

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

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 (\pm 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 ($U = 316$, $P = 0.58$).

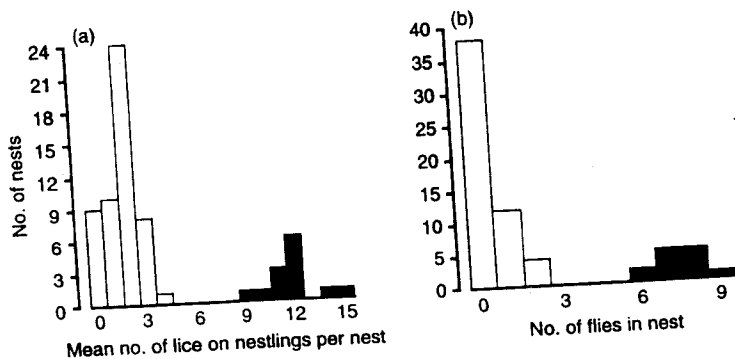


Fig. 1. (a) Distribution of chewing lice on nestlings 35–37 days old. (b) Distribution of louse flies (maximum observed) in nests. Open bars are donor (low-load) nests; shaded bars are recipient (high-load) nests.

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 ($U = 0$, $P < 0.0001$).

No haematzoa 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,

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nestlings in low- and high-fly nests did not differ significantly in asymptotic mass ($F_{1,57} = 0.25$, $P = 0.62$), growing period ($F_{1,57} = 0.43$, $P = 0.51$), growth rate ($F_{1,57} = 0.24$, $P = 0.63$), Richards shape parameter ($F_{1,57} = 0.04$, $P = 0.85$), fledging mass ($F_{1,57} = 0.00$, $P = 1.00$) or fledging age ($F_{1,57} = 0.14$, $P = 0.71$).

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 ($F_{1,57} = 59.86$, $P < 0.001$), slower growth rates ($F_{1,57} = 13.26$, $P = 0.001$), higher Richards shape parameters ($F_{1,57} = 4.65$, $P = 0.04$), and fledged at a later age ($F_{1,57} = 4.75$, $P = 0.03$) than did nestlings in 1994. However, there was no significant difference in growing period ($F_{1,57} = 0.49$, $P = 0.49$) or fledging mass ($F_{1,57} = 0.53$, $P = 0.47$) between the two years.

Nestlings from broods of two had higher asymptotic mass ($F_{1,57} = 16.19$, $P < 0.001$), longer growing periods ($F_{1,57} = 4.78$, $P = 0.03$), lower Richards shape parameters ($F_{1,57} = 16.07$, $P < 0.001$), and higher fledging mass ($F_{1,57} = 11.84$, $P = 0.001$) than nestlings from broods of three [with no difference in growth rate ($F_{1,57} = 0.03$, $P = 0.86$) or fledging age ($F_{1,57} = 0.89$, $P = 0.35$)]. There was also a marginally significant year \times brood size interaction with regard to

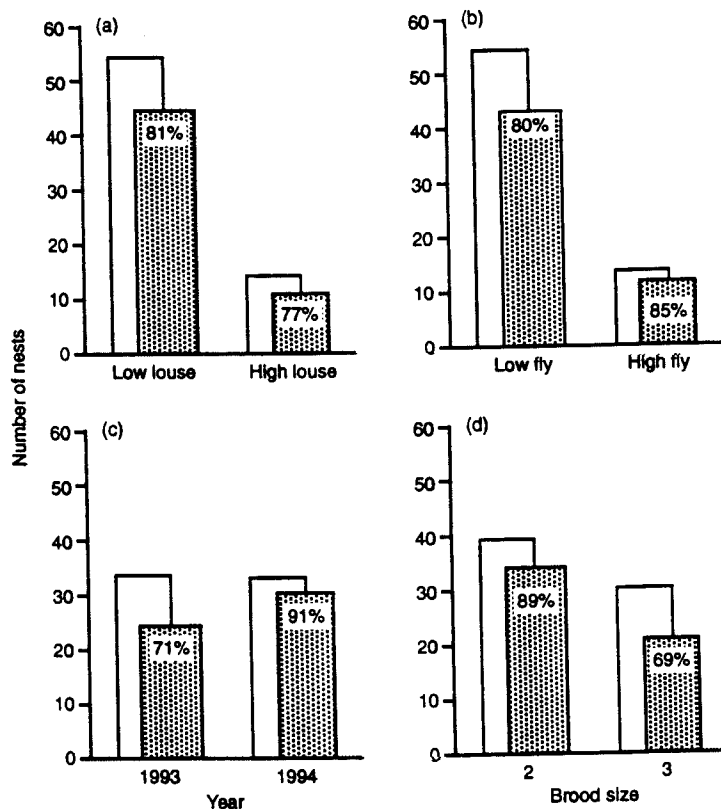


Fig. 2. Number of nests that fledged all young (stripped bars) contingent upon sample size (open bars) in nests with (a) low versus high louse loads, (b) low versus high fly loads, (c) nestlings hatched in 1993 versus 1994, and (d) nests with broods of two versus three. Values in bars are the percentages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

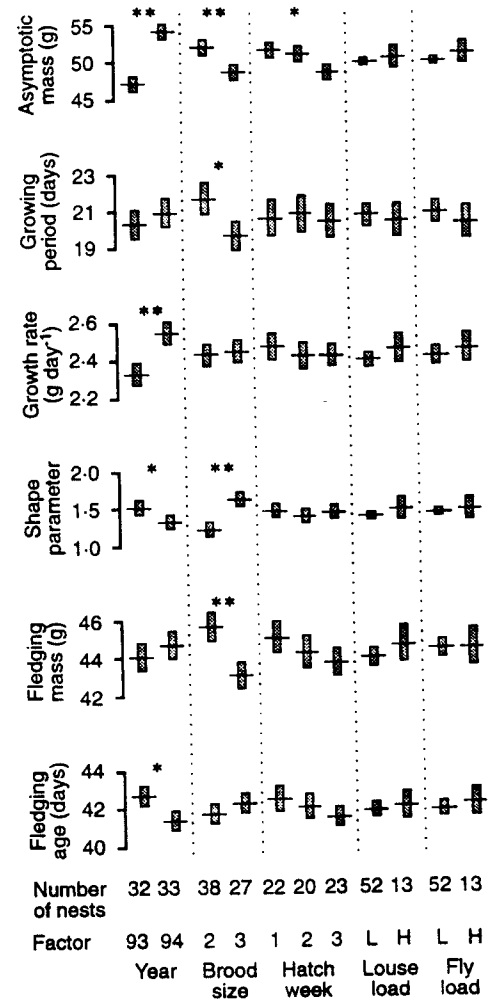


Fig. 3. Impact of various factors on components of nestling growth. Values are Means (\pm SD) adjusted for all other factors (as fitted to the data by 'General Linear Model' analyses). For parasite loads L = low-load nests, H = high-load nests; * $P < 0.05$, ** $P \leq 0.001$.

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 (55.0 ± 1.11 for broods of 2 compared with 53.12 ± 1.09 for broods of 3) ($F_{1,57} = 4.07$, $P = 0.05$).

Nestlings hatched in weeks 1 and 2 had higher asymptotic mass ($F_{2,57} = 4.43$, $P = 0.02$) than nestlings hatched in week 3 (Fig. 3), but there was no difference in growing period ($F_{2,57} = 0.10$, $P = 0.91$), growth rate ($F_{2,57} = 0.43$, $P = 0.65$), Richards shape parameter ($F_{2,57} = 0.15$, $P = 0.86$), fledging mass ($F_{2,57} = 1.25$, $P = 0.30$) or fledging age ($F_{2,57} = 1.10$, $P = 0.34$).

The power of the analyses to detect a 0.75 'effect size' of either parasite on any component of nestling growth was 70% at $\alpha = 0.05$ (two-tailed). If the type error probability is increased to $\alpha = 0.10$ (which can be done for parasite effects in this study with

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).

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, $\chi^2 = 9.33$, $P = 0.002$]. 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

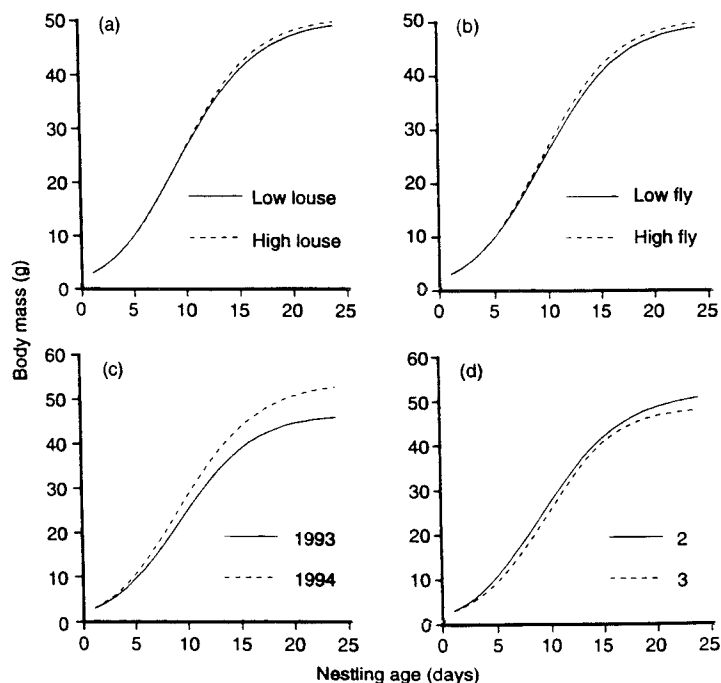


Fig. 4. Impact on nestling growth (to asymptotic body mass) of (a) louse load, (b) fly load, (c) year and (d) brood size. Curves were generated by fitting mean parameters for each group of nests back into the modified Richards growth model used.

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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