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Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*)

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Summary

1. Parasites that are transmitted vertically from parent hosts to offspring are expected to be relatively benign, because their fitness depends on successful host reproduction. The effects of two species of vertically transmitted ectoparasite on the reproductive success of swifts (*Apus apus L.*) were tested. Populations of the Chewing Louse, *Dennyus hirundinis (L.)* (Phthiraptera: Menoponidae), and the Flightless Louse Fly, *Crataerina pallida (Latreille)* (Diptera: Hippoboscidae), were experimentally manipulated, effectively converting the natural aggregated frequency distribution of each species into a bimodal distribution of high and low loads.

2. Neither parasite had any effect on nestling growth or fledging success, even though parasite loads were boosted above natural levels and host environmental conditions were poor during part of the study, thus increasing the chances of detecting an effect of the parasites.

3. In contrast to parasite load, year, brood size and hatch date were all significantly related to components of nestling growth. Year and brood size were also significantly related to fledging success.

4. These results are consistent with theoretical models suggesting that vertically transmitted parasites evolve reduced virulence because they depend on host reproduction for dispersal to new hosts.

Key-words: Chewing Lice, Hippoboscidae, Louse Fly, Phthiraptera, virulence

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Introduction

Ectoparasites are known to reduce several components of avian fitness (Lehman 1993; Brown, Brown & Rannala 1996) and influence a range of host life-history variables (Møller 1996). Some ectoparasites, however, appear to have little or no effect on the host (Clayton & Tompkins 1994, 1995). Observational studies of Chewing Lice and Louse Flies on Swifts (*Apus apus*) and of Louse Flies on Alpine Swifts (*Apus melba*) showed no correlation between parasite load and host condition, survival or reproductive success (Hutson 1981; Lee & Clayton 1995; Tella *et al.* 1995). One possible reason for the apparent avirulence of swift lice and flies is that observational studies lack the inferential power required to detect subtle effects. Parasites generally show an aggregated frequency distribution among hosts, with most individuals having few parasites and a few individuals having many parasites (Anderson & Gordon 1982). Subtle effects of such parasites may be overlooked unless very large samples are studied (Booth, Clayton & Block 1993).

An alternative explanation for avirulence is that Swift Lice and Flightless Louse Flies, both of which are vertically transmitted from parent hosts to their offspring, have evolved reduced virulence. All else being equal, vertically transmitted parasites are expected to be less virulent than parasites capable of horizontal transmission to unrelated hosts because the fitness of vertically transmitted parasites is tightly linked to the reproductive success of the host (Anderson & May 1982; Ewald 1983; Clayton & Tompkins 1994). In reducing host fitness, vertically transmitted parasites reduce their own fitness, thus selecting for a reduction in virulence.

An experimental field study was conducted to test whether vertically transmitted ectoparasites of swifts have an impact on host reproductive success. Lice and Louse Flies were transferred among nests to convert the aggregated distributions of these parasites (Lee & Clayton 1995) into bimodal distributions of high- and low-load nests. The growth and fledging success of nestlings in high- and low-load nests were then

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compared. Nestling body mass is known to be influenced by environmental factors such as weather (Bryant 1978), and is often correlated with post-fledging size and survival in birds (Boag 1987; Magrath 1991). Body mass is therefore a component of fitness that parasites might easily affect (Møller 1994). For example, Johnson & Albrecht (1993) reported a slight impact of haematophagous ectoparasites on the body mass of nestling House Wrens, even though they detected no impact of ectoparasites on haematocrit, tarsal growth or feather growth.

The effect of several non-parasite factors (year, brood size and hatching date) on nestling growth and fledging success was also examined. These variables are known to have strong effects on the reproductive success of Swifts (Lack & Lack 1951; Lack 1956a) and are also known to interact with parasite effects on avian hosts (de Lope *et al.* 1993; Møller 1993). Finally, blood and faecal samples were taken to check nestlings for endoparasites. Both Chewing Lice and Louse Flies act as vectors for avian endoparasites (Baker 1967; Balashov 1984), transmission of which may be one of the fitness costs of ectoparasite infestation of Swifts (Dutton 1905).

Materials and methods

BACKGROUND

Swifts (*Apus apus* (Linnaeus)) are aerial, insectivorous birds that breed in Eurasia and overwinter in sub-Saharan Africa (small numbers winter in northern India and Arabia) (Chantler & Driessens 1995). The Swifts in this study were breeding in nest boxes in the tower of the Oxford University Museum of Science. Swifts have used these boxes annually since 1948 (Lack 1956b). Birds in the museum colony normally arrive from the South African wintering grounds during the first week of May. A clutch of two to three eggs is laid several weeks later and is incubated for three weeks. Young birds fledge in late July or early August at a mean age of 41 days post-hatching (range = 37–51, n = 96) (Lee & Clayton 1995). Soon after fledging they begin the long migratory flight to Africa. Swifts do not breed until four years of age (Perrins 1971); they often use the same nest site each year.

The most common species of Chewing Louse on Swifts is *Dennyus hirundinis* (Linnaeus). It is a 'permanent' ectoparasite that completes its entire life cycle on the body of the host (Lee & Clayton 1995). *D. hirundinis* feeds on dermal debris, blood and host eye-fluid (Rothschild & Clay 1952; Bromhall 1980; Lee & Clayton 1995).

The Flightless Louse Fly *Crataerina pallida* (Latreille) (which has vestigial wings) is a nest-based parasite that feeds on Swift blood (Bequaert 1953). Adults feed about every five days and take up to 25 mg of blood per feeding (Kemper 1951); this amount is nearly 5·0% of the total blood volume of an adult Swift (Lee & Clayton 1995). The life cycle of *C. pallida* is attuned to that of its host, with adult flies emerging during early summer from pupae that have overwintered in the nest (Marshall 1981). There are no records of adult flies on wintering Swifts in Africa (Zumpt 1966).

D. hirundinis populations are relatively easy to quantify (Lee & Clayton 1995). The eggs, which are glued to the feathers with a glandular cement, are large enough to see with the naked eye (1 mm long) and are white, making them easy to detect in the host's dark plumage. The post-hatching stages, consisting of three nymphal instars and the adult, are also relatively large and easy to see. Populations of *D. hirundinis* are usually fairly small and are therefore tractable (fewer than 12 adults per host) (Lee & Clayton 1995).

C. pallida populations are also easy to quantify (Lee & Clayton 1995). Adult flies are large (7 mm) and easy to observe on the host or in its nest. The pupae are large (4 mm) and black, making them easy to see in the nest, particularly in the Museum Tower, where each nest is in a solidly constructed nest box. Like Swift Lice, Louse Flies occur in small, tractable populations (fewer then 5 adults per nest) (Lee & Clayton 1995).

Transmission of *D. hirundinis,* which requires direct contact among individual Swifts, is constrained by the fact that Swifts spend all of their time flying when away from the nest (Lack 1956b). The main route of dispersal for Swift Lice is vertical transmission from adult birds to their offspring in the nest (Lee & Clayton 1995). Lice are presumably also exchanged between mated adults. Some horizontal transmission may occur between unrelated males during prolonged fights over nest boxes at the start of the breeding season (Lack 1956b). DNA fingerprinting reveals little extra-pair paternity in the museum swift colony (less than 5·0%) (Jeremy Blakey, unpublished data), making extra-pair copulations an unlikely route of louse transmission.

Louse Flies, unlike lice, are capable of efficient locomotion away from the body of the host (Marshall 1981). Nevertheless, there is little horizontal transmission of the flightless *C. pallida* among nests in the studied colony (Lee & Clayton 1995; D. M. Tompkins, personal observations). The present study was carried out over two host breeding seasons; there was a strong correlation between number of pupae in nests at the end of the first breeding season and number of emerged flies in nests at the beginning of the second breeding season (Spearmann $\rho = 0{\cdot}84$, $n = 36$, $P < 0{\cdot}001$). In addition, nests with high numbers of flies at the beginning of a breeding season (natural loads or experimentally increased; see below) maintained high numbers through to the end of that season. Nests with low numbers of flies at the beginning of a breeding season (natural loads or experimentally decreased) maintained low numbers through to the

end of that season. Even under conditions of high density, flies did not transmit horizontally between nests. The nearest neighbour distance for each nest in this study was 0·23 m, but most nests were much further away (nest boxes in the Museum Tower are arranged in pairs). An independent 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 96 flies (6·25%) dispersed between different nests in Summer's (1975) study, which had a nearest-neighbour distance of 0·13 m. Thus, Flightless Louse Flies, like lice, are mainly transmitted vertically.

EXPERIMENTAL PROTOCOL

The study was carried out in May–August 1993 and 1994. Lice and Louse Flies were manipulated by manually transferring them from donor (low-load) to recipient (high-load) nests. Nests were assigned treatments by using a randomized block design. Nests containing at least two nestlings were blocked into groups of three nests based on brood size (two or three nestlings) and hatching synchrony (eggs hatching within a span of 4 days). One nest in each block was randomly assigned as a recipient. The other two nests were assigned as donors. Nests with brood sizes of one were also used as donors, but were excluded from all analyses.

The goal of the transfers was to boost the parasite loads of recipient nests above the natural loads observed in the swift colony during May–August 1992 (see Lee & Clayton 1995). Several donor nests were required to create each high-load recipient nest. Over the course of two field seasons a total of 13 high-louse nests (eight in 1993, five in 1994), and 13 high-fly nests (six in 1993, seven in 1994) were created. This left 44 nests with low loads of both parasites (23 in 1993, 21 in 1994). Three nests in 1993 were given high loads of both parasites (these nests are already included in the sample sizes for high-load nests given above). Nests with high parasite loads in the first year of the study were assigned as low-load nests in the second year.

Nests were checked between the hours of 0800 and 1200 every day in 1993 and every other day in 1994. Adults were normally away foraging at this time of day, except for a one-week period of non-stop brooding immediately after the eggs hatched. At each visit, nestling mass was measured to the nearest 0·1 g with a pesola spring balance. Nestmates were distinguished by clipping the tip of one toenail.

Lice were moved from adult birds in donor nests to nestlings in recipient nests when the nestlings were 16–18-days old. This is the age at which transmission of lice, from adults to nestlings, begins (Lee & Clayton 1995). Lice are never seen on nestlings before this age (Lee & Clayton 1995; D. M. Tompkins, personal observations). Swifts in donor nests were examined for periods of 10 min under a headlamp; Lice and Louse Flies observed were removed with a pooter or forceps and placed in a 1·5-ml microcentrifuge tube. Within several hours the parasites were transferred to nestlings in recipient nests. Lice not captured during the initial transfer were moved from donor nestlings during a second bout of transfers when recipient nestlings were 25–27 days of age. When nestlings reached pre-fledging age (35–37 days) their Louse populations were quantified as described in Lee & Clayton (1995).

Flies were moved from donor to recipient nests when both contained nestlings 1–3-days old. Throughout the study, nests and nestlings were searched for flies every 1–2 days for a period of 1 min with illumination from a headlamp. Any flies encountered in donor nests after the initial transfer were distributed evenly among recipient nests. At the end of the breeding season (2 weeks after the departure of all birds) the contents of each nest box were thoroughly examined for newly deposited fly pupae to check for evidence of flies that had been missed previously.

When nestlings were 25–27 days of age a blood smear was taken to check for blood parasites. Smears were fixed in 100% ethanol and stained in Giemsa's solution. Faecal samples were also taken from nestlings 25–37-days old to check for coccidean parasites. Samples were collected whenever defaecation was observed (0800–1200). Faecal samples were stored in 2·5% potassium dichromate and treated with saturated NaCl solution to float off coccidia. Blood and faecal samples were searched for parasites using 10× and 40× objectives of a phase-contrast microscope.

STATISTICAL ANALYSES

A modified Richards sigmoid growth model (Brisbin, White & Bush 1986) was fitted to the body mass measurements of each nestling. As body-mass recession occurs in Swift nestlings prior to fledging (Lack & Lack 1951) growth curves were fitted from hatching through two days after the maximum recorded mass was attained (approximately 25 days of age). Three parameters for each growth curve were predicted: asymptotic mass, growing period (hatching through age at asymptote) and the Richards shape parameter (m). Near m = 2·0, 0·67, 0·0 or when $\rightarrow$ 1·0, the Richards model becomes the logistic, von Bertalanffy, monomolecular or Gompertz models, respectively (Richards 1959). A fourth parameter, mean growth rate, was calculated by dividing asymptotic mass by growing period. Measurements of fledging mass and age were taken from the raw data. Mean parameter values per nest were analysed by using 'General Linear Models', incorporating year, brood size, hatch date, louse load and fly load as separate factors. All non-significant interaction factors were discarded.

Only nestlings that survived to fledge were included in the analyses. Mean hatching dates were assigned to one of three weeks in order to test for temporal trends in reproductive success (all nests hatched between 14 June and 4 July in 1993, and between 21 June and 11 July in 1994).

Fledging success was analysed non-parametrically by using contingency tests. Nestlings that disappeared before the minimum fledging age (37 days) (Lack 1956b) were presumed to have fallen through the hole in the floor that forms the entrance to each nest box (Lack 1956b). Dead nestlings were occasionally recovered at the base of the tower.

To investigate the possibility of Type II errors in the analyses of parasite effects on components of nestling growth, a statistical power test was carried out (Lipsey 1990). Johnson & Albrecht (1993) reported a slight impact of haematophagous ectoparasites on nestling body mass that had an 'effect size' of approximately 0·75. 'Effect size' is the difference in the mean of the variable under consideration in two experimental groups divided by the common standard deviation (Cohen 1988). An 'effect size' of 0·75 was used to calculate the power of this study to detect effects of ectoparasites on Swift nestlings that were equal in magnitude to those detected in the Johnson & Albrecht study (equivalent to a difference in swift nestling growth rate of approximately 0·04 g day^{-1}).

Results

PARASITE LOADS

High-louse, high-fly and low-load nests had similar parasite loads before manipulation: mean (± SD) louse loads on nestlings 16–18-days old were 0·44 ± 0·61 lice per nestling in low-louse nests, compared with 0·46 ± 0·97 lice per nestling in high-louse nests (Mann–Whitney $U = 303$, $P = 0·57$). Mean fly loads in nests of nestlings 1–3-days old were 1·20 ± 2·55 flies in low-fly nests, compared to 1·00 ± 1·53 flies in high-fly nests ($U = 316$, $P = 0·58$).

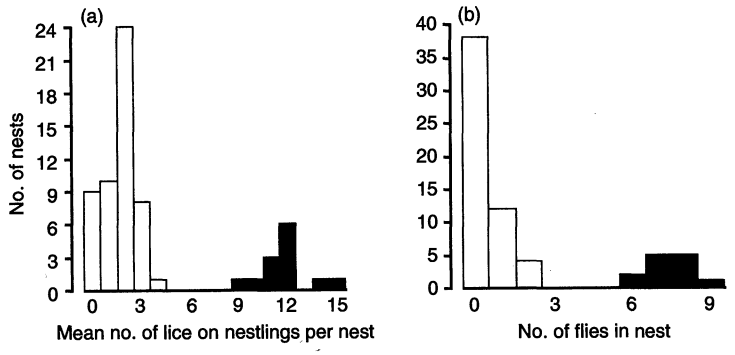

Fig. 1. (a) Distribution of chewing lice on nestlings 35–37 days old. (b) Distribution of louse flies (maximum observed) in nests. Open bars are donor (low-load) nests; shaded bars are recipient (high-load) nests.

Experimental transfer of lice between nests had the desired effect. At the 25–27-day old census, low-louse nests had a mean of 0·48 ± 0·58 lice per nestling compared with 3·46 ± 0·88 lice per nestling in high-louse nests ($U = 1$, $P < 0·001$). At the 35–37-day old census, low-louse nests had a mean of 1·65 ± 1·01 lice per nestling compared with 11·69 ± 1·44 lice per nestling in high-louse nests (Fig. 1a) ($U = 0$, $P < 0·001$).

In comparing fly loads, the maximum number of flies observed at any one count was used. This minimized the chance of missing flies temporarily away from the nest attached to foraging adult hosts. As *C. pallida* has but one generation per year, with flies emerging more or less synchronously in the spring (Lee & Clayton 1995), this approach would not have been confounded by short-term increases in Louse Fly populations. Over the course of the study a mean maximum of 0·37 ± 0·62 flies was observed in low-fly nests compared with 7·39 ± 0·87 flies in high-fly nests (Fig. 1b) ($U = 0$, $P < 0·001$). At the end of the breeding season low-fly nests contained a mean of 0·09 ± 0·35 new pupae compared with 9·54 ± 3·28 new pupae in high-fly nests ($U = 0$, $P < 0·000\,1$).

No haematozoa were detected in any of the blood samples examined ($n = 89$). Likewise, no coccidia were detected in the faecal samples examined ($n = 182$).

NESTLING SURVIVAL

Neither parasite had a significant effect on fledging success (Fig. 2). Forty-four of 54 low-louse nests fledged their entire brood, compared with 10 of 13 high-louse nests (Fisher exact $P = 0·49$). Forty-three of 54 low-fly nests fledged their entire brood, compared with 11 of 13 high-fly nests (Fisher exact $P = 0·78$). In contrast, year did have a significant effect on fledging success (Fig. 2c): 24 of 34 nests fledged their entire brood in 1993, compared with 30 of 33 nests in 1994 ($\chi^2 = 4·41$, $P = 0·04$). Brood size also had an effect on fledging success (Fig. 2d): 34 of 38 nests with broods of two fledged their entire brood, compared with 20 of 29 nests with broods of three ($\chi^2 = 4·41$, $P = 0·04$). Hatch week had no significant effect on fledging success: 14 of 18 nests (78%) with eggs hatching in week 1 fledged their entire brood, compared with 15 of 20 nests (75%) with eggs hatching in week 3 (Fisher exact $P = 0·57$).

NESTLING GROWTH

Neither parasite had a significant effect on any component of nestling growth (Figs 3 and 4). Nestlings in low- and high-louse nests did not differ significantly in asymptotic mass ($F_{1,57} = 0·10$, $P = 0·75$), growing period ($F_{1,57} = 0·30$, $P = 0·58$), growth rate ($F_{1,57} = 0·53$, $P = 0·47$), Richards shape parameter ($F_{1,57} = 0·44$, $P = 0·51$), fledging mass ($F_{1,57} = 0·62$, $P = 0·44$), or fledging age ($F_{1,57} = 0·02$, $P = 0·90$). Likewise,

nestlings in low- and high-fly nests did not differ significantly in asymptotic mass ($F_{1,57} = 0{\cdot}25$, $P = 0{\cdot}62$), growing period ($F_{1,57} = 0{\cdot}43$, $P = 0{\cdot}51$), growth rate ($F_{1,57} = 0{\cdot}24$, $P = 0{\cdot}63$), Richards shape parameter ($F_{1,57} = 0{\cdot}04$, $P = 0{\cdot}85$), fledging mass ($F_{1,57} = 0{\cdot}00$, $P = 1{\cdot}00$) or fledging age ($F_{1,57} = 0{\cdot}14$, $P = 0{\cdot}71$).

On the other hand, year, brood size and hatch week all had significant effects on components of nestling growth (Figs 3 and 4). Nestlings in 1993 had lower asymptotic mass ($F_{1,57} = 59{\cdot}86$, $P < 0{\cdot}001$), slower growth rates ($F_{1,57} = 13{\cdot}26$, $P = 0{\cdot}001$), higher Richards shape parameters ($F_{1,57} = 4{\cdot}65$, $P = 0{\cdot}04$), and fledged at a later age ($F_{1,57} = 4{\cdot}75$, $P = 0{\cdot}03$) than did nestlings in 1994. However, there was no significant difference in growing period ($F_{1,57} = 0{\cdot}49$, $P = 0{\cdot}49$) or fledging mass ($F_{1,57} = 0{\cdot}53$, $P = 0{\cdot}47$) between the two years.

Nestlings from broods of two had higher asymptotic mass ($F_{1,57} = 16{\cdot}19$, $P < 0{\cdot}001$), longer growing periods ($F_{1,57} = 4{\cdot}78$, $P = 0{\cdot}03$), lower Richards shape parameters ($F_{1,57} = 16{\cdot}07$, $P < 0{\cdot}001$), and higher fledging mass ($F_{1,57} = 11{\cdot}84$, $P = 0{\cdot}001$) than nestlings from broods of three [with no difference in growth rate ($F_{1,57} = 0{\cdot}03$, $P = 0{\cdot}86$) or fledging age ($F_{1,57} = 0{\cdot}89$, $P = 0{\cdot}35$)]. There was also a marginally significant year × brood size interaction with regard to asymptotic mass. The difference between asymptotic mass for nestlings in different brood sizes was greater in 1993 [49·63 ± 1·10 (SD) for broods of 2 compared with 43·96 ± 1·17 for broods of 3] than in 1994 (55·01 ± 1·11 for broods of 2 compared with 53·12 ± 1·09 for broods of 3) ($F_{1,57} = 4{\cdot}07$, $P = 0{\cdot}05$).

Nestlings hatched in weeks 1 and 2 had higher asymptotic mass ($F_{2,57} = 4{\cdot}43$, $P = 0{\cdot}02$) than nestlings hatched in week 3 (Fig. 3), but there was no difference in growing period ($F_{2,57} = 0{\cdot}10$, $P = 0{\cdot}91$), growth rate ($F_{2,57} = 0{\cdot}43$, $P = 0{\cdot}65$), Richards shape parameter ($F_{2,57} = 0{\cdot}15$, $P = 0{\cdot}86$), fledging mass ($F_{2,57} = 1{\cdot}25$, $P = 0{\cdot}30$) or fledging age ($F_{2,57} = 1{\cdot}10$, $P = 0{\cdot}34$).

The power of the analyses to detect a 0·75 'effect size' of either parasite on any component of nestling growth was 70% at $\alpha = 0{\cdot}05$ (two-tailed). If the type I error probability is increased to $\alpha = 0{\cdot}10$ (which can be done for parasite effects in this study without

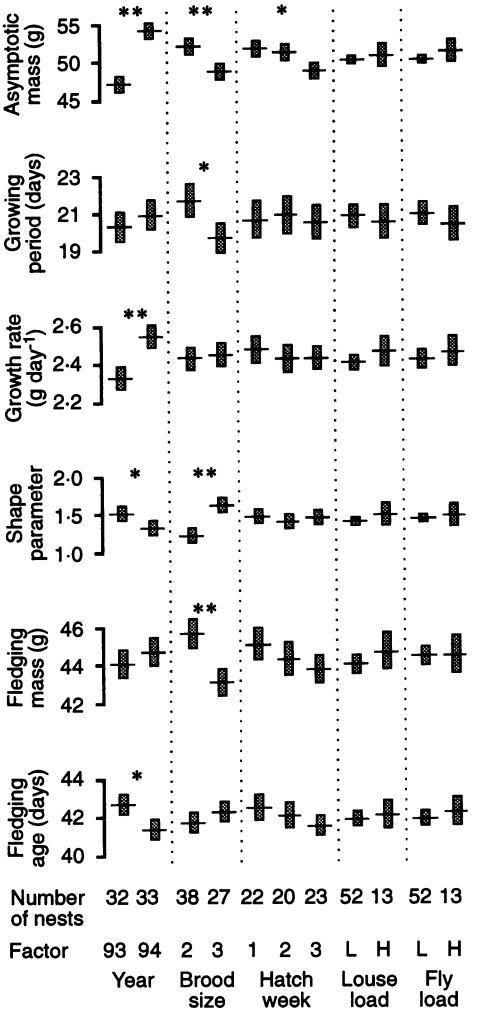

Fig. 3. Impact of various factors on components of nestling growth. Values are Means (± SD) adjusted for all other factors (as fitted to the data by 'General Linear Model' analyses). For parasite loads L = low-load nests, H = high-load nests; * $P < 0{\cdot}05$, ** $P \leq 0{\cdot}001$).

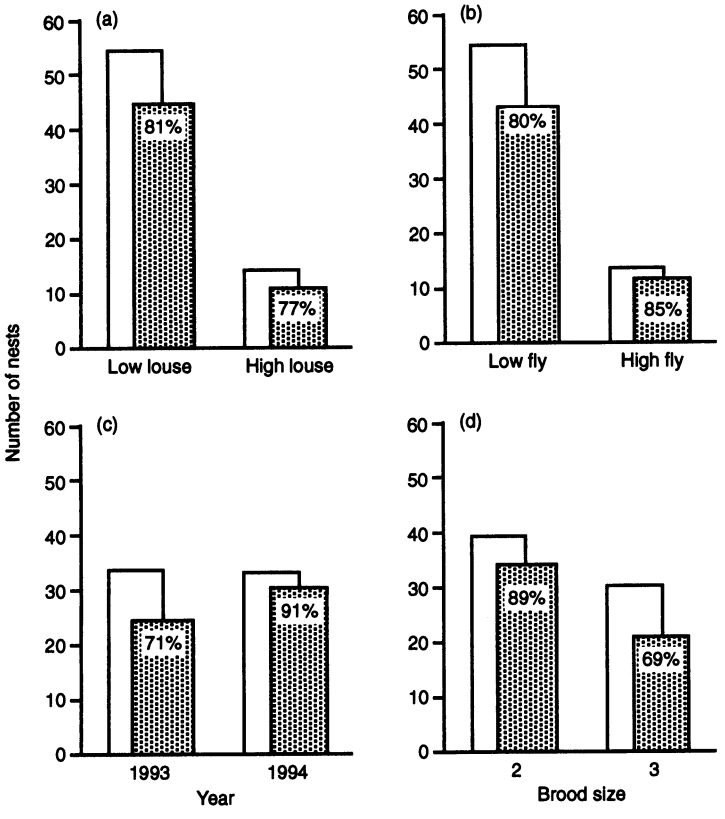

Fig. 2. Number of nests that fledged all young (stripped bars) contingent upon sample size (open bars) in nests with (a) low versus high louse loads, (b) low versus high fly loads, (c) nestlings hatched in 1993 versus 1994, and (d) nests with broods of two versus three. Values in bars are the percentages of nests that fledged all young.

shifting any result to significance) power increases to 80%, which is the standard level of statistical power recommended for experimental research (Cohen 1988). Thus, the power of the high-load versus low-load comparisons was adequate.

Discussion

Our manipulations of ectoparasite load were effective. High-load nests had significantly more lice and flies than low-load nests (Fig. 1). The number of parasites in high-load nests exceeded natural loads by a considerable margin. The median number of lice on high-louse nestlings 25–27-days old was six-fold greater than the natural median observed on birds of the same age in the tower colony in 1992 (3·0 versus 0·5) (P. Lee, personal communication). The median number of lice on high-louse nestlings 35–37-days old was more than twice the natural median observed on birds of the same age in 1992 (12 versus 5). The median number of flies in high-fly nests was seven times the natural median observed in the tower colony in 1992 (7 versus 1).

There was no significant effect of either ectoparasite on any component of nestling survival (Fig. 2) or growth (Figs 3 and 4), despite the fact that the experimental manipulations of both parasites were of sufficient power to detect even slight effects. This result is striking in light of the fact that 1993 was a very bad year for Swift reproduction in Oxford owing to heavy rainfall (see below).

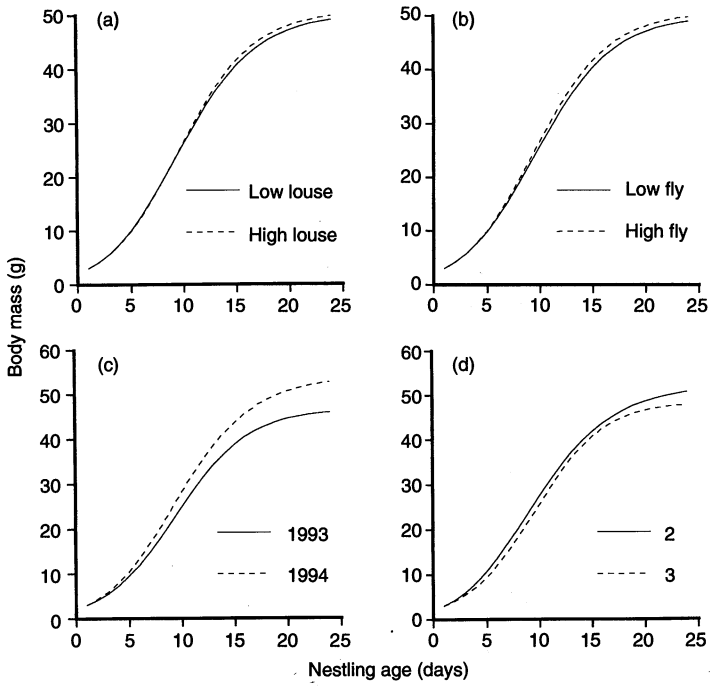

Fig. 4. Impact on nestling growth (to asymptotic body mass) of (a) louse load, (b) fly load, (c) year and (d) brood size. Curves were generated by fitting mean parameters for each group of nests back into the modified Richards growth model used.

Nestlings in 1993 suffered higher mortality, had lower asymptotic mass, slower growth rates, higher Richards shape parameters, and fledged at a later age than those in 1994 (Figs 2, 3 and 4). Yearly differences in the condition of Swift nestlings have been documented previously (1947–56) (Lack 1956a), with rainfall being the major causal factor, owing to reduced food abundance in wetter conditions (Koskimies 1950) (greater rainfall during the nestling period led to lower nestling body mass). The proportion of days on which rain fell during the six-week period after the first nestlings hatched in 1993 was much greater than in 1994 [28 of 42 days (67%) in 1993, 14 of 42 days (33%) in 1994, χ^2 = 9·33, P = 0·002]. In fact, 1993 was wetter than the worst year recorded (1953) in Lack's (1956a) ten-year study, when rain fell on only 27 of the 42 days (64%).

Several non-parasite factors, in addition to year, were also significantly related to components on nestling survival (Fig. 2) and growth (Figs 3 and 4). Nestlings from broods of two suffered lower mortality, had higher asymptotic mass, longer growing periods, lower Richards shape parameters and higher fledging mass than nestlings from broods of three. An effect of brood size on nestling growth and mortality has been documented previously in altricial birds (Klomp 1970), including Swifts (Lack & Lack 1951; Lack 1956a). The effect is due to reduced food provisioning per capita in larger broods, even though overall food delivery by adults increases (Martins & Wright 1993a). The effect of brood size on asymptotic mass was greater in 1993 than in 1994, presumably because adults were less able to provision larger broods in the poorer weather (Martins & Wright 1993b).

Time of hatching within a season also had a significant effect on one component of swift reproduction. Earlier-hatched nestlings had significantly higher asymptotic mass than later hatched nestlings (Fig. 3). Effects of later hatching on Swift nestlings have been documented previously (Lack & Lack 1951) and may be due to decreased food abundance later in the season (Koskimies 1950). The abundance of aerial insects in southern England has been shown to decrease from July through August (Bryant 1975).

A recently proposed alternative hypothesis for the lack of detectable effects of parasites on nestlings is that adults compensate young with high parasite loads through increased provisioning of food (Johnson & Albrecht 1993; Møller 1994). Adults will be better able to compensate in 'good' years (warm and dry) than in 'bad' years (cold and wet) (de Lope *et al.* 1993). In our study, 1993 was an extremely bad year in which adults would have had difficulty compensating for any effects of parasites. The fact that we detected no effect or trend of an effect of parasites on any component of nestling survival or growth strongly suggests that parental compensation is not the

explanation for the avirulence of Swift Lice and Louse Flies. The lack of any interaction between parasite loads and year in their effects on nestling growth reinforces this point.

It is clear from our experiments that Swift Lice and Louse Flies are avirulent. Even when boosted to unnaturally high loads, no effect of either parasite could be detected. The results of our study are consistent with the theoretical prediction that vertically transmitted ectoparasites evolve to become relatively avirulent, because they depend on successful host reproduction for direct transmission to host offspring (Clayton & Tompkins 1994). Our conclusion could be strengthened by comparing the effects of the vertically transmitted parasites in this study with the effects of horizontally transmitted ectoparasites, such as dermanyssid mites (Clayton & Tompkins 1994, 1995), on the same species of host. Unfortunately, the birds in our study colony were not host to these or other horizontally transmitted ectoparasites.

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