Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success

PATRICIA L. M. LEE and DALE H. CLAYTON
Department of Zoology, University of Oxford

Abstract. 1. We censused ectoparasite populations of adult and nestling swifts over the course of the host's breeding season. Nearly all of the birds were infested with chewing lice and two-thirds of the nests were infested with louse flies. Feather mites were observed but not quantified.

2. Lice and louse flies both showed aggregated distributions among hosts. Louse eggs, hatched lice and adult louse flies had negative binomial distributions, whereas the aggregated distribution of louse fly pupae was not adequately described by negative binomial or Poisson models.

3. Transmission of lice from parents to offspring was documented. A comparison of the age structure of lice on parents and offspring indicated that most transmission was by nymphal lice.

4. Host reproductive success and survival appeared to be independent of the number of lice or louse flies. Neither parasite correlated with the number, body mass, or date of fledging of young birds, nor with the overwinter survival of adults. We caution, however, that experimental manipulations of parasite load are required for a definitive test of the impact of ectoparasites on evolutionary fitness components.

Key words. Transmission, virulence, lice, Phthiraptera, louse fly, Hippoboscidae, Diptera, bird, Apodidae.

Introduction

Although numerous studies have tested the impact of ectoparasites on their hosts (reviewed by Lehmann, 1993), far less attention has been given to the ecology of the ectoparasites themselves. This is regrettable because some ectoparasites are among the most tractable of all animal populations. In the case of 'permanent' ectoparasites, which complete their entire life cycle on the host (Schmidt & Roberts, 1989; Lehane, 1991), the parasite niche is delineated entirely by the host's integument. This makes it possible to collect accurate data on the population structure of permanent ectoparasites using simple unobtrusive counts (Clayton, 1991a). The principle aim of the present study was to collect such data for the chewing louse, *Dennyus hirundinis* (Linnaeus) (Phthiraptera: Menoponidae), a permanent parasite of the swift (*Apus apus* (Linnaeus)). By collecting data from breeding birds and their offspring we hoped to measure vertical trans-

Correspondence: Dr Dale Clayton, Department of Zoology, South Parks Road, Oxford OX1 3PS.

mission (parent to offspring) of chewing lice in a wild host population for the first time. The most detailed study prior to ours is that of Rust (1974), who measured louse populations of pocket gophers, but not transmission of lice among individual hosts.

We also collected data on the wingless louse fly, *Crataerina pallida* (Latreille) (Diptera: Hippoboscidae), another ectoparasite of swifts, but one which does not complete the entire life cycle on the host's body. In addition, we conducted a preliminary test of the impact of lice and louse flies on host reproductive success and survival.

Swifts are aerial, insectivorous birds which breed in Europe and overwinter in southern Africa. The swifts in this study were breeding in nest-boxes in the tower of the Oxford University Museum of Science. Swifts have been using these boxes since they were set up in 1948 (Lack, 1956). Birds in the museum colony normally arrive from the South African wintering grounds during the first week of May. Eggs are laid 2–3 weeks later and are incubated for 3 weeks. Young birds fledge at a mean age of 41 days post-hatching (range = 37–51, *N* = 96) in late July and early August and immediately begin the long migratory

flight to Africa. Swifts do not breed until 4 years of age (Perrins, 1971), after which they normally return to the same nest-box each year. Mate fidelity among years is high (Weitnauer, 1947; Lack, 1958).

D.hirundinis feeds on feathers, dermal debris, blood and eye fluid (Rothschild & Clay, 1952; Bromhall, 1980). On several occasions during this study we noted blood oozing from crushed abdomens of this species of louse. Blood feeding has also been documented for other species of Menoponid lice (Wilson, 1933; Crutchfield & Hixson, 1943; Kalamarz, 1963; Seegar *et al.*, 1976; Agarwal *et al.*, 1983; Saxena *et al.*, 1985; Triverdi *et al.*, 1990).

Louse flies feed solely on blood (Bequaert, 1953). Adult *C.pallida* feed approximately every 5 days and they may take up to 25 mg per feeding (Kemper, 1951). This represents nearly 5.0% of the total blood volume of an average swift, assuming total volume to be approximately 10% of a bird's body weight (Campbell, 1988).

Transmission of *D.hirundinis* among individual hosts is constrained by the fact that swifts spend most, if not all, of their time flying when away from the nest. Swifts do not perch in trees because of their short legs and weak feet, nor do they perch on the ground because their long wings make vertical take-off difficult (Lack, 1956). The main route of dispersal for swift lice is thought to be vertical transmission from adult birds to their offspring in the nest (Dubinin, 1947). Horizontal transmission (transmission between unrelated hosts) may also occur between mated adults and between unrelated males engaged in prolonged fights over nest-boxes (Lack, 1956). DNA profiling reveals little extra-pair paternity in the Oxford swift colony (<5.0%, J. Blakey, unpublished), making extra-pair copulations an unlikely route for louse transmission.

Unlike lice, which are confined to the body of the host, *C.pallida* is more capable of locomotion off the host. For example, we sometimes observed louse flies on our clothing. Nevertheless, there appears to be very little horizontal transmission of *C.pallida* among nests (Lee, pers. obs.). A mark–recapture experiment (Summers, 1975) showed little horizontal transmission of the congeneric species *Crataerina hirundinis*, which lives in the nests of house martins (*Delichon urbica*). Only six of ninety-six marked flies moved between nests in Summer's (1975) study.

Lice on swifts are easy to quantify for several reasons. *D.hirundinis* eggs, which are glued to the feathers with a glandular cement, are white in colour and large enough (1 mm long) to see easily in the host's plumage. Adult lice are also large and easy to see (males: 2.4 mm long; females: 3.2 mm). Nymphal instars are smaller, yet their unsclerotized cuticles are light in colour, making them relatively easy to see against the host's black plumage. *D.hirundinis* has fairly small, tractable populations (less than twelve adults per host).

Louse flies on swifts are also easy to quantify. Adult flies are large (7 mm) and easy to observe on the host or in its nest. Although flies are active during the host's breeding season, they overwinter as pupae in the nest (Hutson, 1981). There are no records of adult flies on wintering

swifts in Africa (Zumpt, 1966). The pupae, which are deposited in the nest after completion of the larval stage inside the female fly, are glossy black and fairly large (4 mm), making them easy to see. Louse flies also occur in small, tractable populations (less than twenty adults per nest).

Materials and Methods

Parasite counts. Parasites on adult and nestling swifts and in their nests were counted periodically over the course of the host's breeding season (May–August 1992). To reduce the risk of abandonment, adult birds were examined only after their eggs hatched. They were removed from the nest-box at night for up to 1 h. This was not detrimental to swift nestlings, which are unusual among altricial birds in not requiring continuous brooding by the parents (Lack, 1956). With one exception, there were no cases of abandonment or nestling mortality due to our handling procedures.

Prior to examination, each adult's feet were wrapped in surgical tape to minimize struggling and immobilize the sharp claws. Each bird was replaced in the nest-box after being handled and was prevented from leaving by blocking the entrance. Adults usually calmed down within minutes, after which the entrance was unblocked.

Each bird's plumage was searched with the aid of a 2× jeweller's headset under a 60 W lamp. All feather tracts were examined systematically and forceps were used to check the bases of feathers as well as their distal regions. Because swifts are small-bodied (about 43 g), it was possible to examine each bird's plumage thoroughly in under 30 min. It was not necessary to restrict counts to subsamples of plumage, as for larger birds (cf. Clayton, 1991a).

Most adult birds were examined for parasites between early June and early July, when the young were less than 2 weeks of age and not yet infested with lice. A few late breeding adults were examined in late July. To document changes in louse load over time, a sub-sample of adults ($N = 31$) was rechecked an average of 3 weeks after the first parasite count (range 9–32 days). A smaller subsample ($N = 11$) was rechecked again about 12 days after the second count (range 9–14 days).

Nestlings were examined in the daytime while the parents were out foraging. The young birds were checked on the first day after hatching, then re-examined from one to ten times depending on survivorship. After removing nestlings, but prior to examining them for parasites, the nest was searched for parasites for a period of 1 min with illumination from a hand-held light. Thus nestlings were examined in conjunction with an examination of their nest. Nests were also searched at regular intervals early in the study prior to egg laying and hatching.

When counting ectoparasites we tallied the number of louse eggs, hatched lice and louse flies on each bird. We also counted the number of hatched lice, louse flies and pupae in the nest cup. Louse flies were often observed in the nest, but lice were rarely observed off the host's body.

All lice were aged and sexed on the basis of the following criteria: adults are more heavily sclerotized than nymphs and darker in coloration; females are 20% larger than males (Clay & Hopkins, 1950; Ledger, 1971). No attempt was made to separate nymphal instars or to sex louse flies during parasite counts.

Indices of parasite load. Two measures of parasite load were used: prevalence and intensity. For lice, prevalence was the proportion of birds infested and intensity was the number of lice on an individual bird. Mean intensity was the average number of lice per bird, including uninfested birds, analogous to Marshall's (1981a) 'infestation rate' and Margolis *et al.*'s (1982) 'relative density'.

For louse flies prevalence was the proportion of nests infested (flies in nest cup and/or on nestlings) and intensity was the number of flies in an individual nest and/or on its nestlings. Mean intensity was the average number of flies per nest, including uninfested nests. In calculating louse fly loads for nests, most of which were examined more than once over the course of the study, we used the maximum number of flies at any one count. This reduced the chance of missing flies that were temporarily away from the nest on foraging adults. As *C.pallida* has but one generation per year, with flies emerging more or less synchronously in the spring (Huston, 1981; pers. obs.), this approach should have been not confounded by short-term increases in louse fly populations.

Relationship of parasite load to host reproduction and survival. The relationships of parasite load to fledging success, date of fledging and prefledging body mass were examined for nests from which data were collected within a week of fledging (*N* = 26 nests). Prefledglings, defined as nestlings >35 days old, were weighed to the nearest 0.1 g with a Pesola balance.

For this analysis the louse loads of sibling young were averaged to avoid pseudoreplication (Hurlbert, 1984). Because nestlings sometimes fledged prior to examination, the values for some nests do not represent a mean for all of the young reared in that nest. However, a comparison of the parasite data from birds in 'complete' (*N* = 19) nests

with data from 'incomplete' (*N* = 7) nests did not differ significantly (Mann-Whitney tests: $Z = -0.88$, $P = $ ꞏꞏ (for louse eggs on nestlings) and $Z = -0.09$, $P = $ ꞏꞏ (for hatched lice on nestlings)). The two categories were therefore combined for the analyses.

Overwinter survival of adults was estimated by checking the ring numbers of birds returning to the tower in ꞏꞏ The relationship of louse intensity to the probability of returning was analysed using a logistic regression model generated by Statistix Analytical Software, v4.0(2). All birds in this analysis were examined for parasites over a 10 day period (10–19 June 1992).

Statistical analyses. As the parasite data were not normally distributed we used nonparametric statistics for most of the analyses, which were performed using Statistix SE+Graphics™, v1.02, 1988. Expected negative binomial distributions of parasites were generated using Statgraphics Statistical Graphics System v5.1, and expected Poisson distributions were generated using Minitab v8.1. Frequencies were aggregated in the tails of the distributions to make expected frequencies >5 for chi-square tests.

Results

Eighty-seven adult swifts, 118 young and fifty-two nests were examined for parasites over the course of the study. Most individual birds were infested with lice and about two-thirds of the nests were infested with louse flies (Table 1). *Eureum cimicoides*, another chewing louse sometimes found on swifts, was not present in our colony. The feather mites *Eustathia cultrifera* and *Chauliacia securigera* (Acarina: Eustathiidae) were observed but not counted. No other ectoparasites were seen during the study.

Frequency distributions of parasites among hosts were aggregated: most birds had few parasites, whereas a few had many (Fig. 1). Observed distributions of hatched lice and emerged louse flies were not different from negative binomial distributions (Chi-square tests: $\chi^2 = 13.37$, $df = 12$, $P = 0.34$; $\chi^2 = 2.49$, $df = 5$, $P = $ ꞏꞏ

Table 1. Prevalence and intensity of ectoparasites infesting adult and prefledgling swifts.

| Ectoparasite	Prevalence	Age/sex	Range per bird/nest	Mean intensity ± SE
Dennyus hirundinis	94% of adult birds (*N* = 87)	Eggs	0–73	8.8 ± 1.3
		Hatched lice	0–12	1.9 ± 0.2
		Nymphs	0–12	0.9 ± 0.2
		Males	0–4	0.6 ± 0.1
		Females	0–4	0.5 ± 0.1
	92% of prefledging birds (*N* = 49)	Eggs	0–8	1.4 ± 0.3
		Hatched lice	0–18	6.0 ± 0.6
		Nymphs	0–12	2.7 ± 0.4
		Males	0–11	1.7 ± 0.3
		Females	0–6	1.6 ± 0.2
Crataerina pallida	67% of nests (*N* = 52)	Pupae	0–9	1.7 ± 0.4
		Emerged flies	0–5	1.0 ± 0.2
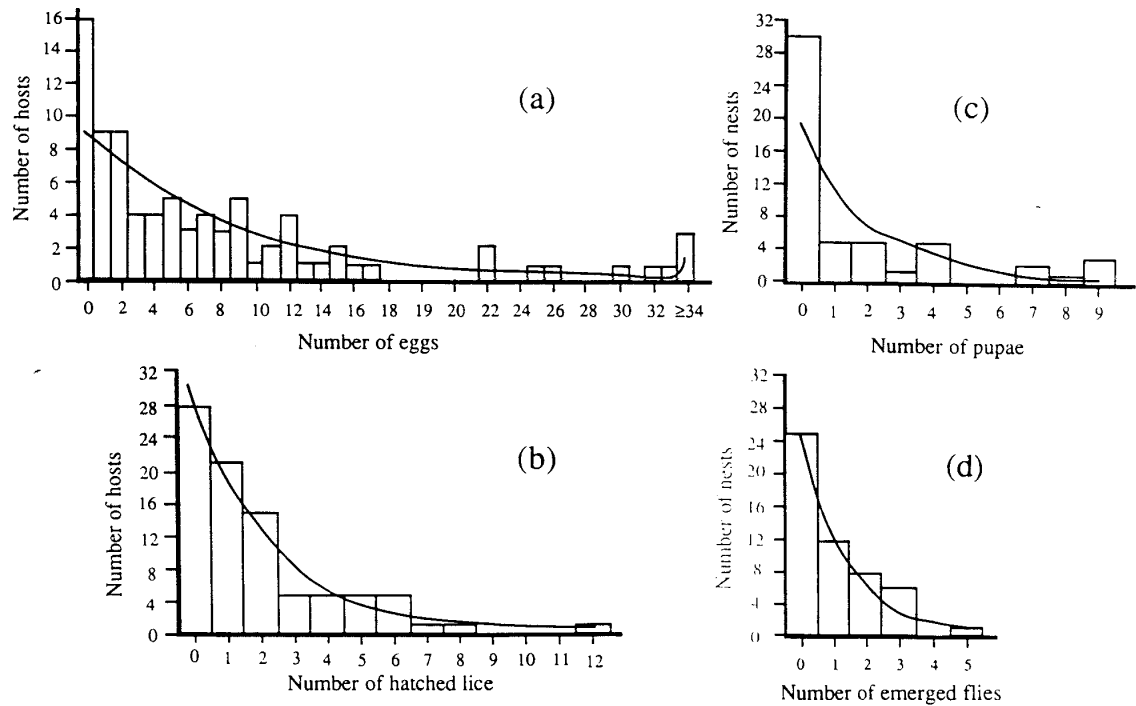
Fig. 1. Observed frequency distributions (bars) of *D.hirundinis* (a) eggs ($k = 0.6$, mean $= 8.8$, $s^2 = 145.2$) and (b) hatched lice ($k = 1.1$, mean $= 1.9$, $s^2 = 5.2$) on adult swifts ($N = 87$). Observed distrubutions of *C.pallida* (c) pupae ($k = 0.3$, mean $= 1.7$, $s^2 = 7.4$) and (d) emerged flies ($k = 1.7$, mean $= 1.0$, $s^2 = 1.4$) in swift nests ($N = 52$). Expected negative binomial distributions are shown as curves.
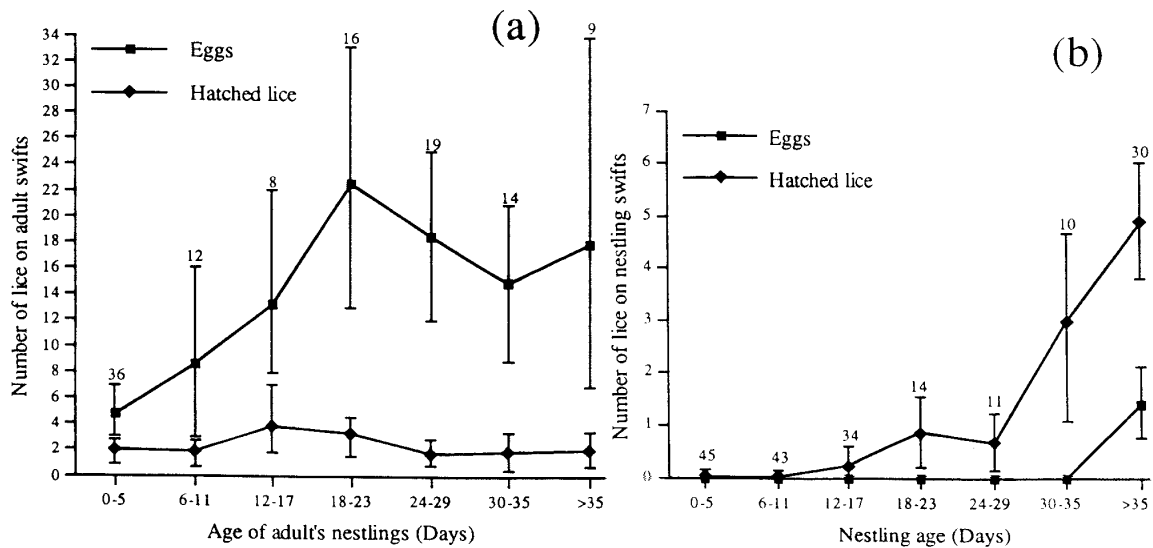

Fig. 2. Mean intensity of eggs and hatched lice on (a) adult and (b) nestling swifts over the course of the study. Error bars are 95% boot-strapped confidence intervals. Values above error bars are the number of birds examined during each interval. The data include repeat examinations of the same birds among intervals, but no repeats within intervals.
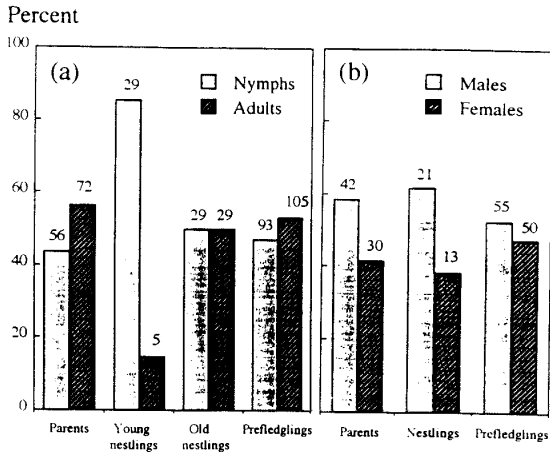
Percent

Fig. 3. (a) Age ratios of lice infesting parents ($N = 69$). young nestlings (<24 days old: $N = 20$), old nestlings (24−35 days old: $N = 17$) and prefledglings (>35 days old: $N = 30$). Numbers of lice are shown above bars. (b) Sex ratios of lice infesting parents ($N = 69$). nestlings ($N = 37$) and prefledglings ($N = 30$). None of the data include repeat examinations of the same birds.

and $\chi^2 = 0.62$, df = 3, $P = 0.89$ respectively). The distribution of louse fly pupae did not fit a negative binomial distribution ($\chi^2 = 10.84$, df = 3, $P = 0.01$) (Fig. 1c), nor a Poission distribution ($\chi^2 = 22.45$, df = 3, $P = 0.0001$).

Prefledgling swifts (>35 days of age) had significantly more hatched lice than adults ($Z = -0.42$ (male lice); $Z = -5.01$ (female lice); $Z = -5.04$ (nymphs); $P < 0.0001$ for all). But prefledglings had significantly fewer louse eggs than adults ($Z = -5.35$, $P < 0.0001$). The mean intensity of hatched lice on mated adults, examined when their offspring were less than 2 weeks of age, did not correlate with the mean intensity of lice on their prefledgling offspring (Spearman rank correlation: $r_s = 0.20$, $P = 0.38$, $N = 20$). However, the mean intensity of louse eggs on mated adults was significantly correlated with the mean intensity of hatched lice on their prefledglings ($r_s = 0.58$, $P = 0.01$, $N = 20$).

The temporal dynamics of louse populations on adult and nestling birds showed different patterns. The number of hatched lice on adults remained fairly constant over time (Fig. 2a) and was not correlated with count date ($r_s = 0.08$, $P = 0.36$), nor with the age of an adult's nestlings ($r_s = -0.71$, $P = 0.42$). In contrast, the number of louse

eggs on adult birds was correlated with count date ($r_s = 0.5$, $P < 0.0001$) and nestling age ($r_s = 0.42$, $P < 0.0001$).

For nestlings both the number of hatched lice and the number of eggs were correlated with age ($r_s = 0.57$ and $r_s = 0.33$, $P < 0.0001$ for both). Nestlings had few hatched lice until they were about 2 weeks of age, after which louse intensities increased rapidly (Fig. 2b). However, nestlings were free of louse eggs until they reached prefledging age (>35 days old).

The ratios of adult to nymphal lice on parents, old nestlings (well feathered) and prefledglings were not significantly different ($\chi^2 = 2.0$, df = 1, $P = 0.16$; $\chi^2 = 0.0$, df = 1, $P = 1.0$; $\chi^2 = 0.73$, df = 1, $P = 0.39$) (Fig. 3a). In contrast, most of the lice on young nestlings were nymphs ($\chi^2 = 16.94$, df = 1, $P < 0.0001$).

The ratio of male to female lice was not significantly different on adult swifts ($\chi^2 = 2$, df = 1, $P = 0.16$), prefledglings ($\chi^2 = 0.24$, df = 1, $P = 0.63$) or nestlings ($\chi^2 = 1.88$, df = 1, $P = 0.17$) (Fig. 3b).

Relationship of parasite load to host reproduction and survival

Data were collected for prefledglings in twenty-six nestboxes. One to three birds fledged from each of these boxes between 21 July and 1 August. None of the three components of reproductive success (number fledged, fledging date or body mass) was significantly correlated with parasite prevalence or intensity (Table 2). Mean body mass of prefledglings was $45.4\,\text{g} \pm 0.8\,\text{SE}$ (range 35.5−57.0 g). There was a marginally nonsignificant, positive correlation between louse intensity and prefledgling body mass (Table 2). Furthermore, the body mass of louse-free nestlings ($39.8\,\text{g} \pm 2.5\,\text{SE}$; $N = 3$ nests) was significantly lower than that of louse-infested nestlings ($46.1\,\text{g} \pm 0.8\,\text{SE}$; $N = 23$ nests, Mann-Whitney test: $Z = -2.21$, $P = 0.03$). However, the number of young fledged from louse-free nests did not differ significantly from the number fledged from louse-infested nests ($Z = -1.23$, $P = 0.22$), nor was there a significant difference in the mean fledging dates of young from the two groups ($Z = -0.81$, $P = 0.42$).

Fly-free nests ($N = 16$) did not differ significantly from fly-infested nests ($N = 10$) in the number ($Z = -0.27$, $P = 0.79$), timing ($Z = -0.24$, $P = 0.81$) or body mass ($Z = -1.45$, $P = 0.15$) of young birds fledged.

Of thirty-six adult swifts examined for lice on 10−19 June 1992, nineteen (53%) returned to the tower in 1993,

Table 2. Spearman rank correlation coefficients between ectoparasite intensities and fitness components of prefledgling swifts (values for siblings averaged, $N = 26$ nests). (P values in parentheses.)

Host fitness component	Dennyus hirundinis		Crataerina pallida		Total hatched/emerged ectoparasites
	Eggs	Hatched lice	Pupae	Emerged flies	
Fledging date	0.218 (0.27)	0.087 (0.66)	−0.095 (0.64)	0.048 (0.81)	0.104 (0.60)
No. fledged	0.277 (0.17)	−0.063 (0.75)	0.076 (0.70)	0.050 (0.80)	−0.038 (0.85)
Body mass	0.001 (0.99)	0.375 (0.06)	−0.051 (0.80)	0.216 (0.28)	0.337 (0.09)

a rate similar to previous years (Perrins, 1971). Neither the number of louse eggs (coefficient = -0.07, $P = 0.23$) nor the number of hatched lice (coefficient $= 0.47$, $P = 0.08$) was significantly correlated with the probability of adults returning.

Discussion

We surveyed populations of lice and louse flies on adult swifts and their offspring over the course of the host's breeding season. Nearly all birds had chewing lice and two-thirds of the nests were infested with louse flies. The numbers of both lice and louse flies varied considerably among individual hosts (Fig. 1). Both groups of parasites showed aggregated distributions, as reported for other species of lice (Eveleigh & Threlfall, 1976; Fowler & Williams, 1985; Clayton & Tompkins, 1994b) and for louse flies (Marshall, 1981a). Louse eggs, hatched lice and adult louse flies had negative binomial distributions. However, the aggregated distribution of louse fly pupae was not adequately described by a negative binomial or a Poisson distribution.

Parasites usually show aggregated distributions among hosts (Anderson & May, 1982). Several factors appear to contribute to this, including heterogeneity of host behaviour, effective immunity of hosts, direct reproduction within hosts, and spatial heterogeneity in the distribution of infective stages (Anderson & Gordon, 1982, Anderson & May, 1982). Any of these factors may have contributed to the aggregated distributions of lice and louse flies observed in our study.

The intensity of hatched lice that we observed on adult birds was low and remained fairly constant during the study, ranging from two to four lice per bird. This is similar to intensities reported for other species of *Dennyus* on swifts comparable to *Apus apus* in body size (e.g. *Chaetura* and *Cypseloides*; Clayton *et al.*, 1992). The ratio of male to female lice did not differ significantly from unity. This is the case for most species of bird lice (Marshall, 1981b; Wheeler & Threlfall, 1986; Clayton *et al.*, 1992).

The intensity of louse flies was also low, averaging just one fly per nest. To our knowledge, this is the first study to quantify louse flies in swift nests.

The intensity of lice on young birds changed considerably over the course of the study. Young birds were infested with lice as early as 2 weeks of age, by which time the tips of their developing feathers had emerged. However, louse eggs were not observed on nestlings until after 5 weeks of age. Thus the lice on young nestlings must have come from the parent birds. Nestlings had no contact with birds other than their parents while in nest (pers. obs.). The number of eggs on parents was significantly correlated with the number of hatched lice on their offspring.

Transmission of lice from parents to offspring was mainly by nymphs. Significantly more nymphs than adult lice were present on young nestlings, whereas there was no age bias in the lice of older nestlings, prefledglings or adult birds (Fig. 3a). Apparently, one reason for the relatively

constant number of lice on adult birds over time (Fig. 2a) was that nymphs hatching from the growing population of eggs soon dispersed to young birds in the nest.

Adult lice were not moving onto nestlings to lay eggs. Nestlings had no eggs until they reached prefledgling age (Fig. 2b), despite the fact that they were well feathered by 3 weeks of age, providing a substrate for lice. The generation time of most lice is about a month (Marshall, 1981a). Therefore one would expect nymphs transmitted to nestlings to mature and begin laying eggs 3–4 weeks later. This is precisely when the first eggs were detected on nestlings. Experiments with marked lice could shed further light on the details of louse transmission. However, Phthirapteran lice can be sensitive to direct handling (Rust, 1974; Clayton, 1991a) so we avoided marking in the present study.

Many authors have assumed that bird lice disperse primarily by vertical transmission from parents to their offspring (e.g. Boyd, 1951; Rothschild & Clay, 1952; Woodman & Dicke, 1954; Blagoveshchenskii, 1959; Ash, 1960; Dogiel, 1964; Brock, 1967; Baum, 1968; Foster, 1969; McGroarty & Dobson, 1974; Eveleigh & Threlfall, 1976; Marshall, 1981a; Rankin, 1982; Fowler & Williams, 1985; Wheeler & Threlfall, 1986; Borgia & Collis, 1990; Clayton, 1990). Our study is the first to actually measure vertical transmission of lice in wild birds. We documented the timing and rate of transmission by both adult and nymphal lice, as well as the rate of deposition of louse eggs.

Two implications of vertical transmission have received attention recently in the literature. The first is the suggestion that vertically-transmitted parasites should evolve reduced virulence, as their fitness is closely tied to that of the host (Anderson & May, 1982; Ewald, 1983; Lehmann, 1992, 1993). This hypothesis was confirmed by Clayton & Tompkins (1994a, b), who showed that lice have no impact whatsoever on the reproductive success of captive pigeons (*Columba livia*), compared to horizontally transmitted mites which drive reproductive success to zero. Pigeon lice were transmitted vertically from parents to offspring after the tips of the developing feathers had emerged.

Vertical transmission is also relevant to the theory of parasite-mediated sexual selection (PMSS). One model of PMSS predicts that female hosts will choose mates on the basis of traits which allow them to avoid males with parasites that might be transmitted vertically to offspring in the nest or to the females themselves (Møller, 1990; Clayton, 1991b). Our results confirm that bird lice are suitable candidates for such a process, as suggested by several authors (Borgia & Collis, 1990; Clayton, 1990; Møller, 1990; Spurrier *et al.*, 1991).

Relationship of parasite load to host reproduction and survival

None of the components of host reproductive success that we measured correlated with parasite intensity. Neither the intensity of lice nor that of louse flies correlated with

the number, body mass, or date of fledging of young birds. Parasites were also independent of the overwinter survival of adult birds. Although it is tempting to conclude from these data that swift lice have no impact on the host — particularly as they are vertically transmitted — to draw such a conclusion would be premature. Correlational data such as these are not sufficient to test for potential effects of parasites on components of host fitness. Controlled manipulations of parasite numbers are required for a more definitive test of the impact of parasites on the host (Booth *et al.*, 1993; Lehmann, 1993; Clayton & Tompkins, 1994a, b). Such manipulation in this study would have interfered with its principle aim, which was to document the natural population biology of swift lice.

The aggregated distribution of parasites among hosts means that relatively few individuals are heavily parasitized. Nevertheless, high intensities of parasites on a small fraction of the host population could still represent a strong agent of selection on host phenotypes (Clayton *et al.*, submitted). Experimental manipulations that increase the proportion of hosts with high intensities, while keeping within the range of naturally occurring intensity, are extremely useful for testing the impact of parasites on components of host fitness (Booth *et al.*, 1993; Clayton & Tompkins, 1994a, b).

In our study there was a significant relationship between parasite prevalence and one component of host reproduction: twenty-three louse-infested nests contained significantly heavier nestlings than did three louse-free nests. This surprising result suggests a reversal of the causal arrow discussed above; large nestlings may be capable of supporting more lice than small nestlings. But just as manipulations of parasite load are needed to test for effects of parasites on host fitness, manipulations of nestling growth would be needed to test for an impact of nestling size on louse populations. Given the reciprocal nature of host—parasite interactions, it is important to test the impact of host parameters on the survival and reproductive success of parasites, as well as the impact of parasites on the survival and reproduction of hosts. To our knowledge, reciprocal studies of this kind have not been performed.

Acknowledgments

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