Laying Eggs in a Neighbor's Nest: Benefit and Cost of Colonial Nesting in Swallows

Abstract. *Intraspecific brood parasitism (laying eggs in another's nest) occurs widely in colonial cliff swallows (Passeriformes: Hirundinidae:* Hirundo pyrrhonota*). In colonies consisting of more than ten nests, up to 24 percent of the nests were sometimes parasitized by colony members. Laying eggs in a conspecific's nest may be a benefit of coloniality for parasitic individuals and simultaneously may represent a cost to host individuals within the same colony.*

Some animals routinely breed by laying eggs in nests not their own. Most often these species parasitize the reproductive effort of other species (*1–4*), but individuals might also parasitize nests of conspecifics. That intraspecific brood parasitism should be most common in colonies of densely nesting organisms because a parasite's chances of locating a suitable host improve dramatically with increased numbers and proximities of synchronously nesting neighbors has been argued (*5*). Although intraspecific brood parasitism has been searched for in colonial species (*6*), it has been reported only for certain noncolonial birds, particularly waterfowl (*7–10*), and for an insect (*11*). In these species it apparently occurs only occasionally and is difficult to investigate without large samples of marked individuals. Thus, the extent and selective importance of intraspecific brood parasitism remain unknown (*12*). I now report the occurrence of prevalent intraspecific brood parasitism in a colonial animal, the cliff swallow (*Hirundo pyrrhonota*), and suggest that this phenomenon may be a benefit of coloniality to some individuals and a cost to others.

Table 1. Number of eggs laid and number of young fledged for parasitized and unparasitized cliff swallow nests in a Nebraska colony, 1983. Success of host nests in which two eggs appeared in 1 day and of host nests where parasites were observed was significantly less ($P < 0.05$, Mann-Whitney U test) than the success of nests not known to have been parasitized.

Number of eggs laid			Number of young fledged		
$\bar{x}$	S.D.	*N*	$\bar{x}$	S.D.	*N*
*Nests not known to have been parasitized**					
3.6	0.7	156	3.0	1.2	155
Host nests where two eggs appeared in 1 day†					
3.0	1.5	20	2.3	1.0	20
Host nest where the act of parasitism was observed†					
2.8	0.9	6	2.7	0.5	6
Nests of known parasites					
4.0	0.0	4	3.3	0.5	4

*Includes only those initiated before the date of the last parasitism in the colony, because late-starting nests suffer heavy nestling mortality attributed to cimicid bugs. †Does not include parasitic eggs or parasitic nestlings.

At the study site in Keith County, southwestern Nebraska, the cliff swallow nests in colonies ranging in size from one to more than 3000 nests (mean colony size, 275; $N = 62$). The large colonies are among the largest and most dense aggregations known for any land vertebrates in North America. The swallows build gourd-shaped nests out of mud and place them in clusters under the eaves of bridges, buildings, and culverts and on natural cliff faces. Cliff swallows arrive in southwestern Nebraska in early May, begin egg-laying in late May, and usually fledge their young by mid-July. Breeding within each colony is highly synchronous. Evidence of close relatedness among nesting adults within each colony is lacking (*13*).

During a 1982–1983 study of the benefits and costs of sociality in cliff swallows, two kinds of evidence for widespread intraspecific brood parasitism in these birds were found. Daily examination of the pattern and timing of egg deposits in more than 700 nests at 17 colonies (*14*) revealed that in many instances more than one egg per day appeared in a clutch (Fig. 1). Since no species of bird is known to lay more than one egg in less than 24 hours (*15, 16*), this observation implied that the presence of two or more eggs in a nest per day could be attributed to two or more females laying eggs in the same nest (*17*).

This indication of parasitism was confirmed by direct observation in 1983. A 190-nest cliff swallow colony was observed intensively throughout the period of egg-laying, with particular attention being directed to a subsample of 30 nests. Approximately three-fourths of the nest owners in the sample were individually color-marked before egg-laying (*18*). We observed five cases in which known, marked individuals entered neighboring nests and laid single eggs while the owners were away (*19*). One individual was responsible for two of these parasitisms. All five parasitisms were perpetrated by females that also had clutches of their own (Table 1) (*20*). No behavioral or morphological differences seemed to exist between host and parasitic females. All of the host and parasite nests were within 2.1 m of each other in the colony and were separated by, at most, a ten-nest distance. A sixth parasitism occurred when two eggs appeared in one of the sample nests within a 29-minute period, but the parasitizing individual escaped detection. The parasites all laid eggs within 60 seconds of entering the host's nest; this speed of laying is similar to that reported for some interspecific brood parasites (*1, 16*). One parasite was able to lay an egg in 15 seconds while the nest owner was present but fighting another intruding conspecific in the nest entrance. Cliff swallows are monogamous, and all host and parasitic females had their own mates (*21*).

Both the host nests in which parasitisms were observed and those in which parasitisms were inferred were less successful than nests not known to have been parasitized in the 1983 colony (Table 1). Lower success was due largely to smaller clutches being laid by the hosts. Possibly the parasites selected hosts that had smaller clutches to minimize competition among host and parasitic nestlings, but in most cases parasites must somehow have selected these hosts before the hosts had completed laying. This would require subtle assessment by parasites of hosts' future fecundities. It is perhaps more likely that the addition of a parasite's egg during a host's egg-laying period mimicked completion of a clutch and resulted in a tactile-hormonal response leading to cessation of laying by the host (*16, 22*). Nonetheless, parasitisms seemed to depress host fitness (Table 1) and, if so, could represent an important cost of colonial breeding to host individuals (*23*).

The parasites benefited by parasitizing other nests in the colony. The parasites all fledged offspring from their own nests (Table 1); in addition, all eggs identified

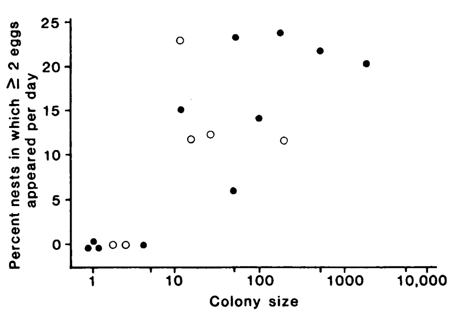

Fig. 1. Percent nests in which ≥ 2 eggs appeared per day versus colony size for 17 Nebraska cliff swallow colonies. Two or more eggs laid per day were interpreted as evidence of intraspecific brood parasitism. Colonies studied in 1982 are shown with a closed circle; those in 1983 with an open circle.

as belonging to a parasite hatched, and the nestlings were raised by the hosts. The parasites increased their expected reproductive output for the year by one to two offspring.

There was an overall increase in parasitism as a function of colony size ($r_s = 0.75$, $P < 0.001$), but there was no correlation between colony size and the percentage of nests parasitized for colonies consisting of more than ten nests ($r_s = 0.17$, $P > 0.05$) (Fig. 1). Thus, the chances of an individual being parasitized in all colonies of more than ten nests may be constant. The cost of intraspecific brood parasitism may therefore influence only whether or not birds choose very small colonies (*24*). The effect of increasing colony size to more than ten nests on the success of parasites is not clear.

Other evidence suggests (i) that intraspecific brood parasitism in cliff swallows involves two related adaptations on the part of the parasites and (ii) that it is even more prevalent than these data indicate. Eggs from presumed parasites occasionally appeared in host nests several days after the hosts had begun incubation, yet the parasites' eggs hatched at the same time as the hosts' eggs ($N = 6$) (*25*). This implies that eggs belonging to parasites may require less incubation time than host eggs, an adaptation reported for interspecific parasites (*1*, *3*). Furthermore, cliff swallows tried continually to enter neighboring nests in the colony. When owners were away, intruders tossed out single eggs (*26*). These egg displacements may have been perpetrated by parasites that subsequently replaced the tossed eggs with eggs of their own. If parasites removed eggs and replaced them, the daily nest checks (Fig. 1) underestimated the frequency of brood parasitism. Extensive and continuous observations of marked individuals within a colony, coupled with electrophoretic parental exclusion analyses, are needed to evaluate further the prevalence of this reproductive strategy in the cliff swallow.

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14. All nest examinations were made at 0800, approximately 2.5 hours after sunrise or later, after all nest owners had laid their eggs for the day. Cliff swallows lay in the early morning each day, as do other swallows [R. W. Allen and M. M. Nice, *Am. Midl. Nat.* **47**, 606 (1952)]. In 1983 nests at one colony were checked at 1-hour or less intervals throughout several days; only two eggs (1.1 percent, $N = 168$) deposited by owners after 0800 were found. Thus, irregularities observed in laying were unlikely to have been caused by variations in owners' laying times [see (*6*)].
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17. Irregular laying patterns have been used to infer occasional intraspecific brood parasitism [T. E. Morse and H. M. Wight, *J. Wildl. Manage.* **33**, 284 (1969); Y. Yom-Tov, *Ibis* **122**, 234 (1980); M. O. G. Eriksson and M. Andersson, *Bird Study* **29**, 49 (1982); M. S. Dhindsa, *Notornis* **30**, 87 (1983)].
18. Swallows were mist-netted and their white forehead patches colored in distinctive combinations with UniPaint and Decocolor paint marking pens. Marked birds did not appear to behave differently from unmarked birds, nor did other birds seem to react to them in any unusual ways. Sexes of birds were inferred from later copulation attempts and from observing birds parasitizing nests.
19. Nests were examined whenever owners left them unattended and whenever neighbors entered and then exited unattended nests after remaining inside for longer than 10 seconds. In this way any eggs appearing in an unattended nest after a neighbor had entered were verified to have been laid by the neighbor and not the owner. Nest examinations were made with a dental mirror and flashlight within 30 seconds, and disturbances to the colony during the examinations were minimal.
20. One female parasitized a nest 3 days before she began laying eggs in her own nest. Two females parasitized nests on the day after they had completed laying eggs in their own nests. The remaining female parasitized one nest on the day after her own clutch was completed and parasitized a second nest between laying the second and third eggs in her own nest. On that day she did not lay any eggs in her own nest. She also skipped a day between laying her first and second eggs and may have parasitized yet another nest on that day undetected. This same female later lost an egg in her own nest when the owner of the nest immediately adjacent entered her nest and tossed out an egg while she was absent [see (*26*)]. These parasitic females' own clutches did not seem to be parasitized in turn by other birds.
21. In contrast to bank swallows (*Riparia riparia*) [M. D. Beecher and I. M. Beecher, *Science* **205**, 1282 (1979)] and purple martins (*Progne subis*) [C. R. Brown, *Auk* **92**, 602 (1975)], promiscuity and polygyny are apparently rare among male cliff swallows that maintain nests in a colony. Females that mated with or were fertilized by the same male were not observed to lay eggs in the same nest.
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23. If brood parasitism is a significant cost, one might find host defenses that would minimize it, the most obvious defense being intraspecific egg recognition. However, in a series of 12 egg transfer experiments, no egg discrimination abilities were detected in cliff swallows. Eggs transferred from other nests remained in host nests until hatching in all cases. Possibly cliff swallows have evolved other defenses, such as nearly constant nest guarding by one or both members of a pair during the egg-laying period (inasmuch as parasitisms usually occurred only when a nest was left unattended).
24. My ongoing research suggests that benefits associated with social facilitation of foraging and, secondarily, benefits associated with predator avoidance increase with colony size up to sizes of at least 1600 nests. Costs associated with buildups of cimicid bugs also tend to increase with colony size. The benefits and costs attendant on foraging and ectoparasites may be the most important influence on the birds' choice of colony size.
25. C. R. Brown, unpublished data.
26. Swallows were observed destroying neighbors' eggs. Egg destruction increased with colony size ($r_s = 0.81$). In a colony of 1600 nests, 13 percent suffered losses attributed to conspecifics. However, incidents of an egg destruction and a parasitism in the same nest by the same individual at the same time were not seen.
27. I thank Mary Bomberger, Karen Brown, Laura Jackson, and Todd Scarlett for field assistance. Supported by an NSF Predoctoral Fellowship, Princeton University, Bache Fund of the National Academy of Sciences, Frank M. Chapman Fund of the American Museum of Natural History, Sigma Xi, Alpha Chi, Raymond and Kathryn Brown, and the University of Nebraska's Cedar Point Biological Station. I thank the director of the station, John Janovy, Jr., for assistance and permission to work there and E. Bitterbaum, M. Bomberger, E. Greene, J. Hoogland, H. Horn, J. Loye, R. May, T. Root, D. Rubenstein, J. Seger, P. Sherman, and D. Wilcove for comments on the manuscript.

30 November 1983; accepted 8 March 1984

Behavioral Sensitivity to Purinergic Drugs Parallels Ethanol Sensitivity in Selectively Bred Mice

Abstract. *Behavioral responses to an adenosine receptor agonist and antagonist were examined in mice genetically selected for differential sensitivity to the soporific effects of ethanol. Both ethanol and the adenosine receptor agonist* L*-phenylisopropyladenosine had greater sedative and hypothermic effects in ethanol-sensitive "long-sleep" mice than in ethanol-insensitive "short-sleep" mice. Long-sleep mice were also more sensitive to the excitatory behavioral effects of theophylline, an adenosine receptor antagonist. These data suggest that adenosine may be an endogenous mediator of responses to ethanol.*

The mechanism by which ethanol produces its effects on the brain remains obscure. One of the most promising techniques for studying the effects of this drug has been the selective breeding of two mouse lines (SS, short-sleep mice, and LS, long-sleep mice), which differ in central nervous system sensitivity to the depressant effects of ethanol (*1*). Characterizing the differences between these two lines of mice may help to establish which neuronal systems are specifically