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Host resources govern the specificity of swiftlet lice: size matters

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Summary

1. An important component of parasite diversity is the specificity for particular host taxa shown by many parasites. Specificity is often assumed to imply adaptive specialization by the parasite to its host, such that parasites are incapable of surviving and reproducing on 'foreign' hosts.
2. Specificity, however, need not be due to adaptation to particular hosts. Some parasites may be specific simply because they are incapable of dispersing among host taxa. For example, 'permanent' parasites like chewing lice spend their entire lifecycle on the body of the host and require direct contact between hosts for dispersal.
3. The role of adaptive constraints in parasite host-specificity has seldom been tested in natural populations. We conducted such a test by comparing the relative fitness of host-specific lice experimentally transferred among closely related species of cave swiftlets in northern Borneo.
4. The survival of lice in most of these transfers was significantly reduced in proportion to the mean difference in feather barb size between the donor and recipient species of hosts. Thus, adaptation to a particular resource on the body of the host does appear to govern the specificity of swiftlet lice.
5. In transfers where lice survived, microhabitat shifting on the body of the host was observed, whereby the mean barb diameter of the feathers on which the lice occurred was held 'constant'.

Key-words: Apodidae, bird, host-specificity, parasite, Phthiraptera.

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Introduction

Parasites represent more than half of all animal diversity (Price 1980). The host-specificity of many parasites is a major contributor to their diversity. Host-specificity is sometimes considered *prima facie* evidence for adaptive specialization by parasites, i.e. it is taken as evidence that parasites are incapable of surviving and reproducing on 'foreign' hosts (Secord & Kareiva 1996). Parasite specificity, however, may be maintained simply by limited dispersal among host species; adaptation need not play a role. Although limited dispersal will often be a contributing factor to host-specificity, the importance of adaptive specialization to a particular host requires explicit testing.

The adaptive specialization hypothesis can be tested by comparing the fitness of host-specific parasites transferred to 'foreign' host taxa with the fitness of controls transferred to new individuals of the 'usual' host. If parasite fitness on usual and foreign hosts does not differ, specificity is not governed by adaptive constraints. Such tests have seldom been carried out in natural populations of animal parasites. The major objective of this study was to test the potential role of adaptive constraints in the pronounced host-specificity of chewing lice (Insecta: Phthiraptera). Chewing lice are obligate ectoparasites of birds and mammals that complete their entire life-cycle (egg, three nymphal instars, adult) on the body of the host (Marshall 1981). Most species depend on the warm, humid conditions near the skin of the host and are unable to

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survive off the host for more than a few days or hours. Transmission of lice to new hosts is largely vertical, i.e. from parents to offspring in the nest (Clayton & Tompkins 1995; Lee & Clayton 1995). Thus, chewing lice may be host-specific simply because they are incapable of dispersing among host taxa.

We studied chewing lice on four sympatric species of cave swiftlets (Apodiformes: Collocalliini) in northern Borneo. Swiftlets comprise two genera of aerial, insectivorous birds found in the Indo-Australian region (Lee *et al.* 1996). Members of the genus *Aerodramus* nest in the dark interior of caves, where they navigate by echolocation. Members of the genus *Collocalia*, which are not capable of echolocation, nest in lighted areas near cave entrances. Both genera attach their nests to cave walls or build them on ledges in caves. *Collocalia* spp. sometimes also nest on human structures such as buildings and bridges.

The morphological similarity of many species of swiftlets has led to a reliance on molecular and behavioural characters, including details of nest structure, in their classification (Lee *et al.* 1996). Two of the four species we studied, the white-nest swiftlet [*Aerodramus fuciphagus* (Thunberg)] and the black-nest swiftlet [*Aerodramus maximus* (Hume)], construct nests solely or largely of saliva; these nests are harvested on a regular basis for the Chinese birds' nest soup industry (Tompkins 1997). The other two species, the mossy-nest swiftlet [*Aerodramus salanganus* (Streubel)] and the glossy swiftlet [*Collocalia esculenta* (Linnaeus)], produce nests constructed largely of vegetation.

The four swiftlet species are parasitized by six species of chewing lice belonging to the genus *Dennyus* (suborder Amblycera). Although bird lice can have a negative impact on host fitness (Booth, Clayton & Block 1993), feeding primarily on feathers, dermal debris and blood, a recent experimental study revealed no significant effect of *Dennyus hirundinis* on the fitness of the common swift (*Apus apus*; Tompkins, Jones & Clayton 1996). Species of *Dennyus* found on swiftlets comprise the subgenus *Collodennyus*, members of which vary in host-specificity (Clayton, Price & Page 1996). Swiftlets are also host to another genus of chewing louse, *Eureum*, but it was found on only 0·3% of the 1381 birds examined in this study (see below). In contrast, *Dennyus* spp. were present on 23·3% of these birds.

We studied Bornean swiftlets and their lice at Gomantong Caves (5°31′N, 118°04′E), a limestone complex 30 km south of Sandakan, Sabah, Malaysia. Approximately 1·5 million swiftlets nest at Gomantong in mono-specific clusters high on the walls and ceilings of the caves (Francis 1987). We compared the survival of three species of lice transferred among the four species of swiftlets to the survival of control lice, transferred between individuals of the same host species. We also compared the microhabitat distributions of lice on different hosts and examined the relationship of louse survival to microhabitat use on different host species.

Materials and methods

HOST-SPECIFICITY OF LICE

We quantified the host-specificity of *Dennyus* lice by collecting them from at least 200 adults or nestlings of each of the four swiftlet species. Adult birds were removed directly from their nests in Gomantong Caves using nets attached to long poles. Nest type is the most reliable way to identify swiftlet species, particularly in the case of the cryptic species *A. salanganus* and *A. fuciphagus* (Medway 1966; Lee *et al.* 1996). Nestlings were removed from the nest by hand; nests were reached with ladders up to 15 m in length or using climbing ropes suspended from the ceiling of the cave. After examination for lice (see below), birds were banded with a numbered aluminium band and released or returned to the nest.

Since *C. esculenta* nests are highly inaccessible at Gomantong Caves (most are over 20 m above the ground), lice from this species were also collected at a colony of ≈1500 birds nesting under a house ≈35 km from Gomantong (16 km west of Sandakan: 5°52′N, 117°59′E). *C. esculenta* attach their nests to wooden support beams under the house, which is raised on stilts 3 m off the ground. The colony, which has nested at this site for over 30 years (K. Chong, personal communication), breeds during the same months as the birds at Gomantong (February–September). The same species of lice occur on *C. esculenta* under the house and at Gomantong.

The four species of swiftlet were searched for lice using a visual examination method (see Clayton & Walther 1997) with illumination from a headlamp. The plumage of each bird was searched thoroughly, paying particular attention to the flight feathers, which is where *Dennyus* lice spend most of their time (Tompkins 1996). Lice were removed with forceps and preserved in 70% EtOH and later mounted on microscope slides to be identified using keys in Clayton *et al.* (1996). Hands and nets were checked carefully between birds to prevent erroneous host records or accidental transfers.

When searching birds to recover lice at the end of transfer experiments (see below) the following pattern of visual examination was used. First, dorsal and ventral surfaces of each flight feather were examined while deflecting the greater covert feathers with forceps to reveal the base of the flight feather. The body of the bird was then examined, starting with the head and neck, and then moving down the dorsal and ventral surfaces, again deflecting feathers with forceps. Using this approach it was possible to collect data on the microhabitat distribution of each louse before removing it with the forceps. Young nestlings, prior to feather emergence, were examined for lice by carefully searching the entire surface of their skin.

Since *Dennyus* spp. are relatively large (≈2 mm long), fairly sedentary and normally present in small

numbers (Lee & Clayton 1995), all of the adult lice on an adult swiftlet could be collected in under 3 min (nestlings required less time). We tested the efficiency of the collection method by removing the adult lice from 25 adult *C. esculenta*, killing the birds for use as museum vouchers, then placing each dead bird in a sealed paper bag for a minimum of 18 h. *Dennyus* and other Amblyceran chewing lice are known to abandon the body of a dead host as it cools down in order to find a new live host (Marshall 1981). No adult *Dennyus* were found in the 25 bags or on any of the carcasses upon removal from the bags.

FITNESS OF LICE ON FOREIGN HOSTS

Transfer procedure

The major goal of this study was to test whether host-specificity in swiftlet lice is governed by adaptive constraints. We did this by comparing the relative fitness of three species of *Dennyus* lice transferred among three species of swiftlets. The fitness component we measured was survival of lice on foreign hosts relative to survival of control lice transferred to new individuals of the usual host. This experimental design controlled for natural mortality of lice on the usual host, as well as unwanted side-effects of the transfer procedure.

We used nestling birds as donors and recipients in the transfer experiments. Nestlings were used because, with the exception of parents and nest mates, they seldom come into contact with other birds prior to fledging from the nest. This simplified the monitoring of parasite survival because it made it unnecessary to survey the host population at large. Since the population of swiftlets at Gomantong exceeds 1·5 million individuals, such a survey would not be feasible. Transferring lice between nestlings of different host species was made possible by the overlapping breeding schedules of the four species of swiftlets at Gomantong (Francis 1987).

Although swiftlets spend at least 5 weeks in the nest after hatching, they do not grow enough feathers to support *Dennyus* until about 2 weeks prior to fledging from the nest. Lice rapidly disperse from parent birds to nestlings at this point in juvenile development (Lee & Clayton 1995). This delay in transmission constrains the opportunity for monitoring louse survival because, once fledged, swiftlets seldom return to the vicinity of the nest (unpublished data). We transferred adult lice to nestlings at the age when natural transmission from the parents occurs; 10 days later we collected all of the lice from each nestling before it had a chance to fledge. The lice were immediately preserved in 70% EtOH. Later, they were mounted on microscope slides and identified by a taxonomist (R. D. Price) who was blind to experimental treatments. Since lice were not identified until after the transfer experiment, we were blind to the identity of all lice during the field work. Transferred lice not recovered from nestlings were assumed to have died during the 10-day period (see below for details). Ten days is an appreciable fraction of the adult lifespan of chewing lice, which averages 24 days (Table 4·3 of Marshall 1981). Ten days also exceeds the amount of time *Dennyus* can survive off the host; most individuals die within 36 h of removal (Fig. 1).

Three of the four swiftlet species at Gomantong have brood sizes of 1–2 nestlings. The fourth species (*A. maximus*) has a brood size limited to one nestling. In order to equilibrate host density across the transfer experiments, we restricted transfers for all host species to nests containing a single nestling. This was not difficult because at least half of the nests of every species at Gomantong normally contain one nestling. Recipient nestlings were chosen haphazardly from available singleton nests. The use of singleton nestlings further eliminated the possibility of louse dispersal between nest mates.

Two male and two female lice were transferred to nestlings in each experiment. Four was the maximum number of adult lice observed on nestlings prior to the transfer experiments (although natural loads of up to nine adult lice per bird were later observed; unpublished data). *Dennyus* spp. are relatively easy to sex, even under field conditions, because females are 15–20% larger than males (Clayton *et al.* 1996). One member of each sex was placed on the primary feathers of each wing of the recipient nestlings. We did not mark lice in this study because the standard methods of marking ectoparasites (Marshall 1981) have negative effects on louse survival (personal observation). Since the lice transferred to foreign hosts seldom, if ever, occur on those hosts naturally (see Table 1) it was an easy matter to identify experimental lice recovered from foreign nestlings at the end of the experiments. On the other hand, accounting for individual unmarked lice recovered from control nestlings was not possible because they could not be dis-

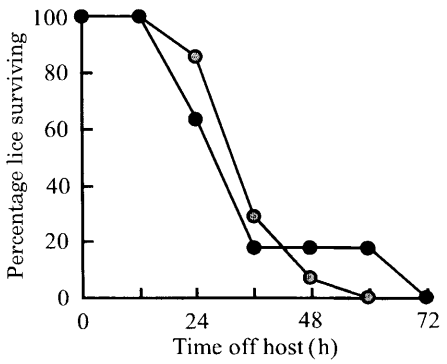


Fig. 1. Survival of 25 adult chewing lice (14 males and 11 females) removed from *Collocalia esculenta* nestlings and maintained in aerated vials at ambient temperature and humidity. Shaded points = male lice; closed points = female lice.

Table 1. Numbers of lice collected from swiftlets in this study. Percentages, which are a measure of host-specificity, are the proportion of each louse species that was present on each species of host (mean number of each louse species on each host divided by the sum of the mean numbers of that louse across all host species). Species of lice included in transfer experiments, described later, are in bold. Values in bold indicate novel host records (compared with current host lists in Clayton *et al.* 1996)

Dennyus species	Host species *C. esculenta* (n = 240)	*A. salanganus* (n = 398)	*A. fuciphagus* (n = 207)	*A. maximus* (n = 536)
distinctus	35 (98·7%)	0	0	**1 (1·3%)**
somadikartari	99 (99·5%)	0	0	**1 (0·5%)**
carljonesi	0	23 (5·3%)	177 (77·2%)	104 (17·5%)
simberloffi	0	**2 (8·9%)**	1 (8·6%)	25 (82·5%)
thompsoni	0	**1 (10·4%)**	1 (20%)	9 (69·6%)
wellsi	0	80 (97·3%)	0	**3 (2·7%)**

tinguished from lice of the same species occurring naturally on those nestlings. To estimate the survival rate of transferred lice on controls we used the total number of lice recovered from nestlings, minus the 'background' abundance of lice on singleton nestlings not involved in the experiments (sample sizes equal to the control groups).

Transfer of C. esculenta *lice to* A. salanganus

The first transfers were from *C. esculenta*, the smallest-bodied species of swiftlet in the study (mean wing-chord of 98 mm, estimated from five adults), to *A. salanganus*, the next smallest species (mean wing-chord of 117 mm, again estimated from five adults). We transferred the host-specific lice *Dennyus distinctus* (Ferris) and *Dennyus somadikartai* (Clayton, Price & Page) (see Table 1) from *C. esculenta* nestlings at the house colony to 25 *A. salanganus* nestlings at Gomantong. We also carried out control transfers of these lice to 25 new *C. esculenta* nestlings at the house. Lice for experimental and control transfers were gently removed from donor nestlings with forceps and placed in plastic Eppendorf tubes for 3 h. They were then placed on the wings of recipient nestlings. The 3-h period was necessary to allow for travel between donor nests at the house and experimental nests at the cave. *Dennyus* lice can withstand 3 h off the body of the host with no apparent side-effects (Fig. 1).

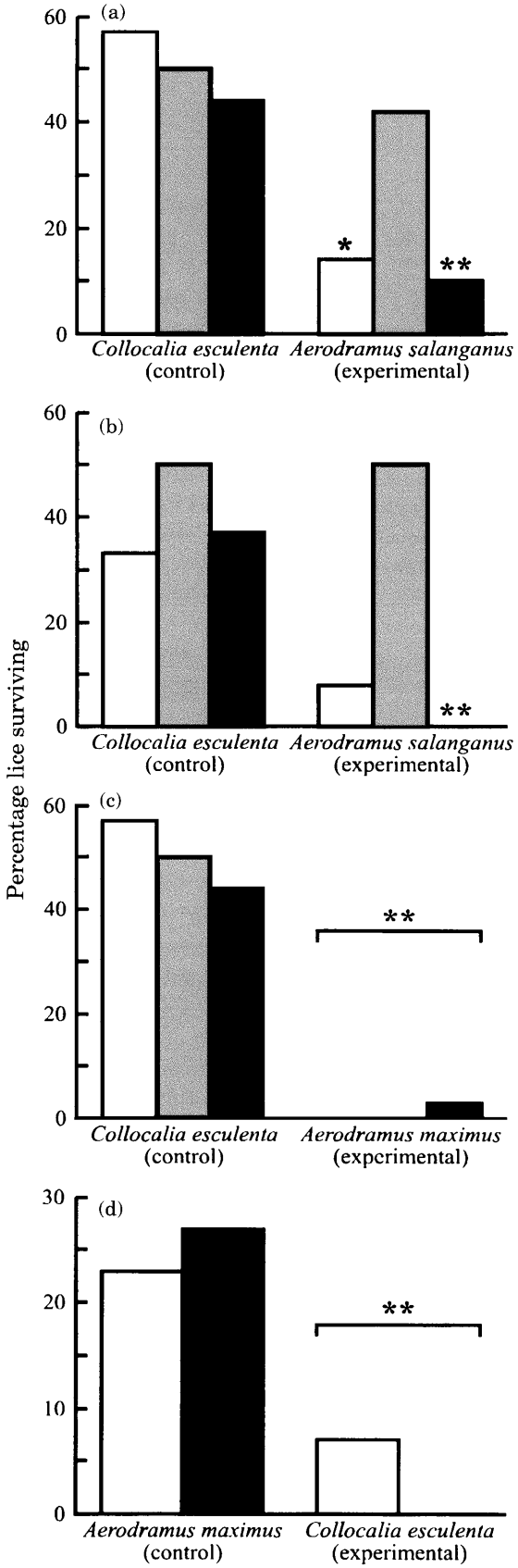
The two species of lice were transferred in proportion to their natural abundance on *C. esculenta*. Males of these species cannot be distinguished morphologically and females cannot be distinguished without microscopic examination of slide mounted specimens (Clayton *et al.* 1996). Therefore, although it was possible to identify female lice following recovery from hosts at the end of the transfer experiment, it was not possible to tally the ratio of the two species transferred at the beginning of the experiment. Instead, we assumed that the relative abundance of the lice in our transfers was equal to the relative abundance of the two species in the background collections of lice from other nestlings (described above).

Transmission of *D. distinctus* or *D. somadikartai* away from recipient nestlings during the experiment would, of course, lead to erroneous survival estimates. Two types of transmission could conceivably occur: (1) back-transmission from nestlings to parents; and (2) horizontal transmission from recipient nestlings to non-experimental nestlings in adjacent nests. To check for back-transmission we collected all lice from both parents of 18 of the 25 *A. salanganus* nestlings at the end of the experiment. Although both *D. distinctus* and *D. somadikartai* were recovered from recipient nestlings (see Fig. 2a), no individuals of either species were found on the parent birds. The lack of back-transmission is not surprising since most *Dennyus* lice normally disperse from parent hosts to offspring prior to the latter fledging (Lee & Clayton 1995).

To test for horizontal transmission of lice between nestlings at adjacent nests, we collected all lice from nestlings in 108 *A. salanganus* nests adjacent to the 25 nests containing recipient *A. salanganus* nestlings. No *D. distinctus* or *D. somadikartai* were found on any of the adjacent nestlings. The lack of horizontal transmission is not surprising because the inefficient locomotion of *Dennyus* off the body of a host prevents transmission between hosts not in direct physical contact (Lee & Clayton 1995; Tompkins *et al.* 1996).

Transfer of C. esculenta *lice to* A. salanganus *cross-fostered into* C. esculenta *nests*

Ambient temperature in the cave was lower than that under the house (mean midday temperature of 25·2 vs. 31·8°C), and ambient humidity in the cave was higher than that under the house (mean midday relative humidity of 85·1 vs. 65·4%). These differences might have influenced the survival of lice in the first transfer experiment. The second experiment tested for this possibility by transferring lice to foreign host nestlings moved into the usual host's environment. *D.*



distinctus and *D. somadikartai* were transferred from nestlings of the usual host *(C. esculenta)* to 15 singleton *A. salanganus* nestlings cross-fostered into *C. esculenta* nests. Control transfers to 15 singleton *C. esculenta* nestlings cross-fostered into new *C. esculenta* nests were also carried out. Cross-fostering was carried out 5 days prior to the transfer of lice. Nests with singleton *A. salanganus* nestlings were removed from the cave and kept in a closed container at ambient temperature for 2 h. Each nestling was then moved into a foster *C. esculenta* nest from which the resident singleton nestling was simultaneously removed and placed in another active nest not involved in the experiment. The same procedure was followed for the cross-fostering of *C. esculenta* control nestlings. Lice were transferred to the cross-fostered nestlings exactly as described in the first experiment.

Transfer of C. esculenta *lice to* A. maximus

In the third experiment *D. distinctus* and *D. somadikartai* were transferred to 25 singleton nestlings of *A. maximus*, an even larger foreign host living in the cave (mean wing-chord of 132 mm, estimated from five adults). Lice were also transferred to 25 *C. esculenta* nestlings to serve as controls. *A. maximus* builds nests in denser colonies than *A. salanganus*, with adjacent nests often sharing a common nest wall. For this reason, we again checked for horizontal transmission by collecting all of the lice from nestlings in 57 nests immediately adjacent to the 25 experimental nests. As before, foreign lice were not found on any of the adjacent nestlings.

Reciprocal transfer of A. maximus *lice to* C. esculenta

The fourth and final experiment was a reciprocal of the third experiment. To accomplish this we transferred the louse *Dennyus carljonesi* (Clayton, Price & Page) from *A. maximus* to *C. esculenta* (see Table 1). Due to logistical difficulties reaching large numbers of *A. maximus* nests, which are limited to the upper walls

Fig. 2. Survival of lice transferred from the usual host species to a foreign host species, relative to survival of control lice transferred to new individuals of the usual host species. *Dennyus distinctus* and *D. somadikartai* transferred from *Collocalia esculenta* to (a) *Aerodramus salanganus* nestlings (a larger foreign host); (b) *A. salanganus* nestlings cross-fostered into *C. esculenta* nests; and (c) *A. maximus* nestlings (an even larger foreign host). Open bars = female *D. distinctus*; shaded bars = female *D. somadikartai*; closed bars = male *D. distinctus/somadikartai*, which cannot be told apart (Clayton *et al.* 1996). (d) Reciprocal transfer of *D. carljonesi* from *A. maximus* to *C. esculenta* nestlings (a much smaller foreign host). Open bars = female *D. carljonesi*; closed bars = male *D. carljonesi*. Asterisks denote significant differences from controls; * $P < 0.05$, ** $P < 0.01$.

and ceilings of Gomantong Caves, we used adult birds as donors of lice for this experiment. *D. carljonesi* was transferred from adult *A. maximus* to singleton nestlings in 15 *C. esculenta* nests. Control transfers to 15 singleton *A. maximus* nestlings were also carried out.

FEATHER DIMENSIONS

> ... a plumage that is similar, a feather structure that is similar, such a similar substrate may facilitate transfer to a new host (Mayr 1957).

Feather size can be a determinant of host-specificity in avian ectoparasites. For example, Syringophilid mites can survive only in feather shafts of a certain diameter (Kethley 1971; Kethley & Johnston 1975). Swiftlet lice may likewise require feathers of a certain size for survival. To compare feather dimensions of the different species of swiftlets in this study we collected feather samples from the museum voucher specimens we prepared. Swiftlet lice spend most of their time on flight feathers (Tompkins 1996); we therefore measured samples of primary, secondary and tail feathers from five adult specimens of each species of swiftlet in the study. Barb diameters of the following 12 feathers from one side of each specimen were estimated (numbering from outermost to innermost): primaries number 2, 4, 6 and 8, secondaries 2, 3, 4 and 5, and tail feathers 1, 2, 3 and 4. For each feather, the diameters of five barbs, chosen haphazardly from a 25-mm^2 region situated midway along the shaft, and midway between the shaft and the distal edge of the feather vane, were measured under $\times 800$ magnification using an ocular micrometer. Measurements were to the nearest 1·25 μ and the mean of the five barbs was used as an estimate of mean barb diameter for each feather. Measurements were then averaged across feathers to estimate the mean barb diameter of each of the three flight feather tracts of each bird examined. Finally, the overall mean barb diameter of flight feathers was estimated for each bird by averaging measurements across feather tracts. Feather barbs were measured on two separate occasions from one individual of each swiftlet species in order to calculate the repeatability of the measurements (Lessells & Boag 1987). Repeatability was high for each feather tract examined ($r > 0{\cdot}90$; $P < 0{\cdot}01$).

DISTRIBUTION OF LICE ON HOSTS

Foreign hosts

Feather size varies considerably among the feather tracts on a single host (see results). Hence, even if feather size is an important component of louse survival, it may be possible for lice to survive on foreign hosts simply by shifting their distribution on the body of the host. We explored this possibility by noting the feather tract from which each louse was collected at the end of the transfer experiments. Previously collected data on the mean barb diameters of different feather tracts (see above) allowed us to quantify differences in preferred microhabitat on usual vs. foreign hosts.

Usual hosts

Variation in microhabitat use could be important in the ability of generalist lice to survive on hosts with different body sizes. To test this possibility we transferred the generalist louse *D. carljonesi* (see Table 1) among its three usual host species, which vary in body size (mean wing-chord of 132 mm for *A. maximus*, vs. 118 mm for *A. fuciphagus*, vs. 116 mm for *A. salanganus*). Lice were obtained from *A. maximus* adults and transferred to 15 singleton *A. fuciphagus* nestlings and 15 singleton *A. salanganus* nestlings. Control transfers to 15 *A. maximus* nestlings at new nests were also carried out. As in the previous transfer experiments, all lice were removed from nestlings 10 days following transfer and the location of each louse in the plumage was noted. Since all transfers were to usual hosts, survival rates of all transferred lice (not just the lice on controls) were estimated by subtracting background abundances from total numbers of lice recovered.

Results

HOST-SPECIFICITY OF LICE

A total of 562 adult *Dennyus* were collected from 1381 swiftlets (Table 1). Single individuals of *D. distinctus* and *D. somadikartai* were collected from *A. maximus*. These novel host records show that *Dennyus* lice are, in fact, capable of dispersing to foreign hosts. Additional novel host records were established during our survey. These included *Dennyus simberloffi* (Clayton, Price & Page) and *Dennyus thompsoni* (Ledger) collected from *A. salanganus*, and *D. wellsi* (Clayton, Price & Page) collected from *A. maximus*. These records are not surprising since at least one species of louse, *D. carljonesi*, is already known to occur on all three species of *Aerodramus* (Table 1).

FITNESS OF LICE ON FOREIGN HOSTS

Transfer of C. esculenta *lice to* A. salanganus

The first transfer experiment involved the host-specific lice *D. distinctus* and *D. somadikartai*. These species were transferred from *C. esculenta* nestlings under the house to *A. salanganus* nestlings in the cave. Overall, significantly fewer transferred lice survived on *A. salanganus* than on control birds (Fig. 2a; $\chi^2 = 14{\cdot}86$, d.f. = 1, $P < 0{\cdot}001$). Further analysis revealed significant variation in the survival of lice depending on their species and sex. Only two of 14 female *D. dis-*

tinctus survived on the foreign host, compared with eight of 14 controls ($\chi^2 = 5{\cdot}60$, d.f. = 1, $P = 0{\cdot}02$). In contrast, 15 of 36 female *D. somadikartai* survived on the foreign host, compared with 18 of 36 controls ($\chi^2 = 0{\cdot}50$, d.f. = 1, $P = 0{\cdot}48$). Only five of 50 male lice survived on the foreign host, compared with 22 of 50 controls ($\chi^2 = 14{\cdot}66$, d.f. = 1, $P < 0{\cdot}001$); male *D. distinctus* and *D. somadikartai* cannot be told apart morphologically (Clayton *et al.* 1996).

Transfer of C. esculenta *lice to* A. salanganus *cross-fostered into* C. esculenta *nests*

The second experiment, designed to control for differences between the house and cave in temperature and humidity, involved *C. esculenta* lice transferred to *A. salanganus* nestlings cross-fostered into *C. esculenta* nests. The results were similar to those of the first experiment: overall, significantly fewer lice survived on *A. salanganus* than on the usual host (Fig. 2b; $\chi^2 = 8{\cdot}04$, d.f. = 1, $P < 0{\cdot}005$). Only one of 12 female *D. distinctus* survived on the foreign host, compared with four of 12 controls (Fisher exact $P = 0{\cdot}16$); the result was not significant because of the low survival of controls (cf. previous experiment). Survival of female *D. somadikartai* on the foreign host was equivalent to that on controls (nine of 18 in both cases; $\chi^2 = 0{\cdot}00$, d.f. = 1, $P = 1{\cdot}00$). As before, there was a significant reduction in the survival of male lice on the foreign host, with none of 30 lice surviving on the foreign host, compared with 11 of 30 lice on controls ($\chi^2 = 13{\cdot}47$, d.f. = 1, $P < 0{\cdot}001$).

A direct comparison of the first and second experiments revealed no significant overall difference in the survival of lice transferred to *A. salanganus* in the cave vs. *A. salanganus* cross-fostered into *C. esculenta* nests ($\chi^2 = 0{\cdot}67$, d.f. = 1, $P = 0{\cdot}41$). Further comparisons showed no significant difference in the survival of female *D. distinctus* (Fisher exact $P = 0{\cdot}56$), female *D. somadikartai* ($\chi^2 = 0{\cdot}34$, d.f. = 1, $P = 0{\cdot}56$) or the survival of males of the two species combined (Fisher exact $P = 0{\cdot}09$). Therefore, ambient conditions were not a major factor in the survival of *C. esculenta* lice transferred to *A. salanganus* nestlings.

Transfer of C. esculenta *lice to* A. maximus

In the third experiment, *D. distinctus* and *D. somadikartai* were transferred from *C. esculenta* nestlings under the house to *A. maximus* nestlings in the cave. Survival was severely depressed on *A. maximus*, with only one of 100 lice surviving, compared to 48 of 100 control lice (Fig. 2c; $\chi^2 = 59{\cdot}71$, d.f. = 1, $P < 0{\cdot}001$).

Direct comparison of the results of experiment 1 (Fig. 2a) and experiment 3 (Fig. 2c) showed that significantly fewer *C. esculenta* lice survived on *A. maximus* than on *A. salanganus* ($\chi^2 = 21{\cdot}67$, d.f. = 1, $P < 0{\cdot}001$).

Reciprocal transfer of A. maximus *lice to* C. esculenta

In the fourth experiment *D. carljonesi* was transferred from *A. maximus* adults in the cave to *C. esculenta* nestlings under the house. Only two of 60 lice survived on *C. esculenta*, compared to 15 of 60 control lice transferred to *A. maximus* nestlings in the cave (Fig. 2d; $\chi^2 = 11{\cdot}58$, d.f. = 1, $P < 0{\cdot}001$). Thus, survival of *A. maximus* lice transferred to *C. esculenta* was nearly as low as the reciprocal survival of *C. esculenta* lice transferred to *A. maximus* (Fig. 2c).

FEATHER DIMENSIONS

Although feather barb diameter showed a high degree of overlap among the four swiftlet species (Fig. 3), mean barb diameter increased significantly across feather tracts in the following sequence: secondaries < primaries < tail feathers (Kruskal–Wallis $H = 40{\cdot}64$, $P < 0{\cdot}001$). Overall mean barb diameter was positively correlated with wing chord (Spearman $r = 0{\cdot}81$, $P < 0{\cdot}001$).

DISTRIBUTION OF LICE ON HOSTS

Foreign hosts

The only transfer experiments in which lice were able to survive on a foreign host were transfers of female *D. somadikartai* to *A. salanganus*, a larger-bodied swiftlet than the usual host *C. esculenta* (Fig. 2a,b). A com-

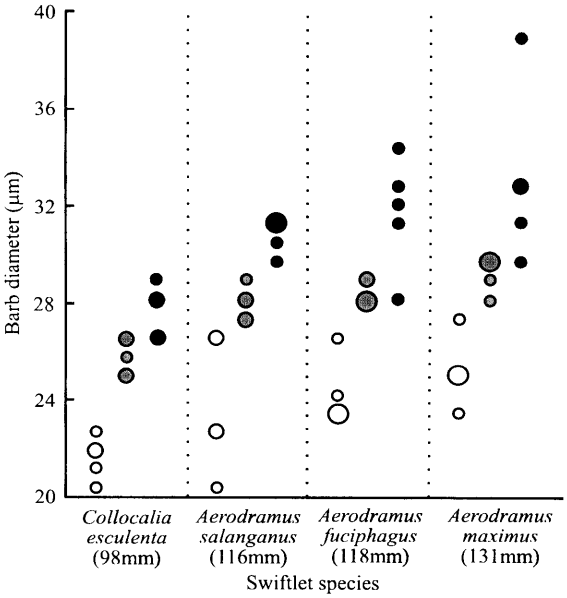


Fig. 3. Feather barb diameters of adult swiftlets (in microns). Point size is proportional to the number of individual birds (1–3); each value is the mean diameter of four feathers from a given feather tract (see text). Open points = secondary feathers; shaded points = primary feathers; closed points = tail feathers. Values in parentheses are the mean wing-chords of the five individuals of each species from which feather dimensions were measured.

parison of the distribution of this louse on the foreign and control hosts revealed a significant preference for finer-grained secondary feathers on the foreign host; 11 of the 24 female *D. somadikartai* (45·8%) recovered from foreign hosts were collected from secondary feathers, compared with only two of the 27 (7·4%) recovered from control hosts ($\chi^2 = 9{\cdot}87$, d.f. = 1, $P < 0{\cdot}005$). Analysis of the barb diameters of feathers preferred by this louse on the usual host showed that they are significantly larger on the foreign host (Fig. 4a; Mann–Whitney $U = 50$, $P < 0{\cdot}001$). However, analysis of the barb diameter of feathers actually used by this louse on the foreign host revealed no significant difference compared to the usual host (Fig. 4a; $U = 275$, $P = 0{\cdot}36$). In other words, when moved to a larger-bodied host, female *D. somadikartai* essentially hold barb diameter constant by shifting their microhabitat distribution.

Usual hosts

As expected, there was no significant difference in the survival of *D. carljonesi* when transferred among its three usual host species; 12 of 60 lice survived on *A. fuciphagus* and 14 of 60 lice survived on *A. salanganus*, compared with 15 of 60 control lice transferred to new *A. maximus* individuals ($\chi^2 = 0{\cdot}44$, d.f. = 2, $P = 0{\cdot}80$). A comparison of the distribution of this louse among the three host species showed no significant difference in feather tract use, notwithstanding a trend for increased use of the tail feathers on *A. fuciphagus* and *A. salanganus*; 30·8% of the *D. carljonesi* recovered from these hosts were collected from tail feathers, compared with only 6·7% recovered from *A. maximus* (Fisher exact $P = 0{\cdot}08$). Analysis of the barb diameters of feathers preferred by this louse on *A. maximus* showed that they are significantly smaller on the other two hosts (Fig. 4b; Kruskall–Wallis $H = 13{\cdot}27$, $P = 0{\cdot}001$). However, analysis of the barb diameters of feathers actually used by this louse on the two smaller hosts revealed no significant difference compared to *A. maximus* (Fig. 4b; $H = 2{\cdot}82$, $P = 0{\cdot}24$). Thus, *D. carljonesi* holds barb diameter more or less constant among three usual host species by altering its microhabitat distribution.

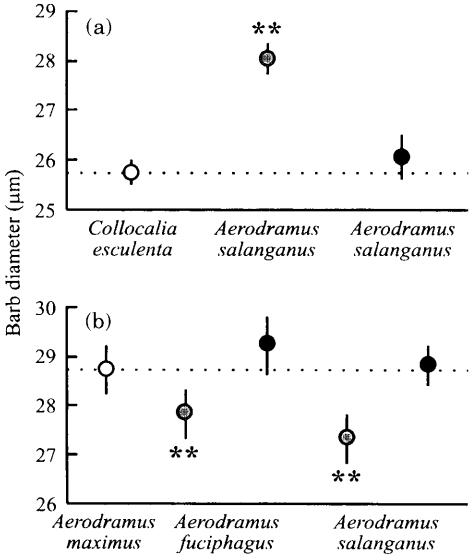


Fig. 4. (a) Mean (±1 SE) feather barb diameter of microhabitat of female *D. somadikartai* on different hosts: open circle = *C. esculenta* microhabitat from which lice were transferred, shaded circle = the same microhabitat on *A. salanganus* (a foreign host), and filled circle = microhabitat on the foreign host where experimental lice were found. (b) Mean (±1 SE) feather barb diameter of microhabitat of *D. carljonesi* on different usual hosts: open circle = *A. maximus* microhabitat from which lice were transferred, shaded circles = the same microhabitat on the two smaller host species, and filled circles = microhabitats on the two smaller host species where experimental lice were found. Asterisks denote significant differences from controls. ** $P < 0{\cdot}01$.

Discussion

Any role of reduced fitness on foreign hosts, in the maintenance of parasite host-specificity, would be preempted if parasites never had an opportunity to disperse to those hosts under natural conditions. For this reason, we started by examining the host distributions of large numbers of lice collected from the four species of swiftlets in the study, all of which are sympatric with overlapping habitat. These distributional data enabled us to measure how often lice occur on the 'wrong' host, termed 'straggling' by parasitologists (Rozsa 1993). At least two opportunities for straggling of swiftlet lice exist. First, passive dispersal could conceivably occur during mid-air collisions between swiftlets as they forage in close proximity, and as thousands of individuals return to their nests each night using common cave entrances (personal observation). A second, more likely possibility is that lice may disperse actively between different host species nesting in close association. As a rule, swiftlets tend to nest in monospecific clusters; however, we sometimes observed overlap between the tips of the flight feathers of different species nesting in close proximity. In particular, *Aerodramus maximus* occasionally nested quite close to the nests of the three other species in the study. Interestingly, *A. maximus* was the only species that shared lice with all three of these species, including *Collocalia esculenta* (Table 1). In contrast, *C. esculenta* was never observed to nest near *A. salanganus* or *A. fuciphagus*, and it never shared lice with either of these species. These two *Aerodramus* species, which shared three species of lice (Table 1), sometimes nested in close proximity to one another.

Although collecting records can reveal cases of straggling among host species, it is impossible to know from such data alone whether stragglers are capable of surviving on foreign hosts. Stragglers may have dispersed to a foreign host shortly before being

collected. Measuring the fitness of stragglers requires an experimental approach in which the survival of lice transferred to foreign hosts is compared with that of controls transferred to new individuals of the usual host species. The main goal of this study was to carry out such transfers to determine whether host-specificity is governed by adaptive constraints.

FITNESS OF LICE TRANSFERRED AMONG HOSTS

We transferred three species of lice to foreign hosts. The fitness of most of these lice was reduced, compared with controls transferred to new individuals of the usual host (Fig. 2). The sole exception, female *Dennyus somadikartai* transferred to *A. salanganus*, will be discussed below. Our results thus indicate that the host-specificity of most swiftlet lice is governed by adaptive constraints.

The outcome of these experiments is striking, considering two factors: (1) for logistical reasons it was necessary to limit fitness comparisons to a 10-day test of survival, with no data on reproductive success being collected; (2) survival of most control lice was also low ($\approx 50\%$), reducing the probability of detecting a reduction in the relative fitness of experimental lice. Natural senescence may have contributed to the low survival of control lice, since 10 days is a significant fraction of the expected lifespan of *Dennyus* spp. (see methods). Unwanted side-effects of the experimental procedure, which required keeping lice in a vial for 3 h during transfers, were probably also factors reducing survival. The particularly low survival of *D. carljonesi* controls ($\approx 25\%$; Fig. 2d) may have been due to the fact that adult birds were used as donors for this species, instead of nestlings which were the source of the other two species of lice used in transfer experiments. Lee & Clayton (1995) showed that the ratio of nymphal to adult *Dennyus* on nestling swifts (*Apus apus*) is far higher than that on adults. This means that lice from younger donors will themselves be younger, on average, than lice from older donors. Younger lice have a higher probability of surviving a 10-day experimental window. Our data are consistent with this scenario; control lice from adult donors showed double the mortality of control lice from nestling donors.

Not all lice on foreign hosts had reduced survival; the survival of female *D. somadikartai* transferred to *A. salanganus* was nearly equivalent to that of controls (Fig. 2a,b). This is not to say that *D. somadikartai* is capable of establishing viable populations on *A. salanganus*; the survival of male *D. distinctus/somadikartai* transferred to *A. salanganus* was quite low. *D. somadikartai* could conceivably colonize *A. salanganus* if females were capable of parthenogenesis, which is known for some species of chewing lice (Marshall 1981). However, another obstacle to colonization of *A. salanganus* by *D. somadikartai* is that dispersal opportunities from *C. esculenta* to *A. salanganus* appear limited, as discussed earlier.

Various authors (e.g. Rozsa 1993) have suggested that competitive exclusion by resident lice may play a role in host-specificity. Competition was unlikely to have played a role in the reduced survival of lice transferred to foreign hosts in our study because the background loads of recipient hosts were very low. The mean abundance of lice on foreign hosts was a mere 0·56 lice per *C. esculenta* nestling, 0·13 lice per *A. salanganus* nestling, and 0·20 lice per *A. maximus* nestling. In any case, there is no rigorous evidence that inter-specific competition actually occurs among chewing lice (Page, Clayton & Paterson 1996).

THE IMPORTANCE OF FEATHER BARB SIZE

The only case in which survival of lice was not reduced on a foreign host, relative to controls, involved female *D. somadikartai* transferred from *C. esculenta* to *A. salanganus*. Comparison of feather tract use on these two hosts revealed that the lice held barb size constant by shifting their microhabitat distribution on the foreign host (Fig. 4a). Similarly, transfers of the generalist louse *D. carljonesi* showed that it, too, held feather barb size constant by shifting microhabitat distribution when transferred among hosts (Fig. 4b).

Louse survival was significantly related to the mean preferred barb size on the donor host, relative to the mean available barb size on the recipient host. Relative survival dropped appreciably when the discrepancy in barb size exceeded 2 μ, regardless of the direction of the difference (Fig. 5). Survival was reduced when lice were transferred to smaller hosts (Fig. 5: G, H), as well as when they were transferred to larger hosts (Fig. 5: E, F, I–L). The 2-μ threshold may explain the differential survival of male and female *D. somadikartai* transferred from *C. esculenta* to *A. salanganus* (Fig. 2a,b). The preferred barb size of male *D. somadikartai* and male *D. carljonesi* (the louse usually found on *A. salanganus*) differed by more than 2 μ (25·0 vs. 27·7 μm), whereas that of female *D. somadikartai* and female *D. carljonesi* differed by less than 2 μ (25·7 vs. 27·5 μm). *Dennyus* spp. grasp feather barbs using paired tarsal claws, each of which measures ≈ 25 μ in length (Clayton *et al.* 1996). Thus, 2 μ is only 8% of the length of a tarsal claw.

Why is the survival of lice so closely attuned to such small changes in the feather barb size? Small changes in feather barb size may interfere with the ability of lice to hang onto the host, particularly during flight. Swiftlets spend many hours flying each day since they are aerial insectivores that feed only on the wing. Of course, nestlings do not fly so difficulty hanging onto hosts may not have been a factor in the reduced survival of lice transferred in this study. On the other hand, the nestlings in our study spent a good deal of time vigorously flapping their wings to exercise them before leaving the nest (personal observation). This

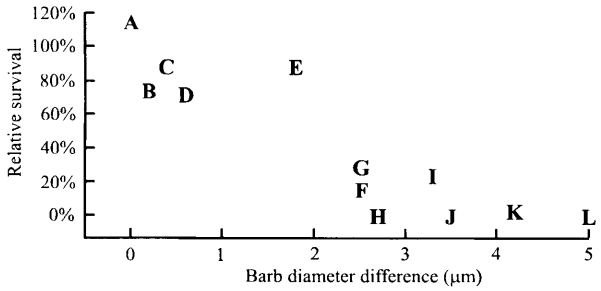


Fig. 5. Relative survival of lice experimentally transferred between host species in relation to the difference between the mean barb diameter of the preferred microhabitat on the donor host species vs. the mean barb diameter of available microhabitat on the recipient host species. Points A–D are transfers of lice between usual hosts; points E–L are transfers of lice to foreign hosts (louse, donor host Æ recipient host): A = female *D. carljonesi*, *A. maximus* Æ *A. salanganus*; B = male *D. carljonesi*, *A. maximus* Æ *A. salanganus*; C = male *D. carljonesi*, *A. maximus* Æ *A. fuciphagus*; D = female *D. carljonesi*, *A. maximus* Æ *A. fuciphagus*; E = female *D. somadikartai*, *C. esculenta* Æ *A. salanganus*; *F* = male *D. distinctus/somadikartai*, *C. esculenta* Æ *A. salanganus*; *G* = female *D. carljonesi*, *A. maximus* Æ *C. esculenta*; H = male *D. carljonesi*, *A. maximus* Æ *C. esculenta*; I = female *D. distinctus*, *C. esculenta* Æ *A. salanganus*; J = female *D. somadikartai*, *C. esculenta* Æ *A. maximus*; K = male *D. distinctus/somadikartai*, *C. esculenta* Æ *A. maximus*; L = female *D. distinctus*, *C. esculenta* Æ *A. maximus*. Values for transfers of lice from *C. esculenta* to *A. salanganus* are the mean results of two experiments, one with *A. salanganus* nestlings in their own nests, the other using nestlings cross-fostered into *C. esculenta* nests (see text). Survival was inversely related to the difference in barb size, across all transfers (A–L; Spearman $r = -0{\cdot}87$, $P < 0{\cdot}001$), and across just those transfers involving foreign hosts (E–L; $r = -0{\cdot}74$, $P = 0{\cdot}04$).

could have had a negative impact on the survival of lice transferred to foreign hosts with barb diameters that differed from those found on the usual host.

Alterations in barb size presumably have an impact on the locomotory agility of *Dennyus* spp., although we did not test this possibility in our study. Impaired locomotion may have reduced the ability of lice to avoid preening [the principle defence of most birds against chewing lice (Marshall 1981)]. However, we doubt that preening played an important role because nestling swiftlets seldom preened (personal observation) and were never observed to be preened by their parents. Furthermore, swiftlets and their relatives (Apodidae) have tiny bills in relation to body size, suggesting that preening may not be a very important defence against ectoparasites in this particular family of birds.

Variation in microclimate among feather tracts may be another factor influencing the survival of lice on foreign hosts. The surface temperature of birds varies considerably at different sites on the body. For example, surface temperatures in oystercatchers *(Haematopus ostralegus)*, when ambient temperature was 10°C, varied between 26°C at the base of the primaries and 42°C under the folded wing (Marshall 1981). Since the secondaries of swiftlets are normally covered by a folded wing, the temperature of this feather tract will normally be higher than that of the primaries. Assuming host-specific lice are adapted to the microclimate of the feather tract in which they occur on the usual host, moving to a new feather tract might cause a reduction in survival.

PHYLOGENETIC CONSIDERATIONS

Our study suggests that the fitness of host-specific lice is governed to some extent by the quality of microhabitat available on different species of hosts. Another factor that may correlate with louse fitness is the phylogenetic history of the hosts. Reed & Hafner (1997) measured the fitness of host-specific chewing lice transferred among captive pocket gopher taxa. Their results showed an inverse relationship between louse fitness and the phylogenetic distance between the donor and recipient hosts. In contrast, our results do not show a clear correlation of louse fitness with host phylogeny. As shown in Fig. 6, the phylogenetic distance between *C. esculenta* and *A. salanganus* is equivalent to that between *C. esculenta* and *A. maximus*, since these comparisons share the same most recent common ancestor. Despite this similarity, lice transferred from *C. esculenta* to *A. salanganus* (Fig. 5: E, F and I) had higher survival than lice transferred between *C. esculenta* and *A. maximus* (Fig. 5: J–L). The difference in survival of lice transferred over these

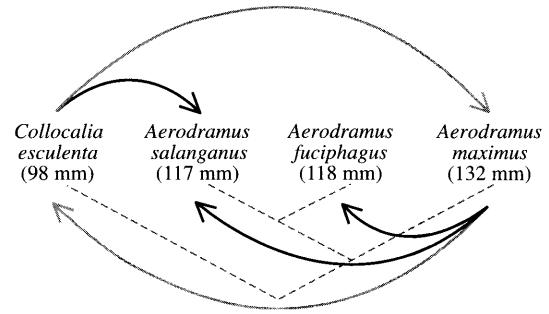


Fig. 6. Summary of the experimental transfers of *Dennyus* lice among swiftlet species, in relation to host phylogeny. Black lines show transfers where lice survived, grey lines indicate transfers where louse survival was near zero. Values in parentheses are the mean wing-chord of five adults of each swiftlet species. Dashed lines show host phylogenetic relationships (from Lee *et al.* 1996).

phylogenetically equivalent distances was related to the unequal differences in feather barb size of the two pairs of hosts.

Conclusions

The host-specificity of *Dennyus* lice on swiftlets appears to be governed by the availability of a particular resource on the body of the host, i.e. flight feathers with suitable dimensions. Such dependence on host morphology is also apparent for lice on mammals. Pocket gopher lice use a groove on the underside of their head to attach themselves to host hair shafts (Reed 1994). Across species, the width of this groove is correlated with the width of the hair shaft of the host. Hence, like *Dennyus*, host-specificity of mammalian chewing lice is related to the quality of the microhabitat provided by the host.

Adaptation to particular hosts is not surprising in the case of permanent parasites, such as chewing lice and Syringophilid mites (Kethley 1971), which spend their entire life cycle on the host. Adaptation might be expected to be less specific in the case of non-permanent parasites. The distribution of non-permanent ectoparasites on swiftlets at Gomantong suggest that this may be true. Whilst the four swiftlet species we studied are host to six *Dennyus* spp., they are host to only four species of hippoboscid louse-flies (R. Peterson, personal communication; Maa 1980). Louse-flies are more mobile parasites found in the nest, as well as on the body of the host (Tompkins *et al.* 1996). These four swiftlet species also share a single species of cimicid bug, which is a highly mobile, nest-based parasite that makes brief forays onto the body of the host to feed (Usinger 1966).

Our results show that, although swiftlet lice are capable of dispersing to foreign hosts (passively or actively), survival is severely reduced unless the feather morphology of the foreign host is quite similar to that of the usual host. Thus, host-specificity is reinforced by the adaptive constraints imposed by host morphology. Lice can moderate the severity of these constraints somewhat by altering their microhabitat distribution on the host. Survival of host-specific lice on foreign hosts does not appear to be correlated with host phylogeny. This implies that current ecological conditions play a more important role than phylogenetic history in maintaining the host-specificity of chewing lice.

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