Asynchronous hatching in a blue tit population: a test of some predictions related to ectoparasites

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Abstract: Although much attention has been devoted to understanding the adaptive value of size hierarchies within broods of altricial birds, current hypotheses are the subject of much debate. Recently it has been suggested that parasites could play a role in promoting the establishment and maintenance of a nestling size hierarchy within broods. For example, the "tasty chick hypothesis" stipulates that the last-hatched chick in asynchronously hatching clutches would have the least efficient immune system, resulting in subsequent parasite aggregation on this chick and hence reducing parasitic pressure on the other chicks of the brood. From data collected during four breeding seasons and after experimental removal of the last-hatched chick, we tested three predictions based on variation in chick body characters within broods in a Corsican blue tit (*Parus caeruleus ogliastrae*) population exposed to high levels of ectoparasites (*Protocalliphora* spp.). None of the predictions were fully supported and alternative explanations could not be excluded. In particular, there was no evidence for aggregation of parasites on the last-hatched chick or for a beneficial role of this chick with respect to the others, be it "tasty" or not. Thus, our results are not consistent with the hypothesis that mechanisms responsible for size hierarchies within broods have evolved to alleviate the negative effect of parasites on the fitness of their host.

Résumé : Bien que la valeur adaptative de la hiérarchie selon la taille au sein des couvées d'oiseaux nidicoles ait fait l'objet de plusieurs études, les hypothèses au sujet des causes de cette hiérarchie sont toujours le sujet de nombreuses discussions. Tout récemment, il a été suggéré que des parasites contribuent peut-être à promouvoir l'établissement et le maintien d'une hiérarchie basée sur la taille des oisillons au sein de la couvée. Par exemple, l'hypothèse de « l'oisillon délicieux » suppose que le dernier éclos des oisillons d'une couvée à éclosions asynchrones a le système immunitaire le moins efficace résultant en une accumulation de parasites sur cet oisillon, ce qui réduit la pression de parasitisme sur les autres oisillons de la couvée. Des données récoltées au cours de trois saisons de reproduction et le retrait expérimental du dernier oisillon dans certaines couvées, nous ont permis de vérifier trois hypothèses conçues d'après la variation des caractéristiques corporelles des oisillons au sein des couvées dans une population de mésanges bleues de Corse (*Parus caeruleus ogliastrae*) exposée à des infections graves d'ectoparasites (*Protocalliphora* spp.). Aucune des prédictions ne s'est vérifiée entièrement et les hypothèses de rechange n'ont pu être rejetées. En particulier, il n'y a aucune indication d'une accumulation de parasites sur le dernier éclos des oisillons, ni d'un rôle bénéfique particulier de cet oisillon envers les autres, si « délicieux » soit-il. Nos résultats ne corroborent pas l'hypothèse selon laquelle les mécanismes responsables de la hiérarchie en fonction de la taille au sein d'une couvée sont apparus pour contrecarrer les effets négatifs de parasites sur le fitness de leurs hôtes.

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Introduction

In many altricial birds, several factors, such as hatching asynchrony, egg-size differences, or nestling feeding asymmetry, result in nestling size hierarchies within broods (Lack 1966; Parsons 1970; Clark and Wilson 1981). In the first adaptive hypothesis proposed to explain this phenomenon, size hierarchies within broods were considered a mechanism for adjusting brood size to current food resources (Lack 1947). However, no fewer than 18 hypotheses have been proposed to explain the significance of hatching asynchrony, of which 9 consider nestling hierarchy produced by hatching asynchrony to be adaptive (for reviews see Stenning 1996; Stoleson and Beissinger 1995). The most recent, the "tasty chick hypothesis" (Christe et al. 1998), suggests parasitism as the main factor promoting the establishment and maintenance of nestling size differences within broods. This hypothesis proposes that in systems in which chick behaviour

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cannot prevent parasite attack (such as systems with mites), parasites aggregate on the last-hatched chick (LHC) because that chick would have the least efficient immune system. The resulting effect would be a reduction of the parasitic load on the other nestlings, which, as a result of the sacrifice of the tasty chick, should grow better (Christe et al. 1998). When parasitic pressure is very high, such a strategy could even prevent failure of the entire brood (Christe et al. 1998). Alternatively the smallest chick could be more vulnerable to parasites for nongenetic reasons, for instance if sibling competition determines the position of chicks in the nest (e.g., Johnson et al. 1991).

Regardless of the defence mechanism employed against parasites (e.g., behavioural, physiological, genetic) and the type of ectoparasite involved, hypotheses related to the adaptive role of asynchronous hatching in the context of parasitism make at least three predictions: (*i*) within-brood variation in nestling body size and haematocrit will be greater in infested nests than in uninfested ones because parasite aggregation on the weakest chick is expected to be detrimental to the growth of this chick but advantageous to that of the others; (*ii*) the LHC, which is expected to endure parasite aggregation, will remain smaller than the other nestlings as long as parasitic pressure is high; (*iii*) under high parasitic pressure, the fate of the brood will be closely related to the presence or absence of the LHC. Nestlings in infested nests from which the LHC was experimentally removed will be lighter than those in nests from which the LHC was not removed. Conversely, in uninfested nests, the LHC will provide no benefits to its siblings, and the earlier it is removed, the greater the advantage for its siblings because there is one less nestling to be fed.

The aim of this study was to test whether ectoparasites play a role in maintaining differences in nestling body characters in a blue tit (*Parus caeruleus ogliastrae*) population on the island of Corsica. The Corsican blue tit provides a good model for examining relationships between patterns of asynchronous hatching and ectoparasite intensity, for several reasons. (*i*) Hatching asynchrony, and hence brood hierarchy, is very common in this population; more than 80% of the broods include a chick born 1 day or more after its siblings (95% in 1999). (*ii*) During the breeding season this population is systematically and heavily infested by haematophagous larvae of blow flies (*Protocalliphora* spp.). With a prevalence of over 90% and parasite loads reaching 150 larvae per nest, this population has the highest blow fly infestation rate so far recorded in Europe (Blondel 1985; Hurtrez-Boussès et al. 1999). (*iii*) Previous studies on this population have demonstrated the negative impact of these ectoparasites on the body size and especially on the haematocrit of nestlings (Hurtrez-Boussès 1996; Hurtrez-Boussès et al. 1997*a*, 1997*b*, 1998), but not on nestling mortality (Hurtrez-Boussès et al. 1997*b*). (*iv*) Previous studies suggest that larvae of *Protocalliphora* spp. aggregate on nestlings (e.g., Merino and Potti 1995). Adult blow flies lay their eggs in the nest material after the chicks hatch. The larvae develop over a period of 15 days (three larval stages) by sucking the blood of nestlings, and take the largest quantities of blood when the chicks are ca. 9 days old (Bennett and Whitworth 1991; Johnson et al. 1991; Hurtrez-Boussès et al. 1997*a*, 1997*b*). (*v*) Other ectoparasites, such as ticks, mites, and fleas, are extremely rare

and their effects are probably negligible (Hurtrez-Boussès 1996). (*vi*) The isolation of this population within the island (Blondel et al. 1999) is likely to favour the evolution of local adaptations to environmental constraints, including parasitism.

Methods

The habitat is an old forest of holm oak (*Quercus ilex*) at 100–300 m elevation (for a detailed description of the study site see Blondel 1985). In the study plot, 137 nest boxes were evenly distributed at a density of ca. 2/ha; about 60 pairs of blue tits breed annually on this site. They usually start laying around 10 May and have a clutch size of 6.3 ± 1.24 (mean ± SD) eggs, which they incubate for 14 days. The young leave the nest at ca. 21 days of age (Blondel 1985; Blondel et al. 1993).

Chick development follows a fixed pattern in terms of colour change, plumage development, and mass gain (Perrins 1979; J. Blondel, unpublished data). The LHC from each nest was identified using both plumage-development patterns and body mass at 2 days post hatching.

Nestlings are infested by two species of blow flies, *Protocalliphora falcozi* and *Protocalliphora azurea* (Hurtrez-Boussès 1996). The larvae of these flies parasitize chicks only (Hurtrez-Boussès 1996). They remain in the nest material from which they move up to take a blood meal several times a day, so they are not permanently fixed on their host, which made it impossible to determine the number of parasites per chick. Furthermore, since we failed to find any morphological criteria for distinguishing the two species at larval stages, the species have been pooled in our analyses (cf. Hurtrez-Boussès et al. 1997*a*, 1997*b*).

In 1994, 1995, 1996, and 1999, about one-third of the nests were randomly chosen and treated efficiently to eliminate parasites, using insecticides (1994), a microwave oven (1995, 1996), or a tissue screen to prevent adult female blow flies laying in the nest (1999) (for details see Hurtrez-Boussès et al. 1997*b*). Nests were collected after the chicks fledged in 1994, 1995, and 1996 and when the chicks were 15 days old in 1999. Nests were carefully checked in the laboratory and *Protocalliphora* spp. larvae and pupae were counted.

In 1994, 1995, and 1996, chicks were weighed at 2, 5, 9, and 15 days of age to the nearest 0.1 g using a Pesola spring balance (see Hurtrez-Boussès et al. 1997*b*). In 1999 they were weighed with an electronic balance to the nearest 0.01 g at 2 days of age and with a Pesola spring balance at 5, 9, and 15 days of age. They were ringed when 5 days old. At day 15, their tarsus length was measured and 20 µL of blood was collected from each chick into a microtube and centrifuged (3 min at 13 000 rpm) to determine the haematocrit (cf. Hurtrez-Boussès et al. 1997*a*).

In 1999 we tested the role of the LHC. We removed the LHC from randomly chosen treated ($n = 7$) and untreated ($n = 10$) nests when it was 2 days old. In other nests, another nestling was removed at the same age to compare nests using the same experimental procedure ($n = 4$ treated nests versus $n = 11$ untreated nests). Finally, in a number of control nests, no chick was removed ($n = 6$ treated nests versus $n = 9$ untreated nests). All the removed nestlings were put in

Table 1. Numbers (mean ± SD) of blow fly (*Protocalliphora* spp.) larvae (instars II and III and pupae) per nest per year in treated and untreated nests of Corsican blue tits (*Parus caeruleus ogliastrae*).

Year	Untreated nests	Treated nests	Z*	P
1994	56.13 ± 4.88 (*n* = 8)	5.80 ± 3.23 (*n* = 5)	–2.72	0.007
1995	42.67 ± 4.76 (*n* = 15)	19.86 ± 3.23 (*n* = 7)	–2.01	0.04
1996	78.43 ± 4.89 (*n* = 7)	0 ± 0 (*n* = 3)	–2.31	0.02
1999	37.90 ± 4.99 (*n* = 30)	0.18 ± 0.73 (*n* = 17)	–5.10	0.0001

*Mann–Whitney test.

Table 2. Coefficients of variation (mean ± SD) of various body characters according to the age of nestlings and treatment (1994, 1995, 1996, and 1999).

Body character	Untreated nests (*n* = 36)	Treated nests (*n* = 19)
Body mass		
At 2 days of age	23.54 ± 9.45	23.19 ± 9.98
At 5 days of age	15.60 ± 6.15	14.47 ± 4.65
At 9 days of age	9.28 ± 4.56	8.11 ± 4.21
At 15 days of age	5.95 ± 4.02	5.33 ± 2.28
Tarsus length (at 15 days of age)	2.42 ± 0.98	2.40 ± 1.04
Haematocrit (at 15 days of age)	13.36 ± 6.83	9.12 ± 5.31

Note: There were 46.25 ± 26.96 larvae per untreated nest and 5.34 ± 10.01 larvae per treated nest (mean ± SD).

Table 3. *F* and *P* values from the MANOVA, with transformed coefficients of variation of body mass, tarsus length, and haematocrit at day 15 as dependent variables according to treatment (treated, untreated), year (1994, 1995, 1996, 1999), brood size (2, 3, 4, 5, 6, 7), and interaction terms (results of the Hotelling–Lawley trace).

Explanatory variables	F	P >F
Treatment	0.34	0.80
Year	0.12	0.99
Brood size	0.29	0.83
Treatment × year	0.12	0.99
Treatment × brood size	0.36	0.78
Year × brood size	0.14	0.99
Treatment × year × brood size	0.19	0.98

"host" great tit (*Parus major*) or coal tit (*Parus ater*) nests from which they fledged safely.

The three predictions mentioned above were first tested using the data collected in 1994, 1995, and 1996, to which we added data from the control nests in 1999. The third prediction (data collected in 1999) was tested using the three different nest types (reduced broods without the LHC, reduced broods with the LHC, and control nests). Nestling condition was estimated through body mass, tarsus length, and haematocrit (cf. Hurtrez-Boussès et al. 1997*a*). To test the first prediction we used the coefficient of variation of body mass, tarsus length, and haematocrit for each brood. For the other two predictions we used brood mean values, excluding body size (i.e., body mass and tarsus length) of the LHC. The effects of treatment and presence or absence of the LHC were tested on mean nestling characters using ANOVA (multiway) and multivariant analysis of variance (MANOVA) (see Sokal and Rohlf 1981; Cody and Smith 1991) after arcsine square-root transformation. We controlled for effects of year, brood size, and the interaction between these two factors and treatment and (or) LHC removal. We did not consider chick mortality because previous studies using the same samples had shown that chick mortality did not differ significantly among nest categories, including in 1999 (Hurtrez-Boussès et al. 1997*b*; J. Blondel, unpublished data). Analyses were performed using the SAS computer program. All *P* values are two-tailed.

Results

Test of prediction 1 (within-brood variation)

The number of blow fly larvae differed significantly between treated and untreated nests, regardless of the year and methodology used (Table 1).

Parasite treatment had a significant effect on nestling growth patterns (MANOVA with parasite treatment, year, brood size, and their interactions as explanatory variables and body mass, tarsus length, and haematocrit at 15 days of age as dependent variables: $F_{[4,10]} = 5.80$, $P = 0.01$ for the variable treatment). ANOVAs with Bonferroni corrections gave similar results (data not presented).

However, neither treatment nor its interactions with year and (or) brood size affected the coefficient of variation of chick body mass and tarsus length within broods (Tables 2 and 3). For infested nests, the number of ectoparasites had no effect on nestling character variation (multiway ANOVA with parasite load of the nest, year, brood size, and the interactions between these variables as explanatory variables, all $P > 0.7$ for body mass, tarsus length, and haematocrit at day 15).

Test of prediction 2 (body mass of nestlings)

In both treated and untreated nests, the LHC was significantly smaller than the other chicks until 9 days post hatching (Table 4). Consistent with this prediction, a significant difference in body size at 15 days post hatching was found between the LHCs and the other chicks in the nest for the untreated nests only (Table 4). However, haematocrit did not differ between the LHC and the other chicks in either the treated or the untreated nests (Table 4).

Test of prediction 3 (effect of the presence or absence of the LHC on brood performance)

Experimental removal of a chick revealed no effect of nest type (removal of the LHC, removal of any other chick, control), brood size, or their interaction terms on mean body mass, mean tarsus length, or mean haematocrit at day 15 (Table 5). There was no significant difference between body

Fig. 1. Body characters of Corsican blue tit (*Parus caeruleus ogliastrae*) nestlings in relation to the type of chick removed at 2 days of age and parasite treatment (data for 1999). (*a*) Untreated nests. (*b*) Treated nests.

■ LHC was removed at 2 days of age

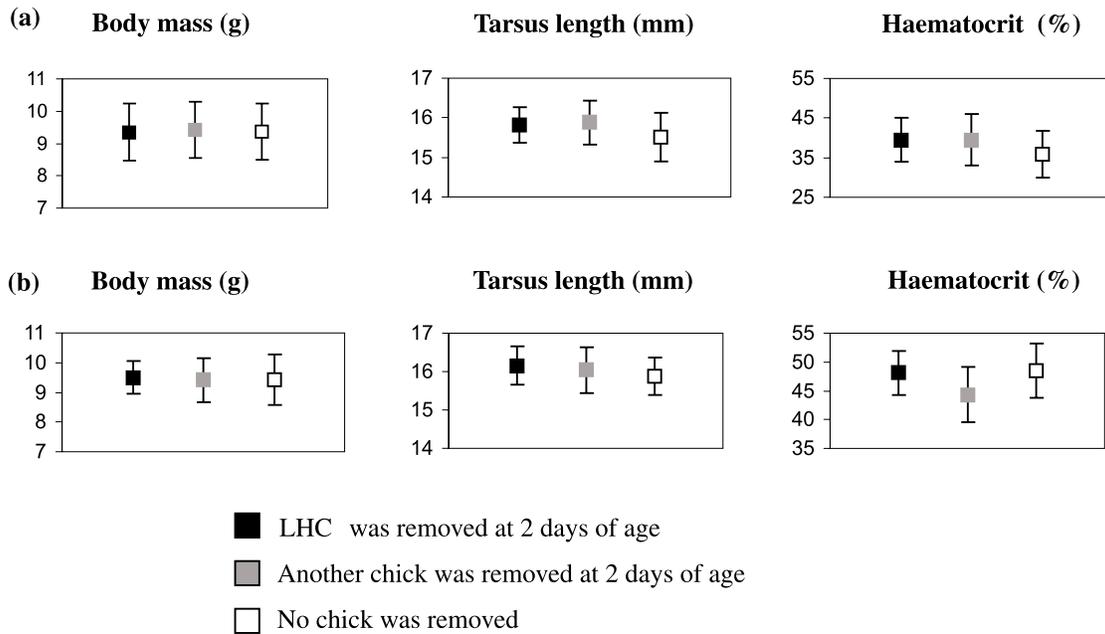▨ Another chick was removed at 2 days of age

□ No chick was removed

Table 4. Body mass, tarsus length, and haematocrit (mean ± SD) according to the age and type of nestlings (last-hatched chick (LHC) versus other chicks) and parasite treatment (1994, 1995, 1996, and 1999).

Variable	Untreated nests ($n = 39$)			Treated nests ($n = 19$)		
	LHC	Other chicks	p (paired t test)	LHC	Other chicks	p (paired t test)
Body mass						
At 2 days of age	1.23 ± 0.29	1.99 ± 0.54	<0.001	1.31 ± 0.29	1.96 ± 0.45	<0.001
At 5 days of age	3.60 ± 0.74	4.72 ± 0.65	<0.001	3.83 ± 0.65	4.93 ± 0.69	<0.001
At 9 days of age	7.21 ± 1.11	8.16 ± 0.93	<0.001	7.52 ± 0.86	8.51 ± 0.70	<0.001
At 15 days of age	9.08 ± 1.14	9.44 ± 0.82	0.003	9.59 ± 0.86	9.63 ± 0.76	0.64
Tarsus length (15 days of age)	15.61 ± 0.60	15.79 ± 0.56	0.02	15.88 ± 0.83	15.94 ± 0.59	0.51
Haematocrit (15 days of age)	38.79 ± 9.05	39.31 ± 6.85	0.76	44.58 ± 5.35	49.90 ± 4.61	0.10

Table 5. *F* and *P* values from the MANOVA, with mean body mass, tarsus length, and haematocrit at day 15 as dependent variables in relation to parasite treatment, type of chick removed, brood size, and interaction terms in 1999 (results of the Hotelling–Lawley trace).

Explanatory variables	F	$P > F$
Treatment	0.72	0.55
Type of chick removed	0.92	0.49
Brood size	1.83	0.17
Treatment × type of chick removed	1.07	0.39
Treatment × brood size	1.11	0.37
Type of chick removed × brood size	0.92	0.49
Treatment × brood size × type of chick removed	1.02	0.18

characters of nestlings from the different nest types, which suggests that the LHC plays no beneficial role in relation to parasitism (Fig. 1). In reduced nests without the LHC, nestlings even tended to be larger in infested nests than in control nests (e.g., tarsus length and haematocrit; Fig. 1).

Discussion

Our results are based on samples that are admittedly rather small, which could be a problem because of the low statistical power of tests to detect differences between treatments. We think, however, that the results are conservative because the trends observed in this study were sometimes opposite to those predicted.

Our results do not support the idea that the larvae of *Protocalliphora* spp. affect variance in body characters within broods of Corsican blue tits. Contrary to prediction 1, variance in body-size measurements and haematocrit did not differ significantly between infested and treated broods. Within infested broods, there was no significant relationship between the variance in nestling body characters and parasite load. This suggests that larvae of *Protocalliphora* spp. do not aggregate on a single chick. Although it was not possible to demonstrate aggregation patterns within broods, exploitation of all chicks by parasites is most likely. This may explain why previous studies also showed a positive correlation between brood size and parasite load (Hurtrez-Boussès et al. 1997*a*, 1997*b*).

Only prediction 2, that the LHC will remain smaller than the other chicks in infested nests, is supported. However, the haematocrit was not significantly lower in the LHC than in the other chicks, which suggests that the LHC did not sustain a higher level of parasitic attack. Our results could therefore be explained by greater sibling competition in more stressful environments, where the LHC would suffer more than its siblings from the adverse conditions in parasitized nests (for instance, see Hahn 1981; Mock and Ploger 1987).

Finally, the results of the experiment conducted to assess the influence of the LHC on the body size and haematocrit of its siblings do not support our third prediction. First, no significant difference was observed when nests from which the LHC was experimentally removed at day 2 were compared with nests from which a nestling other than the LHC was removed at the same age. In addition, nestlings from reduced broods without the LHC did better than those from control nests when exposed to parasitic pressure. Thus, it seems that removing the smallest chick in the hierarchy tended to improve feeding conditions for the remaining chicks because there were fewer to feed. This confirms the results of previous experimental manipulations of brood size (Blondel et al. 1998).

In this study we used an indirect approach (i.e., no measure related to the immune system nor the number of parasites feeding on individual chick) to test the potential role of the LHC in relation to parasitism. However, our results indicate that asynchronous hatching cannot be considered an efficient mechanism for protecting the brood against attacks by *Protocalliphora* spp. in this Corsican blue tit population.

In conclusion, our study does not support any of the three hypotheses, including the tasty chick hypothesis proposed to explain the role of some ectoparasites in promoting a nestling size hierarchy in altricial birds. Further investigations on other species are necessary before generalizations can be made. As was suggested by Poiani (1993), Richner and Heeb (1995), and Christe et al. (1998), a reduction in clutch size (and hence brood size) could be a strategy to prevent ectoparasitism. Selection for such a strategy would not be unlikely in this population of blue tits, since the prevalence of blow flies is nearly 100% and parasite intensities are always very high. This would explain why the clutch size is so low in this highly parasitized population. Further experiments should be carried out to measure the selective effects of parasites on clutch size.

Acknowledgements

References

Bennett, G.F., and Whitworth, T.L. 1991. Studies on the life history of some species of *Protocalliphora* (Diptera: Callophoridae). Can. J. Zool. **69**: 2048–2058.

Blondel, J. 1985. Breeding strategies of the Blue Tit and Coal Tit (*Parus*) in mainland and island Mediterranean habitats: a comparison. J. Anim. Ecol. **54**: 531–556.

Blondel, J., Dias, P.C., Maistre, M., and Perret, P. 1993. Habitat heterogeneity and life-history variation of Mediterranean blue tits (*Parus caeruleus*). Auk, **110**: 511–520.

Blondel, J., Maistre, M., Perret, P., Hurtrez-Boussès, S., and Lambrechts, M.M. 1998. Is the small clutch size of a Corsican blue tit population optimal ? Oecologia, **117**: 80–89.

Blondel, J., Dias, P.C., Perret, P., Maistre, M., and Lambrechts, M.M. 1999. Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. Science (Washington, D.C.), **285**: 1399–1402.

Christe, P., Møller, A.P., and de Lope, F. 1998. Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. Oikos, **83**: 175–179.

Clark, A.B., and Wilson, D.S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. Q. Rev. Biol. **56**: 253–277.

Cody, R.P., and Smith, J.K. 1991. Applied statistics and the SAS programming language. Simon and Schuster Co., North Holland, N.Y.

Hahn, D.C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. Anim. Behav. **29**: 421–427.

Hurtrez-Boussès, S. 1996. Interactions hôte–parasite : le système mésange bleue – *Protocalliphora* en région méditerranéenne. Ph.D. thesis, University of Montpellier II, Montpellier, France.

Hurtrez-Boussès, S., Blondel, J., Perret, P., and Renaud, F. 1997a. Relationship between intensity of blowfly infestation and reproductive success in a Corsican population of blue tits. J. Avian Biol. **28**: 267–270.

Hurtrez-Boussès, S., Perret, P., Renaud, F., and Blondel, J. 1997b. High blowfly parasitic loads affect breeding success in a Mediterranean population of blue tits. Oecologia, **112**: 514–517.

Hurtrez-Boussès, S., Blondel, J., Perret, P., Fabreguettes, J., and Renaud, F. 1998. Chick parasitism by blowflies affects feeding rates in a Mediterranean population of blue tits. Ecol. Lett. **1**: 17–20.

Hurtrez-Boussès, S, de Garine-Wichatitsky, M., Perret, P., Blondel, J., and Renaud, F. 1999. Variations in prevalence and intensity of blow fly infestations in an insular Mediterranean population of blue tits. Can. J. Zool. **77**: 337–341.

Johnson, L.S., Eastman, M.D., and Kermott, L.H. 1991. Effects of ectoparasitism by larvae of the blow fly *Protocalliphora parorum* (Diptera: Calliphoridae) on nestling House Wrens *Troglodytes aedon*. Can. J. Zool. **69**: 1441–1446.

Lack, D. 1947. The significance of clutch size. Ibis, **89**: 302–352.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.

Merino, S., and Potti, J. 1995. Mites and blowflies decrease growth and survival of nestling pied flycatcher. Oikos, **73**: 95–103.

Mock, D.W., and Ploger, B.J. 1987. Parental manipulation of optimal hatching asynchrony: an experimental study. Anim. Behav. **35**: 150–160.

Parsons, J. 1970. Relationship between egg-size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature (Lond.), **228**: 1221–1222.

Perrins, C.M. 1979. British tits. Collins, London.

Poiani, A. 1993. Small clutch sizes as a possible adaptation against ectoparasitism: a comparative analysis. Oikos, **68**: 455–462.

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

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Co., New York.

Stenning, M.J. 1996. Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. Trends Ecol. Evol. **6**: 243–246.

Stoleson, S.H., and Beissinger, S.R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. *In* Current ornithology. Vol. 12. *Edited by* D.M. Power. Plenum Press, New York. pp. 191–270.