between nests after laying, and 6% of all nests contain eggs that are carried into them (Brown & Brown 1988a). Our findings on transfers of eggs are summarized elsewhere (Brown & Brown 1988a) and in this paper we focus mainly on brood parasitism in the classic sense, that is, by laying eggs in other individuals' nests. We return to egg transfers in the Discussion section of this paper, however, when considering the adaptive significance and evolution of cliff swallow brood parasitism in the broad sense.

STUDY ANIMAL AND STUDY SITE

Cliff swallows are small migratory passerines that nest in colonies throughout much of western North America. The species nests commonly from the

Lower Sonoran through the Transition zones to about 3000 m, but rarely at higher altitudes (Grinnell & Miller 1944). Cliff swallows arrive in the southern and coastal parts of their breeding range in March and arrive in most other areas (including our study area) by early May. Most cliff swallows leave North America in August and September for their wintering range, which extends from southern Brazil to Argentina and Chile (American Ornithologists' Union 1983). The birds build gourd-shaped nests out of mud pellets, and their nests are attached underneath overhanging rock ledges on the sides of cliffs and canyons. Relatively recently, cliff swallows in some areas have begun nesting under the eaves of bridges, buildings, highway culverts, and other artificial structures that offer an overhanging ledge and a rough vertical substrate for nest attachment. The birds feed exclusively on insects caught in flight, and colonies serve as information centres in which individuals unsuccessful at finding food locate and follow successful colony residents to ephemeral prey sources (Brown 1986). Cliff swallows occur in a wide variety of habitats, although open fields for feeding and a body of water as a mud source are usually located close to each colony. The birds are highly social in all of their activities, feeding, preening, mud-gathering and loafing in large groups (Emlen 1952; Brown 1985). The species is usually single-brooded, and hematophagous ectoparasites are responsible for much of the observed nestling mortality (Brown & Brown 1986). The cliff swallow's general biology has been studied well (Emlen 1941, 1952, 1954; Mayhew 1958; Samuel 1971; Grant & Quay 1977; Withers 1977; Brown 1985).

This study, part of continuing long-term research on the social behaviour of cliff swallows, was conducted in southwestern Nebraska, U.S.A., near the University of Nebraska's Cedar Point Biological Station, from May to August, 1982–1987. Cliff swallows are abundant in this area, and have probably increased in recent years with the construction of highway culverts and bridges upon which they can nest. However, these birds probably occurred in southwestern Nebraska before the appearance of artificial structures, nesting on bluffs and outcrops along the North Platte River and on cliffs in other parts of the state (Nichols, cited in Pearson 1917). We studied colonies that were located on bridges, in highway culverts, on irrigation structures, and on natural cliff sites along the

south shore of Lake McConaughy. During 1982–1987, there were 276 cliff swallow colonies totalling 97 980 nests in or near the study area in Keith, Garden, and Lincoln counties (Brown 1985). Colony size ranged from two to approximately 3500 nests ($\bar{X} \pm SD = 355 \pm 561$ nests), and birds also nested solitarily.

METHODS

Checking Nest Contents

Study colonies were named and, where possible, all nests were numbered and their progress followed throughout the nesting season. In large colonies, we could study only a sample of the nests, and in these cases we selected nests from all accessible parts of the colony. We reached cliff swallow nests with aluminium ladders, or canoed, swam, or waded to the bases of cliff sites or into culverts where ladders were unnecessary. Nests were marked by writing chalk numbers on the nearby concrete substrate (for colonies using bridges or culverts) or by driving nails with numbered heads into the cliff face (for cliff colonies). Nests were checked each day or every other day, beginning as soon as nest construction began or as soon as an existing nest was occupied (this was usually indicated by the appearance of fresh mud on the nest's neck). We observed nest contents with a dental mirror and a small flashlight inserted through each nest's mud neck. It was occasionally necessary to chip away pieces of dried mud from the neck to insert the mirror, but it was not necessary to alter the nest appreciably, and birds quickly repaired any damage. Cliff swallows continually added fresh mud to all nests, those studied and those not studied, suggesting that repair brought on by our activity did not lead to much additional energetic or time demands on the birds. Removal of small amounts of mud from the necks of cliff swallow nests has little adverse effect on the birds' reproductive success (Hamilton & Martin 1985; C. Brown, personal observation). Once all the eggs of a cliff swallow clutch had hatched, we did not disturb that nest again until the 10th day after hatching, at which time we recorded the number of surviving nestlings present. Because cliff swallows lay their eggs early each morning (Brown 1984), no nest checks were made prior to 0800 Mountain Daylight Time to avoid possible disruption of natural egg-laying patterns. For criteria

used in separating different groups of cliff swallow nests as different colonies, see Brown & Brown (1986). In this paper 'colony size' refers to the number of active nests and does not include unused nests, which occurred commonly in many colonies.

Capturing, Marking, and Observing Colour-marked Birds

At selected culvert colonies cliff swallows were captured in mist nets strung across the culvert entrances. The birds' white forehead patches were coloured in unique one-, two- and three-colour combinations using UniPaint and Decocolor paint-marking pens. We used light blue, light green, red, orange, pink, yellow, white (unpainted feathers), silver, black and, to a lesser extent, gold. Except for black, the colours used were light and the shape of the birds' forehead patch remained unchanged. When birds were at their nests, usually only their heads were visible as they sat inside their nests. Coloured leg bands were not practical. All colour-marked birds also received standard United States Fish and Wildlife Service bands. Colour-marked birds did not appear to behave differently from unmarked birds, nor did other birds seem to react to them in any unusual ways. Cliff swallows were sexed by cloacal protuberance, a method that is about 90% accurate early in the season (C. Brown, unpublished data). Colour marking began at most colonies soon after the birds arrived in the spring and just prior to egg laying. Paint remained fresh and visible on the feathers for 7–10 days, after which time birds were recaptured and the colour marks reapplied. From 20 to 120 nests at each colony were selected as focal nests for observations. About 75% of the nest owners in these nests were colour-marked (or individually recognizable by plumage irregularities).

Nest ownership by individuals was determined by observing which colour-marked birds were routinely associated with a given nest. Focal nest positions and numbers were mapped, and we referred to the map for a nest's number whenever an interaction occurred among birds. Because of the ease of access by us to colonies located in culverts, all observations of birds' behaviour at their nests were made in culvert colonies. However, because the nests in the centre or at the opposite ends of these colonies were difficult to impossible for us to see from any given vantage point, our observations were necessarily confined to the

20–60 nests closest to the colony's edge on any given culvert wall. We made observations from chairs about 5 m from a culvert's entrance. Cliff swallows habituated quickly to our presence and ignored us as long as we remained outside the culvert, making blinds unnecessary.

One or two observers, often working simultaneously, observed intensively the focal nests for approximately 75% of daylight hours, beginning prior to or during egg laying at each colony. Observations were continued until all egg laying in the focal nests had stopped and all birds were incubating. Since cliff swallows are highly synchronous nesters (Brown & Brown 1987), the time of observation at each colony was about 2 weeks. As a result, all focal nests were observed during their egg-laying period but only some (the earlier-starting ones) were watched intensively for a major portion of their incubation period. All interactions among colour-marked nest owners and unmarked non-owners at nests were monitored and recorded. Observations were conducted at five colonies, consisting of 125, 190, 345, 750 and 1100 nests, respectively.

Our goal was to observe directly birds laying eggs in other individuals' nests. Therefore, we examined nests whenever owners left their nests unattended and whenever neighbours entered and then exited unattended nests after remaining inside for longer than 10 s. In this way any eggs appearing in an unattended nest after a neighbour had entered were verified to have been laid by the neighbour and not the owner. We examined nests by entering the culvert quickly and checking the contents of the nest in question and then exiting quickly. These disturbances to the colony were minimal, and often birds remained inside their nests and carried on seemingly normal activity less than a metre away while we examined a nest. To avoid disruption during a colony's egg-laying period, we did not mark eggs as they were laid. We were never present at colonies for either nest examinations or observations prior to 0800 hours.

Inferring Parasitisms Based on Nest Checks

An accurate way to infer whether a brood parasitism has occurred in a nest is by the temporal sequence of egg laying. Birds do not lay more than one egg during any 24-h period (e.g. Warren & Scott 1935; Sturkie 1965; Murton & Westwood

1977). Thus, appearance of more than one egg in a nest per day is evidence of more than one female laying in the nest. We considered any cliff swallow nest with more than one egg appearing per 24-h period as having been parasitized. In addition, any nest which had a single egg appearing 3 or more days prior to the laying of the rest of the clutch was also considered as having been parasitized. This was because parasites were often directly observed to lay eggs in nests slightly before the hosts began laying there (see Results). Using a criterion of 3 days before the putative host began laying was conservative and probably resulted in many parasitisms being overlooked. We observed no instances of a colour-marked female laying eggs in her own nest and then skipping 3 or more days before laying more eggs there, so we doubt that any egg added 3 or more days before the appearance of the rest of the clutch was in fact laid by the nest owner. Finally, nests which had single eggs appear and then disappear by the time of our subsequent nest check were also considered as having been parasitized. This was because nest owners removed parasitic eggs that appeared in their nest if the eggs appeared far enough in advance of their own egg laying (see Results). This kind of brood parasitism differed in an important way from other kinds: it was never successful because the putative hosts removed the parasitic eggs. Therefore, in our analyses we distinguished 'egg-removed' parasitisms from all other inferred parasitisms based on nest checks. We use the term egg-removed parasitisms as a convenient means of describing putative parasitic eggs added and then removed from nests. Unless noted otherwise, analyses based on inferred parasitisms combined all nests with relevant data from all colonies studied.

Measuring Nesting Synchrony

For some analyses we investigated the relationship between intraspecific brood parasitism and the degree to which nests were synchronized with each other. For each colony the modal clutch initiation date (i.e. date of first laying in a nest) was determined and the standard deviation of clutch initiation date was calculated (see Brown & Brown 1987). A single standard deviation was 2–5 days for most colonies. Each nest was then assigned, based on its clutch initiation date, to the appropriate number of standard deviations on either side of the

modal date. We thus compared relative intra-colonial synchrony of all nests, allowing us to pool data from different colonies.

Statistical Analyses

All statistical analyses were performed on an IBM XT personal computer, using the PC Statistician software (Madigan 1983), or on a Texas Instruments 59 programmable calculator. All statistical tests were two-tailed. Because data were not distributed normally, non-parametric statistical tests were used (Siegel 1956). Sample sizes for different analyses often differed slightly because not all information was available for every nesting attempt or observation. Some analyses did not require complete information, while others did. For chi-squared goodness-of-fit tests, categories were lumped together when necessary to achieve expected frequencies of ≥ 5 .

RESULTS

Natural History of Parasitism

We observed 27 actual parasitisms in which the identities of both the host and parasite were known. These parasitisms were distributed among all five colonies where observations were made: one parasitism (3.7% of those observed) each in the 125- and 345-nest colonies; five (18.5%) in the 190-nest colony; nine (33.3%) in the 750-nest colony; and 11 (40.7%) in the 1100-nest colony. In all observed parasitisms, parasitic females maintained nests of their own in addition to parasitizing others. In nine cases (33.3%) the parasite's and host's nests were located adjacent to each other within the colony (15 cm or less separating them), and in 13 cases (48.1%) the parasite's and host's nests were separated by two–five nests. Thus, only five (18.5%) parasites travelled more than five nests away to parasitize a nest, the farthest distance between a parasite's and its respective host's nest being 198 cm. Parasitisms tended to occur at virtually any time during the day: 11 (36.7%) occurred between 0800 and 0959 hours; nine (30.0%) between 1000 and 1159 hours; three (10.0%) between 1200 and 1359 hours; six (20.0%) between 1400 and 1559 hours; and one (3.3%) at exactly 1600 hours ($N=30$ observed parasitisms for which time of day was known). This contrasts with normal egg laying by individuals in their own

nests in which 98.8% of eggs were laid prior to 0800 hours (Brown 1984).

Beginning prior to egg laying and continuing into the early stages of incubation, virtually all cliff swallows frequently tried to enter neighbouring nests in their respective colonies. This activity at times was almost continuous, as individuals repeatedly visited different nests in obvious attempts to gain entrance. These trespass attempts were in general perpetrated by birds that had nests of their own. Known nest owners often sat inside their own nests, apparently watching activity around them. Periodically they would dart out of their own nest, try to enter a neighbour's, and then dart back to their own nest. This behaviour was not that of 'lost' birds trying to find their own nest. Trespass attempts may be related in part to brood parasitism. In 22 of 27 cases (81.5%) a parasitism occurred in a host nest that had been left unattended momentarily. Cliff swallows guarded their nests heavily, and nests were seldom left unattended. As a result, trespass attempts by neighbours were rarely successful. In one case a parasite gained entrance to a nest and laid an egg there while the nest owner was present but while the owner was fighting another intruder in the nest (Brown 1984). In the four remaining cases (14.8%) a parasitic female entered a host nest while the male owner of the nest was present. In each case he tolerated the parasite while she laid an egg. In two of these cases the parasite, to our knowledge, never returned again to that host nest, but in the other two cases the parasitic female periodically returned to the host nest during the subsequent week and appeared to incubate the entire clutch there when the resident host female was absent. These parasitic females continued to be tolerated by the host males until they eventually ceased incubation at the host nests and confined their activities to their own nests.

Since parasitisms tended to occur when nests were left unattended, we watched especially for brood parasitisms during bad weather when birds left the colony to forage and during colony alarm responses when many nest owners were flushed from their nests. Four parasitisms (14.8%) occurred on cool (less than 16°C), cloudy, and rainy days when overall nest guarding was less intense than normal. One parasitism (3.7%) occurred during a colony alarm at an unidentified stimulus, when the host left its nest momentarily unattended in response to the alarm. There was no evidence that parasites gave 'false' alarm calls

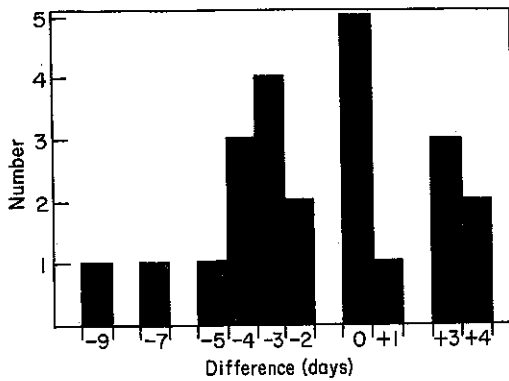


Figure 1. Frequency distribution for difference in days between the date that each known parasitic cliff swallow laid its first egg and the date that its known host laid its first egg. For example, if a parasite first laid on 20 May and its host first laid on 25 May, the difference would be -5 days.

(sensu Munn 1986) to flush potential hosts from their nests. Actual laying of parasitic eggs occurred in time periods of 15–120 s while parasitic females were inside unattended host nests.

Seasonal Chronology of Parasitism

For parasitisms in which the identities of both the parasite and host were known by direct observation, we examined the dates on which each laid their first egg (whether in their own nest or not). Small differences in the dates of first laying for each observed parasite and its host (Fig. 1) indicated that individuals in each class tended to be relatively synchronized in time with each other. This is not surprising, partly because cliff swallow colonies are highly synchronous (Brown & Brown 1987). Observed parasites tended to parasitize other nests before they had begun laying in their own nest, often 2–3 days before, although a few females parasitized nests well after they had begun laying in their own nest (Fig. 2). Observed host nests were often parasitized slightly before or on the same day the host herself began laying (Fig. 3).

For parasitisms inferred on the basis of laying patterns, we examined when in the laying period the parasitic egg appeared. For this analysis we used only those parasitisms detected by more than one egg appearing per day during laying. Of 285 nests containing parasitic eggs based on more than one egg laid per day, 235 (82.4%) had parasitic eggs appearing during the first 2 days of the host's egg-laying period, 13 (4.6%) had parasitic eggs appearing during the remaining days of the host's egg-laying period, and the time of appearance of

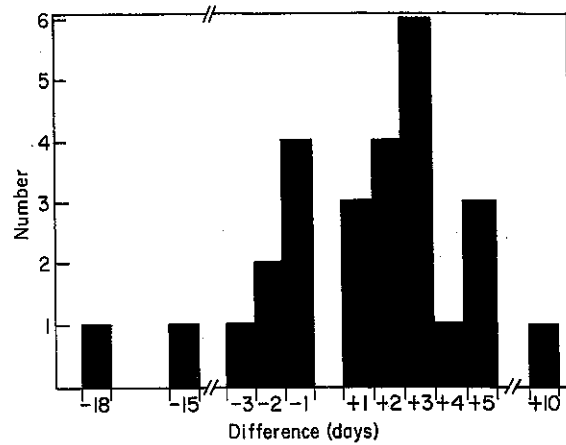


Figure 2. Frequency distribution for difference in days between the date that each known parasitic cliff swallow laid its first egg in its own nest and the date that it laid in a known host's nest.

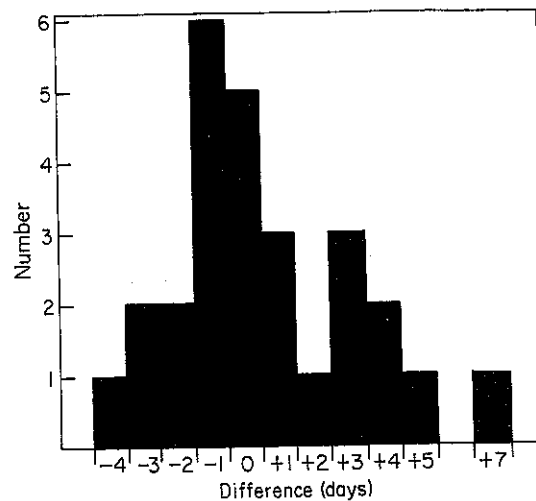


Figure 3. Frequency distribution for difference in days between the date that each known parasitic cliff swallow laid in a host's nest and the date that the host first laid in the nest.

parasitic eggs in the remaining 37 nests (13.0%) was unclear.

We also examined seasonal patterns in the occurrence of inferred brood parasitisms. All cliff swallow nests initiated during 5-day intervals, beginning with the earliest on 8 May and concluding with the latest on 28 July, were combined. We compared the percentage distribution of nest initiation dates for all nests in all colonies with that for all nests suffering inferred brood parasitisms (Fig. 4a) and with that for all nests suffering egg-removed parasitisms (Fig. 4b). Distributions for both classes of parasitisms differed significantly

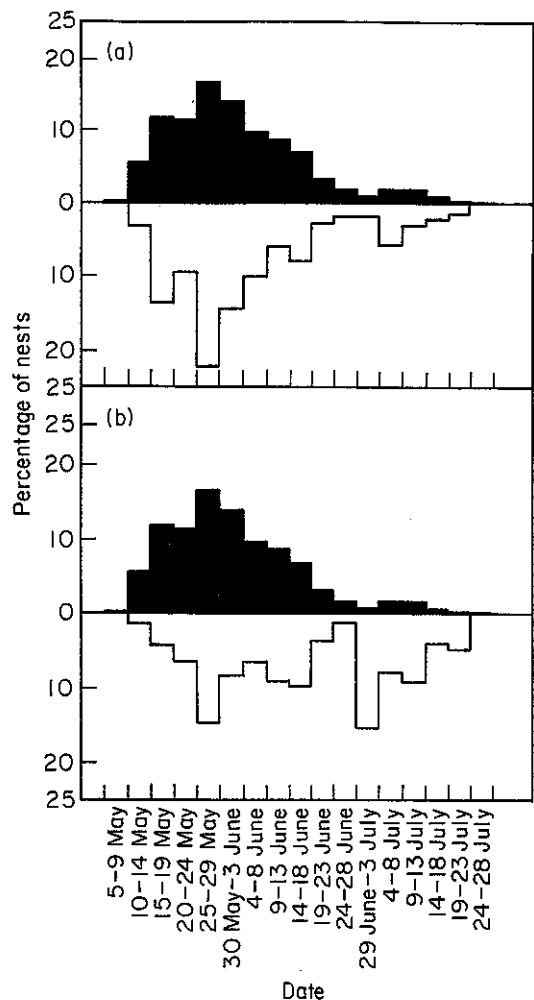


Figure 4. Percentage distributions of cliff swallow nests beginning egg laying during 5-day intervals for (a) all nests (■; $N=4302$ nests) versus those that suffered one or more inferred brood parasitism (□; $N=330$); and for (b) all nests (■; $N=4302$) versus those that suffered one or more egg-removed parasitism (□; $N=150$). The distributions in (a) differed significantly ($\chi^2=24.4$, $df=11$, $P=0.011$); the distributions in (b) also differed significantly ($\chi^2=184.2$, $df=11$, $P<0.001$).

from the overall distribution of nest initiation dates (Fig. 4). The distribution of inferred parasitisms tended to match more closely the overall distribution, but nests with inferred parasitisms occurred disproportionately more often earlier in the season (Fig. 4a). Nests with egg-removed parasitisms occurred disproportionately more often later in the season (Fig. 4b).

Parasitism and Colony Synchrony

We examined whether the incidence of parasitism varied with respect to a nest's temporal position within a colony, i.e. with synchrony. Synchronous nesting could be of benefit to a potential host

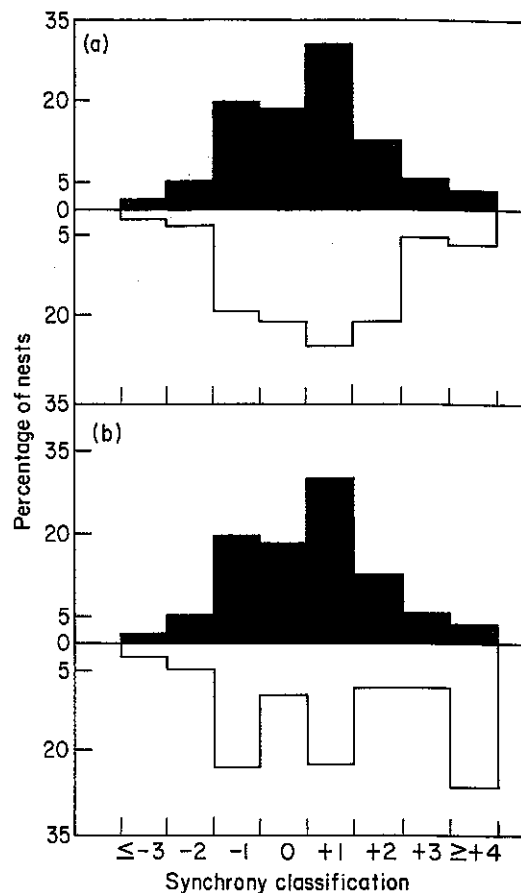


Figure 5. Percentage distributions of cliff swallow nests in each synchrony classification for (a) all nests (■; $N=4171$) versus those that suffered one or more inferred brood parasitism (□; $N=320$); and for (b) all nests (■; $N=4171$) versus those that suffered one or more egg-removed parasitism (□; $N=137$). The distributions in (a) differed significantly ($\chi^2=22.0$, $df=7$, $P=0.002$); the distributions in (b) also differed significantly ($\chi^2=136.5$, $df=7$, $P<0.001$).

by diluting its chances of being parasitized, which is analogous to avoiding predation in the same way. We compared the distribution of synchrony categories (see Methods) for nests suffering inferred parasitisms with the distribution for all nests from all colonies (Fig. 5a). The distributions differed significantly, with parasitized nests being slightly more represented across all synchrony categories than nests in general (Fig. 5a). This means that nests initiated during the peak period of nesting within each colony may have a lower probability of being parasitized. We also compared the distribution of synchrony categories for nests with egg-removed parasitisms with the distribution for all nests from all colonies (Fig. 5b). These distributions differed significantly, with egg-removed parasitisms represented disproportionately among nests in the later synchrony categories, especially

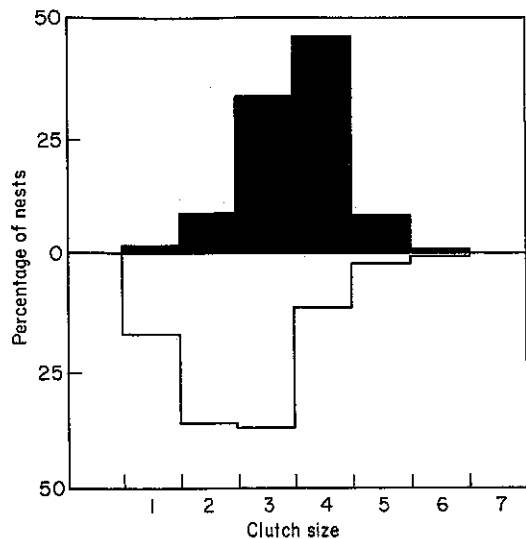


Figure 6. Percentage distributions of cliff swallow nests containing clutch sizes of one–seven eggs for all nests (■; $N=4935$) versus those to which parasitic eggs were added (□; $N=330$). The distributions differed significantly ($\chi^2=598.4$, $df=5$, $P=0.001$); clutch of seven excluded from the statistical analysis because of inadequate sample sizes.

the category equal-to-or-greater-than +4 (Fig. 5b). This means that nests initiated after the peak period of nesting in a colony have a higher probability of suffering an egg-removed parasitism.

Clutch Sizes of Parasitized Nests

We examined the clutch sizes of those nests that were parasitized and whether parasites might select hosts randomly with respect to a host's clutch size. We compared the percentage distribution of clutch sizes in all nests in all colonies with that of clutch sizes of all nests in which an inferred parasitism occurred (Fig. 6). Only nests for which the clutch size was considered definitive were used in this analysis, i.e. we used only nests that survived past the laying-period (until laying stopped). Egg-removed parasitisms were not included here because by definition they were added to nests not containing any eggs. Clutch size in this analysis was the clutch size laid by the host, exclusive of any parasitic eggs. The distributions differed significantly; parasitized nests had disproportionately smaller clutch sizes (Fig. 6). This indicates either that parasites actively select hosts with smaller clutch sizes or that the presence of a parasitic egg or eggs causes hosts to reduce the number of eggs that they lay.

Cliff swallows seldom have clutches larger than

six eggs (Fig. 6). We detected only seven clutches (of 4942; 0.14%) larger than seven eggs: three clutches of nine eggs each and one clutch each of 11, 12, 13 and 15 eggs. All of these supernormal clutches had multiple eggs appearing within single 24-h periods and were assumed to have been parasitized heavily. None of the nests with supernormal clutch sizes occurred among our nests with colour-marked owners.

Survivorship of Parasitic Eggs

We examined how often parasitic cliff swallow eggs were known to survive to produce fledged offspring as a measure of the success of brood parasitism. There were 38 instances of a parasitic egg being added to an observed nest of either a colour-marked host or parasite (detected by either direct observation or laying patterns). In 13 cases (34.2%) the parasitic egg was known to have hatched and produced offspring because all eggs in the nest survived. In 20 cases (52.6%) the parasitic egg may have survived to produce fledged offspring, but we do not know for sure because either some eggs were lost before fledging or some eggs did not hatch or some nestlings were lost before fledging, and because parasitic eggs and nestlings were not marked. In only five cases (13.1%) did the parasitic egg definitely not survive, once because the entire nest fell and four times because parasitic eggs were removed by the nest owners (see below).

Among all nests in all colonies containing an inferred parasitism ($N=385$ parasitic eggs), 127 eggs (33.0%) were definitely known to have hatched and produced offspring; survivorship status of 155 eggs (40.3%) was unclear, and 103 eggs (26.7%) were definitely known not to have survived because the nests containing them failed. Egg-removed parasitisms were not included in this analysis because by definition all of them ($N=150$) did not survive.

We also examined overall nest survivorship for parasitized nests. A nest containing at least one live nestling on the 10th day after hatching was considered a successful nest and a nest without any nestlings alive as an unsuccessful nest. For nests with inferred parasitisms, 86 were unsuccessful ($N=328$; 26.2%). This compares to nest survivorship of all the nests in our study population in which 1102 were unsuccessful ($N=4708$; 23.4%; $\chi^2=1.35$, $df=1$, $P=0.25$).

Table I. Reproductive success of known parasites, hosts and birds not observed to be either parasites or hosts*

	Parasite			Host			Birds not observed to be parasites or hosts		
	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N
Total eggs laid	4.00 ^a	0.16	24	3.29 ^b	0.14	21	3.58 ^b	0.05	288
Self-laid eggs in own nest	2.87 ^a	0.17	24	3.14 ^b	0.14	21	3.58 ^c	0.05	288
Own young fledged from own nest	2.86 ^a	0.16	21	2.00 ^b	0.23	19	2.86 ^a	0.08	269

* For each row means with different superscripts differed significantly ($P < 0.05$, Mann-Whitney U -test).

Reproductive Success of Known Parasites and Hosts

We examined reproductive success of known parasites and hosts for our sample of colour-marked birds. For comparison we also examined reproductive success of colour-marked individuals not known to have been either a parasite or a host. Known parasites laid significantly more eggs (counting those in their own nest plus the ones they laid parasitically) than did host females or females not known to be hosts or parasites (Table I). However, parasites laid significantly fewer of their own eggs in their own nests than did either hosts or non-hosts/non-parasites (Table I). Parasites fledged significantly more of their own offspring from their own nests (not counting parasitic offspring) than did hosts, but there was no difference between parasites and non-hosts/non-parasites in the number of offspring fledged from one's own nest (Table I). Known hosts laid significantly fewer eggs of their own and fledged significantly fewer offspring than did non-hosts/non-parasites (Table I).

This analysis indicates that known parasites laid more eggs in total than other individuals. Parasites raised more offspring than did hosts, and, when adding their parasitically raised offspring (which we were unable to quantify beyond knowing that at least about a third survived; see previous section), also raised more offspring than did non-hosts/non-parasites. Host individuals paid a cost of a reduction in almost one fledged offspring, on average.

Multiple Parasitisms of Hosts

We examined whether known colour-marked hosts tended to be parasitized only once, or multiply. Seven of 21 known hosts (33.3%) were parasitized again subsequent to their initially being

parasitized. Three of these hosts were parasitized twice, three were parasitized three times, and one was parasitized four times. The mean number of parasitic eggs added to all 21 host nests in our observed sample was 1.57 (SD = 0.93, SE = 0.20).

Among nests with inferred parasitisms based on laying patterns ($N = 330$; nests with egg-removed parasitisms not included), 42 (12.7%) were parasitized a second or third time. Of those 42 nests, 39 (92.9%) were parasitized twice, and three were parasitized three times. The discrepancy in the percentage of host nests multiply parasitized between samples based on direct observation and samples based on parasitisms inferred from nest checks only (33.3 versus 12.7%), occurs because nest checks probably underestimated the frequency of multiple parasitisms. When nests are checked only once a day or once every 2 days, multiple parasitisms occurring just prior to a host's start of egg laying, or just after a host's cessation of egg laying, would be inferred only as a single parasitism concurrent with egg laying by the host.

Multiple Parasitisms by Parasites

We examined whether parasites were ever known to parasitize more than one nest. In our sample of colour-marked birds, three of 24 parasitic females (12.5%) were directly observed to parasitize a second nest. Two of these females parasitized the same nest twice. In each case the first parasitic egg had been removed by the host (see later section) before the second parasitism happened. In addition, of the remaining 21 known parasitic females, four (19.0%) skipped laying an egg in their own nest on a day (other than the known day they parasitized another nest) during the egg-laying period. This suggests that they parasitized a second

nest undetected by us. Thus, the evidence suggests that up to 29.2% of parasites may multiply parasitize the same nest or parasitize more than one nest.

Costs of Being a Parasite

We examined whether individuals incurred any costs of being a parasite, the most likely such cost being increased time spent away from their own nests while searching for unattended host nests. This could result in parasites themselves being more likely to be parasitized by other individuals. The cost of leaving one's own nest unattended, even momentarily, was illustrated when a male owner left his nest and attempted an intrusion into a neighbouring nest. While he was fighting with the owner of the neighbouring nest, another neighbour parasitized his unattended nest. Of 24 different colour-marked females known to be parasites, 13 (54.2%) suffered observed or inferred parasitisms in their own nests (inferred parasitisms in these cases were detected by more than one egg appearing per day during laying or an egg appearing in the parasites' nests on the same day they parasitized someone else). Of these 13 parasitized parasites, six (46.1%) suffered multiple parasitisms (a second egg was added after they were initially parasitized). The mean number of parasitic eggs added to the 13 nests of parasitized parasites was 1.46 ($SD = 0.52$, $SE = 0.14$). There was a total of 19 parasitic eggs laid in the nests of the known parasites; 12 of these eggs (63.2%) were added on the same day that these parasites parasitized another nest. Leaving one's nest to search for host nests to parasitize apparently entails risk to a parasite of being parasitized itself.

Parasitism and Egg Removal

Cliff swallows commonly enter unattended neighbouring nests within their colonies and toss out single eggs. Neighbours engage in this behaviour, and it does not appear related to nest take-over attempts. The adaptive significance of egg-tossing in cliff swallows is obscure (Brown & Brown 1988b), although Brown & Brown (1988a) reported a probable link between egg removal and physical transfer of eggs into nests. If cliff swallows remove eggs concurrent with parasitism (as suggested by Brown 1984), this could drastically affect our estimates of parasitism based on nest checks.

A total of 23 instances of cliff swallows removing eggs from nests were directly observed (for details

see Brown & Brown 1988b). In only one of these instances was an egg removal directly associated with parasitic egg laying. At 1136 hours on 15 May 1987 in a colony of 1100 nests, female BKB entered an unattended nest 33 cm from her own. Immediately upon entering she tossed out the single egg that was present in the nest (an egg that the owner had presumably laid that day). BKB then retreated into the nest's interior, laid an egg, and within about 1 min returned to her own nest. This observation was the only direct evidence that cliff swallows might remove eggs from host nests at the same time that they laid parasitic eggs.

Although nest checks alone would not reveal simultaneous egg removal and parasitism, nest check data could be informative if parasites tended to visit nests and remove eggs either before or after they parasitized the nest. We examined whether nests with inferred parasitisms tended to show a higher incidence of single egg removal by conspecifics than did non-parasitized nests. Excluding egg-removed parasitisms, 37 nests ($N = 330$; 11.2%) with inferred parasitisms had evidence of a single egg being removed at some time during incubation and after the parasitism had occurred. Among presumed non-parasitized nests, 442 ($N = 4899$, 9.0%) had similar evidence of egg removals. Egg removals did not occur disproportionately more often among parasitized nests ($\chi^2 = 1.78$, $P = 0.18$). There is thus little direct or indirect evidence at present that parasitic cliff swallows routinely remove eggs either before or after they parasitize host nests.

There was evidence, however, that nest owners might sometimes remove parasitic eggs that had been laid in their nests. We observed three cases of colour-marked nest owners tossing single eggs out of their own nests. In all three cases an observed or inferred parasitism had occurred in that nest within 3 h preceding the toss-out. One of these nests suffered egg-removed parasitisms at least four different times, and the male owner definitely tossed out at least two of these parasitic eggs. Another nest in our observed sample was parasitized at least three times. Each parasitic egg in this nest disappeared within hours of being laid, and we saw the male owner toss out at least one of these eggs. These observations contrasted with a series of experimental additions of eggs to cliff swallow nests (Brown 1984). In this experiment we added single eggs to 12 nests in various stages of egg laying and incubation, mimicking parasitism. None of these

Table II. Results of experiments to test whether cliff swallows would remove eggs from their nests if an egg was added prior to egg laying

Nest no.	No. days prior to laying that egg was added	Egg removed	How soon egg was removed after addition
164A	1	No	—
361	1	No	—
500	1	No	—
48	3	No	—
126	3	Yes	Within 48 h (all subsequent eggs also lost)
681	5	Yes	Within 24 h
706	7	Yes	Within 24 h
491	8	Yes	Within 5 h
688	8	Yes	Within 24 h
492	10	Yes	Within 0.5 h
687	10	Yes	Within 24 h
675	18	Yes	Within 5 h

eggs was removed, and we have not directly observed any colour-marked hosts remove parasitic eggs from their nests once they began laying their own eggs.

In 1987 we did another series of egg additions to nests at a colony containing 1100 nests, this time adding eggs to nests before egg laying had started. Single eggs were collected from nests in unobserved parts of the colony and added to nests from 1 to 18 days before egg laying in each nest began (Table II). We then checked for presence or absence of eggs in these nests at least twice a day until either no eggs remained or egg laying started. Results indicated that at about 3 days prior to laying, a potential host would be likely to accept a foreign egg (Table II). Any egg added 5 or more days prior to a host's own start of egg laying was removed (Table II). This experiment suggests that a parasite cannot successfully parasitize a nest before about 3–4 days prior to the host's own egg laying. This result is in close agreement with direct observations of parasitic egg laying, in which no nest was parasitized more than 4 days before the host began egg laying (Fig. 3). Cliff swallows can apparently recognize and will remove parasitic eggs but only if the eggs are laid well in advance of an individual's own start of egg laying.

Parasitism Versus Colony Size

Large colonies could contain more potentially suitable hosts at any given time than small colonies, enhancing a parasite's chances of successfully parasitizing a nest in a large colony. We examined the percentage of nests with at least one parasitism (inferred plus egg-removed) in colonies ranging in size from two to 1600 nests, plus solitary nesters. When all colonies plus solitaries were considered, incidence of parasitism increased significantly with colony size (Fig. 7). However, this effect was largely due to a very low incidence of parasitism among solitaries and in colonies of 10 nests or less in size. When only colonies with more than 10 nests were considered, colony size had no significant effect on the incidence of brood parasitism (Fig. 7). The incidence of parasitism varied extensively between different colony sites.

Estimated Frequency of Brood Parasitism

In a given colony, from 0 to 40% of the nests may contain parasitic eggs based on nest-check data (Fig. 7). But what is the overall incidence of parasitism? Combining all colonies and based on nest-check data alone, there were 487 nests with at least one parasitism ($N=4942$; 9.9%). Nest checks grossly underestimate the frequency of brood parasitism, however. An algebraic expression that describes the estimated number of parasitic eggs and corrects for the fraction of eggs overlooked by nest checks is presented by Frederick & Shields (1986). Their correction uses the number of parasitic eggs detected, not the number of nests with parasitic eggs. We detected a total of 532 parasitic eggs, inferred plus egg-removed ($N=17\,521$ eggs; 3.0%). Frederick & Shields' (1986) correction leads to an estimated 981.4 parasitic eggs (5.6% of total eggs). To derive the total number of nests containing at least one parasitic egg, we assume that the 981.4 eggs were distributed among nests in the same proportion as that actually detected (532 eggs from 487 nests). This leads to an estimated 898 nests ($N=4942$; 18.2%) containing parasitic eggs based on nest-check data alone.

Another way to assess the degree of brood parasitism overlooked by nest-check data is to consider those nests in which brood parasitism was directly observed to occur (by seeing a female lay an egg there) but in which parasitism would have gone undetected through nest checks. In our subsample of nests with colour-marked owners ($N=356$

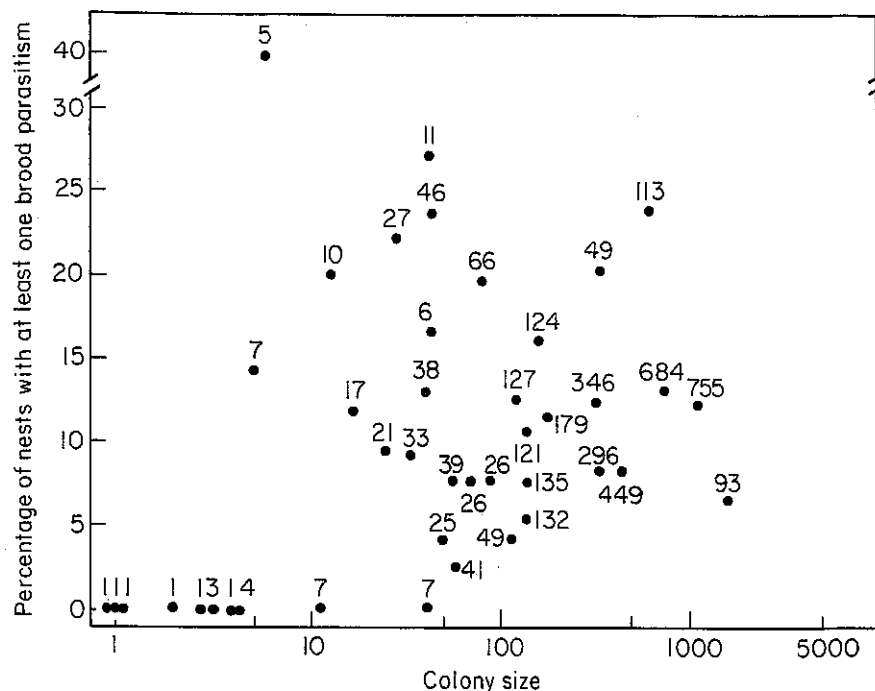


Figure 7. Percentage of cliff swallow nests with one or more brood parasitism versus colony size (number of active nests). Sample size for each colony shown. For all colonies combined, percentage of nests with parasitism increased significantly with colony size ($r_s = 0.40$, $P = 0.008$). For colonies with more than 10 nests only, there was no significant correlation between percentage of nests with parasitism and colony size ($r_s = 0.03$, $P = 0.64$).

nests), 40 brood parasitisms in 38 nests were detected by daily nest checks, 31 parasitisms in 24 nests were detected by direct observation, and three parasitisms in three nests were detected both by daily nest checks and direct observation. Thus, 21 nests in this subsample had known parasitisms that would have been undetected by daily nest checks. For various reasons all 21 would have gone undetected regardless of the frequency of the nest checks. Based strictly on daily nest checks, 318 nests in this subsample had no evidence of parasitism. Thus, a minimal estimate from the subsample of nests with colour-marked owners is that 6.6% of nests (21 of 318) showing no egg-laying irregularities based on nest checks in fact contained parasitisms.

If we combine the percentage of parasitized nests based on actual nest-check data from all nests, 9.9%, with that estimated from Frederick & Shields (1986) as being overlooked by nest checks, an additional 8.3%, we can estimate that 18.2% of all cliff swallow nests in our population are parasitized by conspecifics laying eggs in them. Similarly, we can add the percentage of nests with parasitism detected by direct observation but not by nest checks in the subsample of nests, 6.6%, to the 9.9% obtained from actual nest checks, to estimate that

16.5% of all nests are parasitized. We thus have two different behavioural estimates of the frequency of brood parasitism via parasitic egg laying, 18.2% and 16.5%.

If we conservatively accept the lower percentage (16.5%), we can modify this estimate further. We can add the percentage of cliff swallow nests with eggs physically transferred into them, 6% (Brown & Brown 1988a), because none of these nests was included among those in which parasitisms were detected by nest checks given the criteria used here or by direct observations. Combining these different types of estimates is legitimate because each is for a different subset of the population that would have gone undetected by the others. We conclude from behavioural data that approximately 22.5% of all cliff swallow nests in Nebraska contain one or more eggs not belonging to the owners.

We have conducted a simultaneous biochemical study of parentage in Nebraska cliff swallows, using protein electrophoresis to exclude putative mothers and fathers (Brown & Brown, in press). The observed distribution of parental exclusion types suggested that isozyme mismatches are more likely to result from brood parasitism rather than from extra-pair copulations. Analyses of isozyme data revealed that 19 of 91 nests (20.9%) that had

no evidence of a parasitism based on either nest checks or direct observations of egg laying, in fact contained nestlings unrelated to one or both of their putative parents. If we assume that these nestlings resulted from brood parasitism (Brown & Brown, in press), parasitic egg laying in these 19 nests was overlooked by both nest checks and direct observations (parasitic egg laying in three nests as shown by isozyme analysis was also detected by nest checks). The behavioural estimate of 22.5%, and the isozyme estimate of 20.9%, of all nests as having been parasitized, are probably additive because each is for a mutually exclusive subset of the population. Thus, over 43% of all cliff swallow nests in Nebraska may contain one or more eggs not belonging to the owners. We believe this estimate is probably accurate, although it is potentially an overestimate if the 20.9% isozyme figure in fact contained any mismatched offspring resulting from extra-pair copulations.

How efficient are intensive observations in detecting parasitisms among colour-marked nest owners? We directly observed parasitic egg laying in 31 of the 68 known parasitisms (45.6%) in our sample of nests. The actual efficiency is probably much lower because other undetected parasitisms undoubtedly occurred.

DISCUSSION

Our analyses indicate that intraspecific brood parasitism in cliff swallows is a relatively sophisticated behavioural strategy, and one that has probably been shaped by natural selection. In contrast to the implication inherent in the widely used term 'egg dumping', that birds are perhaps randomly and wastefully dropping eggs of questionable viability into nests, parasitic cliff swallows usually select appropriate host nests that tend to maximize the parasites' probability of future gain.

Selection has probably favoured those parasites who select the best hosts and who parasitize nests at the best time. For example, hosts will not tolerate eggs added to their nests more than 3 or 4 days prior to the start of egg laying (Table II). Direct observation of colour-marked birds revealed that, consistent with the results in Table II, no parasite attempted parasitism more than 4 days before the host began laying (Fig. 3). But within the time period of a host's acceptance of eggs, parasites tended to parasitize nests as early as possible both

prior to and during host egg laying. From the parasite's standpoint, parasitism early in laying enhances the chances that the parasitic egg will hatch or will hatch first. Brood parasitisms tend to occur relatively early in the season (Fig. 4a), which enhances their success because late cliff swallow nests suffer heavy nestling loss and abandonment due to ectoparasites (Brown & Brown 1986). Parasitic eggs were laid in nests that tended to have reduced clutch sizes (Fig. 6). Although this may partly reflect active clutch size reduction by hosts in response to parasitism, it is also possible that parasites are able to assess and select hosts that are likely to have small clutches. Physical transfer of eggs that have been laid (Brown & Brown 1988a) is a behaviourally quite sophisticated way to parasitize nests. Brood parasitism via egg transfers can occur virtually any time during laying and during incubation, greatly expanding the window of time when nests may be successfully parasitized. Finally, removal of a host egg coincident with laying a parasitic egg is another behavioural elaboration of parasitism that is potentially present in some cliff swallows (although seen only once to date). Several kinds of evidence thus indicate that brood parasitism is an adaptive strategy in cliff swallows and not maladaptive or pathological behaviour (see Semel & Sherman 1986). The possibility that these birds become lost within a colony and lay eggs in other nests as a result, is probably remote. In hundreds of hours of watching colour-marked cliff swallows, we have not seen any evidence that these birds become lost with respect to nest locations.

What are the advantages of intraspecific brood parasitism? In this Discussion we use 'parasitism' to include both parasitic egg laying and physical transfer of eggs. Brood parasitism may be best understood in cliff swallows (and perhaps other species) by considering variance in reproductive success (Gillespie 1974, 1977; Rubenstein 1982). Maximizing average fitness is not always the best strategy an animal can choose. When environmental uncertainty affects the likelihood of a reproductive strategy actually manifesting its expected fitness, an individual may often do best by minimizing variance in reproductive success and maximizing the likelihood of at least one offspring surviving to independence (Rubenstein 1982). One way this reduced variance may be achieved is by scattering eggs in several different nests. Scattering eggs works to ensure that at least some offspring will survive. Although this notion was previously

discussed in the context of interspecific brood parasitism (Payne 1977a), reduction of variance via scattering eggs is probably the key to understanding intraspecific parasitism. No previous theoretical treatment of intraspecific brood parasitism has explored the potential advantages of scattering eggs (Yom-Tov 1980; Andersson 1984).

Cliff swallows may stand to gain a great deal by scattering eggs into several nests via either parasitic egg laying or egg transfer. The major causes of nesting failure are hematophagous ectoparasite infestations and falling of nests due to crumbling substrate or poor weather conditions. The number of ectoparasites per nest varies greatly within a colony (C. Brown, unpublished data). The nature of this variation is not understood. Due to life history patterns of the ectoparasites, which increase as the nesting season advances (Loye & Hopla 1983; Brown & Brown 1986), it is probable that a cliff swallow cannot predict relative within-colony patterns of nest infestation at the time of nest site selection and egg laying. Distributing eggs into several nests reduces the chances of an individual's total reproductive failure that year due to ectoparasites and also may enhance the condition and body mass of some of its nestlings that are raised in a less-infested nest. If ectoparasite infestations begin to be obvious to nest owners late in incubation (which appears to be the case at least for later-nesting birds; Brown & Brown 1986), physical transfer of eggs to a less-infested nest becomes increasingly advantageous. In fact, transfer of eggs often occurs late in incubation (Brown & Brown 1988a). Similarly, nesting failures caused by rock slides and extreme weather conditions are relatively common in cliff swallows (C. Brown, unpublished data; C. Hopla & J. Loye, personal communication). For example, a single thunderstorm on 20 June 1987 destroyed at least 1400 cliff swallow nests on cliff faces along Lake McConaughy. Some colonies were destroyed entirely, but many had a few surviving nests. Small microgeomorphic differences along the cliff faces, such as degree and direction of overhang and exposure and substrate composition, led to some nests surviving this catastrophe. Birds who lost their nests on the relatively late date of 20 June in our study area probably did not re-nest. Scattering eggs into several nests ensures that at least some offspring will survive if late summer nesting failures happen.

Our data indicate that the overall probability of a cliff swallow nest fledging at least one offspring is

0.766. If a female has only one nest, her probability of success is 0.766. If she has two nests (her own plus one which she parasitized) her probability of having at least one offspring in a successful nest is 0.950; with three nests (her own plus two which she parasitized) her probability is 0.989, and so on (from Rubenstein 1982). In the case of Nebraska cliff swallows in which nesting success is usually relatively high, there is little further theoretical gain on average from parasitizing more than four nests.

However, when nest failure rates are high, individuals gain disproportionately more from each nest they parasitize. Nesting success can vary between cliff swallow colony sites (Brown & Brown 1987). This variation could affect the maximum number of nests an individual might be expected to parasitize locally and the advantages it might receive from risk-spreading. To test whether environmental uncertainty in fact leads to increased risk-spreading via brood parasitism, for each of our colonies we compared the percentage of parasitized nests (inferred plus egg-removed) with the percentage of nests unsuccessful at fledging young. Colonies where reproduction is more uncertain should have higher rates of parasitism. This prediction was supported (Fig. 8). There was a significant correlation between the percentage of parasitized nests per colony and percentage of unsuccessful nests per colony (Fig. 8). Uncertainty of reproduction is thus a better predictor of a colony's degree of parasitism than is colony size (Fig. 7). This correlation is not an artefact of parasitized nests being more likely to fail, because parasitized nests were not more likely to fail than nests in general (see Results). This analysis (Fig. 8) suggests that cliff swallows may assess the degree of uncertainty in their colonies relatively early in the nesting season, at least by the time egg laying (and thus parasitism) starts. These birds may be using subtle cues to predict, among other things, future degree of ectoparasite infestation and likelihood of nest loss at a site. This analysis (Fig. 8) also suggests that brood parasitism in cliff swallows is perhaps a phenotypically flexible strategy that individuals may or may not employ depending on the nature of the colony they occupy at any given time.

If brood parasitism is a strategy to maximize probability of fledging at least one offspring, one would expect little multiple parasitism of nests (Payne 1977a). A parasite would do better to spread its eggs throughout several nests rather than put them all in a single nest. The rarity of

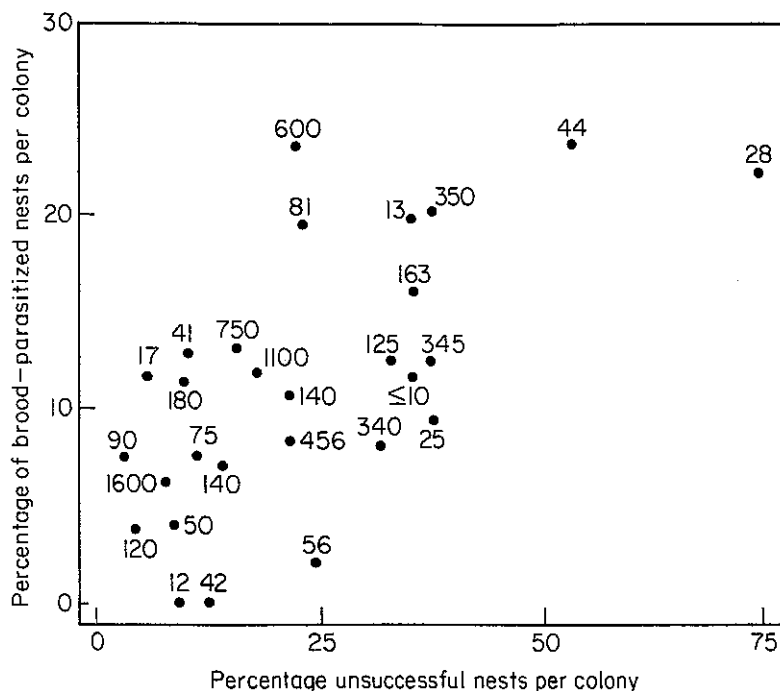


Figure 8. Percentage of brood-parasitized nests (those with one or more parasitically laid egg) per colony versus percentage of unsuccessful nests (those without any nestling alive 10 days after hatching) per colony. There was a significant correlation between the percentage of parasitized nests and the percentage of unsuccessful nests per colony ($r_s = 0.62$, $P < 0.001$). These were the same colonies as those shown in Fig. 7, although some of those in Fig. 7 were not included here because of inadequate sample sizes. Nests from all colonies with 10 nests or less were pooled for this analysis. Total size of each colony is shown.

supernormal clutch sizes in cliff swallows (Fig. 6) supports the notion that the birds are scattering their eggs. The proportion of parasitized nests suffering multiple inferred parasitisms (49 of 487; 10.1%) does not differ significantly from the proportion of all nests parasitized (487 of 4942; 9.8%; $\chi^2 = 0.02$, $df = 1$, $P = 0.88$), meaning that birds are probably not disproportionately seeking out parasitized nests to parasitize a second or third time. (Nest-check data may underestimate the frequency of multiple parasitism, however.)

Another prediction is that an individual would spread its eggs throughout all parts of a colony, if parasites are spreading their eggs in response to environmental uncertainty. Our observations reveal that parasitisms occur among close neighbours (as in other species, Gibbons 1986; Møller 1987). This may be simply because monitoring the activity of close neighbours is most efficient. Ascertaining when distant neighbours leave their nests unattended may be virtually impossible without huge energetic investment (flying back and forth) and without leaving one's own nest often unattended and thus highly vulnerable to parasitism, conspecific egg removal, or even usurpation. But at least with respect to ectoparasitism, a

neighbouring nest may be as likely to be uninfested as one far away (C. Brown, unpublished data), so risk-spreading among neighbours may be the most efficient tactic. The degree to which neighbouring nests vary with respect to exposure to the elements and probability of falling needs to be determined.

With the costs that parasites themselves must potentially pay (being parasitized themselves), the benefits they gain from parasitism may not be obvious if advantages of risk-spreading are not considered. Chances are that a parasite may end up with as many eggs as a host, when the parasite itself is parasitized. This suggests that these birds probably do not parasitize nests to reduce their net brood sizes and thus the costs of parental care (cf. Davies 1988). Only if parasites had consistently smaller brood sizes than non-parasites (they do not, Table I) could reduction of parental care be a possible advantage of intraspecific brood parasitism. However, if birds parasitize nests to spread risk, as argued here, it does not matter if a parasitic individual is itself parasitized, and differences in net brood size among different classes of individuals are not required. This tends to support our interpretation that cliff swallows parasitize nests to spread risk, although we are in the process of

measuring the costs of parental care in a long-term study of marked individuals.

The preponderance of parasitisms among close neighbours probably explains why colony size does not affect the overall incidence of parasitism (Fig. 7; Brown 1984). Once an individual gains about 10 or so neighbours, further increases in colony size may not change the number of close neighbours with whom that individual will interact. Thus, per caput probability of being parasitized is not affected by increases in colony size above that threshold. Individuals nesting in extremely small colonies (or solitarily; Fig. 7) are probably seldom parasitized and seldom have opportunities to parasitize others. It would be interesting to examine the degree of environmental uncertainty associated with small colonies or solitary nesting where the option of risk-spreading is apparently unavailable to an individual. The degree to which the absence of brood parasitism and opportunities to be a brood-parasite in extremely small colonies affects the evolution of coloniality in cliff swallows should be explored.

We found no evidence for the existence of 'professional parasites' in cliff swallows, that is, individuals who did not maintain nests of their own and resorted solely to parasitizing others in order to reproduce. To our knowledge no professional parasites have been documented in any other species known to practise intraspecific brood parasitism (Emlen & Wrege 1986; Gibbons 1986; Møller 1987; certain ducks might be the most likely candidates). Parasitic individuals in all of these species appear to be either ones that simultaneously maintain nests of their own or ones that lose their nests during egg laying and lay their remaining eggs elsewhere. Our data indicate that not all cliff swallows engage in parasitism. Why some individuals do and others apparently do not is a major unanswered question in our research. Intraspecific brood parasitism in cliff swallows may be a conditional risk-spreading strategy based on an individual's age, condition, expectation of survivorship, spatial position in the colony, or other factors.

Is the male cliff swallow a passive observer or an active participant in brood parasitism? Males have an integral role in guarding the nest, usually trading-off with their mate, to ensure that one owner is nearly always present. In most cases males actively repelled visiting females that might have parasitized the nest. We did observe, however, four cases in which a male voluntarily allowed his nest to

be parasitized. If males achieve successful extra-pair copulations with neighbouring females, parasitic eggs laid by those females in neighbouring nests could have been fertilized by the male 'host'. Male cliff swallows do in fact attempt copulations (sometimes forced, other times not forced) with neighbouring females (C. & M. Brown, personal observation). If a male was reasonably certain of having fertilized a parasitic female's eggs, he might not resist her parasitizing his nest. This could be tested by examining whether males are more likely to tolerate intrusions by neighbouring females than by non-neighbouring females, and could explain the instances we observed in which males allowed parasitism of their nest. From the standpoint of a male paired to a parasitic female, he presumably benefits in similar ways to she in risk-spreading via parasitism. Theoretically, males as well as females can parasitize nests by physically transferring eggs, but so far no case of a male transferring an egg has been observed (Brown & Brown 1988a).

Egg-removed parasitisms deserve attention, if only for the suggestion from them that eggs may come cheap in cliff swallows. These sorts of parasitic events accounted for 30.8% (150 of 487) of the total brood parasitisms detected. These parasitisms are unsuccessful because the eggs are removed by either the nest owners or other swallows. Some of these could be bonafide parasitisms added too soon before a host begins laying and are therefore removed. But the temporal pattern of egg-removed parasitisms (Figs 4b, 5b) suggests that they may often be last-ditch efforts by birds faced with unlikely prospects of achieving successful brood parasitisms that year. Egg-removed parasitisms occur disproportionately often late in the nesting season (Fig. 4b), frequently in nests that have recently fledged young and therefore have no resident owners who would care for any eggs. Many late parasitisms occur when large numbers of cliff swallows return to the colony sites after fledging young and go through preliminary phases of courtship and nest defence. This post-breeding nesting behaviour may occur for up to 2 weeks at some colonies after young are reared and before migration in the fall begins (C. Brown, personal observation). Eggs are seldom produced at this stage, other than single parasitic eggs distributed among nests and quickly removed by the transient nest owners. Production of doomed eggs late in the year after birds have completed brood-rearing and as they are preparing for migration suggests that

eggs may be less energetically costly than generally assumed (see Murton & Westwood 1977). If cliff swallow eggs are inexpensive late in the summer, eggs may also be relatively inexpensive early in the summer when birds parasitize nests for real and presumably need to make as many eggs as possible. The seasonal distribution of egg-removed parasitisms was the only indication that parasitic egg laying in cliff swallows might at times be maladaptive and directed at inappropriate nests.

Cliff swallows presently occur in habitats that sometimes differ greatly from the ancestral habitats in which their social behaviour presumably evolved. These birds often nest on artificial structures which could potentially alter the spatial distribution, density and visibility of nest sites. In wood ducks, Semel & Sherman (1986) detected exorbitantly high rates of brood parasitism in a box-nesting population in which nest density and visibility had been greatly increased artificially. Semel & Sherman interpreted the parasitism they observed as pathological behaviour gone amuck, and their study suggests extreme caution for those studying brood parasitism in artificial nesting situations. The problems encountered in wood ducks are unlikely in cliff swallows. Present-day cliff swallow colonies in Nebraska that use bridges and culverts are similar in size, density and shape to colonies located on natural cliff sites in the same area. We have detected few differences of any kind between cliff swallow colonies located on man-made versus natural sites (Brown 1985; C. Brown, unpublished data). It is unlikely that we observed an inflated incidence of parasitism in our main study colonies (which were in culverts), and some of our data on inferred parasitisms did in fact come from colonies located on cliffs.

Andersson (1984) suggested that intraspecific brood parasitism is favoured in species with long laying seasons and marked asynchrony in nesting. Our results show that parasitism can also occur in highly seasonal, synchronous breeders. The degree to which synchrony affects opportunities for parasitism depends on how many eggs each parasite lays and when hosts are parasitized. If each parasite produces relatively few parasitic eggs and is able to place some of those eggs in host nests immediately prior to a host's laying or early during laying (as seems to be the case for cliff swallows), the parasite will then have the remainder of the colony's peak egg-laying period to parasitize additional hosts or lay in its own nest. A high degree of host nesting

synchrony thus does not necessarily drastically reduce a parasite's opportunities.

That host individuals might actively reduce their clutch sizes upon being parasitized was suggested by Brown (1984). If cliff swallows are indeterminate layers, parasitic eggs added to a host's nest early in laying could lead to a tactile-hormonal response (see Weidmann 1956) causing hosts to reduce their own egg output to achieve a normalized clutch inclusive of the parasitic egg. Hosts ultimately lay small clutches (Fig. 6). The other possibility is that parasites are able to assess in advance which females are likely to lay small clutches and preferentially parasitize those (Brown 1984). We have nothing new to report relevant to this, and the two alternatives remain possible. Experimentally adding eggs to a large sample of nests might resolve the issue.

Other than nest-guarding, cliff swallows do not exhibit any well-developed anti-parasitism defences. Egg removal prior to laying serves as an incidental parasitism preventive, but this may reflect more a tendency to simply remove any large foreign object in the nest. These birds often remove from their nests large chunks of dried mud, many the size of an egg, that break off during nest construction. Removal of foreign objects days prior to laying may be a manifestation of nest sanitation behaviour and not defence against parasitism per se. Cliff swallows are unable to recognize their own eggs (Brown 1984). Spot patterns of cliff swallow eggs could conceivably allow for individual recognition, and thus lack of egg recognition in these birds is surprising. Perhaps the dark interior of the domed-over nest makes visual discrimination of subtle differences in spotting unreliable. Hosts that nest during the peak of synchrony within a colony may stand a lower per caput chance of being parasitized (Fig. 5a). This is probably only an incidental effect of synchrony, however, and, given the relatively small anti-parasite advantage, it seems unlikely that reproductive synchrony evolved mainly in response to intraspecific brood parasitism. Lack of defensive measures against intraspecific brood parasites (other than nest-guarding) seems to be a general pattern in all species studied thus far (Lanier 1982; Emlen & Wrege 1986; Gibbons 1986; Møller 1987).

If host individuals have no evolved defences (or ineffective ones) against brood parasitism, then parasitism either does not represent an important cost to hosts or the cost is balanced by other

benefits. Hosts appear to pay a cost of almost one fledged offspring per nesting attempt, on average (Table I). This means a cost of one potential fledged offspring per year since cliff swallows usually raise only one brood each season.

Assuming that intraspecific brood parasitism is costly for hosts, this cost can be recouped directly by the hosts if they themselves resort to parasitism. At least 13 different females were known or suspected to be both parasites and hosts. We have been unable to measure the incremental gain in fitness to a parasite (i.e. number of fledged offspring) that results strictly from parasitic egg laying, but this gain could be enough to compensate a host who is also a parasite. The gain could be achieved either by a host parasitizing another nest during the same season it is parasitized or by parasitizing nests in subsequent seasons. Cliff swallows live for several years, and thus strategies available to an individual across seasons throughout its lifetime must be considered. Looked at slightly differently, the cost of being parasitized for a host can be balanced, evolutionarily, if parasites themselves are parasitized. Since there is a documented cost to being a parasite, incremental loss in fitness to a parasite resulting from the cost of parasitism could be enough to offset the parasite's incremental gain in fitness resulting from parasitism. This could equalize relative fitness between hosts and parasites. As a result, there might be little selection against being a host, explaining the lack of host defences.

Selection may not have favoured effective host defences in cliff swallows for two other reasons. First, advantages of colonial nesting (predator avoidance, social foraging via information centres) may be great enough to overcome the cost of parasitism to a colonially nesting host. The alternative of not nesting in a colony, even though parasitism would be unlikely, might be worse. Second, hosts and parasites may be related. Andersson (1984) emphasizes that under appropriate conditions of relatedness, brood parasitism among kin will be favoured for both host and parasite. Andersson's model was developed for ducks but is potentially applicable to any species. We are presently unable to evaluate the degree of relatedness among hosts and parasites in cliff swallows. Although we initially assumed low to no degrees of relatedness among colony residents, we have discovered that annual return rates of Nebraska cliff swallows to their natal areas are

relatively high for a migratory songbird (C. Brown, unpublished data). We are presently collecting long-term data to evaluate how often kin may settle near, and interact with, each other.

The most important conclusion arising from our study is that at least 22%, and perhaps as many as 43%, of all cliff swallow nests in southwestern Nebraska contain one or more eggs not belonging to the nest owners. Population biologists typically count offspring as a measure of reproductive success and use reproductive success to estimate fitness. If relatedness within families cannot be assumed, how much more difficult will it be to accurately measure individual fitness in natural populations?

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