

Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift

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Summary

1. Parasitism is a non-negligible cost of reproduction in wild organisms, and hosts are selected to partition resources optimally between current and future reproduction. While parents can compensate for the cost of parasitism by increasing their current reproductive investment, such change in resource allocation is expected to carry-over costs on future reproduction.

2. Life history theory predicts that because long-lived organisms have a high residual reproductive value, they should be more reluctant to increase parental effort in response to parasites. Also, when rearing successive infested broods, the cost of parasitism can cumulate over the years and hence be exacerbated by past infestations.

3. We tested these two predictions in the alpine swift *Apus melba*, a long-lived colonial bird that is infested intensely by the nest-based blood sucking louse-fly *Crataerina melbae*. For this purpose, we manipulated ectoparasite load over 3 consecutive years and measured reproductive parameters in successive breeding attempts of adults assigned randomly to 'parasitized' and 'deparasitized' treatments.

4. In current reproduction, fathers of experimentally parasitized broods produced a similar number of offspring as fathers from the deparasitized treatment, but the rearing period was prolonged by 4 days. Fathers that were assigned to the parasitized treatment in year x produced significantly fewer fledglings the following year $x + 1$ than those of the deparasitized treatment. The number of young produced by fathers in year $x + 1$ was correlated negatively with the number of days they cared for their brood in the previous year x . We also found a significant interaction between treatments performed over 2 successive years, with fathers of parasitized broods suffering a larger fitness loss if in the past they had already cared for a parasitized brood rather than for a deparasitized one. Similar effects of parasitism, although partly non-significant ($0.05 < P\text{-values} > 0.10$), were found in mothers.

5. Altogether, our results show that parasites can modify resource allocation between current and future reproduction in long-lived hosts, and that the cost of parasitism can cumulate over the years. It emphasizes the fact that effects of parasites can depend on past infestations and become apparent in future reproduction only.

Key-words: *Apus melba*; cost of plasticity, ectoparasite, hatching asynchrony, Hippoboscidae; life history theory; trade-off between current and future reproduction.

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Introduction

In iteroparous organisms, natural selection favours optimal partitioning of resources over the reproductive attempts and thereby maximizes lifetime reproductive

success. Reproduction entails significant costs to parents, and effort invested in current reproduction is traded-off against survival and effort devoted to future reproduction, as shown experimentally a number of times (review in Stearns 1992; Golet, Irons & Estes 1998). The optimal partitioning of resources between reproductive events is expected to differ between species and environments (Stearns 1992). For instance, short-lived species should invest a significant amount of resources in current reproduction by producing a large number of high-quality offspring because the likelihood of reproducing again is low. In contrast, long-lived organisms should refrain investment in current reproduction because their residual reproductive value is typically high. Environmental factors can also alter trade-off by affecting either the value of current reproductive attempt, survival prospect, or both.

Parasitism is an important environmental component that modulates reproductive success of wild organisms. Broods are frequently heavily infested, and experimental manipulation of parasite load demonstrated that parasites can severely impair the growth and survival of young hosts (review in Clayton & Moore 1997). As a result, host parents are predicted to maximize lifetime reproductive success by adjusting investment in reproduction as a function of how parasites affect their current reproductive success, how investment alters the effect of parasites, and finally how change in investment affects future reproductive success (Forbes 1993; Perrin, Christe & Richner 1996). Accordingly, in several bird species parents modify their behaviour when raising parasitized offspring (e.g. Møller 1994; Christe, Richner & Oppliger 1996a, 1996b; Hurtrez-Boussès *et al.* 1998), which in turn influences the future reproductive success of parents (Møller 1993). As an example, parent blue tits *Parus caeruleus* Linnaeus of experimentally infested broods increased the rate of food provisioning to offspring (Tripet & Richner 1997), and this change in parental behaviour decreased the survival and future reproductive success of the parents (Richner & Tripet 1999). With respect to the effect of parasites on the trade-off resolution of resources allocated between successive breeding attempts, two important issues remain as yet unexplored. First, all model organisms used so far are short-lived species (barn swallow *Hirundo rustica* L., de Lope & Møller 1993; Møller 1993; house martin *Delichon urbica* L., de Lope *et al.* 1993; blue tit: Richner & Tripet 1999; great tit *P. major* L., Fitze, Tschirren & Richner 2004), and hence it remains unclear if parasites have similar effects in long-lived species. Because in the face of poor rearing conditions such as intense parasite infestation, long-lived organisms may favour their survival at the expense of offspring number and quality, they can be predicted to be reluctant to increase parental effort in response to parasitism (Lindén & Møller 1989). Secondly, most studies so far investigated the reproductive cost of parasitism in a single year, and hence the possibility

that effect of parasites cumulate over the years remains unexplored. The effect of parasites on the reproductive success of their hosts may be benign when host parents raise a parasitized brood for the first time but become non-negligible when they care again for a parasitized brood in subsequent reproductive attempts. Survival of nest-based ectoparasites between breeding attempts is common, and hence the level of parasitism in a given year will partly determine level in the next year (e.g. Roulin *et al.* 2001). These two aspects of host-parasite relationships may be important in explaining variation in the effects of parasites on host life-history strategies.

In this paper, we investigated experimentally if the long-lived alpine swift *Apus melba* L. is more reluctant to increase parental effort in response to infestation by the nest-based blood sucking louse-fly *Crataerina melbae* Rondani (Diptera, Hippoboscidae), and if the cost of parasitism cumulates over the years. A previous study demonstrated that in this species developmental plasticity lessens the negative effect of parasitism on nestlings by a reduction of growth rate during heavy infestation followed by an acceleration of growth rate (so-called accelerated growth) once parasites become naturally less abundant. Combined with a longer nestling period (so-called delayed maturation), developmental plasticity allowed parasitized offspring to fledge with a similar body size to parasite-free offspring (Bize *et al.* 2003a). Developmental plasticity is, however, unlikely to be cost-free (Metcalf & Monaghan 2001), and parents may pay part of this cost if extra resources are required for parasitized offspring to adjust growth rate to the dynamics of parasite infestation. This hypothesis predicts that residual reproductive value of parents of a parasitized brood may decline. To test this hypothesis, we manipulated louse-fly load over three successive reproductive seasons, and monitored the effect of this experiment on parental reproductive success and effort measured in the current and future breeding attempts.

Materials and methods

MODEL ORGANISMS

The alpine swift is a 90 g trans-Saharan migrant bird that feeds on insects caught exclusively on the wing. This species is long-lived with age at maturity being reached not before 2 years old and the oldest recaptured bird reported being 26 years old (Arn 1960; Swiss Ornithological Station, personal communication). Alpine swifts reproduce in colonies of a few (< 5) to several hundred pairs in holes located in cliffs or under the roofs of tall buildings. It is socially monogamous with stable pair bonds over several years (Arn 1960; P.B., personal observation). Males and females build an open nest of feathers and dry materials grasped in the air and cemented together with saliva. Breeding pairs commonly reuse the same nest from one year to

the next one. A single clutch is produced per year containing one to four eggs (mean is 2.6) laid at 1-day intervals. Both parents incubate the clutch for 20 days, and feed the offspring up to fledging 50–70 days after hatching (Bize *et al.* 2003a). At birth, nestlings are naked and parents brood them up to 10 days after hatching. The aerial insectivorous diet makes food provisioning highly dependent on weather conditions with almost no food on cold and rainy days (Arn 1960). On sunny days, between 9 o'clock in the morning and 10 o'clock in the evening, parents feed their young one to three times per hour with a single 2.5 g bolus each time containing 10–600 insects (Arn 1960). Parental care stops after offspring have taken their first flight. Breeding adults initiate the moult of primary feathers at the time of hatching.

The 7-mm-long blood-sucking louse-fly *C. melbae* feeds exclusively on adult and nestling alpine swifts (Tella *et al.* 1998). Larvae develop in the maternal abdomen (viviparity) until the prepupal stage when they are released near or inside the host nests, and then pupate immediately (Bequaert 1953). There is one generation of parasites per year, and pupae do not hatch before the following year. *C. melbae* is flightless and can rapidly switch hosts on foot (Bize, Roulin & Richner 2003b). Several hippoboscids fly species have been shown to transmit blood parasites to their host (Baker 1967) but this has not been confirmed for *C. melbae* (Tella *et al.* 1995; P.B., personal observation, $N = 30$ blood smears). Mites *Dermanyssus* sp. (Acarina) and lice *Dennyus* sp. (Mallophaga) also infest alpine swift nestlings, but are relatively rare (Arn 1960; P.B., personal observation). For this reason, we did not consider them in the present study.

GENERAL METHODS

Fieldwork was carried out between May and August 1999–2002 in an alpine swift colony counting 50 breeding pairs located under the roof of a clock tower in Solothurn (47°12'N, 7°32'E), Switzerland. Each breeding season, nests were visited daily to determine laying date of the first egg, clutch size, egg volume, hatching date of the first egg (denoted day 0), hatching asynchrony, fledging date and brood size at fledging. Fifty days after hatching, we also weighed nestlings to the nearest 0.1 g and measured wing length to the nearest mm, and then calculated body condition as the residuals of a linear regression of log-transformed body mass on log-transformed wing length ($F_{1,45} = 17.12$, $P = 0.0002$, $r^2 = 0.28$, $N = 47$ broods). Egg length L and breadth B were measured to the nearest 0.1 mm, and egg volume V was calculated with the formula $V = LB^2\pi/6$, a measure that reflects egg size reliably in the alpine swift (Bize, Roulin & Richner 2002). A brood is said to have hatched synchronously if all siblings hatched within an interval of 24 h, or asynchronously if the brood took more than 24 h to hatch. To test the effect of parasite manipulation in year x on hatching asynchrony in year $x + 1$, only nests with at least two nestlings were con-

sidered. The nestling period was determined as the number of days elapsed between hatching of the first egg and fledging of the last young. In the analysis of the nestling period, we therefore controlled for brood size at fledging. In 2000 and 2001, parental food provisioning rate was recorded 35 days posthatching, which corresponds to the peak of louse-fly infestation (Bize *et al.* 2003a). Using infrared video sensitive cameras (ref. GEH.F.116785, Conrad Electronic AG, Switzerland), nests were filmed during 6 hours (10.00–16.00 h). Feeding rates of male and female parents were calculated as the number of feeding trips per hour. To identify birds on video footage, some body feathers were decoloured with a commercial hairdresser decolouring paste in 2000 and 2001 (Malacarne & Griffa 1987). Feather decolouration did not affect adult returning rate as breeders the following years, nor nest site fidelity, mate fidelity and current and future reproductive success (statistics not shown, all P -values > 0.41). Because a large part of the variation in feeding rate is likely to be explained by weather conditions, we included daily precipitation, measured by the Swiss meteorological station at Bern Liebefeld, 28 km apart from our study colony, as a covariate in the analysis of feeding rate. Daily ambient temperature and wind had no significant effects on feeding rate ($P > 0.40$), and were hence discarded from our final statistical model. Precipitation tends to decrease along the reproductive season of alpine swifts (mean May amount of rain in years 1999–2001 is 119.2 mm, June 137.2 mm, July 125.4 mm, August 112.9 mm). Most breeders were captured a first time while sitting on their eggs, and 73% of them were recaptured while provisioning their young a few days (mean is 5 days) after feeding rate was recorded. The date when adults were captured (day 1 = 1 May) was included as a covariate in the analyses. Each year, non-breeders (33 individuals in 1999, nine in 2000, 33 in 2001 and 31 in 2002) were captured while visiting the colony during daytime between May and July, or while roosting in the colony at night in August. At that time, most adults (70–90%) roost in the colony and thus can be captured easily by closing the colony entrances. Adult body mass and wing length were measured to the nearest 0.1 g and 1.0 mm, respectively, and we calculated an index of adult body condition as explained above for nestlings ($F_{1,79} = 16.69$, $P = 0.0001$, $r^2 = 0.174$, $N = 81$ adults). Louse-flies were searched systematically and counted during a 4-min period by blowing feathers of the whole body. This visual method is efficient, as demonstrated by the strong correlation between numbers of louse flies counted with this method and after having extracted manually louse flies from the plumage ($r = 0.97$, $N = 282$, $P < 0.001$). The number (y) of louse-flies found on adults were $\log(y + 1)$ -transformed to fit a normal distribution. Because primary feathers are moulting symmetrically, we assessed the advancement of moult on one wing solely. Each of the 10 primary feathers of the left wing was scored on a 0–5 scale (0 = old feather; 1–4 = growing new feather;

5 = fully developed new feather) (Newton 1966), and the total primary score (range 0–50) was calculated as the sum of the scores assigned to each primary feather. Because alpine swifts are sexually monomorphic, a drop of blood was collected from the foot of each individual, and their sex determined from blood cell DNA using polymerase chain reaction (PCR) amplification of the *CHD* genes (Ellegren 1996; Griffiths *et al.* 1998).

MANIPULATION OF ECTOPARASITE LOAD

To create two groups of nests differing in ectoparasite load, we transferred louse-flies from a donor brood (referred to as ‘deparasitized brood’) to a receiver one (‘parasitized brood’) over three successive breeding seasons (1999–2001). Treatments were assigned using a randomized block design where a block consisted of two nests with a similar hatching date (Pearson’s correlation between the two nests of each block: $r = 0.95$, $N = 50$, $P < 0.001$), brood size 10 days after hatching ($r = 0.57$, $N = 50$, $P < 0.001$) and number of louse flies 10 days after hatching ($r = 0.45$, $N = 50$, $P = 0.001$). Manipulation of louse-fly load started 10 days after hatching because ectoparasites are rarely found on nestlings before this age (Roulin *et al.* 2003). For each block of nests, louse-flies were collected by hand in the nest cup and on nestlings of both nests, and immediately returned to one of the two nests, chosen randomly. We did not manipulate the number of louse-flies found on the body of adults. Because flies frequently reinfested deparasitized broods, manipulation of ectoparasite load was repeated every 5 days until nestlings were 50 days old. We have demonstrated elsewhere (Bize *et al.* 2003a) that our manipulation was efficient, because nestlings belonging to the ‘parasitized’ treatment bore 2.4 times more louse-flies than nestlings of the ‘deparasitized’ treatment (17 ± 1 vs. 7 ± 1 louse-flies). In total, 11, 20 and 19 blocks of parasitized and deparasitized nests were generated in 1999, 2000 and 2001, respectively.

Sixty-eight per cent of the breeders included in our experiment in year x returned as breeders in year $x + 1$. At that time, the number of louse-flies on their nestlings was either manipulated as described above if adults were included again in the parasitized and deparasitized treatments or, if not, the number of louse-flies per nestlings was counted but not manipulated (referred to as ‘control brood’). Table 1 summarizes how parents were allocated to treatments in year $x + 1$ (parasitized; control; deparasitized) in relation to treatments in year x (parasitized; deparasitized). In fathers, treatments in year $x + 1$ were allocated at random with respect to the treatment in which they were allocated in year x ($\chi^2 = 2.11$, $P = 0.38$), whereas in mothers there was an unexpected bias for females of parasitized brood in year x to rear more frequently a deparasitized than a parasitized brood in year $x + 1$ ($\chi^2 = 9.17$, $P = 0.01$).

Table 1. Allocation of treatments in year $x + 1$ in relation to treatments in year x for father and mother alpine swifts

Treatment in year $x + 1$	Treatment in year x	
	Deparasitized	Parasitized
Fathers ($n = 35$)		
Deparasitized	5	11
Control	4	5
Parasitized	6	4
Mothers ($n = 40$)		
Deparasitized	4	8
Control	6	8
Parasitized	12	2

STATISTICS

The unit of statistical analysis was the adult, and thus separate analyses were carried out for each sex. To avoid pseudoreplication, if an adult was recorded in more than one breeding season we included only its first breeding attempt to test the effect of the manipulation of ectoparasite load performed in year x on reproductive parameters measured in the same year x (i.e. current reproduction). Reproductive parameters measured in the subsequent year $x + 1$ were used to test the effect of treatments in year x on future reproduction in year $x + 1$. Treatment performed in year x (parasitized; deparasitized) and year of treatment (1999, 2000, 2001) were entered as two independent variables in ANOVA models when testing the effect of the manipulation of ectoparasite load in year x on current and future reproduction. As we also manipulated the ectoparasite load between 10 and 50 days after hatching in year $x + 1$, we added the effect of treatment (parasitized; control; deparasitized) performed in year $x + 1$ as an independent variable in the analysis of offspring condition and brood size at fledging in year $x + 1$.

The likelihood of adults returning to the colony the following year, fidelity to mate and nest were analysed with binomial logistic regressions. Alpine swifts are faithful to their breeding colony (Arn 1960; P.B., personal observation), and therefore the estimation of the probability of returning to the colony the following year is unlikely to be flawed by emigration. Adults may, however, skip reproduction and not be caught the following year. Although intense efforts were made each year to capture both breeders and non-breeders (see above), no adult was observed to skip reproduction during the study period. This suggests that estimates of the probability that an adult returns to the colony the following year accurately reflect survival rate. Because adults may change mate from one year to the next one due to the death of their mate, we restricted our analyses of mate fidelity to individuals where the mate remained alive from one year to the next one.

For each reproductive parameter, a full model containing all explanatory factors, covariates and first-order

Table 2. Analyses of variance showing the effects of treatment (parasitized/deparasitized broods) and year (1999/2000/2001) on different measures of current reproduction in father and mother alpine swifts. Sexes are analysed separately. Degrees of freedom (d.f.), *F*-values and *P*-values are reported; significant *P*-values are shown in bold type

Traits measured in year <i>x</i>	Factors	Fathers			Mothers		
		d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Louse fly loads during rearing	Treatment in year <i>x</i>	1,38	0.37	0.55	1,35	8.78	0.005
	Year	2,38	0.49	0.61	2,35	1.48	0.24
Body condition during rearing ^a	Treatment in year <i>x</i>	1,38	0.05	0.83	1,35	2.99	0.09
	Year	2,38	1.61	0.21	2,35	1.41	0.26
Moult score during rearing ^b	Treatment in year <i>x</i>	1,38	0.66	0.42	1,35	0.03	0.87
	Year	2,38	1.19	0.32	2,35	0.99	0.38
Feeding rates ^c	Treatment in year <i>x</i>	1,38	0.31	0.58	1,38	0.06	0.81
	Year ^d	1,38	1.50	0.23	1,38	1.54	0.22
Nestling period ^e	Treatment in year <i>x</i>	1,44	9.88	0.003	1,44	3.91	0.05
	Year	2,44	1.35	0.23	2,44	0.87	0.43
Number of fledglings	Treatment in year <i>x</i>	1,51	3.04	0.09	1,51	2.66	0.11
	Year	2,51	1.08	0.35	2,51	2.84	0.07

^aAfter controlling for the date of capture. Adult body condition decreased with the advancement of the season $F_{1,79} = 8.98$, $P = 0.004$. ^bAfter controlling for the date of capture. Moult score of adults increased with the advancement of the season $F_{1,79} = 174.89$, $P < 0.001$. ^cAfter controlling for daily precipitation. The number of feedings decreased with increasing daily precipitation $F_{1,80} = 46.01$, $P < 0.001$. ^dThe analysis is restricted to 2000 and 2001. ^eAfter controlling for brood size at fledging. The nestling period increased with brood size $F_{1,94} = 4.16$, $P = 0.04$.

interactions was initially fitted. Only significant covariates and interactions were kept in final models. Statistical analyses were carried out with the statistical software JMP IN 4.0 (Sall & Lehman 1996). Throughout the paper, mean values are quoted ± 1 SE, statistical tests are two-tailed and *P*-values less than 0.05 considered to be significant.

Results

EFFECT OF PARASITISM ON CURRENT REPRODUCTION

The number of louse-flies was about eight times lower on parents than on their offspring, measured on the same day (deparasitized broods: 0.7 ± 0.2 louse-flies per parent vs. 4.9 ± 1.3 per nestling, $N = 26$ broods; paired *t*-test: $t = 3.41$, d.f. = 25, $P < 0.002$; parasitized broods: 1.7 ± 0.4 louse-flies per parent vs. 15.4 ± 1.5 per nestling, $N = 26$ broods; paired *t*-test: $t = 9.13$, d.f. = 25, $P < 0.0001$). Mothers of experimentally parasitized broods had significantly more louse-flies on their body than those of deparasitized ones (2.23 ± 0.68 vs. 0.41 ± 0.15 louse-flies, $N = 22$ and 17 individuals, respectively, Table 2). In contrast, we did not detect any significant difference in ectoparasite load between fathers of parasitized and deparasitized broods (1.2 ± 0.3 vs. 0.8 ± 0.2 louse-flies, $N = 22$ and 20 individuals, respectively, Table 2). Within deparasitized nests, louse-flies were found in similar numbers on fathers and mothers (paired *t*-test: $t = 0.43$, d.f. = 10, $P = 0.68$), whereas within parasitized nests louse-flies were more abundant on mothers than fathers (paired *t*-test: $t = -2.48$, d.f. = 14, $P = 0.03$). Moult score and body condition of parents did not differ between the two treatments (Table 2).

At the peak of louse-fly infestation (i.e. 35 days post-hatching), there was no significant difference between treatments on the number of feeding trips per hour in both male and female parents (Table 2). On average, fathers reared their young 4 days longer in parasitized than deparasitized broods (63.2 ± 1.4 vs. 58.9 ± 0.7 days, $N = 23$ and 25 broods, respectively, Table 2). Similarly, mothers cared for their young 2 days longer in parasitized than deparasitized broods (62.5 ± 1.3 vs. 60.1 ± 0.9 days, $N = 24$ and 24 broods, Table 2). The number of fledglings produced by fathers and mothers was similar in the two treatments (Table 2).

EFFECT OF PARASITISM ON RETURNING RATE, NEST SITE AND MATE FIDELITY

Thirty-five of 55 (63.6%) fathers and 40 of 55 (72.7%) mothers that reared an experimental brood in a year *x* were recaptured as breeders in the colony the following year *x* + 1. In both sexes, louse-fly manipulation did not affect their returning probability (69.0% vs. 57.7% for fathers of the parasitized and deparasitized treatments, respectively; logistic regression: Wald $\chi^2 = 1.07$, $P = 0.30$; and 64.3% vs. 81.5% for mothers of the parasitized and deparasitized treatments, respectively; Wald $\chi^2 = 2.54$, $P = 0.11$). The factor 'year' had no significant effect on the returning probability (fathers: Wald $\chi^2 = 2.70$, $P = 0.26$; mothers: Wald $\chi^2 = 5.04$, $P = 0.08$).

Treatments in year *x* affected significantly the number of louse-flies found in nests and on nestlings 10 days after hatching in year *x* + 1 (parasitized nests: 33 ± 5 , $N = 18$; deparasitized nests: 11 ± 3 , $N = 21$; $F_{1,37} = 18.42$, $P < 0.001$). The manipulation of louse-flies in year *x* might therefore also shape the distribution of adults among nests in year *x* + 1. To test this hypothesis, we

Table 3. Analyses of variance showing the effects of treatment in year x (parasitized/deparasitized broods), treatment in year $x + 1$ (parasitized/control/deparasitized broods) and year (1999/2000/2001) on different measures of future reproduction (year $x + 1$) in father and mother alpine swifts. Sexes are analysed separately. Degrees of freedom (d.f.), F -values and P -values are reported; significant P -values are shown in bold type

Traits measured in year $x + 1$	Factors	Fathers			Mothers		
		d.f.	F	P	d.f.	F	P
Adult body condition at incubation	Treatment in year x	1,31	0.38	0.54	1,35	0.01	0.97
	Year	2,31	1.38	0.27	2,35	2.13	0.13
Laying date	Treatment in year x	1,31	0.62	0.44	1,36	0.02	0.88
	Year	2,31	51.49	< 0.001	2,36	46.49	< 0.001
Clutch size	Treatment in year x	1,31	3.18	0.08	1,36	0.01	0.92
	Year	2,31	0.75	0.48	2,36	0.91	0.41
Egg volume	Treatment in year x	1,31	0.44	0.51	1,35	0.41	0.53
	Year	2,31	3.29	0.05	2,35	4.13	0.02
Number of fledglings	Treatment in year x (a)	1,27	22.88	< 0.001	1,32	4.34	0.045
	Treatment in year $x + 1$ (b)	2,27	3.23	0.06	2,32	2.44	0.10
	Year (c)	2,27	2.03	0.15	2,32	1.88	0.17
	Interaction a \times b	2,27	6.60	0.005	2,32	2.45	0.10
Offspring body condition at 50 days after hatching	Treatment in year x	1,25	2.95	0.10	1,25	0.11	0.74
	Treatment in year $x + 1$	2,25	0.40	0.68	2,25	0.05	0.95
	Year	2,25	1.90	0.17	2,25	2.01	0.16

investigated potential treatment effects on mate and nest site fidelity. We did not find any support for this hypothesis, probably because nest site fidelity was high in both sexes (fathers: 88.6%; mothers: 77.5%). Indeed, mate and nest site fidelity was not affected by the manipulation of louse-flies (fathers: Wald $\chi^2 = 0.20$, $P = 0.66$; mothers: Wald $\chi^2 = 0.43$, $P = 0.51$) and by year (fathers: Wald $\chi^2 = 0.10$, $P = 0.95$; mothers: Wald $\chi^2 = 0.19$, $P = 0.91$). Also, divorce rate (fathers: 29.2%; mothers 33.4%) did not differ significantly between treatments and year (effect of treatment: fathers: Wald $\chi^2 = 0.24$, $P = 0.63$; mothers: Wald $\chi^2 = 1.76$, $P = 0.18$; effect of year: fathers: Wald $\chi^2 = 0.68$, $P = 0.71$; mothers: Wald $\chi^2 = 0.86$, $P = 0.65$).

EFFECT OF PARASITISM ON FUTURE REPRODUCTION

For both parents, manipulation of the number of louse-flies in their nest in year x had no significant effect on laying date, clutch size, egg volume and adult body condition measured during incubation in the subsequent year ($x + 1$) (Table 3). Hatching synchrony in year $x + 1$ was not affected by treatments in year x (mothers: logistic regression, Wald $\chi^2 = 0.12$, $P = 0.73$; fathers: Wald $\chi^2 = 0.68$, $P = 0.41$) and by year (mothers: Wald $\chi^2 = 4.22$, $P = 0.12$; fathers: Wald $\chi^2 = 4.13$, $P = 0.13$). Treatment in year x had, however, a significant effect on brood size at fledging in year $x + 1$ with fewer offspring being produced by parents that reared a parasitized compared to a deparasitized brood the year before (Table 3; Fig. 1). Manipulation of parasite load in successive years severely affected reproductive success as indicated by the significant interaction between treatments performed in years x and $x + 1$ in fathers (Table 3). Birds that reared a parasitized brood fledged much fewer young if, in the past, they had already cared

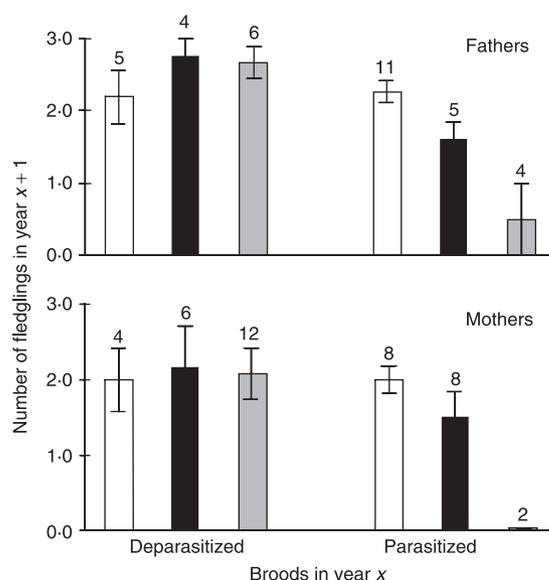


Fig. 1. Mean number of fledglings (\pm SE) produced by parents in year $x + 1$ in relation to the manipulation of ectoparasite load in year x (deparasitized and parasitized nests) and year $x + 1$ (deparasitized nests = white bars; control nests = black bars; parasitized nests = grey bars). The upper graph is for fathers, the lower one for mothers. Sample sizes are indicated above the bars.

for a parasitized brood rather than for a deparasitized one (Fig. 1). We observed a similar reduction in future reproductive success for mothers of parasitized broods (Fig. 1), but this relationship was not significant ($P = 0.10$; Table 3) probably due to the small sample size and unbalanced design (Table 1). Body condition of offspring measured 50 days after hatching in year $x + 1$ was neither affected by treatments performed in year x nor by treatments performed in year $x + 1$ (Table 3).

Life-history theory suggests that future reproductive success is shaped by investment in current reproduction.

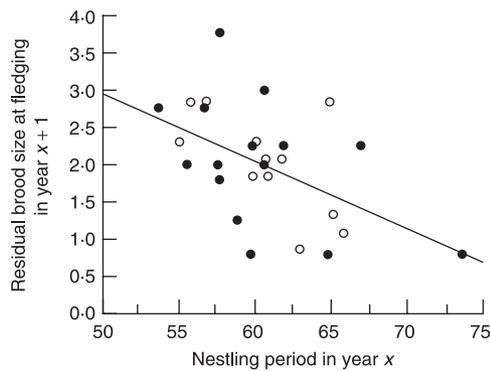


Fig. 2. Relationship between the number of young fledged by fathers in year $x + 1$ and the number of days they cared for their offspring in year x when controlling for the effect of year x and treatment in year x . Open and closed symbols are for deparasitized and parasitized broods in year x , respectively.

To examine this hypothesis, we tested whether the decrease in reproductive success in year $x + 1$ caused by the manipulation of parasite load in year x was associated with the amount of time parents cared for their young in year x . For this purpose, we used an ANOVA with brood size at fledging in year $x + 1$ as the dependent variable, and treatment in year x (parasitized, deparasitized), year (1999, 2000, 2001) and the amount of time parents cared for their offspring in year x as three independent variables. Number of fledglings reared by fathers in year $x + 1$ was related negatively to the number of days they cared for the young in the previous year x ($F_{1,24} = 8.93$, $P = 0.006$; Fig. 2). Effect of treatment was no more significant in this model ($F_{1,24} = 3.57$, $P = 0.07$), suggesting that part of the effects of ectoparasite load manipulation in year x on reproductive success in year $x + 1$ occurred through the parasite-induced prolonged nestling period in year x . The factor 'year' had a significant effect in this model, with fewer young being fledged in 2000 in comparison to 2001 and 2002 (1.71 ± 0.19 , 2.43 ± 0.26 and 2.25 ± 0.25 , respectively; $F_{2,24} = 5.80$, $P = 0.009$). A similar, although non-significant, negative relationship between nesting period and future reproduction was observed in mothers ($F_{1,31} = 3.41$, $P = 0.07$; treatment: $F_{1,31} = 0.68$, $P = 0.42$; year: $F_{2,31} = 1.21$, $P = 0.31$).

Discussion

Parasites are ubiquitous and they can impair the development and survival of their hosts. To maximize lifetime reproductive success, host parents are therefore expected to optimally partition their resource over the reproductive attempts. In the present study, we examined the effect of parasites on current and future reproduction of alpine swift parents. Louse-flies had no significant effect on the current reproductive success of mothers and fathers, but reduced future reproductive success. Even though swifts are long-lived, parasites altered resource allocation behaviour of their host, which in turn affected future reproduction. Further-

more, the significant interaction between treatments in year x and year $x + 1$ demonstrates that negative impact of parasitism can be additive, with parents raising a parasitized brood over two consecutive years achieving a much lower reproductive success in their second attempt in comparison to the first one.

EFFECT OF PARASITISM ON CURRENT REPRODUCTION

Parents can use two non-mutually exclusive strategies to lessen the effect of parasites on their current reproduction. First, by provisioning their offspring at faster rates they can compensate for the energy and nutrients extracted by parasites from nestling, as demonstrated in experimentally infested broods of great (Christe *et al.* 1996a) and blue tits (Tripet & Richner 1997; Hurtrez-Boussès *et al.* 1998; Bouslama *et al.* 2002). There is no evidence for such a strategy in the alpine swift because parents of parasitized and deparasitized broods provided a similar amount of food to their young at the peak of louse-fly infestation. We measured feeding rate in the middle of the nestling period only, and cannot completely exclude the possibility that parents of parasitized broods fed their offspring at a higher rate earlier or later in their development. Indeed, parasitized nestlings were shown to grow their wings at a faster rate than deparasitized nestlings in the second half of their development (i.e. from 40 days onwards; Bize *et al.* 2003a), suggesting that parents of parasitized broods may have provisioned their offspring at higher rates only in the second half of the growing period. Secondly, by caring for their young for a longer period of time, parents can allow their offspring to reach a similar final body size as deparasitized chicks that grew at a faster rate, provided that tissue maturation is flexible (Schew & Ricklefs 1998). A prolonged period of parental care is observed frequently in response to parasites (e.g. Dufva & Allander 1996; Nilsson 2003; Fitze *et al.* 2004). In the present study, the rearing period was increased by 3 days for parents of parasitized broods in comparison to parents of deparasitized broods (see also Bize *et al.* 2003a), and at fledging we did not detect a difference in body size between young of parasitized and deparasitized broods (Bize *et al.* 2003a).

EFFECT OF PARASITISM ON FUTURE REPRODUCTION

Our study demonstrates that louse-flies reduce future reproductive success in alpine swift parents, with parents of parasitized broods producing 26% less offspring at fledging at the subsequent reproductive event than parents of deparasitized broods. A reduction in future reproductive success in parents of experimentally parasitized broods may have been caused by a direct effect of parasites drawing resources from the adults, or indirectly via a reallocation of the resources normally devoted to future reproduction to current reproduction.

Our results are not consistent with the hypothesis that the reduction in reproductive success of parents was a direct effect of parasites. In both treatments, parents were about eight times less infested than their offspring, and hence parasite load was probably too low to affect parents. Furthermore, our manipulation of ectoparasite load in the nest had a significant effect on the number of louse-flies found on the body of mothers but not fathers, and hence does not support a hypothetical direct link between parasite load and future reproductive success in fathers.

In agreement with the hypothesis that parasites can indirectly alter future reproductive success of their hosts, the experimental addition of louse-flies in alpine swift nests prolonged the rearing period by 3 days, and in an ANOVA the length of the rearing period rather than the manipulation of louse-flies explained the reduction in reproductive success of fathers. A similar, albeit non-significant ($P = 0.07$), effect of the rearing period in year x on the reproductive success in year $x + 1$ was observed in mothers. Although alpine swifts have a long rearing period (50–70 days), an increase of the rearing period by only 4.3% (3/70) strongly impaired their future reproductive success. Parents were probably exhausted at the end of the rearing period, and hence rearing offspring for a few extra days may have penalized parents at future reproductive attempts. However, a demonstration of this hypothesis requires an experimental approach by manipulating the length of the rearing period.

Altogether, our results are in accord with life history models that predict a trade-off in resource allocation between current and future reproduction. They show that parasites can affect the behaviour of parental hosts in current reproduction, which in turn can alter their future reproductive success (de Lope *et al.* 1993; Møller 1993; Richner & Tripet 1999; but see Fitze *et al.* 2004). On the other hand, long-lived organisms are predicted to refrain their investment in current reproduction to maintain their residual reproductive value high. Here, parents increased their investment late in the nestling period, and thus may gain more in caring for their parasitized offspring a little bit longer than in abandoning them (Perrin *et al.* 1996).

ADDITIVE EFFECT OF PAST AND CURRENT PARASITISM ON CURRENT REPRODUCTION

Successive manipulations of louse-fly load demonstrate that both past and current levels of ectoparasitism shape reproductive success of fathers. Fathers of parasitized broods produced 81% less young at fledging if, in the past, they had already cared for a parasitized brood rather than for a deparasitized one. A similar, albeit nonsignificant ($P = 0.10$), interaction was observed in mothers. To our knowledge, this is the first experimental evidence for an additive effect of successive manipulation of parasite load. It points out that the effect of current infestation on reproductive success

of their host is exacerbated by past infestation. Hence, manipulation of ectoparasite load over a single reproductive attempt may underestimate the real cost of parasitism on the lifetime reproductive success of their hosts, if cost of parasitism becomes apparent only after host parents faced parasites over several reproductive attempts.

PARASITISM, DEVELOPMENTAL PLASTICITY AND COST OF REPRODUCTION

A previous study on alpine swift illustrated that plasticity in offspring development can compensate for the effect parasites on final size of young via both an accelerated growth phase once parasites become less abundant and a prolonged period of growth (Bize *et al.* 2003a). Here, we show that parents pay the cost of this parasite-induced change in offspring development at the subsequent reproduction. The negative relationship between the duration of parental care in year x and the number of offspring they produced in year $x + 1$ suggests that a delayed maturation in the tissues of parasitized young can require parents to feed offspring during some extra days at the expense of their future reproductive success. Further studies are required to test whether growth acceleration by parasitized nestlings is coupled with a higher parental feeding rate, and in turn with a decrease in future reproductive success. Parents may pay the cost of plasticity in the development of their offspring because selection on young to reach independence is stronger than selection on parents to keep a high residual reproductive success.

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