Weather dependent effects of nest ectoparasites on their bird hosts

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This study reports the relationships between rainfall and ambient temperature with the abundances and prevalences of three species of ectoparasitic arthropods (viz. mites, blowfly larvae, fleas) in pied flycatcher *Ficedula hypoleuca* nests in three different breeding seasons. In addition to its effects on the growth of nestling pied flycatchers, weather conditions were found to determine patterns of abundance and prevalence of ectoparasites. Nest ectoparasites had detrimental effects on the fitness (nestling growth and survival until fledgling) of their hosts, although the effects and the identity of harmful ectoparasites varied across the years. Among the three species of nest ectoparasites, mites had the most consistent harmful effects on nestling growth. Fleas were detrimental in the more cold and rainy year, while blowflies caused nestling mortality in the warmer year. Different host-parasite interactions were present each year, most likely due to the effects of weather on the activity and timing of development of parasite populations.

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Parasitism is an important environmental component of the life cycle of most organisms (Price 1980), including birds (Møller et al. 1990, Loye and Zuk 1991, Møller 1994a). The array of parasites a particular host sustains, each of them with widely differing modes of dispersal, host infection and reproductive rates, means that highly variable effects on hosts can be expected. These effects can be either neutral (Rogers et al. 1991), beneficial (Munger and Holmes 1988) or, more commonly, detrimental (for reviews see Møller et al. 1990, Lehman 1993). Some parasites, e.g. some nest ectoparasites, differ from other parasites in that they are only confronted by the hosts while breeding and their effects are not suffered by the adult hosts outside that part of the yearly cycle; instead, these nest ectoparasites drain resources mostly directly from the offspring, having their larger detrimental effects on growth and survival early in life (e.g. Møller 1990, Richner et al. 1993, Merino and Potti 1995). Some nest ectoparasites also live more or less permanently on the hosts (e.g. Møller 1994b), potentially affecting them throughout their entire lifetime.

Some studies of birds and their nest parasites have shown that the detrimental effects of parasites are accentuated when environmental conditions for their hosts deteriorate, e.g. in situations of food scarcity or late breeding (Møller 1990, de Lope et al. 1993, Merino and Potti 1995). However, almost all studies dealing with birds and nest ectoparasites have viewed the system from the host's point of view, implicitly assuming that the host environment somewhat buffers parasites from the effects of environmental conditions. While this may hold true for endoparasites (which, however, are exposed to 'environmental stress' in the form of host's immune response), this is not certainly the case for ectoparasites, as colonization of hosts by the parasites themselves is known to strongly depend on environmental conditions, host aggregation being one of the most obvious (Poulin 1991). Climate variation is another potential powerful environmental effect to be faced by parasites, especially in the dispersal/colonization stages of finding suitable hosts (Marshall 1981).

Weather conditions are also an important factor affecting the growth and survival of young in popula-

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tions of insectivorous birds (e.g. Bryant 1975, Jarvinen and Vaisanen 1984, Shields and Crook 1987, Elkins 1988, Sasvári and Hegyi 1993). As pointed out by Johnson and Albrecht (1993) the young of aerial and tree-gleaning insectivorous birds may be especially vulnerable to the combined effects of spells of bad weather, which cause impaired food collection by parents and/or food shortages, and nest ectoparasites. Thus, at least among these birds, the impact of ectoparasites may depend on the influence of weather conditions on host performance (de Lope et al. 1993, Johnson and Albrecht 1993). However, both the activity of ectoparasites and the numerical development of their populations may be more influenced by weather (Marshall 1981) than the birds are. The study of interactions between bird hosts and parasites should therefore consider the joint effects of weather on the biology and performance of both components of the system.

We address in this paper the following two questions: 1) do nest ectoparasite abundance or prevalence actually vary with prevailing weather conditions? 2) Has this variation any bearing on the effects of nest ectoparasites on their bird hosts? We illustrate these problems using the system formed by a passerine host, the pied flycatcher *Ficedula hypoleuca* and three arthropods infesting their nests, in a three-year study period with contrasting weather conditions.

Methods

Nest ectoparasite populations and pied flycatchers were studied from 1991 to 1993, in an old deciduous oak *Quercus pyrenaica* forest in central Spain (see Carrascal et al. 1987 for description of the study area). All pied flycatcher pairs bred in nestboxes provided by us, thus allowing an easy control of nestling growth and estimates of nest ectoparasite populations. Nearly all adult breeding birds were captured, weighed (to the nearest 0.1 g) and measured for tarsus length (distance between bending points, to the nearest 0.05 mm), and all nestlings were equally measured at the age of 13 days, when tarsus length has already attained the definitive, adult size (Potti and Merino 1994). We also estimated the abundance of mites in the nest on the basis of a low vs high scoring system when the nestlings were measured (Merino and Potti 1995). Nestling mortality was controlled from hatching to fledging. Usually on the same or the following day that the young fledged, all nest contents were collected in labeled plastic bags, transported to the laboratory, and placed in Berlese funnels for 48 h. The nest material was subsequently dismantled looking for other ectoparasites. As counts of mites in Berlese funnels in 1991 were highly and positively re-

lated to the scoring index of mite abundance used in day 13 of nestling life (Merino and Potti 1995), this index of mite abundance was used when looking for effects on nestling development and survival. We consider that a nest was infected by fleas when adults or larvae were present, but we did not try to quantify their numbers because counts in Berlese funnels do not adequately estimate flea abundance (see Harper et al. (1992) for more adequate flea counting methods). Blowfly numbers were estimated by counting all puparia present among the nest material, and the abundance was categorized by dividing nests in two classes, namely low (below the median) and high abundances (Merino and Potti 1995). Therefore, throughout this paper we will use dichotomous estimates of abundance (low vs high) of mites and blowfly larvae, while prevalences (percentages of nests infested) are used for fleas only.

To investigate the variation of parasite infestations across years and the possibility of interactions among parasite species, we conducted log-linear analysis (Sokal and Rohlf 1981). This procedure is in analogy with an analysis of variance in that total variance of frequency data is partitioned into different factors, making the testing of interactions between them possible. We ran the test hierarchically, beginning with the highest order (4) interaction and proceeding backwards until all terms/interactions retained by the model reached significance ($p < 0.05$), so that dropping any of them would result in a significant lack of fit of the model.

Daily rainfall and ambient temperatures were obtained from records of the meteorological station of Madriguera, a nearby locality (distance 29 km) which vegetation composition and altitude are similar to those of our study area. In our study plots, both the nest ectoparasite populations grow, and the pied flycatcher nestlings hatch, in June (Potti et al. 1987, Merino and Potti 1995), hence our weather analyses were restricted to this month. It is worthy to note that, apart from weather, conditions were similar for both the flycatchers and their ectoparasites throughout all of the study period, as the nestboxes were cleaned in all years before the breeding season (Merino and Potti 1995).

Throughout this paper, the date of laying of the first egg in the nests of pied flycatchers is used as an index of breeding phenology. All statistical tests (Sokal and Rohlf 1981) are two-tailed. Non-parametric statistics were used when the premises for parametric tests were not fulfilled (e.g. number of dead nestlings). Sample sizes (Table 1) differ due to some accidents with collection bottles breaking or lacking alcohol and missing data in a few cases (e.g. scoring of mite abundance was not attempted in some nests due to chilling weather in 1992).

Table 1 Summary of the effects of three nest ectoparasites on nestling growth (mean within-brood measurements) and survival to fledgling in three years. Differences were tested with analyses of variance, after controlling for significant variation due to genetic and environmental factors (see statistics in the Appendix). 0 no significant effect, - reduced growth in infested nests, + increased mortality in infested nests, n sample size (number of nests) * = $p < 0.05$ ** = $p < 0.01$

	1991			1992			1993		
	Mites	Blowflies	Fleas	Mites	Blowflies	Fleas	Mites	Blowflies	Fleas
Tarsus	—*	0	0	0	0	—*	0	0	0
Mass	—**	0	0	0	0	0	—*	0	0
Dead nestlings	0	+*	0	0	0	+**	0	0	0
n	62	68	66	56	74	73	71	74	67

Results

Nest ectoparasites

Three species of parasitic arthropods were found from the nests: the mite *Dermanyssus gallinoides* Moss 1966, the flea *Ceratophyllus gallinae* Schrank 1803, and pupae of the blowfly *Protocalliphora azurea* Fall 1817. *Dermanyssus gallinoides* is a fast-moving mite in which both adults and some nymphal stages are haematophagous (Cheng 1978). Adults of the blowfly *P. azurea* are not ectoparasitic, but female flies search for birds' nests to lay eggs which develop into larvae that take blood meals from their nestling hosts (Bennett and Whitworth 1991). *Ceratophyllus gallinae* is a common ectoparasitic flea of hole-nesting birds, in which only the adults are hematophagous (George 1959, Cheng 1978).

Variation in weather conditions

There were significant differences ($p < 0.01$, Tukey's a posteriori tests from oneway ANOVAs of meteorological data) among the three study years in weather conditions, mostly due to June 1992 being significantly colder and rainy than the same period in 1991 and 1993 (Fig. 1). June 1992 was exceptional in that in 19 days mean temperatures did not exceed 10°C (0 days in 1991 and 1993) and, unlike in 1991 and 1993, periods with rainfall (16 d in 1992 vs 5 and 10 in 1991 and 1993, respectively) were also significantly colder (Spearman rank correlation $r_{s30} = -0.40$, $p = 0.03$). By contrast, rainfall and temperature in 1991 and 1993 were closer to long-term weather conditions in this montane supramediterranean area (Izco 1984), where rainfall in June is usually limited to short-duration evening storms.

Abundance and prevalence of nest ectoparasites

The abundance of the three ectoparasites varied significantly across the three years, with the lowest rates of infestation in 1992 (Fig. 1, mites $\chi^2_2 = 7.82$, $p < 0.01$, blowfly larvae $\chi^2_2 = 9.13$, $p = 0.01$, fleas $\chi^2_2 = 11.51$,

$p < 0.001$). There were no significant relationships between the abundances or prevalences of the three ectoparasites and the hatching date of the nests they were infesting, except for the number of blowfly larvae in 1991 ($r_{s68} = 0.37$, $p = 0.003$, in all other rank correlations $p > 0.10$). We searched for patterns in mite and blowfly larvae abundance and flea prevalence, yearly effects, and possible interactions between different parasite species using log-linear analysis. The four-way interaction among mites, blowflies, fleas and years was not significant ($G = 1.59$, 2 d.f., $p = 0.45$). A hierarchical model fitted to the variation of infestations across years retained an interaction term among the abundance scores of mites and blowfly larvae across years ($G = 6.38$, 2 d.f., $p = 0.04$), so that there existed an apparent effect of repulsion between both parasites, i.e. few nests (<10%) had high abundance scores of both mites and blowflies. The only other term retained by the model, after controlling for the variation among years and abundances of the other nest ectoparasites, was the variation of flea prevalence across years ($G = 8.36$, 2 d.f., $p = 0.015$). Overall, the fit of the log-linear model containing these two terms was adequate (goodness-of-fit, $G = 13.73$, 9 d.f., $p = 0.13$).

When abundances and prevalences of ectoparasites were compared with rainfall and average temperatures in the three study years, a clear pattern emerges (Fig. 1). These differences were parallel to between-year differences in temperatures and rainfall (Fig. 1), although the small number of data points precludes statistical testing. The three nest ectoparasites were less prevalent in the coldest and wettest year (1992), although fleas fared comparatively well that year, in contrast to mites and blowflies (Fig. 1).

Rainfall, temperatures and nestling growth and survival

Variation in mean within-brood fledgling mass and tarsus length can be compared to weather conditions and parasite abundances in Fig. 1. Mass of young was greater, on average, in the warmer year (1991) than in 1992 and 1993 ($F_{2,203} = 15.03$, $p < 0.0001$). In addition, there were differences in mean tarsus length between

years ($F_{2, 203} = 5.02$, $p < 0.001$). A posteriori tests revealed this was due to reduced tarsus growth in 1993, although no differences were found in the rest of pairwise comparisons. The frequency of nests with nestling mortality was higher in 1992 and 1993 than in 1991 ($\chi^2_2 = 10.19$, $p = 0.006$, Fig. 1).

Parasites, nestling growth and survival

Before analyzing the relationships between parasites and measurements of nestling growth we statistically controlled for other factors which are known to influence nestling development, namely breeding date, brood size, and parental size and condition (see Potti and Merino 1994, Merino and Potti 1995). Table 1 summarizes the information on the effects the nest parasites had on the growth and mortality of nestling pied flycatchers in the three study years. As expected, the effects of nest ectoparasites were, when significant, detrimental for nestling growth and survival until fledgling, reducing average nestling mass and tarsus length and decreasing survival in infested nests. However, there was little consistency across years as to the identity of the ectoparasites that were detrimental (Table 1). Mites affected nestling growth in two out of three years, fleas decreased nestling growth and increased mortality in one year and the only effect of blowfly larvae was on nestling mortality in another, different year (Merino and Potti 1995).

Discussion

The changing weather conditions across years may be an important factor affecting the reproductive success of ectoparasites and hence, their hosts. This was shown in this study by 1) the marked temporal variation of infestation rates by ectoparasites, 2) the apparent tight relationship of parasite abundance and prevalence with variable weather conditions, and 3) the differing effects of the three nest ectoparasite species on the survival and average size and mass of pied flycatcher broods. Irrespective of parasite effects, weather effects on nestlings may be related to difficulties on the part of parents to obtain sufficient food for adequate nestling feeding in predominantly aerial-foraging avian species (e.g. Bryant 1975, Shields and Crook 1987, Johnson and Albrecht 1993). Thus, all else being equal, we could expect the effects of nest ectoparasites to be more detrimental in these circumstances. However, the parasites themselves are also badly affected, as climate may be one of the main factors keeping in check insect ectoparasite populations, especially in those species which do not live permanently on their hosts (Marshall 1981). For instance, temperature has been shown to be a determinant influence on the growth, development and activity of some ectoparasites (Marshall 1981, Maurer and Baumgartner 1992). Thus, different weather conditions may account for the large differences among years in prevalences of ectoparasite species whose life cycles are largely decoupled from their temporary hosts, and must also have a bearing on their differing effects on hosts (e.g. compare fleas and blowfly larvae prevalences with the constancy of feather louse prevalences (Potti and Merino 1995)).

Fig. 1 Yearly variation in average (SD) rainfall (mm) and temperatures (°C) (A), ectoparasite abundance scores low vs high, prevalences (percentage of infested nests) are used for fleas, (see text) (B), and average (SD) growth measurements of nestling hosts and percentage of nests with nestling mortality (C).

The between-year variation in blowfly pupae prevalence and abundance was similar to the variation of temperature and rainfall. This fact may be simply explained by paying attention to the life cycle and mode of infestation of this ectoparasite. In spring, gravid blowfly females look for an adequate host nest to lay eggs (Bennett and Whitworth 1991). It should pay to blowfly females to arrive to host's nests at the first hours posthatching, because developmental time of their parasitic, blood-suckling larvae is similar to the time elapsed from hatching to fledgling in their nestling passerine hosts (Bennett and Whitworth 1992). Rainy and cold weather reduces the activity of flies and hence their prospects of breeding success (Bennett and Whitworth 1991, Rogers et al 1991). In 1992, and less markedly in 1993, blowflies could suffer from low temperatures and rainy weather. In 1991 blowflies were responsible for the high mortality of flycatcher nestlings, contrary to the other two years, possibly as a consequence of the higher numbers of this parasite in 1991.

Fleas presumably suffered too from bad weather in 1992, as reflected by their lower prevalence that year. However, the activity of fleas in bad weather may be not so much impaired as that of blowflies because fleas are remarkably adapted to cold temperatures (Marshall 1981), and their mode of transmission differs from that of blowflies in that they may be transported to their hosts' nests by attaching themselves to adult birds inspecting potential breeding and/or roosting holes that are flea-infested from previous years (George 1959, Humphreys 1968, Harper et al 1992, see also Richner et al 1993, Merila and Allander 1995). In addition, fleas appear to be relatively favored by humidity (George 1959, Marshall 1981, Harper et al 1992). Although we did not quantify flea numbers, the latter fact may account for the effects of this ectoparasite on nestlings in 1992, along with the bad condition of nestlings that year. Despite their low prevalence (30%), the effects of fleas could be more severe in 1992 possibly as a consequence of adult fleas parasitizing nestlings in the first days of life, when bad weather did not allow for an adequate feeding of nestlings by flycatcher parents. In years when food is presumably more abundant (i.e. 1991) parental effort may help to compensate the negative effect that fleas may cause on nestling survival. It is interesting to note that fleas, contrary to mites or blowflies, may have their detrimental effects on the first days of nestling life because adult fleas are parasites that need blood meals for forming eggs, while flea larvae do not feed on nestlings. On the contrary both mites and blowfly larvae develop at the expense of host nestlings (Burt et al 1991, Bennett and Whitworth 1991, Johnson and Albrecht 1993) attaining their higher resource demands when the nestlings are nearly fully grown.

Mites produced detrimental effects on nestling growth in 1991 and 1993. Mite populations were apparently affected by the bad weather in 1992. However, at the end of the 1992 season, all nests were infested by mites and their numbers were as high as in 1991. This fact, as well as the lack of effects on nestling development in 1992, were likely caused by a delay in the development of mite populations. Conditions for the development of mite populations were only favorable at the end of the pied flycatchers breeding period, when both temperature and humidity were high (see Burt et al 1991, Maurer and Baumgartner 1992). So, in 1992 mites attained abundances as high as in the other two years, but only when weather conditions improved, and by then the effect they could cause on nestling growth was minimal. Overall, *Dermanyssus gallinoides* mites were striking in their ability to actually infect most (Merino and Potti 1995) pied flycatcher nests all seasons and under highly variable climate conditions. The high population numbers which mites can attain ($\approx 25\,000$ in some nests, Merino and Potti unpubl.) may enable *D. gallinoides* populations to colonize new hosts nests each year. Their mode of colonization of nests in our area remains unknown. Cheng (1978) has reported on the possibility that mites may be transported to the nest by adult birds just as fleas do viz by attaching to birds inspecting suitable nest-sites. However, we have not observed this mite species during inspections of birds recently arrived from spring migration. Also, as nest boxes were not fumigated the possibility remains that some mites overwintered in the boxes and infested pied flycatcher nests the following spring. However, prevalences of mites in recently erected, new clean nest boxes are as high as in old nestboxes (Merino and Potti unpubl.), which runs against the latter argument. We think it likely that some nest boxes may be infested through one or a few gravid individuals transported by the adults among nest materials.

Differences in prevalence and abundance of nest ectoparasites between years may explain some of the differing, apparently inconsistent effects caused on hosts. Among the parasite species here considered, the results of our work across five years (see also Merino and Potti 1995) indicate that mites are rather consistent in their detrimental effects on the growth of nestling pied flycatchers, while fleas and blowflies have more unpredictable effects. Furthermore, the detrimental effects of mites, as in other nest ectoparasites, may be more marked in years when hosts suffer from lack of food (de Lope et al 1993, Møller 1994a) or for birds breeding in poor territories (Merino and Potti 1995). However, as ectoparasite populations suffer environmental effects as well, only those ectoparasites whose life cycle is in some way more "buffered" against some type of environmental stress, namely weather conditions, have the potential to cause detrimental effects on their hosts irrespective of weather conditions. Also,

different environmental conditions during the winter could kill off a variable fraction of ectoparasite populations, thus affecting their abundances previous to the colonization of hosts' nests in the spring

In conclusion, climate conditions have determinant influences on both hosts and their nest ectoparasites, with subsequent highly variable impacts on host fitness. We must be cautious in making generalizations on host-parasite interactions obtained from only one or a few seasons if weather conditions are not controlled. In addition to this already complex scenario, the possibility of interactions between different parasites (e.g. competition for host's resources) and their subsequent impact on host biology should also be considered, as not always these interactions will be in detriment of host fitness (Merino and Potti 1995). Also, a simultaneous integration of host-parasite systems from both the parasites and host's perspectives is needed, as the detrimental effect of parasites might also be interpreted as being caused by reduced parental effort due to a lowered reproductive value of the offspring in presence of parasitism (Forbes 1993, Møller in press). Experimental studies manipulating parasite identities and intensities of infestations, and quantifying parental effort in relation to parasitism and variable environmental conditions are needed to address alternative explanations on the effects of parasitism, and to see whether it is always the offspring who pays its costs (Johnson and Albrecht 1993, Møller in press).

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Appendix

Results of analyses of variance and covariance of mean nestling tarsus and mass and nestling mortality in relation to abundances of nest ectoparasites in the three study years (Table 1). Differences were tested while controlling for laying date and parental measurements as covariates by means of ANCOVAs when those variables had significant influences on nestling growth, non parametric Kruskal-Wallis analyses of variance were used for testing effects on number of dead nestlings MS mean squares

Mites:

- 1991
- Nestling tarsus Laying date MS = 5.04, F = 51.87, $p < 0.001$, Male tarsus MS = 0.63, F = 6.53, $p = 0.01$, Female tarsus MS = 2.56, F = 26.35, $p < 0.001$, Mite abundance MS = 0.40, F = 4.12, $p < 0.05$, Nestling mass Mite abundance MS = 5.67, F = 9.65, $p = 0.003$ Number of dead nestlings H = 0.58, $p = 0.44$
- 1992
- Nestling tarsus Mite abundance MS = 0.17, F = 0.65, $p = 0.43$, Nestling mass Mite abundance MS = 0.32, F = 0.25, $p = 0.63$ Number of dead nestlings H = 0.15, $p = 0.70$
- 1993
- Nestling tarsus Laying date MS = 3.19, F = 17.92, $p < 0.001$, Male tarsus MS = 1.13, F = 6.32, $p = 0.02$, Mite abundance MS = 0.15, F = 0.87, $p = 0.37$, Nestling mass Laying date MS = 6.89, F = 5.14, $p = 0.03$, Female mass MS = 8.53, F = 6.37, $p = 0.01$, Mite abundance MS = 7.61, F = 5.68, $p = 0.02$ Number of dead nestlings H = 0.40, $p = 0.53$

Blowflies:

- 1991
- Nestling tarsus Laying date MS = 4.00, F = 38.88, $p < 0.001$, Male tarsus MS = 0.70, F = 6.82, $p = 0.01$, Female tarsus MS = 3.05, F = 29.69, $p < 0.001$, Blowfly abundance MS = 0.06, F = 0.54, $p = 0.47$, Nestling mass Laying date MS = 3.41, F = 5.34, $p = 0.03$, Blowfly abundance MS = 0.53, F = 0.83, $p = 0.38$ Number of dead nestlings H = 8.00, $p = 0.005$
- 1992
- Nestling tarsus Blowfly abundance MS = 0.43, F = 1.46, $p = 0.23$ Nestling mass Blowfly abundance MS = 1.49, F = 1.14, $p = 0.29$ Number of dead nestlings H = 1.43, $p = 0.23$
- 1993
- Nestling tarsus Laying date MS = 3.21, F = 17.77, $p < 0.001$, Male tarsus MS = 1.05, F = 5.83, $p = 0.02$, Blowfly abundance MS = 0.33, F = 1.80, $p = 0.18$, Nestling mass Laying date MS = 7.51, F = 5.11, $p = 0.03$, Female mass MS = 7.73, F = 5.26, $p = 0.03$, Blowfly abundance MS = 0.32, F = 0.22, $p = 0.65$ Number of dead nestlings H = 0.00, $p = 0.97$
- ### Fleas:
- 1991
- Nestling tarsus Laying date MS = 4.26, F = 39.91, $p < 0.001$, Male tarsus MS = 0.53, F = 4.97, $p = 0.03$, Female tarsus MS = 3.22, F = 30.23, $p < 0.001$, Flea abundance MS = 0.07, F = 0.69, $p = 0.42$, Nestling mass Laying date MS = 7.19, F = 11.31, $p = 0.001$, Flea abundance MS = 1.32, F = 2.07, $p = 0.16$ Number of dead nestlings H = 0.30, $p = 0.58$
- 1992
- Nestling tarsus Flea abundance MS = 1.78, F = 6.42, $p = 0.01$, Nestling mass Flea abundance MS = 3.11, F = 2.37, $p = 0.13$ Number of dead nestlings H = 6.66, $p = 0.01$
- 1993
- Nestling tarsus Laying date MS = 3.87, F = 26.39, $p < 0.001$, Male tarsus MS = 0.80, F = 5.44, $p = 0.02$, Flea abundance MS = 0.36, F = 2.42, $p = 0.13$, Nestling mass Laying date MS = 7.29, F = 5.57, $p = 0.02$, Female mass MS = 5.59, F = 4.28, $p = 0.04$, Flea abundance MS = 1.30, F = 1.00, $p = 0.33$ Number of dead nestlings H = 2.15, $p = 0.14$

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