

Which chick is tasty to parasites? The importance of host immunology vs. parasite life history

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Summary

1. The Tasty Chick Hypothesis (TCH) proposes that hatching asynchrony evolved as an antiparasite strategy. Hosts would benefit if ectoparasites aggregate more on the offspring that are of lowest reproductive value within a brood, i.e. on the last-hatched chicks, because offspring reproductive value generally decreases with hatching rank. The poor body condition of the later-hatched chicks would impair parasite resistance and render them especially attractive to ectoparasites. Thus, the TCH predicts a decline in chick parasite load with hatching order in avian broods.
2. We investigated the main assumption of the TCH that junior chicks are less immunocompetent than their senior siblings. We also examine the prediction of the TCH that junior chicks bear more ectoparasites than their senior siblings.
3. Conform to the assumption of the TCH for hosts, junior chicks in broods of the barn owl (*Tyto alba* L.) showed a lower humoral immune response than their senior siblings. In contrast, the cell-mediated immune response of senior chicks in broods of the great tit (*Parus major* L.) was not significantly greater than that of their junior siblings.
4. In line with the prediction of the TCH for the distribution of parasites among hosts, the fly *Carnus haemapterus* Nitzsch infested junior chicks in larger numbers than senior chicks in both barn owl and kestrel (*Falco tinnunculus* L.) broods.
5. In conflict with the TCH, ticks (*Ixodes ricinus* L.) were distributed randomly with respect to hatching rank in broods of the barn owl and the great tit. Moreover, louse-flies *Crataerina melbae* Rondani infested mainly senior chicks instead of junior chicks in the Alpine swift (*Apus melba* L.).
6. Summarizing, the present descriptive study indicates that the distribution of ectoparasites within-broods is not generally governed by rank-related variation in host defence of chicks as initially suggested by the TCH. We argue that specific aspects of the morphology, life history and ecological requirements of various ectoparasite species need more consideration as to explain the dynamics and evolution of host–parasite interactions.

Key-words: age hierarchy, ectoparasites, hatching asynchrony, host defence, immunocompetence, Tasty Chick Hypothesis.

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Introduction

While ectoparasites are widespread in wildlife populations and often cause a major fitness loss to their hosts,

their ubiquity and effect on host life history is still poorly understood. Deleterious effects of parasites on host reproduction are especially well documented in empirical studies of birds and their nest-based ectoparasites (reviewed by Clayton & Moore 1997). Nest-based ectoparasites feed mainly on nestlings, reduce their growth and survival (e.g. Brown & Brown 1991; Richner, Oppliger & Christe 1993) and hence curtail

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the value of the current host reproduction. The future reproductive output of hosts might also decrease due to enhanced costs of reproduction, if parents increase their daily work rate in order to compensate the loss of resources to ectoparasites (Christe, Richner & Oppliger 1996; Richner & Tripet 1999). To avoid nest-based parasites or reduce their detrimental effects, hosts evolved various behavioural strategies and physiological defence mechanisms. For example, parents may select nest-sites with low loads of ectoparasites (Brown & Brown 1991), desert infested nests (Oppliger, Richner & Christe 1994) or incorporate plants with insecticidal and antipathogenic properties into their nest (Clark & Masson 1985; Petit *et al.* 2002). In addition, susceptible host species have evolved an efficient immune system to resist parasites (Brossard & Girardin 1979; Sorci, Møller & Boulinier 1997).

Under the 'Tasty Chick Hypothesis' (TCH), Christe, Møller and de Lope (1998) recently proposed that parents might enhance their fitness by increasing the magnitude of hatching asynchrony in the threat of heavy parasite infestation. The selective advantage of staggering the times of egg hatching would result from the gradual decline in competitiveness over parental food supply from the first- to last-hatched offspring. Larger senior chicks may bias parental food allocation in their favour (e.g. Price, Harvey & Ydenberg 1996), such that parents face a decline in expected fitness return per offspring with hatching rank. Because junior chicks are fed less frequently the maturation of their immune system would be retarded, and such low resistance would serve as a sink for the prevailing nest-based ectoparasites. Consequently, senior chicks would enjoy reduced parasite loads, and allow parents to produce more high quality offspring and achieve a higher fitness as compared to the situation in synchronous broods with evenly distributed ectoparasites. Christe *et al.* (1998) thus envision hatching asynchrony as a potential antiparasite strategy of the host.

The TCH relies on the fundamental assumption that the last-hatched chicks have an impaired ability to resist parasites. A weakened host defence of junior chicks may result from their poorer condition compared to their older siblings (Magrath 1990; Møller *et al.* 1998). Between-brood studies indicate that chicks in poor condition are less immunocompetent (Saino, Calza & Møller 1997; Brinkhof *et al.* 1999). Alternatively, the immune system of junior chicks is less matured than that of earlier hatched siblings throughout most of the nesting cycle (Apanius 1998). However, the within-brood variation and link between condition and host defence have hardly been investigated (Christe *et al.* 1998; but see Roulin 1998; Bosch & Figuerola 1999). Therefore, the general applicability of the TCH in the sense originally proposed by Christe *et al.* (1998) is still undecided.

Some, so far largely neglected, factors shed doubt on the general applicability of the TCH. First, within-brood variation in immunocompetence may be irrelevant to

the fitness of ectoparasites that feed upon feathers or dermal debris. Secondly, certain ectoparasite species may also select well-feathered early-hatched chicks, irrespective of their higher immunocompetence, because a dense plumage may offer a safe refuge against antiparasite host behaviour, such as grooming (Clayton 1991). Thus, specific features of a host-ectoparasite relationship may even select against a high degree of hatching asynchrony because ectoparasites would reduce the fitness of high quality, first-hatched chicks.

We investigated the main assumption and prediction of the TCH using data on the within-brood variation in immunocompetence and ectoparasite loads of four avian host-parasite systems. The birds involve the barn owl (*Tyto alba*, family Tytonidae), the kestrel (*Falco tinnunculus*, Falconidae), the great tit (*Parus major*, Passeridae) and the Alpine swift (*Apus melba*, Apodidae), and three species of blood-sucking ectoparasites, i.e. the carnid fly *Carnus haemapterus* (Carnidae; Diptera), the European castor-bean tick *Ixodes ricinus* (Ixodidae; Acari) and the hippoboscid fly *Crataerina melbae* (Hippoboscidae; Diptera).

Materials and methods

HATCHING RANK-RELATED IMMUNOCOMPETENCE

Immunocompetence in the barn owl was studied in western Switzerland. The barn owl shows a large degree of hatching asynchrony, as the last-hatched chick can be up to 3 weeks younger than its first-hatched sibling (AR, personal observation). In 1998, AR measured the antibody response towards an injection of sheep red blood cells (SRBC) of nestlings in relation to their hatching rank (eggs hatch at 2–3-day intervals). In 38 broods, in which the oldest nestling was 40 days old (i.e. 2 weeks before the first flight), 0.1 mL of a suspension of SRBC was injected subcutaneously in the neck of all nestlings. Before immunization, and 3, 8, 13 and 18 days after immunization, a blood sample was taken from each nestling to assess the concentration of antibodies specifically directed against SRBC. See Roulin *et al.* (2000) for further details. Chicks were marked with non-toxic colour paint soon after hatching, and their rank by age was thus known throughout the nesting cycle. Chicks were ranked according to hatching order, starting with rank one. Nestlings with a rank below the median hatching rank in the brood were assigned to the 'senior' category, and the remaining to the 'junior' category. In broods of five chicks, the third-hatched chick was assigned to the 'junior' category. The variation in antibody response was investigated with repeated-measures ANOVA, with the mean antibody titre on the 5 consecutive days as repeats, hatching-rank category and nest as factors, and body condition (i.e. the residual of a regression of body mass on wing length at the time of injection) as a covariate.

Immunocompetence of great tit nestlings was studied in 1999 by MB in a nestbox population located in the forest Bremgartenwald near Bern, Switzerland. We obtained an index of T cell-mediated immunocompetence in nestlings using the inflammatory reaction to a subcutaneous injection of phytohaemagglutinin-P (PHA). We used the simplified skin-testing technique (Smits, Bortolotti & Tella 1999) by injecting one wing web when the older chick was 12 days old (fledging takes place at 20 days) with 0.1 mg of PHA, dissolved in 0.02 mL PBS. The difference in the thickness of the wing web prior to injection and 24 (range ± 1) hours later was taken as an index for the T cell-mediated immune response (for further details see Brinkhof *et al.* 1999). Great tit clutches usually hatch over a period of 1–3 days. Chicks were marked provisionally with colour paints at 2 days of age and ringed on day 9 after hatch. Thus, chicks were accurately ranked by age throughout the nesting cycle. We compared the mean PHA-response of senior and junior nestmates using a paired *t*-test.

HATCHING RANK-RELATED ECTOPARASITE LOADS

Carnid fly *Carnus haemapterus* (*Diptera: Carnidae*)

C. hemapterus is a 2-mm-long fly that feeds upon the blood of nestlings of many bird species (e.g. owls, raptors, passerines; Büttiker 1975; AR personal observation). Gravid females deposit between one and 109 pupae in the bird nest (Roulin 1999). Flies produce several generations, and their population size increases from the host hatchling stage through to half the rearing period (Roulin 1998). Close to fledging, nestlings are free of parasites.

In the barn owl, within-brood variation in *C. hemapterus* load was studied in the years 1996–2001 in the same Swiss area. Here we used data collected in 1996 (50 broods), 1998 (38 broods) and 2001 (19 broods) only, because in these years hatching-rank was known for all chicks, because hatchlings were marked individually with colour paints upon hatching. When the first-hatched nestling was 23–34 days old, i.e. the age at which parasite intensity is maximal (Roulin 1998), we counted the number of *C. haemapterus* on the body surface of each chick. This method assesses parasite intensity reliably (Roulin 1998).

The kestrel data come from western Switzerland (57 broods; data from 1996, 1997, 1999 and 2001; AR) and western France near and on the Island of Oléron (27 broods; data from 1999, 2000 and 2001; CB, GB and NB). Kestrel broods hatch asynchronously, usually over a period of 2–7 days. To investigate parasite aggregation in relation to hatching rank, we compared mean number of *C. haemapterus* on senior and junior siblings. Chicks with a wing length above or below the median wing length in the brood were assigned to the 'senior' or 'junior' rank category, respectively (Village

1990). The third-hatched chick in broods of five was also allocated to the 'junior' category. Among broods, the age of the first-hatched chick varied between 6 and 15 days (mean fledging age is 30 days).

European castor-bean tick *Ixodes ricinus* (*Acari: Ixodidae*)

Ixodes ricinus is a 3-mm-long tick that feeds upon the blood of a wide variety of animals. Ticks are unable to run, fly or move quickly, and hence rely on a sit and wait strategy to reach a suitable host. The tick life cycle has four stages, namely egg, larvae, nymph and adult. To survive, moult and reproduce, individuals of the latter three stages obligatory attach to a host to obtain a blood meal (Gray 1998). *I. ricinus* is a well-known vector for several infectious diseases (Humair, Rais & Gern 1999).

Tick load was assessed in 1996, 1998 and 2001 among 159 barn owl broods by examining carefully the body surface of each nestling. In 1998 and 1999, tick load was similarly assessed on 5-day-old chicks in 98 great tit broods. For each bird species, the relationship between hatching-rank categories ('senior' vs. 'junior') and within-brood tick distribution was investigated using the Wilcoxon signed-rank test.

Hippoboscid fly *Crataerina melbae* (*Diptera: Hippoboscidae*)

C. melbae is a large (4.5 mm; Büttiker 1994), blood-sucking parasite that feeds specifically on Alpine swifts (Roulin *et al.* 1998; Tella *et al.* 1998). This viviparous louse-fly has a single generation each year. After completion of the larval stage inside the abdomen of the female, pupae are usually released near or inside the host nest. The genus *Crataerina* is flightless, but able to switch hosts rapidly on foot (Büttiker 1994).

The within-brood distribution of *C. melbae* was studied in an Alpine swift colony located in a tower in Solothurn, Switzerland in 1999 (21 nests), 2000 (24 nests) and 2001 (29 nests). For 198 chicks in total, fly load was assessed on days 10, 30 and 50 after hatching. Clutch size ranges from one to four eggs, which hatch over 1–2 days. All nests were monitored daily and to determine the hatching rank order hatchlings were individually marked with colour paint before being ringed. To study the within-brood distribution of *C. melbae*, we compared the parasite-load on the younger chick with the mean load on the older nestmates.

STATISTICS

Statistical analyses were carried out with the JMP statistical package (Sall & Lehman 1996). The number (x) of *C. haemapterus* and *C. melbae* found on senior and junior chicks was $\log_{10}(x + 1)$ transformed to obtain a normal distribution. For reasons of simplicity, we used the 'junior' and 'senior' rank categories instead of the

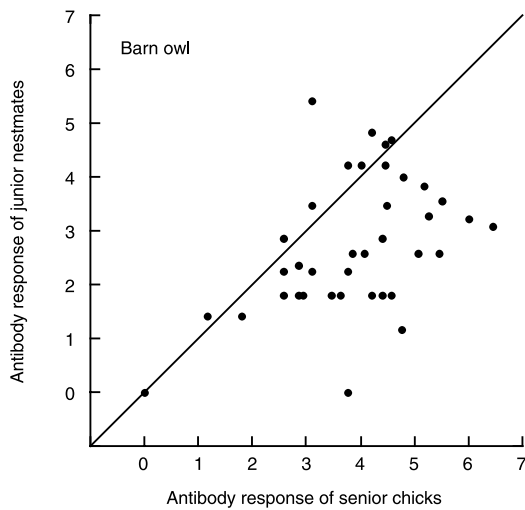


Fig. 1. Within-brood relationship between the anti-SRBC antibody production (mean of peak response on days 8 and 13 after immunization) of senior and junior barn owl chicks. Dots above the diagonal indicate broods in which juniors had a greater humoral immune response than their senior siblings.

actual hatching rank of each chick or the exact hatching span between two successive chicks in all statistical tests. This approach allowed a powerful test of the overall within-brood distribution of ectoparasites envisioned by the TCH, while avoiding the more complex statistical models needed when considering the exact rank of each chick. Statistics are two-tailed and P -values smaller than 0.05 were considered as significant. Means are quoted ± 1 SE.

Results

HATCHING RANK-RELATED IMMUNOCOMPETENCE

In the barn owl, senior chicks showed a stronger antibody response to SRBC than their junior siblings (repeated measures anova controlling for nest: $F_{1,36} = 11.83$, $P = 0.001$; interaction between time-course of the immune response and hatching rank category (i.e. senior vs. junior): $F_{4,33} = 3.18$, $P = 0.03$; Fig. 1); the antibody response was not associated with body condition ($F_{1,36} = 0.39$, $P = 0.53$). Senior great tit chicks were significantly heavier than their junior siblings ($t_{74} = 8.04$, $P < 0.001$), but showed a similar inflammatory response to PHA ($t_{74} = 0.74$, $P = 0.23$).

HATCHING RANK-RELATED ECTOPARASITE LOADS

Carnid fly C. haemapterus

In barn owl nests, mean number of *C. haemapterus* per chick per nest was 50 ± 5 (range = 1–273). Juniors bore twice as many *C. haemapterus* than senior siblings (62 ± 6 vs. 33 ± 4 ; paired t -test on $(\log_{10} + 1)$ transformed data: $t_{106} = 10.2$, $P < 0.001$; Fig. 2). In kestrel

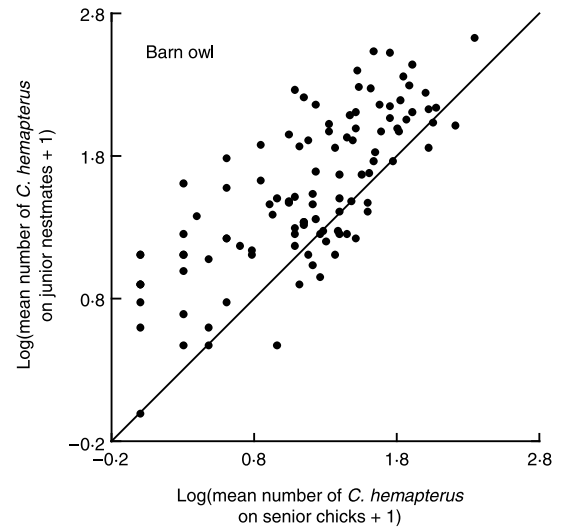


Fig. 2. Within-brood relationship between the mean number of *C. haemapterus* on senior and junior barn owl chicks. Dots above the diagonal indicate broods in which juniors were more parasitized than their senior siblings.

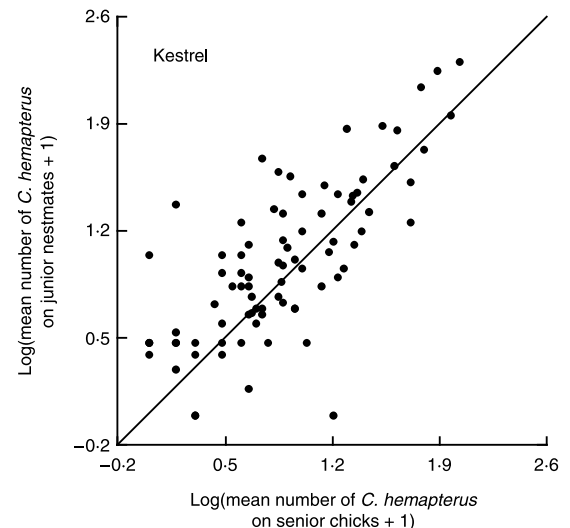


Fig. 3. Within-brood relationship between the mean number of *C. haemapterus* in senior and junior kestrel chicks. Dots above the diagonal indicate broods in which juniors were more parasitized than their senior siblings.

broods, mean parasite intensity was 15 ± 3 (range = 0.5–130). Juniors had more *C. haemapterus* on their body than their senior siblings (21 ± 4 vs. 14 ± 2 ; paired t -test on $(\log_{10} + 1)$ transformed data: $t_{83} = 3.4$, $P < 0.001$; Fig 3).

Tick I. ricinus

In 42 of the 159 barn owl broods (26%; mean brood size = 5.0), we found one to four ticks per brood (1.3 ± 0.1). In four cases, senior and junior siblings had the same number of ticks; in 18 broods most ticks were found on senior chicks, and in 18 other broods on junior chicks (Wilcoxon matched-pair signed-rank test comparing number of ticks on senior and junior nestmates: $Z =$

Table 1. Mean number (\pm SE) of louse-fly *C. melbae* per nestling on seniors and junior sibling Alpine swifts in relation to age. Pooled data from broods in 1999 ($n = 21$), 2000 ($n = 24$) and 2001 ($n = 29$)

Age (days)	Senior nestlings	Junior siblings
10	3.2 \pm 0.5	1.9 \pm 0.3
30	18.6 \pm 1.5	14.4 \pm 1.4
50	7.6 \pm 0.8	8.2 \pm 0.8

0.13, $n = 36$, $P = 0.90$). In 63 of the 98 monitored great tit nests (63%) we found one to 10 ticks per brood (2.45 ± 0.32). In five cases, senior and junior siblings had the same number of ticks on their body; in half of the 58 other broods with ticks, juniors had more ticks than their older siblings, as expected by chance ($Z = 0.48$, $n = 58$, $P = 0.63$). Thus, ticks were distributed randomly with respect to hatching ranks in both barn owl and great tit broods.

Louse-fly *C. melbae*

The within-brood distribution of louse-flies on Alpine swift nestlings was analysed using a repeated-measures anova with number of flies at 10, 30 and 50 days as repeats, and nest and rank (junior vs. senior) as factors. Parasite loads were highest on 30-day-old chicks compared to those aged 10 or 50 days ($F_{2,146} = 122.98$, $P < 0.001$; Table 1). Senior chicks bore more louse-flies than junior nestmates ($F_{1,146} = 19.21$, $P < 0.001$; Table 1), especially at an early age (for the interaction between age and the repeats: $F_{2,146} = 7.74$, $P < 0.001$; Table 1). Note that the factor 'nest' was significant ($F_{73,146} = 2.51$, $P < 0.001$), which indicates that parasite numbers assessed on different days differed consistently in level between broods.

Discussion

ASSUMPTION OF THE TCH: WITHIN-BROOD VARIATION IN IMMUNOCOMPETENCE

Variation in bird immunocompetence has become a major focus in ecological and evolutionary studies, as it could improve our understanding of host-parasite interactions. Established methods are the assessment of the degree of the humoral response towards artificially administered antigens (e.g. Deerenberg *et al.* 1997) and of the inflammatory reaction to a subcutaneous injection of the mitogen phytohaemagglutinin-P (e.g. Smits *et al.* 1999). Similar to the findings in house martins (Christe *et al.* 1998) and barn swallows (Saino *et al.* 1997) using PHA-tests, humoral immunity of senior chicks was higher than that of their junior siblings in the barn owl, while cell-mediated immunity was independent of hatching order in great tit nestlings. Thus, three of four studies that, to the best of our knowledge, investigated hatching rank-related variation in host defence, support the basic assumption of the TCH.

The discrepancy between the great tit study and the other three studies might be associated with the degree of hatching asynchrony within broods, which is relatively small in this bird. In such species, within-brood variation in immunity is probably caused mainly by variation in body condition, whereas differences in age-related maturation of the immune system may play a minor role. Body condition may further be independent of hatching order, if parents feed the last-hatched offspring preferentially (Slagsvold 1997; Krebs, Cunningham & Donnelly 1999). In other species, such as the barn owl, which show a high degree of hatching asynchrony, differences in age-related maturation of the immune system may largely determine hatching rank-related variation in parasite resistance (Apanius 1998). Despite its consequences for the within-brood distribution of ectoparasites, age-related within-brood variation in host defence was not considered in the development of the TCH (Christe *et al.* 1998). Ectoparasites are expected to feed upon the last-hatched chicks throughout the rearing period only, if hatching rank-related variation in body condition largely determines immunocompetence. However, if hatching rank-related variation in host-defence is caused mainly by age-related variation in maturity of the immune system, a more even distribution of ectoparasites is expected in the course of nesting cycle, because all nestlings gradually acquire mature resistance. Under such a scenario, there is less scope for ectoparasite-mediated evolution of hatching asynchrony.

PREDICTION OF THE TCH: WITHIN-BROOD VARIATION IN ECTOPARASITE LOADS

The TCH postulates that ectoparasites drive the evolution of hatching asynchrony, as hatching rank-related variation in parasite resistance would lead to a gradual aggregation of parasites on the chicks of lower residual reproductive value (Christe *et al.* 1998). The TCH may be applicable to many host-parasite systems, provided that two conditions are met. First, the net benefit for parasites of feeding upon a given chick should be determined mainly by its degree of immunological resistance to the parasite. Secondly, the benefit for parasites of feeding upon chicks that show an impaired resistance should outweigh the costs of sampling hosts. These two conditions might not always be fulfilled. First, although hosts in good condition are more immunocompetent they also might provide the ectoparasite with more nutrients. Secondly, the costs of sampling hosts may be linked to factors other than within-brood variation in host immunity. Host switching may include an enhanced risk of detection and removal by the host, and this risk may vary with traits of the ectoparasite, such as mode and speed of locomotion, and with traits of the host, such as cleaning behaviour or degree of feathering, or both. In this context, we next discuss potential reasons for the observed difference in the within-brood distribution of

ectoparasites in the four avian host-parasite systems described here.

Within-brood distribution of C. haemapterus

Both in the barn owl and kestrel, *C. haemapterus* were significantly more abundant on junior chicks. This observation and the finding that senior barn owl chicks showed a stronger SRBC-antibody response than junior chicks are consistent with the TCH, assuming that the SRBC response is indicative of the immunological resistance against *C. haemapterus*. However, these findings do not exclude the alternative, not mutually exclusive, hypothesis that flies feed preferentially upon junior chicks because they are less feathered than their older siblings (Kirkpatrick & Colvin 1989; Dawson & Bortolotti 1997; Roulin 1998; Liker *et al.* 2001). This proposition could be tested by assessing the change in the within-brood distribution of parasites following an experimental plumage reduction in senior chicks.

Within-brood distribution of I. ricinus

Tick distribution was not associated with the within-brood rank of chicks in the barn owl and the great tit. A similar result was found in the yellow-legged gull (*Larus michahellis* Naumann; Bosch & Figuerola 1999). Humoral immunocompetence may indicate tick resistance in rabbits (Brossard & Girardin 1979). Generalizing this result, the random within-brood distribution of *I. ricinus* in barn owl broods contradicts the predictions of the TCH, because the antibody response of senior chicks was greater than in junior chicks. One possible explanation for the random distribution of ticks concerns the costs of host switching. Parent birds contract ticks while foraging and infect their offspring at random upon returning to the nest. Ticks have a low locomotion speed, are unable to jump or fly, and consequently the net benefit of moving and finding a less resistant chick may be lower than the net benefit of staying and feeding upon the present chick.

Within-brood distribution of C. melbae

The louse-fly *C. melbae* is highly mobile, which allows the parasite to switch rapidly and sample alternative hosts to find the most profitable one. In our study, louse-flies attacked senior chicks preferentially, which contradicts the predictions of the TCH. Several observations suggest that the within-brood distribution of louse-flies is governed by host variation in feather development rather than parasite resistance. Amid the rearing period flies aggregate mainly on senior chicks, but with age chicks become more similarly feathered, and the ectoparasite is found distributed evenly among siblings. Further, the lowest intensity of infection is found among newly hatched, non-feathered chicks, even under conditions where *C. melbae* is abundant in

the colony (PB, personal observation). As suggested for *C. haemapterus*, a critical test of the proposition that feathering determines parasite loads would imply an experimental reduction of the feathering of individual chicks.

ROLE OF ECTOPARASITES IN THE EVOLUTION OF HATCHING ASYNCHRONY

At least nine hypotheses have been proposed to explain the evolution of inter- and intraspecific variation in the degree of hatching asynchrony (Stenning 1996). With the TCH Christe *et al.* (1998) added a further hypothesis that explicitly predicts a role for parasites. The TCH may explain the evolution of hatching asynchrony in those cases where the most abundant ectoparasites indeed aggregate on junior chicks. However, even though junior chicks might have a poor immunocompetence (Saino *et al.* 1997; Christe *et al.* 1998; present study), the present descriptive study indicates that hatching rank-related host defence mechanisms may be one factor among others, such as feather development, that determines the pattern of the within-brood distribution of ectoparasites. Future studies should therefore include aspects of ectoparasite morphology, life history and ecological requirements as to understand patterns of within-brood variation in ectoparasite load as well as the role of ectoparasites in the evolution of hatching asynchrony.

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