

Selection of high-quality host nests by parasitic cliff swallows

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Abstract. Parasitic cliff swallows, *Hirundo pyrrhonota*, in southwestern Nebraska nest in dense colonies where an individual has many potential host nests it can parasitize. Parasites apparently assessed the nests around them and used nest age early in the season as a cue to select the more protected host nests. Swallows that parasitized nests later in the season, with a longer time to assess their neighbours, preferentially selected nests that were eventually successful at producing fledglings. Parasitic cliff swallows at all stages tended to select host nests that ultimately had the lowest infestations of deleterious, blood-sucking ectoparasites. This represents the first evidence that birds that parasitize conspecifics can make fine-scale assessment of a nest's quality and choose the better of the available nests in which to place their parasitic eggs.

Brood parasitism in birds has attracted considerable interest, and much of the research on interspecific brood parasitism has concerned the ability of host individuals to discriminate a parasite's eggs and take appropriate action to avoid being parasitized (e.g. Rothstein 1975; Robertson & Norman 1976; Payne 1977; Davies & Brooke 1988). Far less attention has been paid to how parasites select host nests that might maximize their expected gain (Mason 1986a, b; Orians et al. 1989), especially in conspecific brood parasites. Although increasing evidence suggests that conspecific brood parasitism is a relatively common reproductive tactic in some birds (e.g. Brown & Brown 1989; Power et al. 1989; Rohwer & Freeman 1989), many aspects of conspecific brood parasitism are still not understood including how host nests are selected by parasites. Do parasitic individuals choose randomly among the potential host nests that are available, or do they parasitize only a subset of the available hosts? If parasites are restricted to a subset of the potential hosts, are the host nests selected of superior quality? If parasites are restricted to parasitizing only inferior host nests (ones often unattended by their owners or ones otherwise likely to fail), conspecific brood parasitism may be a relatively unsuccessful behaviour pattern for most individuals. On the other hand, if parasites are able to identify and successfully parasitize nests that are attended by high-quality owners or nests located in particularly safe sites, brood parasitism may lead to large fitness payoffs for a parasite. Answers to

these questions are essential before we can understand the evolution of conspecific brood parasitism and why some individuals engage in it. To our knowledge, this paper is the first to address whether individuals that parasitize conspecifics assess potential hosts and actively select among those that are available.

Conspecific brood parasitism occurs commonly in colonial cliff swallows, *Hirundo pyrrhonota* (Brown & Brown 1989). These birds nest in dense colonies where there are many host nests that could potentially be parasitized by an individual. Swallow colonies thus provide natural 'choice experiments' on which hosts are preferred by parasites. In this paper we ask whether parasites choose host nests randomly and if nests are not chosen randomly, what cues parasites use to choose among host nests. Specifically, we examined whether nest age, nest success, ectoparasite load or parental quality are associated with nest selection by parasitic individuals.

STUDY ANIMAL AND STUDY SITE

Cliff swallows are small migratory passerines that nest in colonies throughout much of western North America. They 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 South American

winter range. The birds build gourd-shaped nests out of mud pellets that are attached underneath overhanging rock ledges on the sides of cliffs and canyons, and in some areas underneath the eaves of bridges, buildings, highway culverts and other artificial structures. Cliff swallows 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 are highly social in all of their activities; they feed, preen, gather mud and migrate in large groups (Emlen 1952; Brown 1985). The birds are usually single-brooded. In our study area haematophagous nest ectoparasites, principally a swallow bug, *Oeciacus vicarius* (Cimicidae), and a bird flea, *Ceratophyllus celsus* (Ceratophyllidae), feed on nestlings and retard growth, usually killing the nestlings whenever a nest or colony is heavily infested (Brown & Brown 1986).

This study, part of continuing 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, 1982–1989. Cliff swallows are abundant in this area, and have probably increased in recent years with the construction of artificial nesting structures such as highway culverts and bridges. 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 1982–1989, there were 401 colonies of cliff swallows in or near the study area in Keith, Garden and Lincoln counties (Brown 1985). Colony size ranged from two to approximately 3500 nests ($\bar{X} \pm SD = 381 \pm 619$ nests); birds also nested solitarily.

METHODS

Natural History of Brood Parasitism

Brood parasitism among cliff swallows at our study site occurs in two ways: a parasite will (1) furtively enter a nest and lay an egg there (Brown 1984; Brown & Brown 1989) or (2) physically transfer an egg in its beak from its own nest to that of a neighbour (Brown & Brown 1988). Studies of colour-marked birds show that parasitic individuals maintain nests of their own within a colony (where they raise some offspring themselves) and tend to parasitize only those nests within about a

five-nest radius of their own (Brown & Brown 1989). Nests are parasitized when left unattended momentarily. Parasitic egg laying occurs relatively early in the nesting season when many birds begin synchronously laying their eggs, sometimes less than 2 weeks after a colony site is first occupied in the spring. In contrast, physical transfer of eggs occurs on average 10 days later, after incubation in a host nest has begun (Brown & Brown 1988, 1989).

Detecting Brood Parasitism

We have detected brood parasitism in cliff swallows both by directly observing birds parasitizing nests and by indirectly inferring parasitism based on when eggs appear in nests (Brown & Brown 1988, 1989). In this paper we use only inferred parasitisms. Criteria for determining that a nest had been parasitized via egg laying were the appearance of more than one egg per day during laying or the appearance of a single egg in a nest 3 or more days before additional eggs appeared. The criterion for inferring that a nest had been parasitized via egg transfer was the appearance in a nest after incubation began of an egg that hatched at the same time as the rest of the clutch. These criteria are discussed more fully and justified in Brown & Brown (1988, 1989).

Defining Potential Host Nests

To study the preferences of parasites for different host nests, we first had to define which nests were potentially available to a parasite. A nest where parasitism has not been observed cannot automatically be assumed to have been rejected by a parasite. It may be that no parasite lived near enough to it to choose it. Thus, we designated 'spheres of choice' as the areas surrounding nests where parasitism was known to have occurred (Fig. 1). All non-parasitized nests within a five-nest radius of a parasitized nest were assumed to have been available to the parasite but not chosen. We also assumed that a sphere centred on the host nest was the same sphere that the parasite chose from and that the parasite itself lived within five nests of the nest it parasitized. These assumptions seem justified because in 67% of cases where a colour-marked parasite was observed to parasitize a neighbour ($N=27$), the parasite and host either lived in adjacent nests or were separated by only

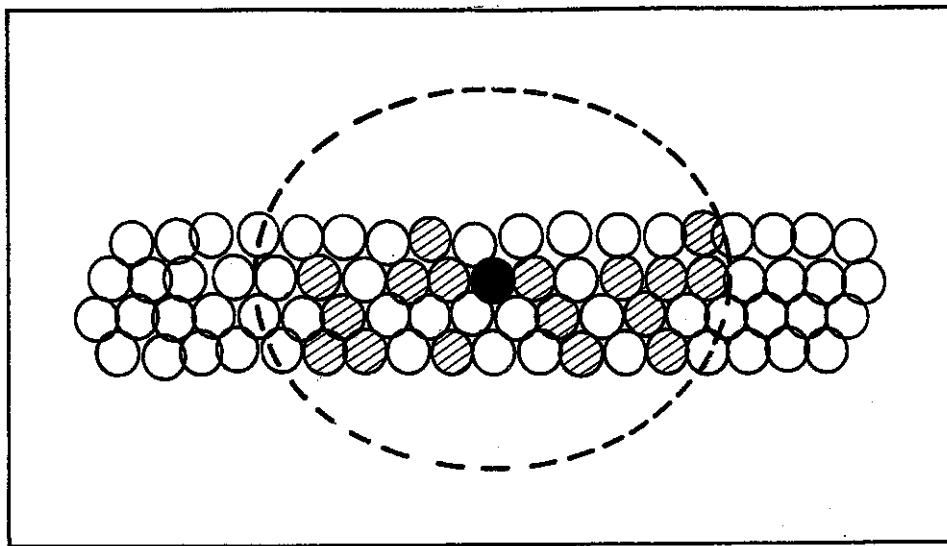


Figure 1. Schematic illustration of a hypothetical sphere of choice surrounding a parasitized cliff swallow nest. The sphere, denoted by a dashed line, contains all nests within a five-nest radius of the parasitized nest (●). Nests within the sphere that were suitable for parasitism based on time of egg laying are shown by ⊗.

one nest. Most of the remaining cases involved birds living within five nests of each other (Brown & Brown 1989).

Within each sphere of choice, only certain nests were at an appropriate stage in the nesting cycle to be parasitized. We assumed that any nest in a sphere was temporally available to a parasite if eggs began to be laid in it between 4 days before and 4 days after eggs began to be laid in the parasitized nest. This period was based on the window of time between when colour-marked parasites were known to lay in a given host nest and when that host (or by analogy another simultaneously available, potential host) laid its first egg (Fig. 3 in Brown & Brown 1989). Defining available nests as only those where birds actually started egg-laying during at most a 9-day interval removed any major effect of degree of nest completion or date on each within-sphere analysis. This definition also meant that the laying dates of parasites and potential hosts overlapped substantially; non-overlap in laying dates can bias conclusions about the choices of parasites (Orians et al. 1989). Spheres often represented a spatial mosaic of temporally suitable and unsuitable nests from which a parasite chose (Fig. 1).

If the value of a given variable (nest age, nest success, ectoparasite load or nestling body mass) was the same for all nests in a particular sphere, that sphere was excluded from our analysis of that variable. We did this because we would not be able to attribute a parasite's choice of nest within such a sphere to a difference in the given variable. (The

percentages of parasitized nests occurring in such spheres are reported in the Results.)

We defined old cliff swallow nests as those which when first occupied in a given year were at least half-built and new nests as those that were newly built or less than half-built when first occupied. A successful nest was one in which nestlings survived to 10 days after hatching (Brown & Brown 1987). Most cliff swallow nestling mortality occurs during the first 10 days.

Calculating Expected Frequencies

Analyses of nest age and nest success required calculation of the expected frequencies of these types of nests if parasitic cliff swallows chose nests strictly according to their availability within spheres. The total number of nests available and the proportion of nests of each type in each sphere varied. Expected frequencies were calculated by combining the proportions of all old and new nests, or all successful and unsuccessful nests, respectively (including the parasitized nest), in each sphere across all spheres. The use of proportions controlled for differences among spheres in the number and type of nest available, and was necessary because each sphere by definition could contain only one nest (the parasitized one) in the 'observed' category regardless of the total number of nests in the sphere. Summing these proportions gave the total number of nests of each type expected based solely on their availability, as illustrated by the example in Table I.

Table I. Example of how expected frequencies were calculated for five spheres of choice containing different numbers of old and new cliff swallow nests

Sphere	Total nests	No. old nests	No. new nests	Proportion of	
				Old	New
1	10	5	5	0.5	0.5
2	15	10	5	0.67	0.33
3	20	12	8	0.6	0.4
4	2	1	1	0.5	0.5
5	36	30	6	0.83	0.17
Expected number =				3.1	1.9
Observed number =				5	0

Ranking Nests

We ranked all nests in each sphere of choice according to the extent of their ectoparasite infestations during the nestling period. We removed all nestlings from their nests at day 10 (Brown & Brown 1986) and counted the numbers of fleas and swallow bugs present on the bodies of the nestlings as our measure of ectoparasite load. The rank of each nest was based on the average number of fleas and bugs present on its nestlings. Each parasitized nest that occurred in a sphere with at least four potential host nests with differing ectoparasite loads was ranked among the non-parasitized nests in that sphere, and the ranks of the parasitized nests were assigned to the appropriate quartile. Brood size did not significantly affect the average number of ectoparasites per nestling per nest (Spearman rank correlations, $P > 0.05$), so all nests were used regardless of brood size. In ranking nests, ties occurred infrequently because, as noted above, we analysed only those spheres that contained nests that exhibited variation in ectoparasite loads. Where ties occurred, each tied nest was given the higher rank (rather than the average of the tied ranks). Using the higher rank for each tied nest was deemed biologically most appropriate, because the ranks reflected only the relative suitability of nests. The absolute differences in ectoparasite load among nests of different ranks within a sphere varied enormously across spheres, and are not presented here. The magnitudes of the ectoparasite loads in nests that were unavailable to any given parasitic swallow were considered irrelevant. What mattered were the loads of the relatively few nests available to each parasite within its own sphere.

For ranking of nestling body masses, we used nests that had been fumigated with a short-lived insecticide to remove all ectoparasites (Brown & Brown 1986). Fumigation was completely effective against swallow bugs, which cause the greatest deleterious effects on nestling cliff swallows (Brown & Brown 1986). Fumigant was applied to nests every 2–3 days throughout the nesting season (for further details on fumigation see Brown & Brown 1986). Nestlings were weighed with a Pesola scale at 10 days of age. Average nestling body mass per nest was ranked for all nests containing broods of the same size as the parasitized nest within a sphere; only spheres with at least four suitable host nests with identical brood sizes were used. Each nest within a sphere was assigned to the appropriate quartile rank.

Because our analyses of both ectoparasite load and nestling body mass were based on relative ranks within each sphere, ranks across spheres were comparable and could be combined for statistical treatment.

RESULTS AND DISCUSSION

Host Selection Based on Nest Age

One important cause of cliff swallow nest failure is the falling of nests, usually a result of rain, wind or wave action. Nests in protected sites within colonies can remain for several years and be re-used. In colonies without enough old nests, birds often begin building new nests in less protected sites where the nests are more likely to fall soon after being built or to be deserted after sustaining structural damage (unpublished data). Thus, one cue as to a nest's stability and the odds of it surviving the elements is whether it is an old or new nest. If a parasite is to maximize the chances that the nest it chooses to parasitize is in a safe site and is likely to withstand the elements, early in the season it should choose an old nest.

Birds that parasitized nests by egg laying chose old nests at a higher frequency than that expected by random choice (Table II). However, birds that parasitized nests by transferring eggs did not show such a preference (Table II). Parasites that transferred eggs probably did not need to use nest age in assessing the nests of neighbours, at least in terms of structural stability, because any new nest still in existence at that stage had already lasted for approximately half of the nesting cycle. In this

Table II. Observed number of old and new nests and successful and unsuccessful nests selected by cliff swallows that parasitized nests by egg-laying (EL) and physical egg transfer (ET), versus the expected number selected if nests were randomly chosen within the pool of nests available to each parasite

Nest selected	Number of nests	
	Observed	Expected*
Old, EL	144	122
New, EL	78	100
	$G = 8.99, P < 0.01$	
Old, ET	79	79
New, ET	64	64
	$G = 0.00, NS$	
Successful, EL	162	163
Unsuccessful, EL	65	64
	$G = 0.02, NS$	
Successful, ET	178	159
Unsuccessful, ET	45	64
	$G = 8.48, P < 0.01$	

*See text and Table I for method of calculating expected frequencies.

analysis we used only parasitized nests that occurred in spheres where the parasite had a choice in nest type, i.e. at least one old and new nest were present. Combining both categories of parasitism, 382 of 747 parasitized nests (51%) occurred in spheres where the parasite had no choice of nest type among the nests available within the sphere.

Host Selection Based on Nest Success

Host nests that were later to be successful at producing at least one fledgling were not chosen by egg-laying parasites more often than expected by random choice (Table II). It may be difficult to predict a host's eventual success at such an early stage in the nesting season. Egg-laying parasites tended to choose nests that were safer in terms of structural stability (i.e. old nests), and so other factors (predation, nestling starvation or ectoparasitism) probably accounted for the differences in nesting success within the spheres of egg-laying parasites. Since egg-laying parasites realized no apparent advantage in nest survivorship by choosing old nests (Table II), the parasites' preference for old nests may not be based on structural stability, but perhaps instead on the quality of the host individuals occupying old nests. Owners of old nests

did not have to spend as much time building nests, and occupancy of an old nest could indicate that individuals are capable of successfully competing for resources and thus might be good parents for parasitic offspring (but see later section on parental quality).

However, egg-transferring parasites preferentially chose host nests that were later successful (Table II). Egg transferrers tended to identify and succeeded in parasitizing those host nests within their sphere that were least likely to fall victim to predation, nestling starvation or ectoparasitism (see next section). In this analysis, we used only parasitized nests that occurred in spheres where the parasite had a choice in nest success. Combining both categories of parasitism, 236 of 576 parasitized nests that were later successful (41%) occurred in spheres where the parasite had no choice; 50 of 160 parasitized nests that were later unsuccessful (31%) occurred in spheres where the parasite had no choice. For egg-transfer parasitisms, nests that had failed prior to the transfer and were thus unavailable to be parasitized were excluded from the analysis.

Host Selection Based on Ectoparasite Load

Among the cliff swallow nests that survive long enough for eggs to hatch, the major source of nestling mortality is loss of nestlings to haematophagous ectoparasites. We examined the ectoparasite loads for all nests that survived to the 10th day after hatching to determine whether brood-parasites discriminated among potential host nests in their propensity to be infested by ectoparasites. If a brood-parasite is able to predict ectoparasite load among host nests and select a less infested one, the chances of its offspring surviving and fledging at a higher body mass (Brown & Brown 1986) are much improved. Extensive variation in ectoparasite load among nests within spheres occurs in Nebraska, although the reasons for this variation are not yet understood (C. Brown & P. Walsh, unpublished data). This analysis examines only nests surviving to day 10 because we had no non-destructive way of measuring ectoparasite load in nests that failed prior to day 10.

Nests that were chosen by both egg-laying and egg-transferring parasites ranked lower in ectoparasite load (both fleas and bugs) than expected if birds chose host nests at random (Fig. 2). This analysis includes only parasitized nests that

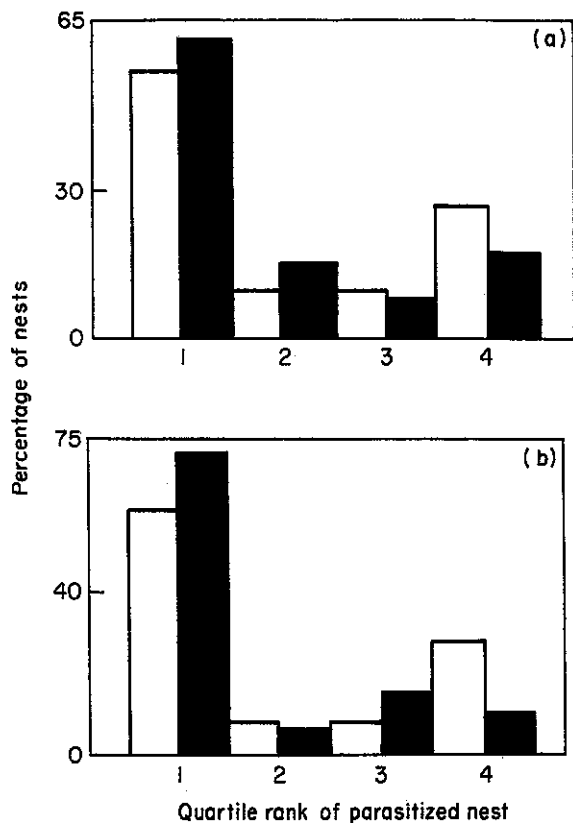


Figure 2. Percentage distribution of cliff swallow nests parasitized by conspecific egg laying (\square) and physical egg transfer (\blacksquare) versus their rank among all suitable nests for extent of flea infestation (a) and swallow bug infestation (b). The nest with the least number of ectoparasites in a sphere ranked 1. Sample sizes for (a) were 86 nests with parasitic egg laying and 66 with egg transfer; for (b), 26 nests with egg laying and 21 nests with egg transfer. Parasitized nests ranked significantly lower in fleas per nestling ($G=22.49$ for nests with egg laying, $G=39.97$ for nests with egg transfer, each $P<0.001$) and in bugs per nestling ($G=16.70$ for nests with egg laying, $G=20.96$ for nests with egg transfer, each $P<0.001$) than would be expected from random choice of host nests.

occurred in spheres where the parasite had a choice of at least four nests with differing flea or bug loads. A minimum of four nests was needed for quartile ranking. Combining both categories of parasitism, 152 of 345 parasitized nests (44%) occurred in spheres where flea loads among all nests were the same; 32 of 98 (33%) occurred in spheres where bug loads among all nests were the same.

When confronted with a choice of host nests, parasitic swallows chose the least infested host in 59% of instances ($N=199$ nests). In all cases where the parasitized nest ranked in the first quartile, the parasitized nest had the lowest absolute rank, meaning the nest chosen was the least infested of all the nests available. The advantage of having offspring in uninfested nests is that the young fledge

in much better condition and their post-fledging survival is probably enhanced (Brown & Brown 1986).

These results show that parasitic cliff swallows are able in many cases to predict the eventual extent of ectoparasitism among potential host nests and select the best nest to parasitize. However, the birds are not always accurate: of the total of 199 parasitized nests (Fig. 2), 14% ranked the absolute highest in degree of infestation within their sphere, suggesting that the swallows that chose those nests had made the worst possible choice. Nevertheless, the birds' ability to assess a nest's propensity later to become infested with ectoparasites is remarkable, because ectoparasites are not active or obvious (at least to humans) on the nests early in the season. The similarity in the patterns for fleas and bugs (Fig. 2) could result from flea and bug loads being correlated. If this were the case, the birds could be making a choice primarily on the basis of 'fleas' or 'bugs', not necessarily on both. However, there was no significant correlation between the flea ranks of parasitized nests and the bug ranks of the same nests (Pearson correlation = 0.206, $P>0.05$, $N=58$). Nests with low flea ranks did not always have low bug ranks, and vice versa, suggesting that the birds might be discriminating on the basis of both types of ectoparasites. The deleterious effects of swallow bugs are well documented (Brown & Brown 1986), and the apparent importance of flea presence in the birds' selection of nests suggests that fleas may have a greater effect on cliff swallows than previously thought.

Host Selection Based on Parental Quality

Parasitic swallows also may use characteristics of the host individuals themselves, rather than the nests per se, as a basis for choosing host nests. Individual host quality could influence the eventual success of a nest (Table II); for example, good quality hosts are probably competent foragers and can provide their nestlings with sufficient food to prevent starvation. Host quality may even provide cues as to propensity to be infested by ectoparasites (Hamilton & Zuk 1982).

It is difficult to measure host quality independently of nest site or ectoparasite load directly, so we used an indirect measure. We examined average nestling body mass of 10-day-old nestlings as an indication of parental foraging efficiency (Hoogland & Sherman 1976; Snapp 1976; Brown

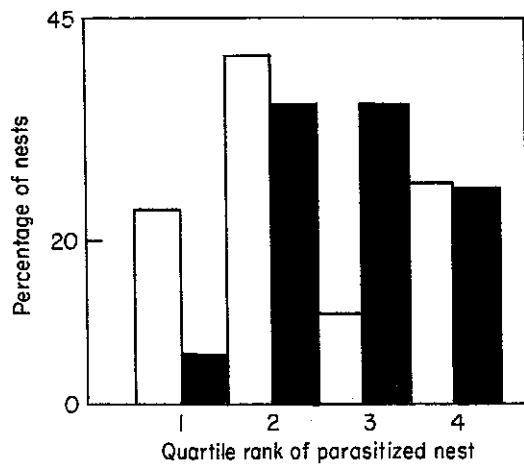


Figure 3. Percentage distribution of cliff swallow nests parasitized by conspecific egg laying (□) and physical egg transfer (■) versus their rank among all suitable nests with the same brood size for average nestling body mass in fumigated colonies. The nest with the highest average nestling body mass in a sphere ranked 1. Sample sizes were 20 nests with parasitic egg laying and 39 with egg transfer. Parasitized nests did not rank significantly higher or lower ($G = 6.20$ for nests with egg laying, $P > 0.05$; $G = 7.79$ for nests with egg transfer, $P = 0.05$) than would be expected from random choice of host nests.

1988). By using only fumigated nests in this analysis, we removed the effects of ectoparasites. We assume that nestling body masses in these nests mainly reflect parental foraging efficiency (Brown 1988).

We ranked average nestling body mass of 10-day-old nestlings from all potential host nests with the same brood size as the parasitized nest within each sphere in fumigated colonies (Fig. 3). In the absence of ectoparasitism, there was no significant difference between the ranks of nestling body mass between brood-parasitized and non-parasitized nests (Fig. 3). This suggests that parasites either do not choose hosts on the basis of inherent parental quality or that nestling body mass is a poor index of host quality. We have not identified any other host characteristics (independent of the nest site itself) upon which parasitic swallows are known to base their choices, but the matter requires further investigation.

Host Selection by Egg-laying versus Egg-transferring Parasites

Because physical transfer of eggs into host nests that have already begun incubation occurs on average 10 days later than parasitism by egg laying, parasitic cliff swallows who transfer eggs have a

longer time in which to assess the nests available within their sphere of choice than parasites who lay eggs at the start of the nesting season. We predicted that egg-transferring parasites should exercise 'better' choice of hosts than egg-laying parasites, because egg transferers presumably have better information on which to base their choice.

Egg-transferring parasites tended to choose host nests that were eventually successful, whereas egg-laying parasites did not (Table II). Apparently, egg-transferers, with more time to assess hosts, tended to predict which host nests within their sphere were most likely to rear offspring successfully and succeeded in parasitizing those. Similarly, the ability of egg-transferring parasites to choose the least infested host nest was better than that of egg-laying parasites. The proportion of the lowest rank (the best nests) was higher and the proportion of the highest rank (the worst nests) was lower for parasites that transferred eggs (Fig. 2), although the differences were not significant (flea ranks: $\chi^2 = 3.14$; bug ranks: $\chi^2 = 2.81$; each, $df = 3$ and $P > 0.05$). Waiting to transfer eggs during incubation may be advantageous in giving the parasite additional time to assess hosts and choose the better one(s).

Assessment of Hosts and Other Issues

The principal unanswered question is how parasitic cliff swallows assess their neighbours. Nest age would seem to be the only obvious cue that individuals can use, especially because choices are made before ectoparasites become numerous in most nests. Swallow bugs and fleas begin reproduction in a colony as soon as it is occupied (Hopla & Loye 1983; Loye & Hopla 1983), but their numbers remain relatively low for several weeks and the effects of swallow bugs are most pronounced on late-nesting swallows (Brown & Brown 1986). Brood-parasites may rely on more subtle cues for host assessment that we have as yet been unable to identify. Individuals frequently attempt to intrude into neighbouring nests throughout the nest-building and egg-laying periods and it is probably during these intrusions that host assessment occurs (Brown & Brown 1989). Exploring the nests of close neighbours may be analogous to assessment of territories in cooperatively breeding birds that remain on their natal territory and watch for vacancies on nearby high-quality territories (Zack & Rabenold 1989).

Given the tenacity and intensity with which cliff swallows guard their nests to prevent parasitic egg laying or transfer (Brown & Brown 1989), the ability of the parasites to exercise their choice in nest to be parasitized is remarkable. Intense nest guarding by nest owners probably prevents some parasites from gaining access to the best host nest, and may account for many of the instances in which parasites chose poorer host nests.

These results suggest that parasitic cliff swallows in many instances can make fine-scale choices of the best possible nest to parasitize. This ability to assess potential hosts is apparently more sophisticated than has been reported in any other conspecifically brood-parasitic species to date, and may equal or exceed the ability of interspecific parasites to assess and choose their hosts. An interspecific parasite that may come the closest to this ability is the European cuckoo, *Cuculus canorus*, in which egg colour of parasites matches that of the most commonly parasitized host species within a population (Davies & Brooke 1988; Brooke & Davies 1988). However, it is not known whether individual cuckoos assess the available hosts and actively choose the ones in which their own eggs will match the host eggs (and thus choose the host nest in which their expected reproductive success is highest), because no 'choice experiments' have been performed with parasitic cuckoos to our knowledge. Egg mimicry generally seems to reflect discrimination by hosts against non-matching eggs (Davies & Brooke 1988; Brooke & Davies 1988) and not necessarily a behavioural preference by parasites for the 'correct' colour. Orians et al. (1989) examined whether interspecifically parasitic brown-headed cowbirds, *Molothrus ater*, laid their eggs randomly among host nests, and found no evidence for active selection or avoidance of hosts, at least as measured in terms of the number of cowbird eggs laid per nest.

Cliff swallows select host nests non-randomly (Table II, Fig. 2). The fact that they can apparently select superior host nests in many cases is further evidence that conspecific brood parasitism in this species is a sophisticated behavioural strategy resulting in fitness payoffs for the parasites, and not the maladaptive or pathological behaviour that has been observed in some species (Semel & Sherman 1986). By adding eggs to nests of high-quality neighbours, parasites gain by increasing the probability of having at least one offspring in a successful nest (in the case of egg-transferring

parasites; Table II) and having those offspring fledge in relatively good, ectoparasite-free condition (for all parasites; Fig. 2). This ability to discriminate among hosts augments the potential advantages of parasitism (e.g. risk-spreading, reduction in parental care; Brown & Brown 1989) but does not itself explain why conspecific brood parasitism occurs in the first place.

Our information on the actual identities of parasitic individuals is confined to less than 30 colour-marked birds that were directly observed parasitizing nests (Brown 1984; Brown & Brown 1989). Using inferred parasitisms and designating spheres of choice was necessary to achieve adequate sample sizes for the analyses reported here, but inferred parasitisms never permit assignment of unequivocal identities to parasites. We know only that it is likely that the parasite lived within the hypothetical sphere. Thus, we are unable to address the question of to what degree average annual reproductive success of known parasites is affected by selection of high-quality host nests. It would seem almost certain that it is enhanced to some degree.

An equally interesting but unresolved issue is whether parasites are individuals who either 'discover' that they have occupied a nest that is soon to be infested with ectoparasites or 'know' that their odds of fledging offspring are low. It seems reasonable that parasites could assess themselves and their own nests as easily as they can assess their neighbours. If so, conspecific brood parasitism may be a reproductive tactic employed only by a subset of the population, which could help explain the apparent variability in the incidence of parasitism between and within cliff swallow colonies (Brown & Brown 1989). This can only be tested by identifying large numbers of known parasites, and no feasible methods presently exist by which this can be done.

By selecting high-quality host nests, parasitic cliff swallows seem to be able to capitalize on the inevitable differences between individuals in either their capacity to hold critical resources (ectoparasite-free nests) or to be successful parents. As a result, parasitic individuals may be at an evolutionary advantage over non-parasitic individuals. Therefore, two further important unanswered questions are why brood parasitism is not more common in cliff swallows and perhaps other birds, and why parental care persists at all in the parasitic individuals. Although we are still unable to measure fitness in parasitic cliff swallows, their

ability to select the better hosts suggests that obligate brood-parasites that do not maintain nests of their own might have as high or higher reproductive success than non-parasites.

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