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Ectoparasites reduce long-term survival of their avian host

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SUMMARY

Few field studies have evaluated whether ectoparasites affect the long-term survival of their adult host, although many studies have examined the impact of parasites on the host's offspring. In the colonially nesting cliff swallow (*Hirundo pyrrhonota*), we manipulated ectoparasite load (of cimicid bugs, fleas, and chewing lice) by fumigating adults and comparing annual survivorship of fumigated birds and non-fumigated control birds captured at the same time. Mark-recapture experiments over an 8-year period revealed that non-fumigated birds had an annual survivorship about 12 % less than that of fumigated birds, on average, but the effects did not vary with colony size. Based on the difference in survivorship between fumigated and non-fumigated birds, we estimated that parasitized individuals had an annual survivorship of 0.38, compared with 0.57 for non-parasitized birds. The parasite-caused reduction in survivorship was the equivalent of the host losing up to one year of lifetime reproductive success. Ectoparasites did not preferentially infest hosts of lower quality, suggesting that all birds in the population were at potential risk of suffering parasitism and the resulting reductions in survivorship. Our results show that obligate ectoparasites such as fleas and lice impose a substantial long-term cost to their hosts and suggest that future studies of ectoparasitism should consider the parasites' effect on annual survival of adult hosts.

1. INTRODUCTION

Parasitism is now generally regarded as costly to hosts. The costs may differ in magnitude among different animals but can be grouped broadly into those paid by the host's offspring directly (reduced growth and survival) and those paid by the parents (reduced survival or increased levels of resource acquisition; Moller 1994*a*). Most work to date has focused on the effects of parasites on the host's offspring, documenting how parasites reduce the number and quality of host offspring that survive (reviewed in Moller *et al.* 1990; Loye & Zuk 1991; Lehmann 1993; Clayton & Tompkins 1994), or how parents adjust resource provisioning of offspring in response to parasite load (Gustafsson *et al.* 1994; Moller 1994*b*).

Surprisingly little data exist to evaluate how parasites affect survival and future reproductive output of adult hosts (parents). This is the case despite the possibly general role of parasitism (operating directly on adult hosts) in sexual selection (see, for example, Hamilton & Zuk 1982; Moller 1990; Clayton 1991; Toft 1991). The few studies that have addressed the effects of parasites on adult survival have generally found little or no evidence that parasitism represents a survival-related cost in natural populations (Lehmann 1993; Clayton & Tompkins 1994, 1995; Lee & Clayton

1995; cf. Hudson & Dobson 1991). However, correlational studies alone are insufficient to demonstrate either an effect or a non-effect of parasites (Lee & Clayton 1995), and studying adult survival is further complicated by the need to follow the same individuals over an extended time to measure any long-term impact of parasites. Such longitudinal data are rarely obtained for most natural populations, and when available have seldom been related to parasite load.

We present here results of a study designed to measure the long-term effect of ectoparasites on a colonially breeding bird, the cliff swallow (*Hirundo pyrrhonota*). We employ an experimental approach involving manipulation of parasite load and combine that with long-term mark-recapture data collected over an 8-year period to measure the impact of ectoparasites on annual survival of their adult hosts. The insects that parasitized cliff swallows in our study were the swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), the bird flea (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*), and two species of chewing lice (Ischnocera: Philopteridae: *Brueelia longa*; Amblycera: Menoponidae: *Machaerilaemus malleus*).

2. METHODS

(*a*) *Study animals and study site*

The cliff swallow is a 20–28 g migratory passerine that breeds throughout most of western North America

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and winters in southern South America. These insectivorous birds build gourd-shaped mud nests and place them underneath overhanging rock ledges on the sides of steep canyons or underneath bridges and the eaves of buildings. Some nests can remain intact, and thus serve as a harborage for nest-based ectoparasites, for 10 or more years. Cliff swallows often breed in dense colonies, with nests stacked together closely, although colony size within a single population varies widely. At our study site, mean ($\pm$s.e.) colony size is 393.0 ($\pm$24.3) nests, ranging from birds that nest solitarily to colonies of 3700 nests in size. Cliff swallows typically have a short breeding season and raise only one brood (Brown & Brown 1995). At our study site, most birds arrive in May and breeding is largely completed by the end of July, at which time the swallows depart, presumably on migration.

The swallow bug lives primarily in the birds' nests. Infestations can exceed 2500 bugs per nest. Bugs frequently disperse among nests within a colony by crawling on the substrate but rarely travel on the bodies of the adult swallows (Rannala 1995; Brown & Brown 1996). Swallow bugs reduce prefledging and postfledging survivorship of nestlings and have other negative effects on the nestlings that survive to fledge (Brown & Brown 1986, 1996; Chapman & George 1991). Fleas live in the birds' nests and also travel for extended periods on the adult cliff swallows. Both fleas and swallow bugs feed on the birds' blood, and the per capita number of each in the nests generally increases with cliff swallow colony size (Brown & Brown 1986, 1996). The chewing lice live entirely on the bodies of the birds; the amblyceran species presumably feeds on blood, the ischnoceran on feathers (Marshall 1981; Clayton 1990; Lee & Clayton 1995). Bugs and fleas, and perhaps the amblyceran lice, are transmitted horizontally among nests within a colony, whereas the ischnoceran lice are transmitted principally vertically from parents to offspring (DeVaney et al. 1980; Clayton & Tompkins 1994).

Our study was conducted in a 150×50 km section along the North and South Platte rivers in southwestern Nebraska near Ogallala (primarily Keith and Garden counties). Within this area, cliff swallows occupy both natural cliff-nesting sites along the southern shore of Lake McConaughy and the North Platte River to the west, and also commonly nest underneath bridges and in highway culverts (Brown & Brown 1996). Our research focused on 25–30 colony sites per year, where birds could be easily mist-netted for capture and recapture.

(b) *Fumigation of birds*

Parasite load was manipulated by removing ectoparasites from cliff swallows via fumigation. After being mist-netted, birds were placed in a wide-mouthed jar with a rubber collar (Wheeler & Threlfall 1986; Brown & Brown 1996). The bird's head protruded from a small hole in the collar, with the rest of the body suspended inside the jar. Ether inside the jar anaesthetized and/or killed the ectoparasites hidden in the bird's feathers, causing them to fall out of the feathers and enabling us to count them inside the jar. Each bird remained in the jar for 20 minutes, and fumigation had no negative effects on cliff swallows (Brown & Brown 1996) or other birds (Fowler & Cohen 1983). All ectoparasites known to us (by visual examination) to be present on a bird's body exclusive of its head were collected in the jar; Fowler & Cohen (1983) found that this method removed 80–90% of lice known to be on birds that were later sacrificed. A total of 5219 birds were fumigated from 1987 to 1992. Non-fumigated birds were handled in similar ways but not placed in the sampling jar. At each colony we fumigated only a portion of the colony residents. Fumigated birds were a random subset of the birds captured in nets at each site. The individuals were chosen for fumigation at approximately uniform intervals over the time of a netting session (whenever a jar became empty, the next bird caught automatically went into it). A bird to be fumigated was chosen without considering any of its physical traits (e.g. size, mass, age, sex) and without knowing its previous capture history.

(c) *Mark-recapture and estimating survivorship*

The annual survivorship of fumigated and non-fumigated birds was estimated using long-term mark-recapture data. Each bird was given a numbered band, and its presence in the study area monitored each year through periodic mist-netting at each cliff swallow colony site (Brown & Brown 1996). Typically between 16000 and 21000 bird-captures in the study area were processed each year (a bird-capture was each time an individual was caught and data collected on it). Cliff swallows often escaped detection in a given year even when known to be alive (by virtue of their being caught in a later year), and therefore we had to follow each yearly cohort for several subsequent seasons in order to achieve consistent survivorship estimates (Brown & Brown 1996). Mark-recapture continued through 1994, giving us two years of recapture for our most recent (1992) cohort and a greater number of years for the earlier cohorts.

We used the computer program SURGE (Lebreton et al. 1992; Pradel & Lebreton 1993) to estimate survival probabilities for cohorts of fumigated birds and cohorts of control birds captured at the same time but not fumigated. SURGE computes survival probabilities using maximum likelihood methods and uses the pattern of recaptures distributed among years to calculate recapture probabilities. In our case recapture probabilities varied among years due to differences in capture effort (Brown & Brown 1996). Recapture probability represents a 'nuisance' parameter (Lebreton et al. 1992) which is used in generating the estimate of survivorship. In most cases we used a survival model in SURGE in which we estimated annual survivorship separately for the first year following fumigation (or, for non-fumigated birds, initial capture) and obtained another estimate for all later years combined (see Kanyamibwa et al. 1990, Pradel & Lebreton 1993). Annual survivorship reported here thus refers specifically to the first year after fumigation. In a few

cases where recapture data for a cohort were too few to allow us to estimate survivorship separately for the first year following fumigation and all later years, we used a model that yielded a single average annual survivorship estimated over all years of data. We used likelihood ratio tests (Kanyamibwa *et al.* 1990; Lebreton *et al.* 1992) to compare survival models for each cohort at each colony, with $p < 0.05$ as the criterion to accept a more complex model.

3. RESULTS

(*a*) *Distribution of ectoparasites on hosts*

Fleas and both species of chewing lice showed a typical contagious distribution among the hosts sampled (figure 1). The majority of cliff swallows had few or no ectoparasites, whereas a small fraction of birds carried relatively large numbers. The observed distribution of parasite species among hosts did not differ significantly from that expected under a negative binomial distribution (B. Rannala, unpublished results). Swallow bugs were found on only 0.34 % of birds ($n = 5219$) placed in the sampling jars (Brown & Brown 1996) and are not included in figure 1.

(*b*) *Effect of ectoparasites on annual survivorship*

Because annual survival probabilities of cliff swallows varied among different colony sites due to a variety of group-size effects (Brown & Brown 1996), we compared fumigated adults only with non-fumigated adults captured within the same season at the same colony. Pair-wise comparisons of annual survival probabilities for fumigated versus non-fumigated birds showed that survival was higher for fumigated birds in 37 of 45 colonies (figure 2); the preponderance of

Figure 2. Difference between annual survival probabilities of fumigated and non-fumigated adult cliff swallows in colonies of different sizes. Fumigated birds had higher survival at colonies above the dotted line and lower survival below the dotted line. The magnitude of the difference in survival probabilities did not vary significantly with colony size ($r_s = 0.04$, $p = 0.81$, $n = 45$ colony sites). In order of ascending colony size, sample sizes (number of birds marked) for fumigated and non-fumigated classes, respectively, for each site were 21, 61; 66, 14; 18, 60; 61, 80; 78, 19; 49, 125; 53, 38; 62, 91; 61, 146; 89, 54; 162, 270; 27, 361; 55, 189; 41, 120; 57, 138; 90, 121; 148, 338; 81, 135; 114, 373; 70, 341; 54, 377; 76, 18; 45, 83; 87, 246; 144, 162; 94, 279; 96, 554; 24, 369; 167, 369; 90, 706; 55, 462; 108, 511; 55, 399; 114; 166; 86, 1292; 570, 4017; 171, 1081; 55, 4455; 55, 328; 295, 639; 143, 1116; 63, 2767; 54, 3072; 84, 301; 135, 252. Sites where either fumigated or non-fumigated classes had n < 15 were excluded, due to problems with estimating annual survival probability for small cohorts.

positive differences was significant (binomial test, $p < 0.0001$). At the relatively few sites where non-fumigated birds had a higher survival probability, in most cases the difference was slight (figure 2). In contrast, at colony sites where fumigated birds had the advantage, their survivorship often differed greatly from that of non-fumigated individuals (figure 2). Colony size had no apparent effect on the magnitude of the difference between survival probabilities of fumigated and non-fumigated birds (figure 2). Survival probabilities of adult males and females are virtually identical in cliff swallows (Brown & Brown 1996), and therefore this analysis was not divided by sex.

The average annual survival probability ($\pm$ s.e.) for fumigated cliff swallows per colony ($n = 45$) was 0.57 (± 0.02), versus 0.50 (± 0.02) for non-fumigated birds exposed to natural levels of ectoparasitism. To compare these survivorships, we used the statistic,

$$\hat{D} = \hat{S}_f - \hat{S}_n, \tag{1}$$

where $\hat{S}_f$ is the survivorship of fumigated birds and $\hat{S}_n$ is that of non-fumigated birds. This statistic has an asymptotic normal distribution with standard error s.e. $(\hat{D}) = \sqrt{(\text{s.e.}(\hat{S}_f)^2 + \text{s.e.}(\hat{S}_n)^2)}$. If the null hypothesis, that there is no difference in survivorship between birds in the two classes, is true, the statistic $\hat{D}$ (equation 1) has expectation of zero. To test this null hypothesis, we constructed a 95 % confidence interval for $\hat{D}$
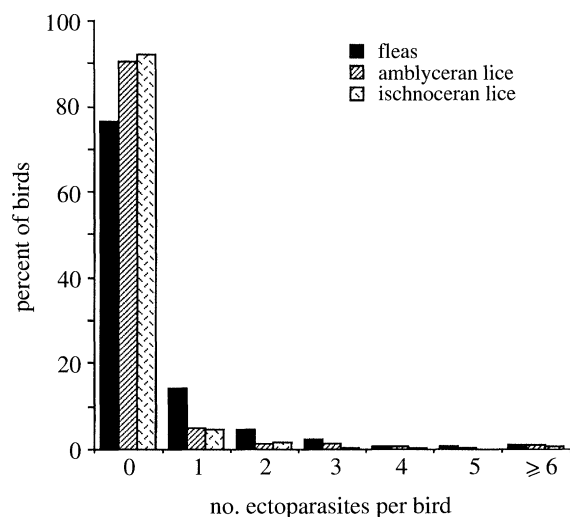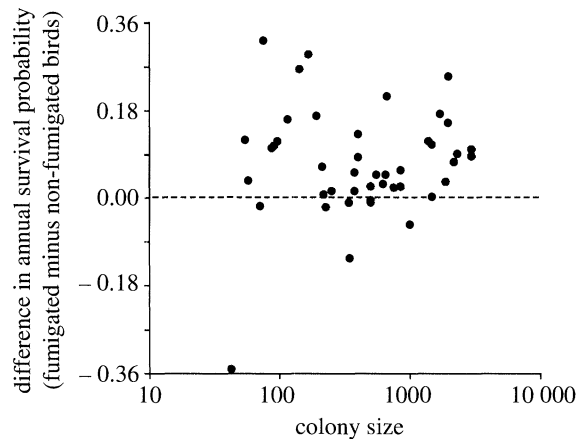

Figure 1. Percentage distribution of adult cliff swallows carrying different numbers of ectoparasites, as removed from birds in parasite-sampling jars during fumigation. For fleas, $n = 5219$ birds from 1987–1992; for amblyceran lice, $n = 2315$ birds from 1992; for ischnoceran lice, $n = 1555$ birds from 1992. Presence of lice was not recorded prior to 1992.

$(\hat{D} \pm 1.96 \times \text{s.e.}(\hat{D}))$ and determined whether it included zero. For the observed values of $\hat{S}_n$ and $\hat{S}_f$, we obtained a confidence interval for $\hat{D}$ of $[0.018, 0.124]$. Because this does not include zero, we reject the null hypothesis of no significant difference in survivorship between the two classes. Fumigated birds had significantly greater overall survivorship than non-fumigated ones.

Because non-fumigated birds also included ones without parasites (e.g. figure 1), we estimated the overall survivorship of the parasitized individuals by examining the difference in the overall survivorships of fumigated and non-fumigated birds. Let $\Delta S = S_f - S_n$, the difference in survivorship between fumigated and non-fumigated birds. Because $S_n = S_f p + S_p (1-p)$, we may represent ΔS as

$$\Delta S = (S_f - S_p)(1-p), \qquad (2)$$

where S_p is the survivorship of birds carrying one or more ectoparasites (i.e. fleas or lice), S_f is the survivorship of birds with no ectoparasites (assumed to be equivalent to that of the fumigated birds), and p is the probability that a particular bird is free of ectoparasites. Equation (2) may be rewritten to obtain an estimator of the survivorship of parasitized birds (S_p),

$$\hat{S}_p = \hat{S}_f - (\Delta\hat{S}/(1-\hat{p})). \qquad (3)$$

The standard error of the estimate $\hat{S}_p$ may be obtained using the method of quadrature (e.g. see Taylor 1982).

Using estimates (see figure 2) of $\hat{S}_f = 0.57$ (± 0.02) and $\hat{S}_n = 0.50$ (± 0.02), and with $\hat{p} = 0.63$ (± 0.01) (see figure 1), we estimate $\hat{S}_p = 0.38$ (± 0.06). Thus, parasitized individuals had an annual survivorship of 0.38, approximately 33% less than that of non-parasitized (fumigated) birds.

The increased survivorship of fumigated birds that we observed might have reflected a greater tendency for parasite-free birds to return to the same breeding colony site the following year, perhaps with the highly infested individuals more likely to disperse elsewhere the next year. We found this to be the case for yearling cliff swallows, which were more likely to return to their natal colony if the nest-based ectoparasite load (i.e. fleas and swallow bugs) there the previous summer had been low (Brown & Brown 1992). If the same pattern held for the older birds that were the focus of this study, we might have been more likely to encounter a fumigated bird the following season, which could have led us to estimate a higher apparent survivorship.

To determine whether this potential bias existed, we examined whether fumigated birds were more likely than non-fumigated birds to return to the same colony site the next year. Among 1060 fumigated birds recaught in a breeding colony the next year after fumigation, 399 (37.6%) returned to the same site. Among 9391 non-fumigated birds from the same initial colonies and years, 5012 (53.4%) returned to their same breeding site the next year. Fumigated birds were significantly *less* likely than non-fumigated birds to be encountered the next year at the same breeding colony ($\chi^2 = 94.4$, d.f. $= 1$, $p < 0.0001$). Thus, parasite-

mediated dispersal of the sort reported by Brown & Brown (1992) is unlikely to have biased our estimates of annual survival.

(c) *Ectoparasites and host quality*

We also examined whether ectoparasitism might have interacted with other phenotypic attributes of hosts to influence annual survivorship. For example, parasites might have more readily infested adults of lower overall health and immunological competence (Nelson *et al.* 1977; Marshall 1981). If so, the contagious distribution of ectoparasites among hosts (figure 1) could have reflected the distribution of susceptible individuals, and this correlation between host health and parasite load might contribute to any apparent 'effect' of ectoparasites on survivorship. However, in our study we chose birds to be fumigated without *apriori* knowledge of their existing parasite load, and therefore the observed increase in survivorship for fumigated individuals (figure 2) can be directly attributed to the fumigation and cannot be explained by inherent, non-parasite-related differences in health among parasitized (i.e. non-fumigated) and non-parasitized (i.e. fumigated) birds.

To test further the apparent independence of parasite load and quality of host phenotype, we estimated annual survivorship of fumigated birds which were carrying, at the time of fumigation, different numbers of fleas. We chose the extent of parasitism by fleas as an index of host quality only because we had the largest sample of birds for whom flea loads were known, compared to the other ectoparasites (figure 1). Average ($\pm$s.e.) annual survivorship of birds that had been carrying 0, 1, 2, 3, and ≥ 4 fleas at the time of fumigation was 0.532 (± 0.016) ($n = 3996$), 0.529 (± 0.038) ($n = 735$), 0.534 (± 0.063) ($n = 246$), 0.511 (± 0.078) ($n = 121$), and 0.534 (± 0.073) ($n = 121$), respectively. Thus, there was no evidence that birds carrying more fleas were inherently 'inferior', at least as measured by their ability to survive when ectoparasites were removed.

4. DISCUSSION

Because fumigation removed all of the ectoparasites present on each cliff swallow, we could not determine which one(s) were responsible for the effects on survivorship (figure 2). We can infer only that the swallow bugs probably had less effect than the other ectoparasites, given the very few that were encountered on adults (Brown & Brown 1996). Fleas probably contributed heavily to the effects on survival, given that they are deleterious to cliff swallows in other ways (Brown & Brown 1992, 1996). Chewing lice also can have negative effects on their avian hosts (Clayton 1990; Clayton & Tompkins 1994, 1995; Lee & Clayton 1995), although not before found to influence probability of annual survivorship for adults. Presumably the ischnoceran louse had less effect than the amblyceran species, because the vertically transmitted ischnocerans are generally less virulent than horizontally transmitted parasites such as fleas and amblyceran lice (Clayton & Tompkins 1994).

Possibly, too, the fumigation killed various mites (Dermanyssidae; see Howell & Chapman 1976) whose removal might also have contributed to higher survivorship among fumigated birds. We saw no mites on cliff swallows in our study area, but mites are hard to detect and might not fall off into the sampling jar when killed (D. Clayton, personal communication).

Regardless of the relative importance of each kind of ectoparasite, the suite of ectoparasites as a whole clearly imposed a substantial long-term cost for adult cliff swallows. The presence of ectoparasites reduced an individual's average annual survival probability by about 33% (from 0.57 to 0.38), translating into a reduction of about 9 months in mean life span for birds that enter the breeding population (calculated using methods of Brownie *et al.* (1985)). Given that a cliff swallow's annual breeding season lasts only 2–3 months, this reduction in mean life span suggests that ectoparasites can cost adult cliff swallows the equivalent of an entire year in lifetime reproductive success.

Colony size had no effect on the extent to which ectoparasites reduced adult cliff swallow survivorship (figure 2). This is unlike the pattern for nest-based ectoparasitism, primarily by swallow bugs, in which the effects increase with colony size (Brown & Brown 1986, 1996). However, the ectoparasites principally affecting adult swallows are fleas, which show only a weak increase in per capita adult infestation with colony size (Brown & Brown 1996), and the chewing lice, which also show either a weak increase or no correlation between per capita adult infestation and colony size (C. R. Brown & B. Rannala, unpublished results). Therefore, with these ectoparasites, an increased cost of parasitism in larger groups would not necessarily be expected.

Hosts of ectoparasites commonly develop acquired immunity to the parasites and their effects (Nelson *et al.* 1977; Randolph 1979; Willadsen 1980; Chiera *et al.* 1985; Marshall 1981), resulting in uneven parasitism among individuals within a host population. Other phenotypic or genetic differences among hosts may make certain ones easier to parasitize (Hamilton & Zuk 1982; Wakelin & Blackwell 1988; Barnard & Behnke 1990; Brown & Brown 1996). However, the relatively constant subsequent survivorship of adults that had been carrying different numbers of ectoparasites prior to fumigation suggested that parasites infest cliff swallows independent of any degree of acquired immunity or other survival-related measures of host 'quality'. The reductions in survivorship (figure 2) therefore are likely caused by ectoparasites without any interacting effect of host quality. Our results are unique in demonstrating that parasites lower adult host survivorship independent of host phenotype. Previous correlational studies have not been able to establish a causal link between parasitism and mortality because of the possibility of a confounding correlation between parasite load and host phenotype.

Ectoparasites may reduce survivorship of adult cliff swallows in several ways. One possible influence they may have is to lower the birds' body mass over the course of the nesting season (see, for example, Senar *et*

al. 1994). Fumigated adult cliff swallows lost less mass during the season, on average, than non-fumigated ones (C. R. Brown & B. Rannala, unpublished results), and thus parasite-free birds were in better physical condition at the start of the stressful fall migration. Greater mass at the end of the breeding season is advantageous, because in cliff swallows body mass is directly correlated with annual survivorship (Brown & Brown 1996). Furthermore, haematophagous parasites such as swallow bugs, fleas, and amblyceran lice cause blood loss that may result in anaemia in their hosts (e.g. Kirkwood 1967; Nelson *et al.* 1977; Marshall 1981; Chapman & George 1991; Lehmann 1993). Parasite-induced anaemia contributes to mass loss and causes increased mortality in some animals (Jellison & Kohls 1938). Although we had no direct measure of the cost of parasite-induced anaemia for adult cliff swallows, Chapman & George (1991) documented its negative effects for nestling cliff swallows.

Another possible way ectoparasites reduced adult survivorship was through feather loss. Chewing lice can remove a substantial amount of feather mass from their avian hosts; the lice usually feed on the downy feathers closest to the bird's skin (Nelson & Murray 1971; DeVaney 1976; Clayton 1990). Feather removal leads to an increased thermal conductance, requiring the host to raise its metabolic rate if it is to compensate (Booth *et al.* 1993). Increases in metabolic rate for small insectivorous birds such as swallows can be costly, especially during bad weather (Prinzinger & Siedle 1988; Bryant 1991), and may therefore influence annual survivorship.

Ectoparasites (especially lice) may also affect host survivorship by serving as vectors for a variety of endoparasitic cestodes and nematodes and some bacteria and viruses (see Marshall 1981; Clayton 1990; Lehmann 1993). Although we lack direct data on the degree to which these endoparasites and pathogens are harmful to hosts in general, it is assumed that they (and their ectoparasitic vectors) are sufficiently deleterious for their presence or absence to represent an important cue for mate choice (Hamilton & Zuk 1982; Borgia & Collis 1990; Clayton 1990, 1991; Hamilton 1990). Finally, ectoparasites may cause their avian hosts to increase their time spent in self-maintenance behavior, especially preening (Cotgreave & Clayton 1994). An increase in preening means less time available for foraging and anti-predator vigilance, with potential consequences for survivorship.

Given these potential costs of ectoparasitism to adult hosts in general and our results for cliff swallows in particular (figure 2), it is clear that studies which ignore the long-term effects of ectoparasites on the survivorship of adult hosts may be neglecting a major environmental component of host fitness. This is especially true for small birds such as cliff swallows in which lifespan is a major determinant of lifetime reproductive success (Clutton-Brock 1988; Newton 1989). Collecting the kind of data necessary to evaluate the impact of parasites on host survivorship requires longitudinal information on the same host individuals, and regrettably few such studies are being sustained in behavioral ecology at present.

REFERENCES

Barnard, C. J. & Behnke, J. M. (eds) 1990 *Parasitism and host behaviour*. London: Taylor and Francis.

Booth, D. T., Clayton, D. H. & Block, B. A. 1993 Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc. R. Soc. Lond.* B **253**, 125–129.

Borgia, G. & Collis, K. 1990 Parasites and bright male plumage in the satin bowerbird (*Ptilonorhynchus violaceus*). *Am. Zool.* **30**, 279–285.

Brown, C. R. & Brown, M. B. 1986 Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* **67**, 1206–1218.

Brown, C. R. & Brown, M. B. 1992 Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology* **73**, 1718–1723.

Brown, C. R. & Brown, M. B. 1995 Cliff swallow. In *The birds of North America* (ed. A. Poole & F. Gill), no. 149. Philadelphia: Academy of Natural Sciences.

Brown, C. R. & Brown, M. B. 1996 *Coloniality in the cliff swallow: the effect of group size on social behavior.* University of Chicago Press.

Brownie, C., Anderson, D. R., Burnham, K. P. & Robson, D. S. 1985 *Statistical inference from band recovery data – a handbook*, 2nd edn. Washington: U.S. Dept. Interior Res. Publ. 156.

Bryant, D. M. 1991 Constraints on energy expenditure by birds. *Acta Cong. Internatl. Ornithol.* **20**, 1989–2001.

Chapman, B. R. & George, J. E. 1991 The effects of ectoparasites on cliff swallow growth and survival. In *Bird-parasite interactions: ecology, evolution, and behaviour* (ed. J. E. Loye & M. Zuk), pp. 69–92. Oxford University Press.

Chiera, J. W., Newson, R. M. & Cunningham, M. P. 1985 Cumulative effects of host resistance on *Rhipicephalus appendiculatus* Neumann (Acarina: Ixodidae) in the laboratory. *Parasitology* **90**, 401–408.

Clayton, D. H. 1990 Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* **30**, 251–262.

Clayton, D. H. 1991 The influence of parasites on host sexual selection. *Parasitol. Today* **7**, 329–334.

Clayton, D. H. & Tompkins, D. M. 1994 Ectoparasite virulence is linked to mode of transmission. *Proc. R. Soc. Lond.* B **256**, 211–217.

Clayton, D. H. & Tompkins, D. M. 1995 Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology* **110**, 195–206.

Clutton-Brock, T. H. (ed.) 1988 *Reproductive success: studies of individual variation in contrasting breeding systems.* Univeristy of Chicago Press.

Cotgreave, P. & Clayton, D. H. 1994 Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour* **131**, 171–187.

DeVaney, J. A. 1976 Effects of the chicken body louse, *Menacanthus stramineus*, on caged layers. *Poultry Sci.* **55**, 430–435.

DeVaney, J. A., Quisenberry, J. H., Doran, B. H. & Bradley, J. W. 1980 Dispersal of the northern fowl mite, *Ornithonyssus sylviarum* (Canestrini and Fanzago), and the chicken body louse, *Menacanthus stramineus* (Nitzsch), among thirty strains of egg-type hens in a caged laying house. *Poultry Sci.* **59**, 1745–1749.

Fowler, J. A. & Cohen, S. 1983 A method for the quantitative collection of ectoparasites from birds. *Ringing Migr.* **4**, 185–189.

Gustafsson, L., Nordling, D., Andersson, M. S., Sheldon, B. C. & Qvarnstrom, A. 1994 Infectious diseases, reproductive effort and the cost of reproduction in birds. *Phil. Trans. R. Soc. Lond.* B **346**, 323–331.

Hamilton, W. D. 1990 Mate choice near or far. *Am. Zool.* **30**, 341–352.

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science, Wash.* **218**, 384–387.

Howell, F. G. & Chapman, B. R. 1976 Acarines associated with cliff swallow communities in northwest Texas. *Southwestern Nat.* **21**, 275–280.

Hudson, P. J. & Dobson, A. P. 1991 The direct and indirect effects of the caecal nematode *Trichostrongylus tenuis* on red grouse. In *Bird-parasite interactions: ecology, evolution, and behaviour* (ed. J. E. Loye & M. Zuk), pp. 49–68. Oxford University Press.

Jellison, W. L. & Kohls, G. M. 1938 Tick-host anemia: a secondary anemia induced by *Dermacentor andersoni* Stiles. *J. Parasitol.* **24**, 143–154.

Kanyamibwa, S., Schierer, A., Pradel, R. & Lebreton, J. D. 1990 Changes in adult annual survival rates in a western European population of the white stork *Ciconia ciconia. Ibis* **132**, 27–35.

Kirkwood, A. C. 1967 Anaemia in poultry infested with the red mite *Dermanyssus gallinae. Vet. Rec.* **80**, 514–515.

Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.

Lee, P. L. M. & Clayton, D. H. 1995 Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecol. Entomol.* **20**, 43–50.

Lehmann, T. 1993 Ectoparasites: direct impact on host fitness. *Parasitol. Today* **9**, 8–13.

Loye, J. E. & Zuk, M. (eds) 1991 *Bird-parasite interactions: ecology, evolution, and behaviour.* Oxford University Press.

Marshall, A. G. 1981 *The ecology of ectoparasitic insects.* London: Academic Press.

Moller, A. P. 1990 Parasites and sexual selection: current status of the Hamilton and Zuk hypothesis. *J. evol. Biol.* **3**, 319–328.

Moller, A. P. 1994*a* Parasites as an environmental component of reproduction in birds as exemplified by the swallow *Hirundo rustica. Ardea* **82**, 161–172.

Moller, A. P. 1994*b* Parasite infestation and parental care in the barn swallow *Hirundo rustica*: a test of the resource-provisioning model of parasite-mediated sexual selection. *Ethology* **97**, 215–225.

Moller, A. P., Allander, K. & Dufva, R. 1990 Fitness effects of parasites on passerine birds: a review. In *Population*

biology of passerine birds (ed. J. Blondel, A. Gosler, J. D. Lebreton & R. McCleery), pp. 269–280. Berlin: Springer-Verlag.

Nelson, B. C. & Murray, M. D. 1971 The distribution of mallophaga on the domestic pigeon (*Columba livia*). *Intl J. Parasitol.* **1**, 21–29.

Nelson, W. A., Bell, J. F., Clifford, C. M. & Keirans, J. E. 1977 Interaction of ectoparasites and their hosts. *J. med. Entomol.* **13**, 389–428.

Newton, I. (ed.) 1989 *Lifetime reproduction in birds.* London: Academic Press.

Pradel, R. & Lebreton, J. D. 1993 *User's manual for program SURGE: version 4.2.* Saint-Georges-D'Orques, France: Avenix.

Prinzinger, R. & Siedle, K. 1988 Ontogeny of metabolism, thermoregulation and torpor in the house martin *Delichon u. urbica* (L.) and its ecological significance. *Oecologia* **76**, 307–312.

Randolph, S. E. 1979 Population regulation in ticks: the role of acquired resistance in natural and unnatural hosts. *Parasitology* **79**, 141–156.

Rannala, B. H. 1995 Demography and genetic structure in island populations. Ph.D. dissertation, Yale University, New Haven, Connecticut.

Senar, J. C., Copete, J. L., Domenech, J. & Von Walter, G. 1994 Prevalence of louse-flies Diptera, Hippoboscidae parasiting [sic] a cardueline finch and its effect on body condition. *Ardea* **82**, 157–160.

Taylor, J. R. 1982 An introduction to error analysis. New York: Oxford University Press.

Toft, C. A. 1991 Current theory of host-parasite interactions. In *Bird-parasite interactions: ecology, evolution, and behaviour* (ed. J. E. Loye & M. Zuk), pp. 3–15. Oxford University Press.

Wakelin, D. & Blackwell, J. M. (eds) 1988 *Genetics of resistance to bacterial and parasitic infection.* London: Taylor and Francis.

Wheeler, T. A. & Threlfall, W. 1986 Observations on the ectoparasites of some Newfoundland passerines (Aves: Passeriformes). *Can. J. Zool.* **64**, 630–636.

Willadsen, P. 1980 Immunity to ticks. *Adv. Parasitol.* **18**, 293–313.