

Adoption as an offspring strategy to reduce ectoparasite exposure

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Adoption occurs frequently in colonial species where both the cost of parasitism and the opportunity for dependent young to find a foster family are typically high. Because ectoparasites show highly aggregated distributions among colony members, we tested two central predictions of the novel hypothesis that adoption is driven by selection on young to reduce ectoparasite load: first, that nest-based ectoparasites cause offspring to seek adoption, and second, that an individual's parasite load will be reduced after it has been adopted. In agreement with these predictions, experimentally infested Alpine swift *Apus melba* offspring sought adoption significantly more often and at an earlier stage than young kept free of ectoparasitic louse-flies. Second, the parasite load of experimentally infested young was reduced after adoption via a redistribution of ectoparasites among the foster family members. Our findings emphasize what we believe to be a novel role for parasites in the evolution of adoption and, by extension, in the emergence of social interactions.

Keywords: adoption; alloparental care; *Apus melba*; coloniality; cost of parasitism; Hippoboscidae

1. INTRODUCTION

Adoption of unrelated young has evolved in a wide range of animals including birds (Pierotti 1988), mammals (Roulin 2002) and fishes (Wisenden 1999). It is usually initiated by dependent young who leave their original family during the course of the rearing period to seek adoption in a neighbouring family (Pierotti 1991), and hence occurs frequently in colonial species where the opportunity to find a foster family is high (Pierotti 1991). Seeking adoption is adaptive when the amount of food that a young can receive in the foster family is greater than in the original one (Pierotti 1991). Although young reared by lower-quality parents (Pierotti & Murphy 1987; Saino *et al.* 1994; Brown *et al.* 1995) and young placed at a lower rank in their brood hierarchy (Pierotti & Murphy 1987; Brown 1998) seek adoption more often, the proximate factors promoting adoption generally remain unclear (e.g. Holley 1981; Tella *et al.* 1997).

Parasitism is a major cost of coloniality. The re-use of breeding sites and old nests favours large populations of nest-based ectoparasites (e.g. Møller 1990) and the prom-

iscuity of colonial members allows horizontal ectoparasite transmission favouring high rates of host exploitation (Anderson & May 1982). Nest-based ectoparasites are usually highly aggregated, with a few broods typically holding a large number of ectoparasites whereas most broods show weak infestation (Shaw *et al.* 1998). In the present paper, we propose that such a distribution allows for offspring strategies to reduce ectoparasite load where, by adoption, the ectoparasites of heavily infested young become redistributed among the nest-mates of a weakly infested foster family (for other strategies of ectoparasite dilution, see Poulin & Fitzgerald (1989) and Mooring & Hart (1992)). This hypothesis leads to two predictions: (i) ectoparasites cause offspring to seek adoption, and (ii) adoption results in a reduced individual ectoparasite load.

We tested these two predictions using the colonial Alpine swift, *Apus melba*, as a model organism. In Alpine swifts, the nestlings are heavily infested by the blood sucking louse-fly *Crataerina melbae* (Diptera, Hippoboscidae) (Roulin *et al.* 1998) and adoption occurs frequently (Arn 1960; Roulin *et al.* 1998). This louse-fly affects growth and development of nestling Alpine swifts (Bize *et al.* 2003). To test the first prediction that ectoparasites cause offspring to seek adoption, we experimentally increased or decreased the ectoparasite load of randomly chosen broods. Each time that a nestling was found in a foster nest, we put it back into its natal nest to assess its frequency of switching nest. With respect to the second prediction that adoption reduces individual ectoparasite load, we transferred experimentally parasitized nestlings into deparasitized broods. As a control, nestlings from experimentally parasitized broods were transferred into other parasitized broods.

2. MATERIAL AND METHODS

(a) *The Alpine swift*

The Alpine swift is a migrant, aerial insectivorous apodiform bird that reproduces in colonies of a few (< 5) to several hundred pairs. It builds open nests located in holes and ledges of cliffs or tall buildings. One clutch of 1–4 eggs (modal clutch is three) is laid per year. Nestlings are heavily infested by the flightless blood-sucking louse-fly *C. melbae* (Roulin *et al.* 1998; Bize *et al.* 2003), an ectoparasite that spends most of its life cycle on the host body. Within colonies this louse-fly shows an aggregated distribution, and severely infests only a limited number of broods (Roulin *et al.* 1998) and adults (Tella & Jovani 2000). Nestlings are physically unable to switch nest before 20 days of age (P. Bize, personal observation) but thereafter switch nests frequently (Arn 1960; Roulin *et al.* 1998). Given that parental care ceases when offspring take their first flight at an age of 50–70 days (Arn 1960), we studied adoption in 20–50-day-old offspring.

(b) *Prediction one: ectoparasites cause young to seek adoption*

Fieldwork was carried out over 3 years (1999–2001) in a colony of Alpine swifts located under the roof of a tower in Solothurn, Switzerland. Two ectoparasite load treatments were created by transferring louse-flies from donor to receiver nests (hereafter denoted 'deparasitized' and 'parasitized' nests). Treatments were assigned using a randomized block design where a block consisted of two nests with a similar clutch size (Pearson's correlations between the two nests of each block: $r = 0.39$, $n = 50$ blocks, $p = 0.005$), hatching date ($r = 0.95$, $n = 50$, $p < 0.001$), brood size 10 days after hatching ($r = 0.57$, $n = 50$, $p < 0.001$) and number of louse-flies 10 days after hatching ($r = 0.45$, $n = 50$, $p = 0.001$). Starting 10 days after hatching, louse-flies were collected by hand for each block from both nests, and then added to one of them, chosen at random. Because new flies frequently invaded deparasitized nests, manipulation of ectoparasite loads was repeated every 5 days until 50 days after hatching. To record nest-switching events, we checked all nests daily between 20 and 50 days after hatching and returned each nest-switcher immediately to its natal nest.

Table 1. Effect of parasite manipulation on nest switching.

(Mean \pm 1 s.e. per nest are reported; sample sizes are in brackets. Significance levels are reported in § 3a.)

variable	deparasitized nest	parasitized nest
age at first nest switching (day)	39.1 \pm 1.9 (13)	33.0 \pm 1.7 (17)
number of nest-switching events per chick	1.3 \pm 0.2 (13)	2.5 \pm 0.4 (17)

(c) Prediction two: young reduce ectoparasite load via adoption

In 2001, we paired seven randomly chosen parasitized broods with seven randomly chosen deparasitized ones from the first experiment (see § 2b). For each pair of nests, we transferred a parasitized nestling into a deparasitized brood for 1 h, mimicking the situation where an infested nestling invades a parasite-free foster family. As a control, one parasitized nestling was transferred into a parasitized brood to measure the change in parasite load of a parasitized individual invading a foster nest where nestlings show a similar parasite load as the nest-switcher. Louse-flies were counted on each nestling both before the transfer into a foster brood and 1 h later. Transferred nestlings were old enough (range of 20–41 days; mean of 31 days) to switch nest on their own. Parasitized nestlings transferred into deparasitized and parasitized foster families did not differ significantly in age (Student's *t*-test: $t = -0.73$, d.f. = 12, $p = 0.48$), body mass ($t = -0.13$, d.f. = 12, $p = 0.90$) and number of ectoparasites counted before transfer ($t = 1.16$, d.f. = 12, $p = 0.27$). Transferred nestlings and their foster nest-mates were also similar in age (paired *t*-test: $t = -0.84$, d.f. = 13, $p = 0.41$) and body mass ($t = 0.78$, d.f. = 13, $p = 0.45$). There was no statistical difference in brood size between parasitized and deparasitized foster families (Wilcoxon two-sample test: $Z = -0.21$, $p = 0.83$).

(d) Statistics

In the first experiment, pseudo-replication was avoided by considering only the first breeding attempt of each breeding pair. This reduced our sample size from 100 to 78 experimental broods. For the same reason, statistical tests were carried out on mean sibling values rather than on individual nestlings of a brood. The number (x) of louse-flies found on nestlings was $\log(x + 1)$ -transformed before analyses to fit a normal distribution. Throughout the paper, mean values are quoted \pm 1 s.e., statistical tests are two-tailed and p -values less than 0.05 are considered as significant.

3. RESULTS**(a) Prediction one: ectoparasites cause young to seek adoption**

Although parasite prevalence was 100% in both treatments, there were significantly fewer louse-flies per nestling over the period 10 to 50 days after hatching in deparasitized than parasitized broods (deparasitized nestlings: 7 ± 1 louse-flies; parasitized nestlings: 17 ± 1 louse-flies) (Student's *t*-test: $t = 6.88$, d.f. = 78, $p < 0.001$). Nestlings of experimentally parasitized broods started to switch nests for the first time 6 days earlier than nestlings of broods where parasites had been removed ($t = 2.38$, d.f. = 28, $p = 0.024$; table 1). They also switched nests 1.6 times more frequently between 20 and 50 days after hatching (Wilcoxon two-sample test: $Z = 2.37$, $p = 0.018$; table 1). The frequency of switching per nestling was non-significantly correlated with age at first switching (Pearson correlation: $r = -0.34$, $n = 30$, $p = 0.07$). The prevalence of nest switching was similar in both treatments (nest switching occurred in 17 out of 38 parasitized broods (44.7%) versus 13 out of 40 deparasitized broods (32.5%); Fisher's exact test $p = 0.35$). The number of nest-switchers per brood did not differ between the parasitized and deparasitized treatments (1.24 ± 0.14 versus 1.38 ± 0.18 nest-switchers, respectively; $Z = 0.77$, $p = 0.44$).

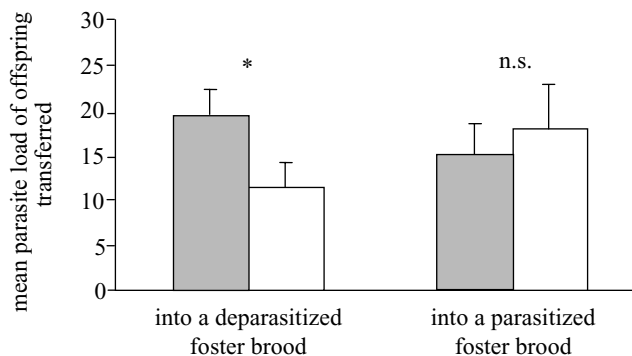


Figure 1. Mean parasite load (\pm 1 s.e.) of nestlings before (filled bars) and after (open bars) transfer to experimentally parasitized and deparasitized foster broods. Significance level is indicated by an asterisk if $p < 0.05$ and n.s. if $p > 0.05$.

(b) Prediction two: young reduce ectoparasite load via adoption

Parasitized nestlings lost 42% of their ectoparasites when transferred into deparasitized foster broods (paired *t*-test: $t = -4.55$, d.f. = 6, $p = 0.004$; figure 1), whereas the ectoparasite load of the parasitized nestlings did not change after transfer to another parasitized foster family ($t = 0.85$, d.f. = 6, $p = 0.43$; figure 1).

4. DISCUSSION

The first experiment shows that Alpine swift nestlings are more prone to switch nest when exposed to severe parasite infestation, and the second experiment demonstrates that parasitized nestlings reduce their parasite load by half after invading parasite-free broods. These findings support our novel hypothesis that, in host–parasite systems where ectoparasites exhibit an aggregated distribution with most parasites being found in a low number of broods (Roulin *et al.* 1998; Shaw *et al.* 1998), seeking adoption may have evolved as an adaptive offspring strategy to reduce ectoparasite load. Indeed, the likelihood that a heavily infested nest-switcher encounters a less-infested foster family and will thereby dilute its ectoparasite burden is high. Louse-flies may also benefit from triggering adoption by the use of hosts as a vehicle to infest other nests. However, the parasite's need to manipulate host behaviour for that purpose is not very high as louse-flies can rapidly walk from nest to nest and spread to most nests even before young swifts start to seek adoption (Roulin *et al.* 1998; P. Bize, personal observation). To our knowledge, this study provides the first experimental evidence that parasites can play a part in the evolution of adoption and, by extension, in the emergence of social interactions. It is an intriguing result because parasites are a major cost in colonial hosts, and hence should rather select for host

spacing and low levels of host social interactions. There are several possible answers to the paradox: (i) louse-flies are highly mobile and spacing of nests within a colony will therefore not lead to a substantial reduction of parasite load; (ii) the benefits of coloniality outweigh the benefits given by a lower parasite load if breeding solitarily; or (iii) the cost of rejection of a nest-switcher by foster parents is higher than the sum of the cost of food sharing with an additional nestling plus the costs arising from an increased parasite load.

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