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. Conforming 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.

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...
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 & Triplet 1999). To avoid nest-based para-

sites 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 par-

ents might enhance their fitness by increasing the mag-

nitude 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 off-

spring with hatching rank. Because junior chicks are 

fed less frequently the maturation of their immune sys-

tern would be retarded, and such low resistance would 

serve as a sink for the prevailing nest-based ectopara-

sites. Consequently, senior chicks would enjoy reduced 

parasite loads, and allow parents to produce more high 

quality offspring and achieve a higher fitness as com-

pared 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 com-

pared 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). Alter-

natively, the immune system of junior chicks is less 

matured than that of earlier hatched siblings through-

out 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 anti-

parasite 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 injec-

tion 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 sub-

cutaneously in the neck of all nestlings. Before immu-

nization, and 3, 8, 13 and 18 days after immunization, a 

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’ cat-

egory, 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 anti-

body response was investigated with repeated-measures 

ANOVA, with the mean antibody titre on the 5 con-

secutive 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.
Immunoocompetence 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. haemapterus 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. haemapterus 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

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

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(x + 1) transformed to obtain a normal distribution. For reasons of simplicity, we used the ‘junior’ and ‘senior’ rank categories instead of the...
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+1) transformed data: \( t_{106} = 10.2, P < 0.001 \); Fig. 2). In kestrel 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+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: \( Z = \)
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 analysis of variance with number of flies at 10, 30 and 50 days as factors. 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 factors. 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 factors. 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 factors.

### Table 1. Mean number (±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)

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Senior nestlings</th>
<th>Junior siblings</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>3·2 ± 0·5</td>
<td>1·9 ± 0·3</td>
</tr>
<tr>
<td>30</td>
<td>18·6 ± 1·5</td>
<td>14·4 ± 1·4</td>
</tr>
<tr>
<td>50</td>
<td>7·6 ± 0·8</td>
<td>8·2 ± 0·8</td>
</tr>
</tbody>
</table>

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.

### 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 administrated antigen (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.
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; Likér 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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References


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