

## *Are clutch and brood size patterns in birds shaped by ectoparasites?*

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Ectoparasites may influence the optimum values of important life history traits such as clutch size and brood size by having different fitness effects for large and for small trait values. We propose here that the life-cycle length of the common ectoparasite species of a host determines whether it is more profitable for the host to raise a large or a small brood. The hypothesis rests on the following argument: (1) the length of an ectoparasite's life-cycle relative to the time-span that the host nestlings are available as a resource determines the total parasite load per nest during the nestlings' growth phase, and therefore (2) also the parasite load per nestling, which in turn (3) determines the parasite impact on the nestlings. Populations of long-cycled ectoparasites (i.e. the life-cycle length of the ectoparasite is similar to the length of time that nestlings take from hatching to fledging) do not build up considerably during the nestling phase and, consequently, parasites become increasingly diluted with an increase in brood size. This predicts no correlation between parasite load and brood size, but a negative correlation between parasite load per nestling and brood size. Larger broods will be favoured and brood size should be reduced only when feeding conditions become increasingly inadequate. In contrast, populations of short-cycled ectoparasites (i.e. the life-cycle length of the ectoparasite is much shorter than the length of time that nestlings take from hatching to fledging) can build up quickly and may reach the carrying capacity given by the number of host nestlings. This predicts a positive correlation between parasite load and brood size, but no correlation between parasite load per nestling and brood size. Smaller broods may then be at an advantage because they can be more adequately provisioned with food. Whether females should adjust clutch size will largely depend on whether they can, when laying their clutch, predict the parasite load after hatching. When future infestation can be predicted, females of species that are commonly infested with short-cycled ectoparasites should lay a smaller clutch, but females commonly infested with long-cycled parasites should lay a larger clutch. When future infestation cannot be predicted at laying, with short-cycled ectoparasites, females should lay a normal clutch and reduce it when the nest becomes infested, but with long-cycled ectoparasites, females should lay a larger clutch and maintain brood size as long as feeding conditions are adequate. If parasite pressure is constant over many breeding seasons, we may expect selection for smaller or larger clutches depending on the cycle length of the common ectoparasite. If parasite pressure fluctuates stochastically, a behavioural response will be more appropriate. Patterns from intra- and interspecific studies are in agreement with most predictions outlined above.

Clutch size in birds varies widely both among and within species and much of this variation has been attributed proximately to variance in phenotypic quality of the parents, variance in food abundance, nest predation, nestling competition, nest parasitism by other birds, phylogenetic inertia, physiological constraints, and ectoparasites (for recent reviews see e.g. Murphy and Haukioja 1986, Godfray et al. 1991, Poiani 1993a, b). Ultimately much of this variation can be understood in terms of variation in reproductive trade-offs, such as clutch size with offspring or adult survival and fecundity (for reviews see Linden and Møller 1989, Dijkstra et al. 1990, Stearns 1992). Ectoparasites can strongly reduce reproductive success (Moss and Camin 1970, Møller et al. 1990, Møller 1993, Richner et al. 1993, Clayton and Tompkins 1994) of their hosts, and are therefore most likely to affect reproductive trade-offs. This life-history point of view predicts that hosts may reduce the impact of parasites by altering their own reproductive effort (Forbes 1993, Poulin et al. 1994).

In this note we address the question of how ectoparasites are expected to influence brood size by considering (1) the relationship between life-cycle length of ectoparasites, host brood size and parasite load, (2) the expected relationship between life-cycle length of ectoparasites and the effect of ectoparasites on nestlings of small and large broods, (3) the expected host response in terms of a change in clutch size and brood size. Empirical evidence supporting the predictions are presented.

### **Parasite life-cycle length, host brood size and parasite load**

Common haematophagous ectoparasites such as mites, fleas, and blowflies differ in the length of their life-cycles. The cycle length in relation to the length of time that host nestlings are available as a resource will to a large extent determine the parasite load during the growth phase of nestlings and around fledging time.

Short life-cycles lead to fast multiplication of the origi-

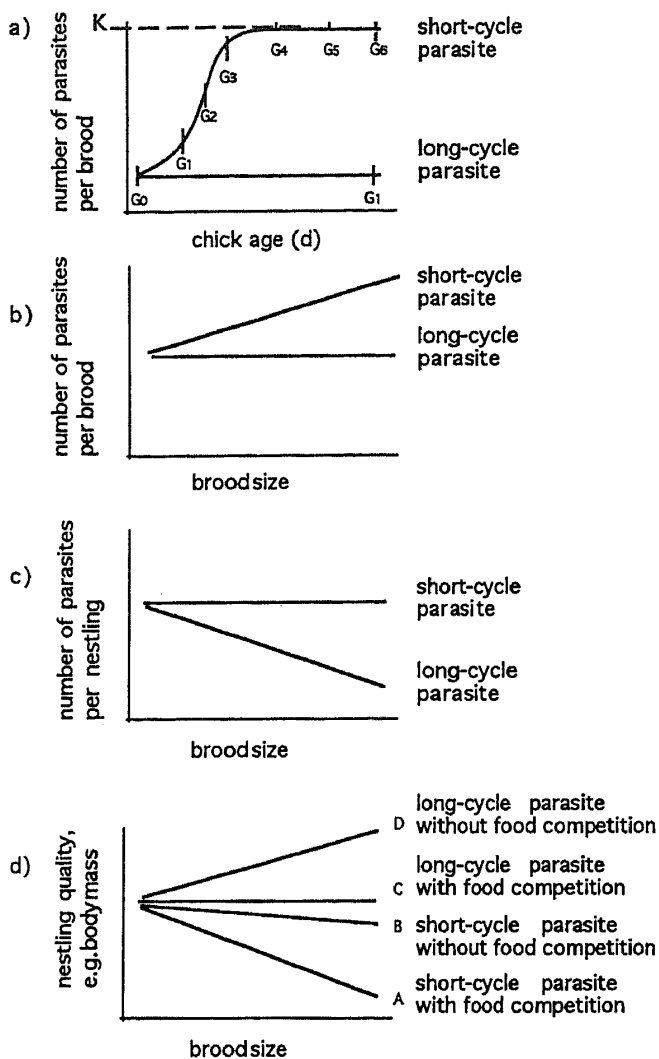


Fig. 1. Consequences of parasite life-cycle length for a) parasite population growth (generations  $G_0$  to  $G_n$ ) during the nestling phase of hosts, b) the number of parasites per brood as a function of host brood size, c) the number of parasites per nestling as a function of host brood size, and d) predicted nestling quality in relation to brood size with long and short-cycled parasites under two levels of food competition among nestlings.

nal ectoparasite population (Fig. 1a, e.g. generations  $G_0$ – $G_6$ ), until the growth is slowed down by resource limitation ( $K$ ) due to increased competition among ectoparasites. Such density-dependent population growth will lead to a correlation between resource level and final parasite load, that is, to a positive correlation (prediction 1) between brood size and total number of ectoparasites (Fig. 1b). There will therefore be no correlation or a much weaker one (prediction 2) between the parasite load per individual nestling and brood size (Fig. 1c). As an example of a short-cycled ectoparasite, the life-cycle length of haematophagous mites is 5–7 d whereas the nestlings of their swallow hosts may take more than 20 d between hatching and fledging (e.g. Møller 1990, 1994), thus allowing the mite population to build up over several generations during the time that nestlings are available as hosts.

Long life-cycles of ectoparasites means that the growth of the parasite population is slow over the time that the nestlings are available as a resource (Fig. 1a, only one or very few ectoparasite generations). If the life-cycle length is as long as nestlings take between hatching and fledging, the parasite load per nest will be independent of brood size and we expect (prediction 3) no correlation between the two (Fig. 1b). Parasite load per individual nestling will then decrease with an increase in brood size, and a strongly negative correlation (prediction 4) between these two variables (Fig. 1c) is expected. In other words, parasites get more diluted in a larger brood than in a smaller one. As an example, life-cycle length of the common hen flea (*Ceratophyllus gallinae*) is 17–30 d, and the host nestlings of tit species (*Parus* spp.) take as little as 18–20 d from hatching to fledging. Population growth of fleas during the nestling time is therefore negligible, and nestlings in larger broods are expected to have lower ectoparasite loads than nestlings in smaller broods.

Empirical evidence confirms prediction (1) of an increase of parasite load per nest with an increase in the host's brood size for short-cycled ectoparasites, and prediction (3) of no correlation for long-cycled parasites. For short-cycled mites (*Dermanyssus hirundinis*) studied by Burt et al. (1991) there was a strong and highly significant and linear correlation of mite load per nest after fledging and host brood size in three different passerine species (house wren *Troglodytes aedon*:  $r=0.95$ ,  $n=61$  nests; tree swallow *Tachycineta bicolor*:  $r=0.92$ ,  $n=18$  nests; eastern bluebird *Sialia sialis*:  $r=0.93$ ,  $n=13$  nests). Brood size alone therefore explained 94% (house wren), 88% (tree swallow) and 90% (bluebird) of total variation in mite load of the three host species. Similarly, it was found that the total load of the tropical fowl mites (*Ornithonyssus bursa*) in nests of barn swallows (*Hirundo rustica*) was significantly (Møller 1991), albeit weakly (A. Møller, pers. comm), correlated with brood size, and in a further study on the house wren, the load of mites (*Dermanyssus hirundinis*) was also positively correlated with host brood size (Johnson and Albrecht 1993). In contrast, for a long-cycled parasite, the hen flea, there was no correlation between parasite load per nest and brood size in both naturally ( $r=-0.09$ ,  $n=74$  nests,  $p=0.43$ ) and experimentally ( $r=-0.31$ ,  $n=35$  nests,  $p=0.07$ ) infested nests (Richner et al. unpubl.) of great tits (*Parus major*). In the latter group there was even a trend for a negative correlation. Harper et al. (1992) also found for several passerine hosts no correlation between the number of fleas per nest (*Ceratophyllus gallinae* and *Dasypsyllus gallinulae*) and the number of hatchlings.

Predictions (2) and (4) are also confirmed. For short-cycled ectoparasites such as mites, there was no relationship between brood size and parasite load per nestling in the three species studied by Burt et al. (1991:113) who state "more nestlings mean more mites, but the number of mites per nestling remains roughly constant". In contrast, for a host infested with the long-cycled hen flea there was

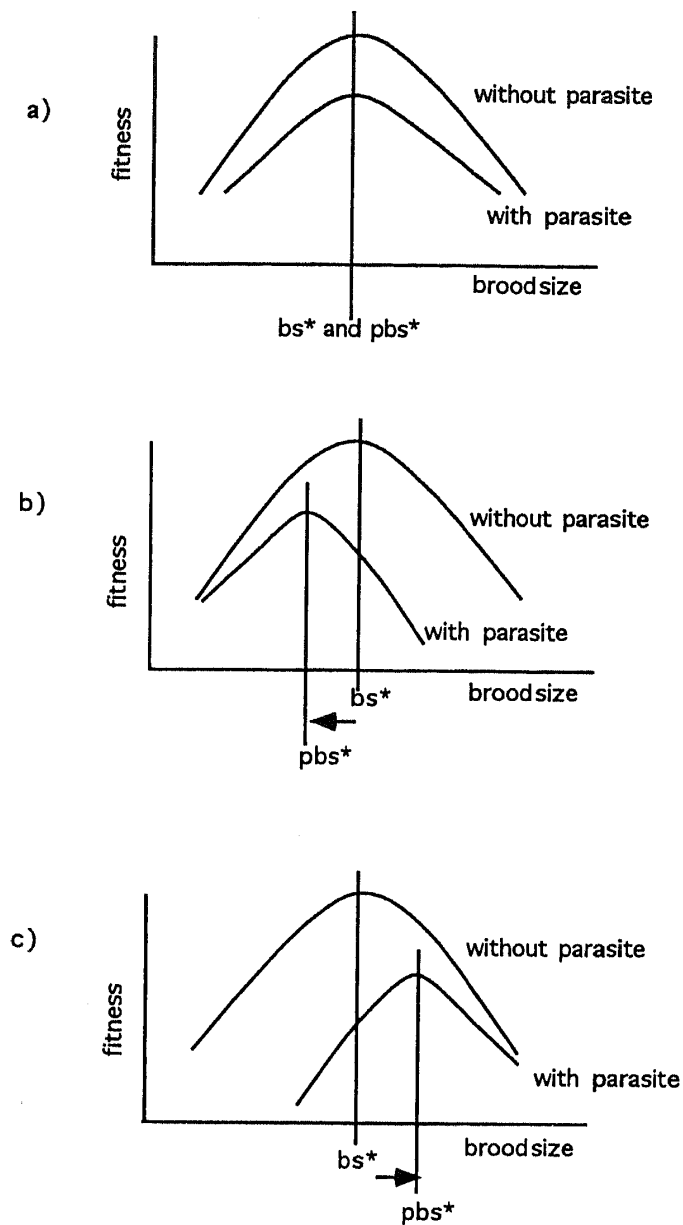


Fig. 2. Fitness with and without ectoparasites in broods of different sizes when a) parasites affect nestlings similarly in all brood sizes, b) parasites have relatively stronger effects on nestlings in large broods, and c) parasites have relatively stronger effects on nestlings in small broods. Optimal brood size with parasites ( $pbs^*$ ) is unchanged in a), but is smaller than optimal brood size without parasites in b), and larger in c).

a strongly negative correlation between brood size and parasite load per nestling (Richner et al. unpubl.) in both naturally ( $r = -0.42$ ,  $n = 74$  nests,  $p < 0.001$ ) and experimentally ( $r = -0.75$ ,  $n = 35$  nests,  $p < 0.0001$ ) infested nests.

### Life-cycle length and effect of ectoparasites on nestlings

For parasites that strongly reduce reproductive success of their hosts, as for example the haematophagous mites and

fleas (Møller 1993, Richner et al. 1993), we can expect that the negative effects of the parasites on their hosts (parasites commonly affect nestling weight) will increase with the number of parasites per nestling. Since, for hosts with short-cycled ectoparasites, the number of ectoparasites per chick is expected to be independent of brood size (Fig. 1c) and food competition increases with brood size, we expect (prediction 5) that nestling quality (e.g. body weight) will decrease with brood size (Fig. 1d, line A). Under exceptionally good feeding conditions competition among nestlings may be unimportant and then we expect no influence of brood size on nestling weight (Fig. 1d, line B) provided that the negative impact of ectoparasites can be compensated by provisioning the nestlings with more food. For nestlings infested with long-cycled parasites, the parasite load per nestling and therefore also the negative effect of the parasites decreases with brood size, and again, food competition increases with brood size. Because of the benefits arising from parasite dilution, we expect (prediction 6) that nestling weights in parasitized broods do not considerably decrease in larger broods (Fig. 1d, line C), or that they may even increase under exceptional food abundance (Fig. 1d, line D).

Empirical evidence supports both predictions 5 and 6. For a short-cycled parasite, the tropical fowl mite, that commonly occur in the nest of barn swallows, the nestling weight was significantly lower in enlarged broods than in reduced and unmanipulated broods (Møller 1993). This is also confirmed by Moss and Camin (1970) who found for infested nests that nestlings in larger broods were lighter than nestlings in smaller broods, and also showed that nestlings in infested broods of a given size  $n$  were of the same weight as nestlings in uninfested broods of size  $n + 1$ . Thus, for short-cycled ectoparasites, it seems that quality of nestlings can only be maintained by a reduction of the number of nestlings. In great tit broods where the ectoparasites had been removed, the nestlings in small broods were significantly heavier than nestlings in large broods ( $17.7 \text{ g} \pm 1.2 \text{ sd}$  versus  $15.6 \text{ g} \pm 1.4 \text{ sd}$ ;  $p = 0.02$ ), whereas in broods that were experimentally infested with a long-cycled ectoparasite, the hen flea, the nestlings in small and large broods were of equal weight ( $14.4 \text{ g} \pm 1.3 \text{ sd}$  versus  $14.1 \text{ g} \pm 1.4 \text{ sd}$ ;  $p = 0.63$ ) (Richner et al. 1993). Thus, it seems that a quality versus number trade-off is possible without ectoparasites, but impossible in the presence of a long-cycled ectoparasite because of the increasing parasite load per chick in smaller broods. A fitness gain may then be realizable rather by the number of nestlings than by their quality.

### Do ectoparasites influence optimal brood size?

If ectoparasites simply lower fitness but have similar effects on nestlings in large and small broods, we expect no effect on optimal brood size (Fig. 2a), and the best

Table 1. Predicted host behaviour in relation to (1) type of ectoparasite and (2) the degree to which the female, when laying her clutch, can predict the parasite load during the nestling phase.

	At laying, parasite load at nestling phase is predictable		At laying, parasite load at nestling phase is not predictable	
	no infestation during nestling phase predicted	infestation during nestling phase predicted	nest remains uninfested during nestling phase	nest becomes infested during nestling phase
host reaction with a short-cycled ectoparasite	lay normal clutch ①	lay smaller clutch do not reduce brood size post-hatching ③	lay normal clutch do not reduce brood size post-hatching ⑤	lay normal clutch reduce brood size post-hatching ⑦
host reaction with a long-cycled ectoparasite	lay normal clutch ②	lay larger clutch do not reduce brood size post-hatching ④	lay larger clutch reduce brood size post-hatching ⑥	lay larger clutch do not reduce brood size post-hatching ⑧

brood size without ectoparasites ( $bs^*$ ) coincides with the best brood size with ectoparasites ( $pbs^*$ ). As outlined above, without an increase in food competition in a larger brood, the parasite cost per chick remains constant over different brood sizes when broods are infested with short-cycled ectoparasites, and we therefore predict no change in optimal brood size. If food competition increases with brood size, as is the more common case, we predict a smaller optimal brood size ( $pbs^*$ ) with ectoparasites (Fig. 2b) than without ectoparasites ( $bs^*$ ). With long-cycled ectoparasites (Fig. 2c) the parasite cost per chick decreases with increasing brood size due to the dilution of the parasites, and this by itself would favour larger broods with ectoparasites ( $pbs^*$ ) than without ectoparasites ( $bs^*$ ). The extent to which larger broods will be favoured, will depend on the importance of the positive dilution effect relative to the negative effect of food competition in a larger brood.

### Should hosts adjust clutch size to ectoparasitism?

Ideally, hosts should lay a clutch of a size that they are subsequently able to raise. For the female, the decision of how many eggs to lay will depend on whether, at laying, the parasite load of the nest after hatching of the chicks can be predicted. A further constraint arises from the fact that brood size after hatching can only be reduced, but not increased by laying more eggs.

In the following comparison we assume that food competition increases with brood size, and that the benefits from parasite dilution are more important than the costs of increased food competition. Two situations may be distinguished: the female can, when laying the clutch, predict whether the nest will or will not be infested during the nestling phase (cells 1–4 in Table 1), or she cannot predict the infestation (cells 5–8). If no infestation is

predicted (cells 1 and 2), the females of both the species commonly infested with short-cycled ectoparasites and the females of species commonly infested with long-cycled ectoparasites should lay a clutch of “normal” size (i.e. the common clutch size for the species adapted to her phenotype and to the predicted food levels without adjustments for ectoparasites). If the infestation is predictable, then the females of the species commonly infested with short-cycled ectoparasites should lay a smaller clutch (cell 3), but the females of species commonly infested with long-cycled ectoparasites should lay a larger clutch (cell 4). If future infestation is not predictable at the time of laying, then clutch size should be adjusted to the case of a future infestation: females of species commonly infested with short-cycled ectoparasites should lay a clutch of “normal” size (cells 5 and 7), but females of species commonly infested with long-cycled ectoparasites should lay a larger clutch (cells 6 and 8).

Empirical support for these predictions comes from both intra- and interspecific studies. Studies on birds infested with mites have shown that the detrimental effects of the parasites are greater in larger broods, but found no adjustment of clutch size (Moss and Camin 1970, Møller 1990, 1991, 1993) as predicted above if females cannot, at laying, predict the parasite load during the growth phase of their nestlings (Møller 1990, 1991, 1993). A study on the long-cycled fleas demonstrated that female great tits that were experimentally infested after laying the second egg laid a larger clutch than unparasitized females (Richner et al. unpubl.). Further support is provided by a recent comparative study (Poiani 1993b) showing that clutch size of some North American and Australian passerine families decreased with an increasing importance of ectoparasitism for each species. Interestingly, and as predicted above, this trend was confirmed for bird species commonly infested by mites (i.e. short-cycled ectoparasites), but not for species commonly infested by dipteran parasites (i.e. long-cycled ecto-

Table 2. Number of studies (listed by Møller 1995) conforming to prediction (cells 1 and 4) that brood size becomes reduced with short-cycled parasites and is not changed with long-cycled ectoparasites; number of studies not conforming (cells 2 and 3).

	reduction of brood size	no change of brood size
with short-cycled parasite	6 studies ①	1 study ③
with long-cycled parasite	2 studies ②	12 studies ④

parasites). In fact the trend was reversed (Poiani 1993b) for such long-cycled parasites, as predicted above.

### Should hosts adjust brood size after hatching?

If females can, at laying, predict whether the nest will later remain free of parasites or be infested, we expect them to lay a clutch of a size that they are able to raise, and we therefore expect that brood size will not be reduced after hatching (cells 1–4 in Table 1). If females cannot predict future infestation but broods remain uninfested, the females of the species commonly infested with short-cycled ectoparasites should not reduce brood size post-hatching (cell 5). The females of species commonly infested with long-cycled ectoparasites had laid a larger clutch and should now reduce brood size (cell 6) to meet the optimal trade-off between number and quality of offspring. If the brood becomes infested, the females of the species commonly infested with short-cycled ectoparasites should reduce brood size (cell 7) due to the increased food competition in larger broods, but the females of species commonly infested with long-cycled ectoparasites should maintain brood size to benefit from the parasite dilution effect (cell 8).

Empirical evidence confirms a reduction of brood size for hosts exposed to short-cycled haematophagous ectoparasites, mainly mites, but maintenance of brood size for hosts exposed to long-cycled haematophagous ectoparasites. Møller (1995) surveys 21 studies where parasite load has been experimentally manipulated, and lists the effects found of haematophagous ectoparasites on brood size. In six studies concerned with short-cycled ectoparasites (cell 1 in Table 2) a reduction of brood size occurs post-hatching, and no alteration of brood size is found in twelve studies with long-cycled ectoparasites (cell 4 in Table 2). Only 3 studies did not conform to the prediction (cells 2 and 3 in Table 2). Thus, 18 studies support our prediction, and 3 do not (Fisher Exact test,  $p = 0.003$ ).

Of the three studies that do not support our predictions, one is concerned with a short-cycled ectoparasite, the

tropical fowl mite on barn swallow hosts in Spain (de Lope and Møller 1993), and the two other ones are concerned with long-cycled ectoparasites, the house martin bug (*Oeciacus hirundinis*) infesting house martins (*Delichon urbica*) (de Lope et al. 1993), and the hen flea infesting great tits (Richner et al. 1993). To some extent, these three exceptions confirm the rule: de Lope and Møller (1993) show that, compared to the Danish populations (Møller 1990, 1991, 1993), the effect of the fowl mite on the barn swallow nestlings in Spain was relatively weak, and therefore a reduction in brood size is predicted for the Danish swallow populations, but to a lesser extent for the Spanish ones. For the house martins infested by house martin bugs, maintenance of brood size is predicted whereas a reduction is listed in Møller's survey. De Lope et al. (1993) show that there is no reduction of brood size for first broods, and that a reduction occurs only in second broods where parasite load is considerably increased, feeding conditions are more inadequate, and parents had suffered already from parasites during their first brood. Under those circumstances, the cost of not reducing brood size may be higher than the benefits arising from parasite dilution. For the study of great tits infested by hen fleas in a comparatively poor habitat (Richner et al. 1993), the data show that brood size is maintained for the largest part of the time that the chicks are in the nest (Richner et al. 1993: Fig. 5), and that the reduction occurs only during the last quarter of the nestling time.

Obviously, for a comprehensive interpretation of the brood-size changes in the studies surveyed by Møller, it should be known whether the female can, at the time she lays her eggs, predict the ectoparasite load after hatching. As an example, this could be possible if there is a strong correlation between parasite load when laying and parasite load when raising the nestlings. For the tropical fowl mite, Møller (1991, 1993) suggested that female barn swallows could not forecast future parasite load. Studies on bird host-ectoparasite systems should address the question of the predictability of parasite loads.

### Do ectoparasites govern clutch size evolution?

As seen from Table 1, hosts of short-cycled ectoparasites should in three out of four scenarios, including predicted and actual status of infestation during the nestling phase, lay a clutch of the common size of the given species. In contrast, the hosts of long-cycled ectoparasites should in three out of four scenarios lay a larger clutch. If the parasite pressure is important over a large number of breeding episodes, we expect that selection will occur and may lead to changes in clutch size. Many studies have found considerable genetic variance for clutch size (e.g. Van Noordwijk et al. 1980), and a response to selection in terms of a change in mean clutch size is

therefore feasible. In contrast, if the parasite pressure between breeding episodes is variable, we expect selection for phenotypic plasticity of clutch size, that is, clutch size will be adjusted by the female in direct response to the current parasite pressure.

Poiani (1993b) has shown that species exposed to mites are characterized by relatively smaller clutches compared to non-parasitized species, in contrast to species exposed to dipteran ectoparasites. These findings might be explained by clutch size changes in response to the life-cycle length of the ectoparasites. As one interesting example, this may also explain why the blue tit, which is one of the most heavily infested host of the long-cycled fleas (Harper et al. 1992; and own observations), lays the largest clutch for a bird of its size.

## Conclusions

Ectoparasites have fitness costs that vary in their magnitude with brood size, and we therefore expect adaptive changes in the number of offspring. Whether an increase or decrease of clutch size or brood size occurs depends on the life history characteristics of the ectoparasite species. Short-cycled parasites can build up a large population over the short time that their main resource, the host's offspring, is available, whereas long-cycled parasites may not even have time to produce a second generation. Short-cycled parasite populations may reach the carrying capacity given by the number of nestlings in a brood, and we therefore expect a positive correlation between total parasite load per nest and brood size, but no correlation between load per nestling and brood size. For long-cycled ectoparasites we expect no correlation between total parasite load and brood size, but a negative correlation between load per nestling and brood size which is due to the effect of greater parasite dilution in larger broods. As food competition among nestlings increases with both parasite load and brood size we expect selection for smaller broods for hosts infested with short-cycled ectoparasites but selection for larger broods when infested with long-cycled parasites, in particular if the benefits from the parasite dilution effect are higher than the costs arising from increased food competition in a larger brood. Whether females can adjust clutch size to counter the effect of ectoparasites on the nestlings will depend on the predictability of the parasite load at the nestling stage at the time when the female is laying her clutch. With short-cycled ectoparasites, unpredictability will not lead to a change in clutch size, but to a reduction of brood size post-hatching. If an infestation can be predicted, females should lay a smaller clutch. With long-cycled parasites, females should lay larger clutches and then maintain the largest possible number of offspring in the nest for both the situation of a nest becoming predictably infested and the situation where future infestation cannot be predicted at the time of laying. An adaptive change of clutch size

may occur if parasite pressure remains constant over many breeding episodes. This paper attempts to provide a framework for observed patterns and will hopefully inspire future experiments and interspecific approaches.

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## References

- Burt, E. H., Chow, W. and Babbitt, G. A. 1991. Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests. – In: Loye, J. E. and Zuk, M. (eds), *Bird-parasite interactions: ecology, evolution and behaviour*. Oxford Univ. Press, New York, pp. 104–122.
- Clayton, D. H. and Tompkins, D. M. 1994. Ectoparasite virulence is linked to mode of transmission. – *Proc. R. Soc. Lond. B* 256: 211–217.
- De Lope, F. and Møller, A. P. 1993. Effects of ectoparasites on reproduction of their swallow hosts: a cost of being multi-brooded. – *Oikos* 67: 557–562.
- , González, G., Pérez, J. J. and Møller, A. P. 1993. Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental condition. – *Oecologia* 95: 234–240.
- Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. and Zijlstra, M. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. – *J. Anim. Ecol.* 59: 269–285.
- Forbes, M. R. L. 1993. Parasitism and host reproductive effort. – *Oikos* 67: 444–450.
- Godfray, H. C. J., Partridge, L. and Harvey, P. H. 1991. Clutch size. – *Annu. Rev. Ecol. Syst.* 22: 409–429.
- Harper, G. H., Marchant, A. and Boddington, D. G. 1992. The ecology of the hen flea *Ceratophyllus gallinae* and the moorhen flea *Dasypsyllus gallinulae* in nestboxes. – *J. Anim. Ecol.* 61: 317–327.
- Johnson, L. S. and Albrecht, D. J. 1993. Effects of haematophagous ectoparasites on nestling house wrens, *Troglodytes aedon*: who pays the cost of parasitism? – *Oikos* 66: 255–262.
- Linden, M. and Møller, A. P. 1989. Cost of reproduction and covariation of life history traits in birds. – *Trends Ecol. Evol.* 4: 367–371.
- Møller, A. P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. – *Ecology* 71: 2345–2357.
- 1991. Ectoparasite loads affect optimal clutch size in swallows. – *Funct. Ecol.* 5: 351–359.
- 1993. Ectoparasites increase the cost of reproduction in their hosts. – *J. Anim. Ecol.* 62: 309–322.
- 1994. Sexual selection and the barn swallow. – Oxford Univ. Press, Oxford.
- 1995. Parasitism and the evolution of host life history. – In: Clayton D. H. and Moore J. (eds), *Coevolutionary biology of birds and their parasites*. Oxford Univ. Press, Oxford.
- , Allander, K. and Dufva, R. 1990. Fitness effects of parasites on passerine birds: a review. – In: Blondel J., Gosler, A., Lebreton, J. D. and McCleery, R. (eds), *Population biology of passerine birds*. Springer, Berlin, pp. 269–280.
- Moss, W. W. and Camin, J. H. 1970. Nest parasitism, productivity and clutch size in purple martins. – *Science* 168: 1000–1003.
- Murphy, E. C. and Haukioja, E. 1986. Clutch size in nidicolous birds. – *Current Ornithol.* 4: 141–180.
- Poiani, A. 1993a. Effects of clutch size manipulations on reproductive behaviour and nesting success in the cooperatively

- breeding bell miner (*Manorina melanophrys*). – *Evol. Ecol.* 7: 329–356.
- 1993b. Small clutch sizes as a possible adaptation against ectoparasitism: a comparative analysis. – *Oikos* 68: 455–462.
- Poulin, R., Brodeur, J. and Moore, J. 1994. Parasite manipulation of host behaviour: should hosts always lose? – *Oikos* 70: 479–484.
- Richner, H., Oppliger, A. and Christe, P. 1993. Effect of an ectoparasite on reproduction in great tits. – *J. Anim. Ecol.* 62: 703–710.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford Univ. Press, Oxford.
- Van Noordwijk, A. J., Van Balen, J. H. and Scharloo, W. 1980. Heritability of ecologically important traits in the Great tit, *Parus major*. – *Ardea* 68: 193–203.