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EMPIRICAL MEASUREMENT OF PARASITE TRANSMISSION BETWEEN GROUPS IN A COLONIAL BIRD

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Abstract. While epidemiological models have suggested that the spread of parasites and infectious diseases often depends critically on the extent of movement by infected individuals between populations, there is little empirical information for any organism on the frequency of between-group parasite transmission or how it varies spatially. The transmission of parasites between discrete social groups or populations may also help determine a host's total parasite or pathogen exposure. We measured the introduction of parasitic bugs (*Oeciacus vicarius*) into colonies of Cliff Swallows (*Petrochelidon pyrrhonota*) by transient birds from outside each group. The transmission of bugs increased strongly as the size of a nesting colony increased. More total transients visited the larger colonies, and the direction of change in transient numbers and the numbers of bugs introduced at a site from week to week tended to vary together. Transients at large colonies were more likely to have previously or subsequently visited other large, infested colonies. The greater likelihood of parasites being introduced into larger colonies by transient birds contributes to an increase in parasite load with increased colony size in Cliff Swallows.

Key words: *Cliff Swallow; coloniality; ectoparasitism;* Oeciacus vicarius; *parasite transmission; parasitism;* Petrochelidon pyrrhonota; *social behavior; swallow bug.*

INTRODUCTION

Understanding the spread of infectious diseases and parasites requires information on the likelihood of transmission. Whenever transmission has been directly measured in natural host–parasite systems (reviews in Anderson and May 1991, McCallum 2000, McCallum et al. 2001, Fenton et al. 2002), it has usually been that between hosts or from vector to host within a group or population (e.g., a city, nesting colony, or herd). However, epidemiological models have suggested that transmission between discrete populations, via immigration of infected or parasitized individuals, is critical for sustaining epidemics and preventing local extinction of parasite populations (Cliff et al. 1981, Loehle 1995, White et al. 1996, Swinton et al. 1998, Grenfell 2001). Yet, perhaps due to the difficulty in empirically measuring the movement of pathogens or parasites between populations, most models have either ignored between-group transmission, assumed that it is negligible, or (more often) that it occurs at a constant, analytically tractable rate (May and Anderson 1984, Bolker and Grenfell 1995, Lloyd and May 1996, Holmes 1997, Beardmore and White 2001).

Transmission between groups may determine in part both a host's total parasite or pathogen exposure and how parasite load varies with group size. Data from a variety of species indicate that rates of parasitism often increase as group size increases (e.g., Brown and Brown 1986, Moore et al. 1988, Rubenstein and Hohmann 1989, Hieber and Uetz 1990, Davies et al. 1991, Côté and Poulin 1995, Hoogland 1995), although in some species the inverse pattern is seen (e.g., Rutberg 1987, Poulin and FitzGerald 1989, Arnold and Lichtenstein 1993, Côté and Gross 1993, Schmid-Hempel 1998). The mechanisms directly responsible for the variation in parasite load in groups of different sizes have been little studied. Theoretical models have suggested that when group formation alters the average distance between uninfected and infected individuals, the probability of encountering an infectious agent will change, and in some cases clustering will reduce parasite or pathogen exposure (Watve and Jog 1997). On the other hand, a group may present a larger ''target area'' for parasites seeking hosts and thus potentially increase the likelihood of parasite immigration to the group (Kuris et al. 1980, Brown and Brown 1996). Testing these scenarios requires empirical information on how often parasites are transmitted between different groups and may also yield insight into factors affecting the evolution of sociality.

By experimentally manipulating hemipteran ectoparasite populations in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*), we measured for the first time in any organism the transmission of parasites between groups. Cliff Swallows nest in colonies that range from 2 to over 3000 nests, and thus are especially suitable for studying how the movement of parasites between groups varies with colony size. We determined how often parasites were introduced into a colony by birds from outside the group by fumigating entire colonies and counting the number of parasites that ap-

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FIG. 1. Swallow bug clinging to the foot of a Cliff Swallow, and thereby able to disperse between colonies. Photo credit: Charles R. Brown.

peared in the weekly interval between fumigations. We also related between-group transmission to the movement of transient birds (hosts) between sites using a large-scale mark–recapture study.

METHODS

Study animal and study site

Cliff Swallows build gourd-shaped mud nests underneath overhangs on the sides of steep cliffs and canyons, or under the eaves of bridges and buildings, throughout much of western North America (Brown and Brown 1995, 1996). These highly social birds are migratory and winter in southern South America. Nests are stacked together closely at a site and often share walls. The principal ectoparasite of Cliff Swallows is a hematophagous cimicid swallow bug (*Oeciacus vicarius*) that is also a vector for an encephalitis-related alphavirus (Brown et al. 2001). Infestations can reach 2600 bugs in a single nest. Swallow bugs typically inhabit the outsides of nests during the day and move inside nests at night, crawling onto the birds primarily to feed. The wingless bugs can disperse between colony sites only by clinging to the legs and feet of a swallow that moves between colonies (Fig. 1). When a transient bird briefly perches on a nest, the bugs crawl off and thus reach new sites. There is some evidence that female bugs are more likely than males to be moved by birds (Loye 1985).

Our study area was near the Cedar Point Biological Station (41°13′ N, 101°39′ W) in southwestern Nebraska. It was ~150 × 50 km and included portions of Keith, Garden, Deuel, and Lincoln counties, primarily along the North and South Platte Rivers. In this area, Cliff Swallows nested on both natural cliffs and artificial structures such as bridges. Colony size was the number of active nests at a site. Mean colony size (n = 1363) was 363 nests, and ranged from 2 to 3700 nests, with some birds nesting solitarily. All nests at a given bridge or cliff represented a nesting colony (Brown and Brown 1996). Each colony site tended to be separated from the next nearest by 1–10 km, although in some cases by as much as 20 km or more. In 1999–2002, we monitored 14 experimental colonies in concrete culverts underneath roads or railroad tracks. These sites were 3.1–44.7 km from each other, and had 18–28 neighboring colony sites within 10 km.

Fumigation and parasite counts

Experimental colonies were first fumigated on or about 10 May each year and weekly thereafter for 10–11 wk, at which time most Cliff Swallows had migrated from the study area. Nests were fumigated by spraying them with a dilute solution of an insecticide, Dibrom, that was highly effective in killing swallow bugs in previous work (Brown and Brown 1986, 1996). To further verify its effectiveness and thus establish that any bugs counted on nests were ones introduced into the colony and not ones surviving the fumigation, we placed 420 bugs (385 instars, 35 adults) in a pan with chunks of nest (dried mud), sprayed the nest pieces, and then assessed survival. No bugs were alive 2 min after spraying. Also, on 15 July 2001 at two large colonies of 955 and 1600 nests, we counted bugs on our nest sample (34 total bugs), sprayed the nests, then recounted before any birds had re-entered the culvert. No living bugs were found on any nest immediately after the fumigation. Finally, in 2002 we compared the percentages of adult and instar bugs in the counts from our experimental colonies with those from a non-fumigated, 525-nest colony in the study area (Fig. 2). Bug counts were taken in the same way at both non-fumigated and fumigated sites. The non-fumigated colony showed a drastic percentage decline in the number of adult bugs in the middle of the season, coinciding with the period of bug reproduction at the site, and then an increase as the instars matured (Fig. 2). In contrast, at our experimental sites, we primarily detected adults throughout the summer, indicating that bugs there were not surviving the fumigation to reproduce. A relatively few instars were found in the experimental sites later in the season (Fig. 2), but these can be explained by immigration of instars on birds, as swallows do carry instars occasionally (Brown and Brown 1996).

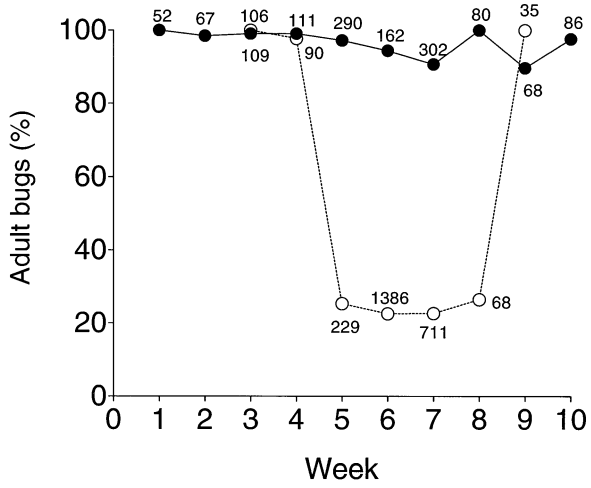

FIG. 2. Percentage of adult swallow bugs among the total bugs counted at weekly intervals in 2002 at four experimental, fumigated colonies (solid circles) and at a non-fumigated colony (open circles) in relation to time of season. The numbers by circles indicate total number of bugs counted that week. Week 1 begins on 19 May.

Weekly counts of parasites at 30 randomly selected nests per site began a week after the first fumigation. We used the same 30 nests each week unless colony size was too small to allow a full 30 (in addition, some nests that we selected fell or became inactive during the season). The outsides of all nests in the sample at a site were visually examined for parasites during the day using a flashlight. Any parasites seen anywhere on the nest or wedged between the nest and the substrate were counted. The number of visible bugs on the outsides of nests was highly correlated with the total number of bugs present in a nest ($r^2 = 0.68$–0.92, depending on nest status), as determined from nests that were collected (Rannala 1995:107). Thus, even if a few bugs inside the nest were missed on a given week, our counts still provide reliable relative indices of bug presence (and the age distributions in Fig. 2 suggest few were missed). Age of the bugs (adult or instar) was also recorded; age can be told by the instars' smaller size and lesser difference in width of the head vs. the abdomen (Usinger 1966). Fumigation of the entire colony (all nests and surrounding substrate) was done immediately after each count, ensuring that any bug counted each week was one introduced from elsewhere since the previous week's fumigation.

Mist-netting and capture protocols

At intervals throughout the season, we caught Cliff Swallows at the experimental colonies by placing a mist net across one end of the culvert. The net was always placed on the upwind end of the culvert with the other end unobstructed (Cliff Swallows enter culverts into the wind, through the downwind entrance), meaning we always caught birds as they exited. This is an effective way to catch naïve birds (transients), who are unaccustomed to avoiding nets at a site. Days on which birds were captured at the experimental colonies (usually with a net open 3–3.5 h per day) ranged from 9 to 33 at a site per season and extended from the period of the birds' arrival until most had departed from the colonies for the year. Total bird captures at the experimental colonies, in order of ascending colony size, were 529, 264, 613, 680, 2478, 2858, 3825, 4180, 4520, 5710, 3477, and 4149 (no capture data were available for the sites with colony sizes of 1 and 110 nests). Additional netting was done at 25–30 colony sites per year in an area of ~375 km^2 surrounding the experimental sites. There were 17 006, 18 717, 16 401, and 19 087 birds captured at all sites during each year of the study (1999–2002), respectively. All birds were banded with U.S. Fish and Wildlife Service bands upon initial capture.

Estimating transients

Transients are defined as birds not resident at a colony that pass through the site on a temporary basis. Those individuals caught only once at a colony include the transient class, but they also may include some residents who just happened to never be caught again. Thus, we had to estimate the fraction of the one-time captures that consisted of transients and (for some analyses) also had to identify specific individuals as transients. We estimated the daily proportion of transients among those birds captured during each netting session with the method of Pradel et al. (1997). By fitting an age-dependent model to the capture data, the ''first-year'' age class can be used to approximate the transients, who, by virtue of not reappearing at a site, have much lower apparent survival, ϕ, than the residents who tend to be caught multiple times. The estimate of ''first-year'' survival allows one to calculate τ_t, the proportion of transients in each time interval ($_t$), as $1 - (\phi_{1t}/\phi_{2t})$, where ϕ_{1t} is apparent survival probability of the ''first-year'' age class, and ϕ_{2t} is apparent survival probability of the ''older'' age class (Pradel et al. 1997). The proportion of transients, τ_t, was multiplied by the number of newly caught birds during each capture session and divided by the number of hours that the net was open that day to produce the number of transients per hour per day. The calculation of τ_t for each netting session (Pradel et al. 1997) specifically excludes the fraction of one-time captures attributed to residents who were never caught again. Survival models were fit, and parameter estimates produced, by the program MARK (White and Burnham 1999). Each colony was analyzed separately, as the number of capture occasions, dates of sampling, and intervals between the occasions were different for each site.

For each colony, the best-fitting model (used to estimate τ_t) was usually one with time-dependent survival probabilities for the ''first-year'' age class, time-constant survival for the ''older'' age class, and time-dependent recapture probability the same among both age

classes. Any differences in recapture probabilities among the different colonies (these tended to vary each day because of differences in weather conditions, time nets were open, etc.) were accounted for in the estimates of ϕ (and thus τ_t) calculated by MARK. Estimates of τ_t and model fitting were done separately for adults and juveniles (birds fledged in the current year) at each site. Juveniles were included because they are known to transport bugs (8 of 135 birds in nets found carrying bugs were juveniles). The number of transients reported reflects the sum of adults and juveniles.

To relate the presence of transients at a site to bug transmission, we examined, for each colony and each week, whether the average number of transients per hour per day and the mean number of bugs introduced per nest increased or decreased from the previous week. We chose to analyze the direction of change because different sites were not netted for transients simultaneously, and changing weather conditions (especially wind speed) between days affected transient activity and capture efficiency. While we sampled all colonies under the same range of weather conditions on a seasonal basis, this was not always possible on a daily or weekly basis. The direction of change in numbers of transients and numbers of bugs per week per site was less sensitive to quantitative biases brought about by different netting conditions on different days.

In analyzing the colony-size histories of transients, we designated specific individual birds as transients if they were caught only once at an experimental site and had been caught at another colony that same year, either before or after having been caught at the experimental site. That these birds were known to have been at two different sites during the breeding season indicates that they were transients at some point during the season. In analyzing the mean size of the colonies that these birds visited, to avoid bias and ensure that the pool of potential colony sizes that transients could have visited was the same among all experimental colonies in a given year, we used only transients previously or subsequently caught at non-fumigated, nonexperimental sites.

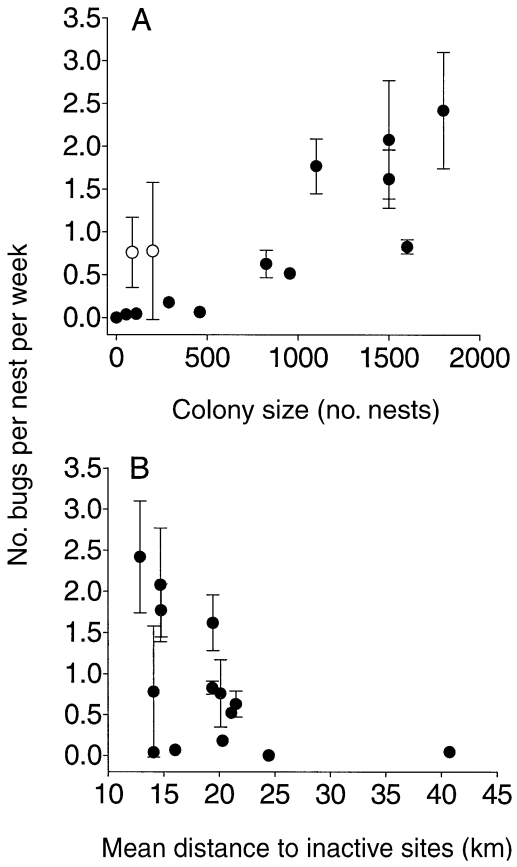

FIG. 3. (A) Mean (± 1 SE) number of swallow bugs transmitted from outside the colony per nest per week over the entire nesting season in relation to Cliff Swallow colony size (number of active nests). Sites designated with an open circle are late-starting colonies that became active in late June, 3–4 weeks after all others. The mean number of bugs increased significantly with colony size for all sites ($r_s = 0.83$, $P < 0.001$, $N = 14$ colonies) and when excluding the late colonies ($r_s = 0.93$, $P < 0.0001$, $N = 12$). (B) Mean (± 1 SE) number of swallow bugs transmitted from outside the colony per nest per week over the entire nesting season in relation to the mean distance (km) to colony sites in the study area that were inactive that year but had been active the previous year (and thus were infested with swallow bugs). Mean number of bugs declined significantly as the mean distance to inactive sites increased ($r_s = -0.55$, $P = 0.04$, $N = 14$ colonies).

RESULTS

Parasite introduction to sites

Counts of immigrant bugs per nest varied significantly among colonies for both adult bugs (repeated-measures ANOVA, $F_{8, 248} = 11.99$, $P < 0.0001$) and for instars ($F_{8, 248} = 4.37$, $P < 0.0001$). The mean number of bugs (of both ages combined) introduced per nest per week increased significantly with colony size (Fig. 3A). The significant effect of colony size ($F_{1,88} = 21.5$, $P < 0.0001$) was independent of the other significant effects of year ($F_{3,88} = 4.6$, $P = 0.005$) and week within the season when counts were made ($F_{12,88} = 2.8$, $P = 0.003$), and the nonsignificant effects of ambient temperature ($F_{1,88} = 2.1$, $P = 0.15$) and time of day ($F_{1,88} = 0.4$, $P = 0.54$, multi-way ANOVA) when counts were made.

Because colony sites that were active the previous year but unused by swallows in the current year tend to have large numbers of bugs seeking to disperse (Brown and Brown 1996), we examined how distance to these sites potentially affected parasite introduction to experimental colonies. The mean number of bugs introduced per nest per week in the experimental colonies declined significantly with an increase in the mean distance to unused colony sites that had been active the previous year (Fig. 3B).

Number of transients

Swallow bugs are transported between colonies by transient birds that briefly visit nests. Of 120 adult Cliff Swallows with bugs still clinging to their feet when caught (Fig. 1), 100 (83.3%) were caught only once at the colony where they were carrying bugs, indicating that they were probably transients there. More transients passed through the larger colonies. Averaged over all days throughout the season, the total number of transient birds per hour per day (as estimated from mark-recapture models) increased significantly with size of the experimental colonies (Fig. 4A).

The direction of the weekly change in transmission of bugs into a site was related to the direction of the weekly change in transient numbers there. Of 94 colony–week intervals, the number of transient birds and the number of bugs varied directly in 58 intervals, varied in opposite directions in 33 intervals, and did not change in 3. The preponderance of intervals in which they varied in the same direction was significant (binomial test, $P = 0.006$).

Colony-size histories of transients

The past history of transient birds and their future activity patterns varied significantly with the colony size of the experimental sites (Fig. 4B, C). Transients caught at the larger experimental colonies either had been caught previously at large nonexperimental colonies (Fig. 4B) or were caught afterwards at large nonexperimental colonies (Fig. 4C). This seemed to reflect an active choice by the transient birds to visit colonies of a particular size and not merely the spatial proximity of sites similar in size, as evidenced by the fact that the average linear distance between the experimental site and the site where a transient was previously or subsequently caught was unrelated to the colony size of the experimental site (previously caught, $r_s = -0.10$, $P = 0.78$; subsequently caught, $r_s = 0.01$, $P = 0.97$). Transients were thus drawn from the same geographic area at all colonies.

Discussion

These results clearly illustrate that between-group transmission of swallow bugs is nonhomogeneous among sites, and that the nests in larger colonies experience much higher per capita rates of bug introduction from outside the colony. The results also demonstrate that the absolute number of transients at a site and their past history are strongly correlated with parasite immigration to a site. Between-group transmission, as documented here, causes greater parasite loads in larger groups in the absence of other effects. This is also the only known mechanism to introduce parasites to new colonies or to sites where bugs have gone extinct (especially if occupied by large numbers of birds).

The increased rates of bug introduction into larger Cliff Swallow colonies are probably caused in part by

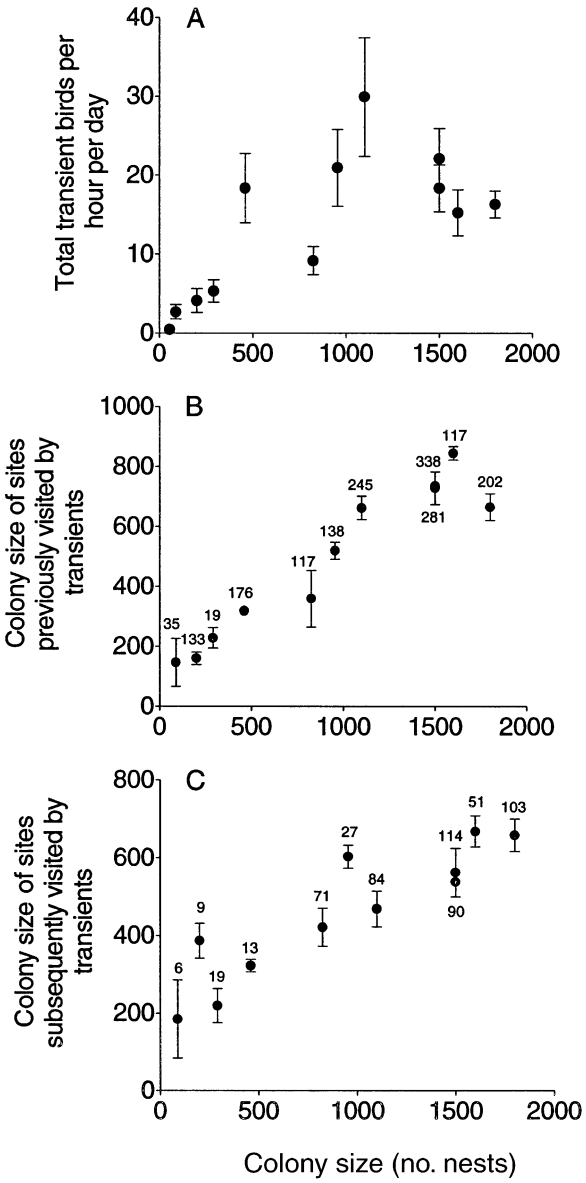

FIG. 4. (A) Mean (± 1 SE) number of transient Cliff Swallows per hour per day over the entire nesting season in relation to Cliff Swallow colony size. The mean number of transient birds increased significantly with colony size ($r_s = 0.66$, $P = 0.02$, $N = 12$ colonies). Total sample sizes (number of birds caught) used to generate the estimates of the number of transients are given in the *Methods*. (B) Mean (± 1 SE) colony size of sites visited by transient Cliff Swallows prior to their capture at an experimental colony in relation to the size of the experimental colony. The numbers by circles indicate sample size (number of birds). Mean colony size visited previously by transients increased significantly with size of the experimental colony ($r_s = 0.94$, $P < 0.0001$, $N = 11$ colonies). (C) Mean (± 1 SE) colony size of sites visited by transient Cliff Swallows after their capture at an experimental colony in relation to the size of the experimental colony. The numbers by circles indicate sample size (number of birds). Mean colony size visited afterwards by transients increased significantly with size of the experimental colony ($r_s = 0.91$, $P < 0.001$, $N = 11$ colonies).

the transients there having preferentially visited other large colonies. Birds that visit large colonies will be more likely to pick up bugs there, simply because those sites have greater average parasite loads (Brown and Brown 1986, 1996). Nonbreeding and post-breeding transients apparently visit different colonies in order to assess the suitability of colony sites for breeding, either in the current season or for next year (Brown et al. 2000). It is not surprising that they would preferentially visit colonies of particular sizes given that these birds show a heritable basis for their choice of breeding colony size (Brown and Brown 2000). There is no evidence that colony residents are responsible for bug immigration, as radio-tracking revealed that individuals do not visit other colonies once becoming established (defined as present four or more days) at a nesting colony (Brown and Brown 1996).

Two other factors may further contribute to the transients that visit the larger colonies being more likely to introduce bugs than the birds visiting small colonies. First, there may be qualitative differences among the birds that visit (and potentially introduce bugs to) different sites. For example, we found that the average level of wing asymmetry among transients increased significantly with colony size (C. Brown and M. Brown, *unpublished data*). Because higher levels of bilateral asymmetry are associated with a greater degree of parasitism in various taxa (reviewed in Møller 1996), including Cliff Swallows (Brown and Brown 2002), greater asymmetry might indicate that transients visiting the larger colonies are more inherently prone to parasitism. Asymmetry can reflect both an individual's past exposure to parasites (especially during development) and its relative condition, which in turn may influence its susceptibility to parasites. If transients visiting large colonies have been more parasitized in the recent past, they may have been more likely to transport bugs between sites. Second, the presence of parasites at a colony is known to influence dispersal in Cliff Swallows (Brown and Brown 1992). While this has been documented only for between-year natal dispersal, it is possible, especially for recently fledged juveniles, that those from highly infested colonies will be more likely to move around after fledging, thus becoming transients and perhaps more likely to introduce bugs to any of the colonies they visit.

The spatial proximity of source sites for parasites may be important in between-group transmission, independent of transient activity. One such source are colony sites that were used the previous year but are unused in the current season. Without a host resource, bugs remaining at these sites cluster at the entrances of empty nests in attempts to disperse. As birds briefly land at nests or brush against them, the bugs crawl onto the birds. Radio telemetry of transient Cliff Swallows indicates that they visit nests at unoccupied colonies at least occasionally (Brown and Brown 1996), and at times these sites are heavily infested with bugs. Swallow bugs may in fact be more likely to disperse from inactive sites, given there is no dependable food source for them there. To distinguish between the effects of distance to parasite sources and the effects of transients per se would require a much larger spatial array of experimental colonies than is practical. However, the data on the average distance transients traveled to reach an experimental colony suggest that transients at all sites are drawn from the same general area and, thus, that the proximity of infested sites alone cannot explain the increased parasite transmission at the larger colonies.

Parasite load in Cliff Swallow colonies, as in most host–parasite systems, is also determined by within-colony factors, chiefly parasite reproductive rates, within-colony transmission, and past history of site use. Our experimental design eliminated parasite reproduction as a cause of the observed patterns (Fig. 3A), but under natural conditions reproduction at a site can greatly increase bug populations (Loye 1985, Rannala 1995). If bug reproductive rate increases with bug density, this would contribute to an increase in parasitism with increased colony size. Within-group transmission (the movement of bugs between nests, largely by crawling on the nest exteriors and substrate) is likely to depend mostly on nest spatial positioning. The number of swallow bugs per nest is inversely related to a nest's nearest neighbor distance (Brown and Brown 1996), probably because closer nest spacing makes movement along the substrate less risky for a bug, especially when the substrate is exposed to direct sunlight and heat, which cause bug mortality. Because of this, we selected experimental colonies that had similar nest densities even though they varied in size. While within-group transmission does not account for our results, this type of transmission ought to be more frequent at sites with closely spaced nests. Finally, large colonies may also support larger parasite populations because, at least in our study area, those sites tend to be more predictably used from year to year (Brown and Brown 1996). Regular use enhances annual bug survival and leads to larger swallow bug populations at the start of each nesting season (Loye 1985, Brown and Brown 1996). Ectoparasite load is also directly correlated with years of colony-site occupancy in Black-legged Kittiwakes (*Rissa tridactyla*; Danchin 1992).

Our experiments and other observations (Brown and Brown 1996) suggest a high capacity for swallow bugs to move between colony sites. For example, at a new colony site in 1989 that had never been occupied before, over 13 000 bugs were introduced in a four-week period (Brown and Brown 1996). These results are consistent with those for other ectoparasites associated with colonial birds, in which lack of parasite population structure among colonies (as determined from genetic markers) suggests a much higher parasite dispersal rate than is often assumed (McCoy et al. 2003).

Some models have suggested that group formation can reduce per capita parasite load whenever uninfected individuals cluster because the average distance to infected individuals is increased (Watve and Jog 1997). Our data do not support such a scenario in a highly mobile host such as the Cliff Swallow, and the opposite seems to occur when hosts preferentially visit groups of particular sizes. The increased transmission of parasites from outside the group into the larger colonies is one mechanism responsible for the positive relationship between parasite load and group size in Cliff Swallows. Over 60 times more parasites, per capita, were transmitted to the largest colony compared to the smallest. Colony formation in Cliff Swallows does not reduce parasitism by bugs, and the results shown here (along with others, Brown and Brown 1996) clearly indicate that ectoparasitism is a cost of coloniality in these birds. The differences in transmission rates among colonies of different size suggest that the migration of parasites or pathogens between spatial groupings is far from constant. Our results also suggest that between-group transmission should be viewed as a potential determinant of a host's total parasite or pathogen exposure, especially when mobile hosts occur in discrete social groups or populations. By knowing, for example, that Cliff Swallows tend to move bugs from large colonies to large colonies, we can predict which sites should be more likely to exhibit epidemics of an encephalitis-related arbovirus vectored by swallow bugs (Brown et al. 2001). Explicit measurement of parasite introduction between populations may assist in predicting the occurrence and spread of other epidemics and parasites in space.

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