by vaginal, cloacal and intravenous routes. Avian Diseases 41:296–303.

MØLLER, A. P. 1990. Sexual behaviour is related to badge size in the House Sparrow *Passer domesticus*. Behav. Ecol. Sociobiol. 27:23–29.

OWENS, I. P. F., AND R. V. SHORT. 1995. Hormonal basis for sexual dimorphism in birds: implications for new theories of sexual selection. Trends Ecol. Evol. 10:44–47.

PEREK, M., M. ELIAN, AND E. D. HELLER. 1969. Microbial flora of semen and contamination of the reproductive organs of the hen following artificial insemination. Res. Vet. Sci. 10:127–132.

PETRIE, M., AND B. KEMPENAERS. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol. Evol. 13:52–57.

PINOWSKI, J., M. BARKOWSKA, A. H. KRUSZEWICZ, AND A. G. KRUSZEWICA. 1994. The causes of the mortality of eggs and nestlings of *Passer* spp. J. Bioscience 19:441–451.

POTTI, J., AND S. MERINO. 1996. Causes of hatching failure in the Pied Flycatcher. Condor 98:328–336.

SEEL, D. C. 1968. Clutch-size, incubation and hatching success in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. Ibis 112:1–14.

SHELDON, B. C. 1993. Sexually transmitted disease in birds: occurrence and evolutionary significance. Phil. Trans. R. Soc. Lond. B 339:491–497.

SHELDON, B. C. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. Proc. Roy. Soc. Lond. B 257:25–30.

SOKAL, R. R., AND J. ROHLF. 1981. Biometry. W. H. Freeman, New York.

SUMMERS-SMITH, J. D. 1963. The House Sparrow. Collins, London.

THIAGRAJIAN, D., A. M. SAEED, AND E. K. ASEM. 1993. Mechanisms of transovarial transmission of *Salmonella enteritidis* in laying hens. Poult. Sci. 73:89–98.

THRALL, P. H., J. ANTONOVICS, AND J. D. BEVER. 1997. Sexual transmission of disease and host mating systems: within-season reproductive success. Am. Nat. 149:485–506.

WESTNEAT, D. F., AND T. B. RAMBO. 2000. Copulation exposes Red-winged Blackbirds to microbes. J. Avian Biol., in press.

ZUK, M., T. S. JOHNSEN, AND T. MACLARTY. 1995. Endocrine-immune interactions, ornaments and mate choice in Red Jungle Fowl. Proc. Roy. Soc. Lond. B 260:205–210.

EFFECTS OF ECTOPARASITES ON NESTLING BODY MASS IN THE HOUSE SPARROW[1]

CARIE B. WEDDLE[2]

Department of Zoology, University of Oklahoma, Norman, OK 73019

Abstract. House Sparrow (*Passer domesticus*) nestlings were screened for ectoparasites; the most common ectoparasite was *Pellonyssus reedi*, a haematophagous mite. Parasite load was used to determine whether: ectoparasites have an effect on chick body mass prior to fledging, relative chick body mass is a within-brood predictor of relative parasite load, and parasite load per brood correlates with brood size. There was a negative correlation between parasite load and chick body mass, indicating that ectoparasites can reduce the quality of host offspring. Within broods, a chick's body mass was not related to its parasite load relative to its siblings' loads, suggesting that these ectoparasites do not preferentially target particular nestlings based on size. No relationship was found between brood size and total parasite load; thus, there was no evidence that within-nests, mite population size is limited by brood size.

Key words: ectoparasites, haematophagous, House Sparrow, mites, parasites, Passer domesticus, Pellonyssus.

Parasites have many diverse and wide-ranging effects on the physiology, morphology, and behavior of their hosts (Forbes 1993, Christe et al. 1994, Poulin 1994). Ectoparasites in particular have been shown to influence both the quality and quantity (viability) of host offspring in several bird species, such as the Great Tit, *Parus major* (Christe et al. 1996) and Cliff Swallow, *Hirundo pyrrhonota* (Brown and Brown 1986, 1996, Chapman and George 1991).

The purpose of this study was to examine the host-parasite relationship between House Sparrows, *Passer domesticus,* and their most common endemic ectoparasite, a haematophagous mite. House Sparrows usually lay 3–5 eggs per clutch, with the hatching to fledging interval averaging 13–15 days (Hegner and Wingfield 1987). Haematophagous mites typically have a 5–7 day life cycle (Richner and Heeb 1995). Thus, two to three generations of mites could potentially be produced per nestling cycle of this host.

I sampled nestling ectoparasite loads to assess their effects on chick quality, as represented by nestling body mass prior to fledging. I also examined whether the distribution of parasites among nestmates could be predicted by relative chick body mass. Richner and Heeb (1995) suggested that, if parasite load at the nestling phase is unpredictable to avian hosts, breeding females may not adjust their clutch size, but instead rely on brood reduction to limit parasite populations. It is possible, however, that the brood reduction process itself could be either facilitated or thwarted by parasites, depending on how the parasites are distributed among host nestmates. A negative relationship between body mass and ectoparasite load might occur if parasites preferentially target smaller, weaker chicks, in which case the effects of parasitism would augment any size differences among chicks, and presumably facilitate brood reduction. Alternatively, a positive relationship could result if parasites prefer to feed on a higher quality food source, such as a larger, healthier chick, which would presumably prolong the brood reduction process.

Finally, I tested Richner and Heeb's (1995) hypothesis that larger brood sizes foster greater ectoparasite population growth for short life-cycled ectoparasites such as haematophagous mites. If the effects of ectoparasitism on optimal clutch or brood sizes of avian hosts vary in response to ectoparasite life-cycle length, this hypothesis predicts a positive correlation between brood size and total parasite load per brood for House Sparrow nestlings experiencing ectoparasitism by haematophagous mites.

METHODS

Ectoparasite sampling was conducted between 30 May and 26 July 1996. House Sparrows were residents of nestbox populations breeding on the University of Oklahoma campus in Norman, Oklahoma; all nesting material in nestboxes had been removed the winter preceding the study. All study nests were censused twice a week to determine laying and hatching dates, clutch and brood sizes, and the approximate time of fledging.

Chicks from each of 37 broods were weighed, banded, and screened for ectoparasites on day 11 posthatch. I sampled ectoparasites using the technique suggested by Griffiths (1978): feathers of each individual chick were combed in a consistent manner over a white piece of paper. I used a broad-tipped camel's hair brush to stroke each of the following surfaces nine times: mid-back, belly, crown, and both sides of the wings. Ectoparasites removed during this process were then collected using a separate, fine-tipped camel's hair brush moistened with alcohol and transferred into a labeled vial of 70% ethyl alcohol.

Blind counts of vial contents were made later under a dissecting scope. With the exception of two feather lice (Mallophaga) that were collected from two different nestlings, all ectoparasites were *Pellonyssus reedi,* Mesostigmata mites of the family Macronyssidae. This mite is a nidicolous species that spends part of its life cycle in the nest and also is found on the host (Radovsky 1994). *Pellonyssus reedi* has four stages in its life cycle: larva, a nonfeeding stage; protonymph, an

active feeding stage; deutonymph, a nonfeeding stage; adult, an active feeding stage in the female (Clark and Yunker 1956). All specimens, regardless of life stage, were included in counting the total ectoparasite number for each individual chick from each nest. Clark and Yunker (1956) suggest that because the deutonymphal and larval stages are relatively short, and are passed in a sheltered environment (usually in the nesting material of the host), these forms are not recovered directly from the host as readily as are the protonymphal and adult (active feeding) stages. I did not include the two feather lice that were found in the totals for those chicks, because the lice were in an advanced state of desiccation, indicating they had likely been dead for some time before the chicks were sampled.

Values of mean parasite load per brood were square-root or natural-log transformed when necessary to achieve approximate normality. *P*-values are two-tailed, with a significance level of $P < 0.05$. All means are given ± SD.

RESULTS

A total of 127 nestlings from 37 broods were screened for ectoparasites. Ectoparasite loads per chick ranged from 0–122 mites, averaging 19.7 ± 20.6. Chicks from broods with high mean ectoparasite loads had lower overall body masses than chicks from broods with relatively low ectoparasite loads. Across broods, mean ectoparasite load correlated negatively with average chick body mass (Fig. 1), both when controlling for brood size effects, and when controlling for seasonal effects. Mean ectoparasite load per brood did not vary with sampling date across the two months that parasites were sampled (partial $r = 0.15$, $n = 38$, $P > 0.3$).

To determine whether mite loads within broods were related to chick weight hierarchies, I ranked chicks within each brood from smallest to largest, based on body mass. I also compared parasite load of the smallest chick in the brood with the mean parasite load of its siblings. Rank within brood was not related to relative ectoparasite load (ln-transformed) in either 3-chick broods (repeated measures ANOVA: $F_{2,26} = 1.3$, $P > 0.2$) or 4-chick broods ($F_{3,39} = 0.4$, $P > 0.7$). There was no difference in the parasite load of the smallest chick in a brood and the mean parasite load of its siblings (Wilcoxon signed-ranks test: $T = 57$, $n = 36$, $P = 0.38$), indicating that position within a sibling size-hierarchy is not a good predictor of the degree of mite infestation.

In a comparison across all multi-chick nests (brood size 2–5), mean ectoparasite load per brood was related to brood size (ANOVA: $F_{3,32} = 3.0$, $P = 0.04$). The larger the brood, the lower the mean number of mites per brood (Fig. 2). Regression analysis revealed no relationship between brood size and total ectoparasite load per brood ($F_{1,35} = 0.3$, $P > 0.5$).

DISCUSSION

The haematophagous mite *Pellonyssus reedi* had negative effects on House Sparrow nestling body mass, measured a few days prior to fledging. Chicks from nests with relatively high ectoparasite loads had lower overall body masses than chicks from nests with relatively low mite loads. Similar effects on nestling weight due to ectoparasitism have been reported for
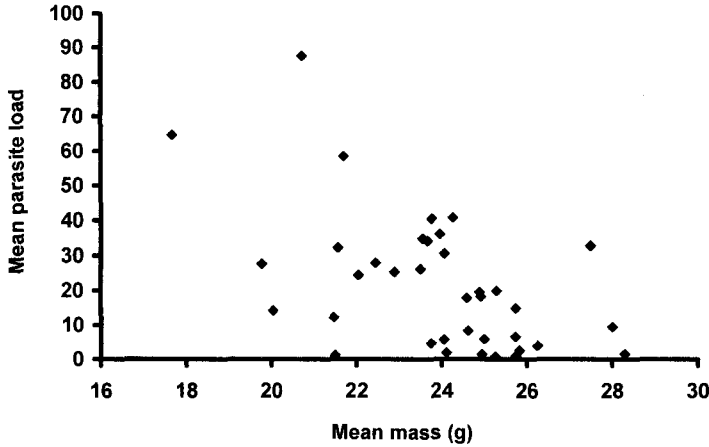
FIGURE 1.   The negative relationship between mean parasite load per brood and mean nestling mass, controlling for effects of brood size (partial $r = -0.58$, $n = 35$, $P = 0.001$) and seasonal effects (partial $r = -0.52$, $n = 35$, $P = 0.001$).

other birds: Chapman and George (1991) found that Cliff Swallow nestlings exposed to three species of endemic ectoparasites [the swallow tick *Argas cooleyi* (Acari: Argasidae); tick *Ornithodoros concanensis* (Acari: Argisidae); and the swallow bug *Oeciacus vicarius* (Hemiptera: Cimididae)] had lower body weights at fledging than nestlings reared in parasite-free nests. Johnson and Albrecht (1993) showed that nestling House Wrens (*Troglodytes aedon*) infested with the haematophagous ectoparasites blow fly larvae *Protocalliphora parorum* (Diptera: Caliphoridae) and mites *Dermanyssus hirundinis* (Mesostigmata: Dermanyssidae) reached their peak body mass at a slightly lower rate than uninfested nestlings.

Ringsby et al. (1998) found that juvenile survival of House Sparrow nestlings is positively related to fledging mass (measured at day 11 post-hatch). This suggests a possible survival disadvantage for highly parasitized nestlings. Individuals that reach fledging age at a significantly lower body mass because they have been more heavily infested as nestlings may have less chance of surviving to enter the breeding population.

Within broods, a House Sparrow chick's body mass relative to that of its siblings does not appear to be a predictor of its relative parasite load. This suggests that *Pellonyssus reedi* does not selectively parasitize chicks based on body mass: the smallest chicks in a brood are no more likely to suffer or be spared from ectoparasites than their larger siblings. Therefore, brood reduction should be neither facilitated nor hampered by infestation. This lack of selectivity on the part of *P. reedi* could actually be advantageous to the mites, given their short life-cycle: if they selectively targeted the weakest chick in a brood, its demise under food-limitation could come sufficiently early to reduce the mites' own reproductive success.
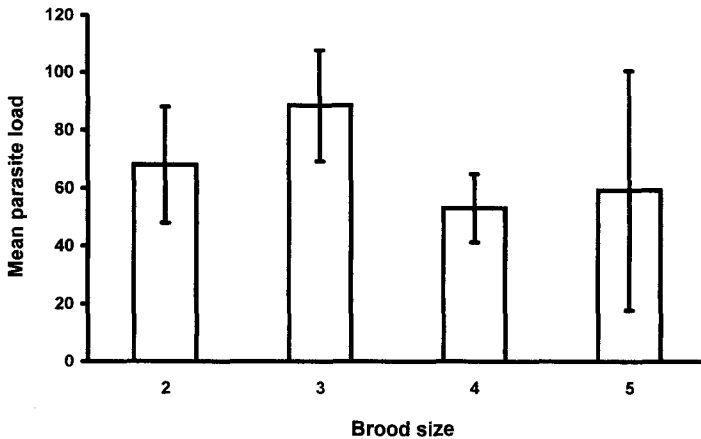

FIGURE 2.   The negative effect of brood size on mean parasite load per brood, in which larger broods experience lower mean parasite loads.

Richner and Heeb (1995) suggested that parasites with short life cycles, such as haematophagous mites, generally have negative effects on the life history traits of their hosts. Short life cycles result in very fast multiplication of the original mite population until carrying capacity is reached. This density-dependent population growth should result in a positive correlation, within-species, between brood size and final parasite load. However, the results of this study did not support this prediction. A significant negative effect of brood size on mean parasite load per nest was found; as brood size increases, the mean number of mites per nest decreases. However, no significant relationship was found in a regression of total parasite load per nest and brood size. Although nonsignificant, the regression analysis suggested a negative relationship between total parasite load and brood size, rather than the positive correlation predicted by Richner and Heeb (1995) for short life-cycled ectoparasites. There is no evidence, therefore, that population size of *P. reedi* is limited by brood size or that these mites may impose directional selection on optimal clutch size in House Sparrows. An interesting future study might be to experimentally manipulate the degree of parasitism experienced by nestlings, recording information on survival to the next breeding season and subsequent reproductive success of manipulated individuals.

LITERATURE CITED

Brown, C. R., and M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

Brown, C. R., and M. B. Brown. 1996. Coloniality in the Cliff Swallow: effects of group size on social behavior. Univ. Chicago Press, Chicago.

Chapman, B. R., and J. E. George. 1991. The effects of ectoparasites on Cliff Swallow growth and survival, p. 69–92. *In* J. E. Loye and M. Zuk [eds.], Bird-parasite interactions: ecology, evolution, and behaviour. Oxford Univ. Press, New York.

Christe, P., A. Oppliger, and H. Richner. 1994. Ectoparasite affects choice and use of roost sites in the Great Tit, *Parus major*. Anim. Behav. 47:895–898.

Christe, P., H. Richner, and A. Oppliger. 1996. Begging, food provisioning, and nestling competition in Great Tit broods infested with ectoparasites. Behav. Ecol. 7:127–131.

Clark, G. M., and C. E. Yunker. 1956. A new genus and species of Dermanyssidae (Acarina: Mesostigmata) from the English Sparrow, with observations on its life cycle. Proc. Helminthol. Soc. Wash. 23:93–101.

Forbes, M. R. L. 1993. Parasitism and host reproductive effort. Oikos 67:444–450.

Griffiths, H. J. 1978. A handbook of veterinary parasitology: domestic animals of North America. Univ. Minnesota Press, Minneapolis, MN.

Hegner, R. E., and J. C. Wingfield. 1987. Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of House Sparrows. Auk 104:470–480.

Johnson, S., and D. J. Albrecht. 1993. Effects of haematophagous ectoparasites on nestling House Wrens, *Troglodytes aedon*: who pays the cost of parasitism? Oikos 66:255–262.

Poulin, R. 1994. Parasite manipulation of host behaviour: should hosts always lose? Oikos 70:479–484.

Radovsky, F. J. 1994. The evolution of parasitism and the distribution of some dermanyssoid mites (Mesostigmata) on vertebrate hosts, p.186–217. *In* M. A. Houck [ed.], Mites: ecological and evolutionary analyses of life-history patterns. Chapman and Hall, New York.

Richner, H., and P. Heeb. 1995. Are clutch and brood size patterns in birds shaped by ectoparasites? Oikos 73:435–441.

Ringsby, H., B. Sæther, and E. J. Solberg. 1998. Factors affecting juvenile survival in House Sparrow *Passer domesticus*. J. Avian Biol. 29:241–247.