ECTOPARASITISM AS A CAUSE OF NATAL DISPERSAL IN CLIFF SWALLOWS[1]

CHARLES R. BROWN AND MARY BOMBERGER BROWN
Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511 USA

Abstract. Nestling Cliff Swallows (*Hirundo pyrrhonota*) in southwestern Nebraska that were relatively heavily parasitized by hematophagous fleas (*Ceratophyllus celsus*) and swallow bugs (*Oeciacus vicarius*) dispersed to nonnatal colonies to breed the subsequent year, whereas nestlings that were relatively lightly parasitized returned to their natal colony to breed. There were no significant differences between dispersers and nondispersers in natal clutch size, natal brood size, relative hatching date, natal body mass, natal nest's distance from the colony's center, and natal nest's age. There were no sex differences in dispersal tendencies. Dispersing birds tended to move to smaller colonies to breed, and in some cases settled in breeding colonies later than nondispersers. Ectoparasitism may be a major cause of natal dispersal in Cliff Swallows and perhaps should be considered another potential cause of dispersal in general, especially in group-living species that may be associated with large numbers of highly co-evolved ectoparasites.

Key words: Ceratophyllus celsus; Cliff Swallow; coloniality; ectoparasitism; Hirundo pyrrhonota; natal dispersal; Nebraska; Oeciacus vicarius; social behavior.

INTRODUCTION

In most animal populations, some individuals upon reaching maturity settle and breed at or near their birthplace, whereas others disperse varying distances to potentially unfamiliar breeding sites (reviewed in Greenwood and Harvey 1982, Chepko-Sade and Halpin 1987, Johnson and Gaines 1990). Natal dispersal can both maintain gene flow between populations and influence social and genetic structure within populations, especially when dispersal occurs preferentially among one sex or age class. Studies on natal dispersal and philopatry have most often measured whether one sex is more likely to disperse (e.g., Greenwood et al. 1979, Greenwood 1980, Dobson 1982, Chepko-Sade and Halpin 1987, Johnson and Gaines 1990) and speculated as to whether the avoidance of either inbreeding or increased competition for resources in the natal area has primarily caused dispersal (e.g., Hoogland 1982, Moore and Ali 1984, Dobson and Jones 1985, Shields 1987, Payne 1991).

Surprisingly few studies have investigated potential genotypic or phenotypic differences, other than sex and age, that characterize dispersers and nondispersers within a population. Studies of small rodents suggested that dispersers differed genetically (with respect to two loci) from nondispersers (Myers and Krebs 1971) and that dispersers had reduced body mass relative to nondispersers (Fairbairn 1978). Among birds, no consistent intrasexual differences between dispersers and nondispersers have been identified, although variables such as population density, time of birth, dominance

status, natal territory quality, natal clutch size, and natal brood size have been examined in some species (reviewed by Pärt 1990).

The potential influence of ectoparasitism on natal dispersal has not been examined in any species to our knowledge. Increasing evidence indicates that parasites have at times major effects on many aspects of host behavior and ecology (e.g., Loye and Zuk 1991). This may be especially true for group-living species that are associated with large numbers of ectoparasites, such as the colonial Cliff Swallow (*Hirundo pyrrhonota*). At our study site in Nebraska, infestations of ectoparasites increase with Cliff Swallow colony size and severely depress nestling body condition and survivorship (Brown and Brown 1986). In this paper we report that natal dispersal in Cliff Swallows can be predicted largely by the extent of ectoparasitism individuals experience as nestlings; those that are relatively heavily parasitized disperse to another colony to breed the subsequent year, whereas those that are relatively lightly parasitized return to their natal colony. We evaluate other potential phenotypic differences among dispersers and nondispersers and suggest that ectoparasitism may be one cause of natal dispersal in Cliff Swallows.

METHODS

Study animals 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 wintering range in South

America. The birds build gourd-shaped nests out of mud pellets, and their nests are attached underneath overhanging rock ledges on the sides of steep cliffs or on artificial structures such as bridges. Some colony sites and individual nests are used repeatedly in successive years, whereas others may be abandoned for intervals of 1–6 or more years before they are used again. Cliff Swallows are highly social in all of their activities; they feed, preen, gather mud, and migrate in large groups.

The Cliff Swallow bug (Hemiptera: Cimicidae; *Oeciacus vicarius*) is the most abundant ectoparasite of Cliff Swallows in our study area. Some nests contain up to 2500 swallow bugs each. The hematophagous bugs feed on both adult birds and nestlings. The bugs are primarily nest ectoparasites, apparently traveling on the adult birds only for brief periods during the summer, and consequently are adapted to long periods during each year or for several consecutive years when their migratory hosts are absent from the colonies (Loye and Hopla 1983, Loye 1985). Swallow bugs are long-lived and begin breeding as soon as a colony is occupied by birds in the spring. The life cycle and basic biology of *O. vicarius* is relatively well known (Usinger 1966, Loye 1985).

The other common Cliff Swallow ectoparasite in our study area is the bird flea *Ceratophyllus celsus* (Siphonaptera: Ceratophyllidae). Fleas are also hematophagous but apparently travel and feed on the adult birds more than do swallow bugs. Fleas reproduce in swallow nests during the summer, spend the winter in the nests, and cluster at the entrances of nests the next spring, jumping on the Cliff Swallows when birds are investigating nests early in the season (Hopla and Loye 1983; C. and M. Brown, *personal observations*). Fleas appear to have small effects on nestling growth rates or nestling survivorship (Brown and Brown 1986), but their short- and long-term effects on adult birds are unknown. Fleas apparently are less able than swallow bugs to withstand multiple-year periods of colony disuse by Cliff Swallows, although the life cycle and basic biology of *C. celsus* is not well known (Hopla and Loye 1983).

Our study was conducted in southwestern Nebraska near the University of Nebraska's Cedar Point Biological Station, in 1982–1991. 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. These birds also occurred in southwestern Nebraska before the appearance of artificial structures, nesting on bluffs and outcrops along the North Platte River. Colonies in our study area were situated on bridges, in highway culverts, on irrigation structures, and on natural cliff sites along the south shore of Lake McConaughy. Mean (± 1 SE) colony size in Keith, Garden, and Lincoln counties was 392 ± 27 nests ($N = 564$ colonies; range 2–3700 nests). Some Cliff Swallows were also solitary nesters.

Marking and recapturing birds

In 1982 we began banding nestling Cliff Swallows with United States Fish and Wildlife Service bands; banding has continued to date. Each bird was banded 10 d after hatching and its body mass measured at that time with a Pesola scale. For each individual we also recorded natal clutch size, defined as the maximum number of eggs laid in its nest; natal brood size, defined as the total number of nestlings alive in the nest 10 d after hatching; relative hatching date, a measure of when within a colony's period of nesting the bird hatched, calculated as the number of standard deviations for that colony either before or after the colony's modal hatching date (see Brown and Brown 1987); the natal nest's linear distance along the substrate from the colony's centermost nest, measured in centimetres; and the natal nest's age, old nests being those in which half or more of the nest already existed when first occupied by birds, and new nests being those in which less than half of the nest existed when first occupied by birds (after Brown and Brown 1986). Sex of nestling Cliff Swallows could not be determined.

Adult Cliff Swallows were captured at colonies by mist-netting at each site repeatedly throughout each nesting season. A breeding colony is defined as any single bridge or highway culvert containing active nests; study colonies were generally between 1 and 65 km apart. The analyses reported here use only birds originally banded as nestlings (or in some cases recently fledged juveniles) and recaptured at a breeding colony the following year. All adults captured since 1986 have been sexed by cloacal protuberance or presence/absence of a brood patch.

Nestlings from three focal colony sites that were active each year of the study constituted the sample of birds used in this paper (see *Results*). These three colony sites varied consistently in size each year: the *small* colony averaged 53 nests over the years of the study (range 6–140 nests) and was the smallest of these sites each year; the *medium*-sized colony averaged 227 nests (range 90–375 nests) and was intermediate in size each year; and the *large* colony averaged 1260 nests (range 125–2350 nests) and was the largest of these sites each year. In addition to the three focal colony sites, we also searched for birds that had dispersed by mist-netting at up to 36 additional colony locations within the approximately 200 × 60 km study area each year (not all of these 36 sites necessarily were active or could be sampled in a given year). Colony size was determined by counting or estimating the maximum number of nests containing eggs.

Measuring ectoparasitism

Extent of ectoparasitism was measured for each nestling Cliff Swallow 10 d after hatching at the time it was banded. All swallow bugs and fleas present anywhere on the bird's body were counted (Brown and Brown

1986). Nestlings were sparsely feathered at that age and ectoparasites could be thoroughly searched for and counted in ≈ 1 min/bird.

Parasite counts from nestlings reflected only the relative degree of parasitism among nests and did not represent the nests' actual parasite loads. Actual parasite loads could be determined only by collecting large numbers of entire nests, which was prohibitively de-
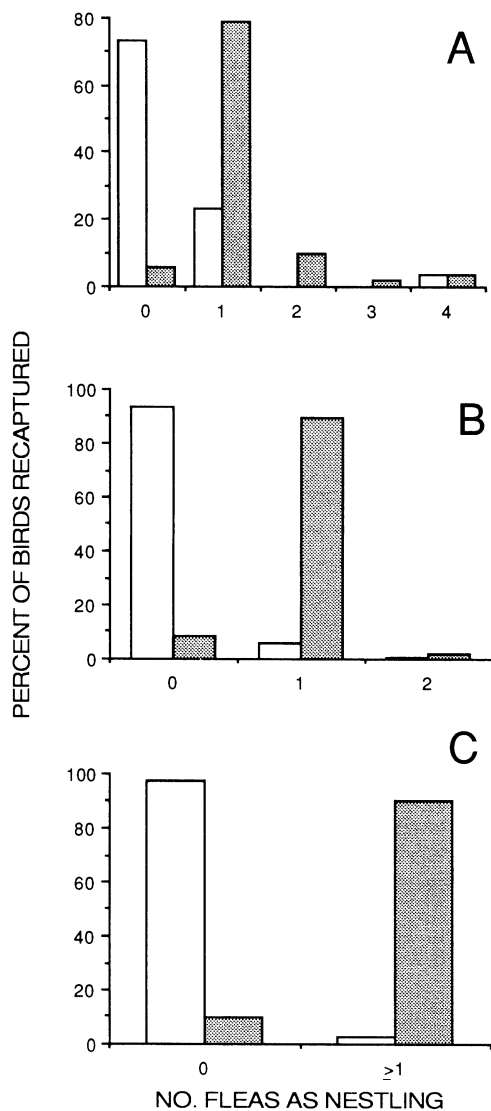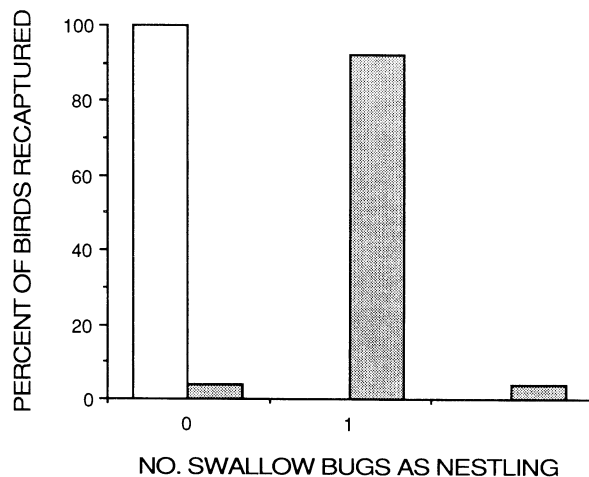

FIG. 2. Percent of Cliff Swallows originally banded as nestlings that were recaptured the following year breeding in their natal colony (open bars) or having dispersed to a nonnatal colony (shaded bars) vs. the extent of swallow bug parasitism they experienced as a nestling in a small colony. $N = 26$ nondispersers, 52 dispersers. The distributions of dispersers and nondispersers with respect to parasitism differed significantly ($P < .0001$, chi-square test), as did the mean level of natal bug parasitism for dispersers and nondispersers ($P < .0001$, Wilcoxon test).

structive. At least for swallow bugs, however, counts on nestlings correlated significantly with a nest's total parasite load, based on a small sample of nests we collected ($r_s = 0.623, P < .001, N = 65$). Nests in which no swallow bugs were found on any of the nestlings averaged 199 ± 27.6 total bugs counted within the nest (mean ± 1 SE, $N = 39$ nests), whereas nests with at least one bug on at least one nestling averaged 565 ± 56.2 total bugs counted within the nest ($N = 26$ nests; Wilcoxon rank sum test, $P < .001$). Fleas were too mobile to be counted accurately in collected nests.

RESULTS

From 1983–1991 we recaptured 1580 birds at a breeding colony that had been banded as nestlings or juveniles the preceding year; 1535 of these (97.1%) had been banded at one of the three focal colony sites. This paper uses data from only the 1535 birds from the focal sites, because each was occupied by Cliff Swallows in each year of the study, and therefore all birds born there each year had the option of returning to their natal colony the following year.

Nestling Cliff Swallows on which one or more fleas (Fig. 1) or swallow bugs (Fig. 2) were counted tended to disperse to another colony to breed the next year, whereas those birds on which no fleas or bugs were found tended to return to breed at their natal colony (Figs. 1 and 2). This pattern held for Cliff Swallows born at all three colonies of different sizes when parasitized by fleas (Fig. 1). Only the small colony could be used in analyses for swallow bugs because the medium and large colonies were in part or fully fumigated

FIG. 1. Percent of Cliff Swallows originally banded as nestlings that were recaptured the following year breeding in their natal colony (open bars) or having dispersed to a nonnatal colony (shaded bars) vs. the extent of flea parasitism they experienced as a nestling in a small (A), medium (B), and large (C) colony. In (A), $N = 26$ nondispersers, 52 dispersers; in (B), $N = 139$ nondispersers, 48 dispersers; in (C), $N = 770$ nondispersers, 106 dispersers. The distributions of dispersers and nondispersers with respect to parasitism differed significantly for all colonies ($P < .0001$ for each, chi-square tests), as did the mean level of natal flea parasitism for dispersers and nondispersers ($P < .0001$ for each, Wilcoxon tests).

in some years to remove bugs, but the fumigant was ineffective against fleas (Brown and Brown 1986).

There were few other differences that distinguished birds that dispersed vs. those that returned to their natal colony. Natal clutch size, natal brood size, relative hatching date, and body mass at 10 d of age did not differ significantly for dispersers vs. nondispersers (Table 1). There was a suggestion that dispersers tended to come from nests located farther from the colony's center, although the differences were not statistically significant (Table 1).

There were no sex differences in dispersal tendency; of 865 birds recaptured and subsequently sexed as males, 158 (18.3%) dispersed to a nonnatal colony, whereas 114 of 577 birds sexed as females (19.8%) dispersed to a nonnatal colony ($\chi^2 = 0.50$, $P = .48$, df $= 1$). Natal nest age similarly had no effect: of 633 birds from old natal nests, 118 (18.6%) dispersed to a nonnatal colony, whereas 65 of 401 birds (16.2%) coming from new natal nests dispersed to a nonnatal colony ($\chi^2 = 1.00$, $P = .32$, df $= 1$).

We calculated the difference in colony size between a bird's first breeding colony and its natal colony for dispersers and nondispersers (Table 1; negative values indicate that the breeding colony was smaller than the natal colony, positive values that it was larger). Birds that dispersed from the medium-sized and large col-

onies moved on average to smaller colonies to breed (Table 1), whereas the birds dispersing from the small colony tended to move to slightly larger colonies (Table 1). Birds that returned to their natal colony site to breed occupied colonies that tended to be larger than their own natal colony had been at that site (Table 1).

Settlement dates at breeding colonies, defined as the first date on which an adult was captured or otherwise known to be present (e.g., by our finding it dead on a road), tended to be slightly later for dispersers than for nondispersers, but the difference was statistically significant only for the medium-sized colony (Table 1).

Birds from the same brood tended to exhibit the same pattern of dispersal or philopatry. There were 128 instances in which two birds from the same brood (putative siblings) were recaptured the following year at a breeding colony; in 126 of these cases (98.4%) both birds either dispersed (3 cases) or both returned to their natal colony (123 cases). There were 16 instances in which three putative siblings were recaptured the following year at a breeding colony, and in all of these cases all three birds either dispersed (2 cases) or all returned to their natal colony (14 cases). Of the 304 birds represented in these sib–sib pairs and triplets, only 14 (4.6%) dispersed to nonnatal colonies, a significantly lower percentage of dispersers than in the overall sample (19.3%, $N = 1535$; $\chi^2 = 39.01$, $P \ll$

TABLE 1. Comparison of Cliff Swallows that dispersed to nonnatal colony to breed vs. returned to natal colony, for birds from three natal colony sites of different sizes that were active each year, 1983–1991.

	Small colony			Medium-sized colony			Large colony		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
Natal clutch size									
Disperser	3.96	0.10	52	4.12	0.16	51	3.97	0.08	94
Nondisperser	3.92	0.15	24	3.93	0.06	157	3.84	0.04	721
Natal brood size									
Disperser	3.65	0.10	60	3.67	0.14	51	3.50	0.06	115
Nondisperser	3.77	0.17	30	3.59	0.06	160	3.34	0.03	807
Relative hatching date									
Disperser	0.065	0.20	46	0.33	0.18	48	0.67	0.20	87
Nondisperser	0.48	0.26	21	0.27	0.13	130	0.82	0.06	706
Natal body mass (g)									
Disperser	23.07	0.50	50	22.40	0.35	48	22.39	0.24	123
Nondisperser	23.21	0.59	26	22.40	0.24	127	22.75	0.09	829
Natal nest's distance from colony's center (cm)									
Disperser	331.4	106.3	43	490.7	39.3	49	305.2	19.3	90
Nondisperser	152.0	26.0	25	459.4	31.6	157	272.2	6.8	689
Size difference between breeding and natal colony (no. nests)									
Disperser	97.3	70.0	62	−133.6 ***	35.6	51	−291.5 ***	78.6	183
Nondisperser	32.0	8.0	31	77.8	9.2	164	287.7	18.8	1044
Date of settlement at breeding colony (first capture date; 01 $=$ 1 May)									
Disperser	45.4	2.0	62	45.4 *	3.3	49	39.8	1.0	180
Nondisperser	39.9	2.2	31	33.0	1.2	161	38.9	0.6	1018

  * $P < .05$, *** $P < .001$; Wilcoxon tests with Bonferroni correction for multiple comparisons. No other variables (except fleas and swallow bugs; Figs. 1 and 2) differed significantly between dispersers and nondispersers. Similar results were obtained with a multiple logistic regression using all variables in Table 1 plus fleas, bugs, sex, natal nest age, and natal colony site. Only fleas, bugs, and size difference between breeding and natal colony contributed significantly to the regression, and there were no significant interaction terms among any of the other variables.

.001, df = 1). This suggests that Cliff Swallows are either more likely to return to their natal colony when they have a surviving sibling, or that dispersing siblings were simply harder for us to locate.

DISCUSSION

Dispersal to nonnatal colonies in Cliff Swallows was strongly associated with natal levels of ectoparasitism. Since dispersal could be predicted by extent of ecto-parasitism and since slight differences in the number of fleas and bugs counted on nestlings (that is, 0 vs. 1) seemed to have had a dramatic effect on whether those birds dispersed the following year (Figs. 1 and 2), a causal relationship between natal ectoparasitism and dispersal is suggested. The swallow bug counts from collected nests indicate that the nestlings that have at least 1 bug on them and that subsequently disperse are coming from nests that have, on average, >350 more bugs than do the nests from which nondispersers come. We are unaware of any previous studies on other species demonstrating such an apparent effect of parasites on natal dispersal.

Ectoparasitism as a cause of natal dispersal in Cliff Swallows is also suggested by the absence of differences between dispersers and nondispersers in other variables with which ectoparasitism might have been associated (Table 1). Date of breeding, in particular, might be a potentially confounding variable, since later hatched chicks of at least one sex tend to be more likely to disperse in Great Tits (*Parus major*; Dhondt and Huble 1968) and Marsh Tits (*P. palustris*; Nilsson 1989). However, there was no significant difference in relative hatching date for dispersing vs. nondispersing Cliff Swallows (Table 1). Because ectoparasitism within a colony is determined relative to when a colony starts (which can be any time between late April and early July in our study area) and not by date per se, relative hatching date is a directly comparable measure of seasonal effects for Cliff Swallows of different classes both within and among colonies (see Brown and Brown 1987). Thus, there is little evidence that birds hatched later in the year are inherently more likely to disperse independent of parasitism (Table 1).

Nest age is another variable that may affect the extent of ectoparasitism and therefore potentially confounds the presumed effect of parasites on dispersal. Earlier analyses indicated that old nests tended to have more ectoparasites (Brown and Brown 1986), although more recent analyses using larger data sets indicate no consistent difference in parasite load between old and new nests (C. and M. Brown, *unpublished data*). Natal nest age per se had no effect on dispersal tendency.

That dispersers are reacting to, and perhaps attempting to avoid, parasites is suggested by the birds' movement, in many cases, to smaller colonies to breed (Table 1). Ectoparasitism varies directly with colony size, and birds can presumably more readily escape parasites by occupying small colonies (Brown and Brown 1986).

Furthermore, siblings tended to exhibit the same pattern of dispersal or philopatry, a result consistent with the notion that individuals respond to the level of parasitism encountered in their natal nest. Siblings exhibiting similar dispersal tendencies also were reported in Great Tits (Dhondt 1979) and Sparrowhawks (*Accipiter nisus*; Newton and Marquiss 1983), although the possible effects of ectoparasites in the natal nest were not mentioned for these species.

We can dismiss, for two reasons, the possibility that birds that had been parasitized the preceding summer were aggressively excluded (for whatever reasons) from their natal colonies by previously unparasitized birds and were thus "forced" to disperse. First, dates of first capture at a breeding colony differed significantly for dispersers vs. nondispersers at only one of the colony sites (Table 1); dispersers should have consistently later settlement dates if they had first tried and failed to settle at their natal colony. Second, we have never observed birds trying to exclude others from a colony site; upon arrival, Cliff Swallows interact only with the relatively few individuals who happen to have occupied nests nearby (Brown and Brown 1989), and birds without nests are ignored.

These results (Figs. 1 and 2) suggest that dispersal decisions in Cliff Swallows may be determined quite early in an individual's life, that is, sometime before it is 24 d old (the average fledging age) while the bird is still exposed to the ectoparasites in its natal nest. The level of parasitism in the natal nest may be used as a simple rule-of-thumb that on average helps a bird avoid colony sites that are likely to be infested from the previous summer. The fact that not all nestlings dispersed the next year in our focal colonies could indicate that not all nests were infested equally, and there is other evidence of inter-nest variation in parasite load within a colony (C. and M. Brown, *unpublished data*; also see Figs. 1 and 2). An effect of ectoparasites on dispersal is perhaps not surprising, given the extremely deleterious effects of parasites, especially swallow bugs, on the birds' reproductive success (Brown and Brown 1986) and behavior (Brown and Brown 1991).

Although Cliff Swallows assess the extent of ectoparasitism among unoccupied nests upon their return in early spring (Brown and Brown 1986), dispersal from (and thus avoidance of) sites known to be infested the previous summer may save the birds critical time during the colony selection phase and enable them to begin breeding earlier in the year. However, the delay in presumably finding a nonnatal colony as reflected in slightly later settlement dates of dispersers (Table 1) may negate some of the ectoparasite-related benefits of dispersing and could itself represent a cost of dispersal. Slightly later settlement dates for dispersers may also reflect longer term physiological effects of being parasitized as a nestling (see Chapman 1973) if these effects subsequently cause later arrival on the breeding grounds.

The results reported here suggest that avoidance of

parasites within the natal environment may be a cause of dispersal in Cliff Swallows and perhaps should be considered another potential cause of natal dispersal in general. This may be especially true for group-living (e.g., colonial) species that are associated with large numbers of ectoparasites (e.g., Hoogland and Sherman 1976, Duffy 1983, Shields and Crook 1987, Rubenstein and Hohmann 1989, Poulin 1991), some possibly highly co-evolved with their hosts. The swallow bug and flea found in our study area are specialized parasites of swallows, rarely occurring on other birds, and exhibit various behavioral and physiological adaptations to their hosts' short and erratic annual availability (Usinger 1966, Hopla and Loye 1983, Loye 1985). Dispersal away from them is apparently one major way that Cliff Swallows respond to these parasites.

LITERATURE CITED

Brown, C. R., and M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

Brown, C. R., and M. B. Brown. 1987. Group-living in cliff swallows as an advantage in avoiding predators. Behavioral Ecology and Sociobiology 21:97–107.

Brown, C. R., and M. B. Brown. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. Animal Behaviour 37:777–796.

Brown C. R., and M. B. Brown. 1991. Selection of high-quality host nests by parasitic cliff swallows. Animal Behaviour 41:457–465.

Chapman, B. R. 1973. The effects of nest ectoparasites on cliff swallow populations. Dissertation. Texas Tech University, Lubbock, Texas, USA.

Chepko-Sade, B. D., and Z. T. Halpin, editors. 1987. Mammalian dispersal patterns. University of Chicago Press, Chicago, Illinois, USA.

Dhondt, A. A. 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologia (Berlin) 42:139–157.

Dhondt, A. A., and J. Huble. 1968. Fledging-date and sex in relation to dispersal in young great tits. Bird Study 15:127–134.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30:1183–1192.

Dobson, F. S., and W. T. Jones. 1985. Multiple causes of dispersal. American Naturalist 126:855–858.

Duffy, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. Ecology 64:110–119.

Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia (Berlin) 32:171–193.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. Journal of Animal Ecology 48:123–142.

Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. Science 215:1639–1641.

Hoogland, J. L., and P. W. Sherman. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecological Monographs 46:33–58.

Hopla, C. E., and J. E. Loye. 1983. The ectoparasites and microorganisms associated with cliff swallows in west-central Oklahoma. I. Ticks and fleas. Bulletin of the Society for Vector Ecology 8:111–121.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449–480.

Loye, J. E. 1985. The life history and ecology of the cliff swallow bug, *Oeciacus vicarius* (Hemiptera: Cimicidae). Cahiers Office de la Recherche Scientifique et Technique Outre–Mer, Serie Entomologie Medicale et Parasitologie 23:133–139.

Loye, J. E., and C. E. Hopla. 1983. Ectoparasites and microorganisms associated with the cliff swallow in west-central Oklahoma. II. Life history patterns. Bulletin of the Society for Vector Ecology 8:79–84.

Loye, J. E. and M. Zuk, editors. 1991. Bird-parasite interactions: ecology, evolution and behaviour. Oxford University Press, Oxford, England.

Moore, J., and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Animal Behaviour 32:94–112.

Myers, J. H., and C. J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecological Monographs 41:53–78.

Newton, I., and M. Marquiss. 1983. Dispersal of sparrowhawks between birthplace and breeding place. Journal of Animal Ecology 52:463–477.

Nilsson, J.-A. 1989. Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. Journal of Animal Ecology 58:619–636.

Pärt, T. 1990. Natal dispersal in the collared flycatcher: possible causes and reproductive consequences. Ornis Scandinavica 21:83–88.

Payne, R. B. 1991. Natal dispersal and population structure in a migratory songbird, the Indigo Bunting. Evolution 45:49–62.

Poulin, R. 1991. Group-living and infestation by ectoparasites in passerines. Condor 93:418–423.

Rubenstein, D. I., and M. E. Hohmann. 1989. Parasites and social behavior of island feral horses. Oikos 55:312–320.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pages 3-24 *in* B. D. Chepko-Sade and Z. T. Halpin, editors. Mammalian dispersal patterns. University of Chicago Press, Chicago, Illinois, USA.

Shields, W. M., and J. R. Crook. 1987. Barn Swallow coloniality: a net cost for group breeding in the Adirondacks? Ecology 68:1373–1386.

Usinger, R. L. 1966. Monograph of Cimicidae (Hemiptera-Heteroptera). Thomas Say Foundation 6.