

Timothy Coppack · Francisco Pulido · Peter Berthold

Photoperiodic response to early hatching in a migratory bird species

Received: 27 June 2000 / Accepted: 22 January 2001 / Published online: 20 March 2001
© Springer-Verlag 2001

Abstract A considerable number of bird species of the northern hemisphere have been breeding earlier over the last few decades, most probably in response to global warming. In migratory birds, there is also a trend towards later departure from the breeding grounds in autumn. Yet it is not known whether this trend in the timing of migration reflects an evolutionary process or is just an immediate phenotypic response to global environmental change. We conducted an experiment with migratory blackcaps (*Sylvia atricapilla*) to investigate how the photoperiodic conditions experienced by birds hatching earlier in the season affect the timing of post-juvenile moult and the onset of autumn migration. In a split-brood experiment, we reared 30 nestlings from six different families and kept them either under a photoperiodic regime simulating conditions 6 weeks before their actual hatching date or under simulated natural photoperiods. Time-shifted birds started moulting at an earlier age compared to controls and showed an early phase of nocturnal migratory activity. Under the influence of long day lengths moult was prolonged and migratory activity was interrupted. However, the termination of moult and the reinitiation of migratory activity were not delayed to the extent that birds compensated for the simulated early hatching date. Thus, we suggest that extant physiological responses to the photoperiod are maladaptive under the novel environmental conditions imposed by a global increase in temperature, leading to earlier autumn migration in juvenile birds with earlier breeding.

Keywords Reaction norm · Adaptive evolution · Climate change · Bird migration · *Sylvia atricapilla*

Introduction

In the last few decades, a large number of bird species breeding in central and northern Europe and North America have started breeding earlier (Crick et al. 1997; Winkel and Hudde 1997; Crick and Sparks 1999; Brown et al. 1999; Dunn and Winkler 1999). At the same time, there is a trend in many migratory bird species to initiate autumn migration later in the season (Enquist and Petterson 1986; Gatter 1992; Bezzel and Jetz 1995; Moritz and Vogel 1995) or at an older age (Bergmann 1998). These opposite trends in the timing of breeding and migration have been attributed to improved conditions on the breeding grounds in spring and autumn, caused by an increase in mean surface air temperature (reviewed in Berthold 1991, 1998). Although field studies provide compelling evidence for shifts in the timing of breeding and migration, it remains unresolved whether these changes are merely phenotypic responses to changes in the environment or whether they reflect adaptive changes in the genetic composition of populations. This question, however, is decisive for assessing the potential of migratory bird species to adapt to global environmental changes (Berthold 1995; Pulido 2000).

In passerine bird species of the temperate zone, the seasonal change in day length is the primary environmental factor controlling endogenous circannual cycles, comprising reproduction, moult, and migration (see, for instance, Gwinner 1986, 1989a; Berthold 1996; Lambrechts et al. 1997). In addition, a number of other environmental factors like local climate, food availability and social stimuli may fine-tune the timing of life-history stages with local conditions (Wingfield et al. 1993; Wingfield and Jacobs 1999). The spatio-temporal programme controlling migratory behaviour, however, is to a large extent genetically determined (Berthold 1996; Pulido 2000) and the photoperiod is the only environmental factor known to be capable of synchronising the migration programme with the season (Gwinner 1996). Blackcaps (*Sylvia atricapilla*) and several other nocturnal passerine migrants complete post-juvenile moult and

T. Coppack (✉) · F. Pulido · P. Berthold
Max Planck Research Centre for Ornithology,
Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell,
Germany
e-mail: coppack@vowa.ornithol.mpg.de
Tel.: +49-7732-150113, Fax: +49-7732-150169

start autumn migratory activity at a younger age if held under short photoperiods (Jenni and Winkler 1994; Berthold 1996). The acceleration of juvenile development by short day lengths, known as “calendar effect” (Berthold 1993), is of functional significance to birds hatched late in the season, enabling them to moult and initiate migration before conditions deteriorate on the breeding grounds. The response in the timing of moult and migration to the photoperiodic environment can be expressed as a reaction norm across a set of hatching dates (Pulido 2000; Pulido et al. 2001). The reaction norm is the full set of phenotypes that a genotype will express in interaction with the full set of environments in which it can survive (Stearns 1992).

Within the range of hatching dates found in southern German blackcaps (3 May–14 August, median: 29 May; Bairlein et al. 1980), the population reaction norm is close to linear (Pulido 2000). Early-hatched birds develop more slowly and thus initiate migration at a relatively older age. However, differences in hatching date are only partially compensated: for every 2 days a blackcap hatches earlier it is only about 1 day older when it initiates migration (Pulido 2000). Earlier hatching would thus lead to earlier migration in autumn, which under the currently improving conditions on the breeding grounds would be maladaptive. Yet we do not know how birds respond to the photoperiodic conditions outside the currently observed range of hatching dates. As fluctuations of global climate have most probably occurred throughout the evolutionary history of blackcap populations (Pulido and Berthold 1998), we may expect very early-hatched birds to respond to their photoperiodic environment in an adaptive way, slowing down the speed of moult during the long days of summer and initiating migration later. However, if blackcaps are not adapted to very early breeding, the short photoperiods experienced by birds hatched before the summer solstice could lead to an acceleration of juvenile development, with the result that moult and migration would occur unseasonably early.

Here we study the reaction norm of the onset of migration in relation to hatching date in the blackcap with the aim of assessing (1) whether a shift towards later autumn migration could be caused by earlier laying dates, and (2) if physiological responses to the photoperiod are adaptive in the range of very early hatching dates. We show that a delay of autumn migration cannot be attributed to phenotypic plasticity in response to the photoperiodic conditions experienced by birds hatching earlier in the season. Furthermore, we suggest that extant reaction norms are possibly maladaptive in conditions favouring very early breeding.

Material and methods

We collected 30 blackcaps from six nests hatched in the environs of Radolfzell (at 47°46'N, 9°E) between 14 and 18 May 1998, and transferred them at an age of 5–7 days to our institute. Each brood was split into two groups, so that each family was represented

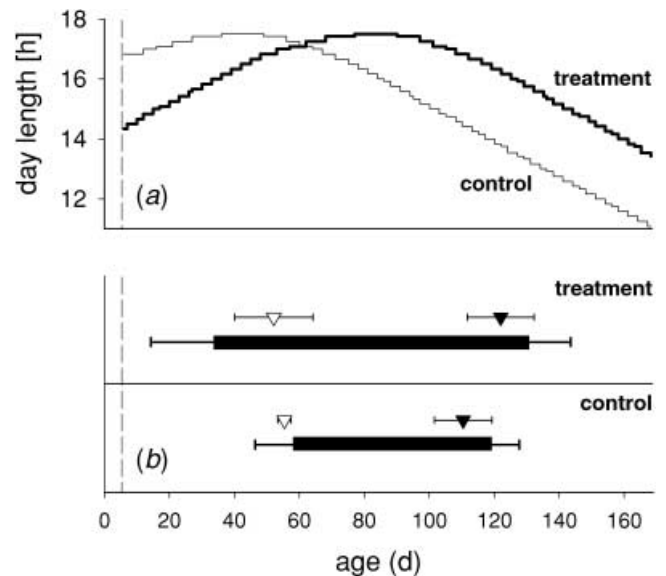


Fig. 1 **a** Simulated day lengths at 47°50'N latitude experienced by the treatment and the control group, and **b** the duration of post-juvenile moult and onset of migratory activity in both groups of blackcaps. Solid bars represent the duration of moult (mean ± SD for onset and termination of moult, $n=15$). Open and filled triangles give mean values (±SD) for the onset of two phases of nocturnal activity. Sample sizes are 10 (treatment) and 3 (control) for the onset of early activity (open triangles), and 14 for the main phase of migratory activity (filled triangles). The vertical dashed lines indicate the beginning of the experiment

with at least two nestlings both in the treatment and in the control group. The treatment group ($n=15$) was exposed to a time-shifted light-dark regime simulating conditions 6 weeks before the actual hatching date (2–6 April) which is approximately 2 weeks earlier than the earliest hatching date recorded since Bairlein et al. (1980) (19 April, U. Querner, personal communication). We chose this treatment in order to obtain a high experimental effect. The control group ($n=15$) was kept under light regimes similar to those experienced by birds of this population in the wild (Fig. 1a). The effective day length was defined as the time between the beginning of civil twilight in the morning and the end of civil twilight in the evening. Light intensity was kept constant at 400 lx during daytime and at 0.01 lx at night. Birds were hand-raised as described by Berthold et al. (1970) and kept in temperature-controlled chambers at 22°C with food and water ad libitum (for details, see Berthold et al. 1990). At the age of 30 days, birds were transferred to individual experimental cages with movable perches which allowed continuous recording of locomotory activity.

The onset of migration was defined as the age at which at least five half-hour intervals of nocturnal activity (migratory restlessness or *Zugunruhe*) were recorded for the first time. There were two bouts of nocturnal activity in most of the treatment birds. We focused our analysis on the second (i.e. the main) phase of migratory activity, as the amount of activity displayed in the first bout was low. We assessed the progress of juvenile moult in each individual bird by weekly inspecting 21 different body feather tracts (described by Berthold et al. 1970). For comparison of the timing of moult and migration we considered not absolute dates but the bird's age relative to its true (control group) or simulated (treatment group) hatching date, because we expected duration of moult and age at onset of autumn migration to be the targets of selection on the timing of migration (Pulido 2000; Pulido et al. 2001).

We used the GLM (generalized linear model) procedure in SAS using type III sums of squares for testing statistical significance of the effects of the experiment (fixed effect), sex (fixed ef-

fect) and of family (random effect), and their interactions. As we found no statistically significant effect of sex, this variable was subsequently omitted. The power of this analysis of variance was estimated using JMP (SAS Institute), using the observed effect and sample sizes.

For testing the slope of the regression of the age at onset of migratory activity on hatching date obtained in this experiment against regression coefficients derived from different hypotheses (e.g. $b=0$, $b=-1$), we generated a bootstrap distribution of regression coefficients by bootstrapping 10,000 times (1) over individuals and (2) over family means. As the distributions differed only little from each other and family effects were non-significant, we estimated 95% confidence intervals for the regression coefficient by the percentile method (Efron and Tibshirani 1993) using individual values.

Results

Blackcaps reared under the time-shifted photoperiodic regime showed significant differences in the timing of juvenile moult and nocturnal activity compared with birds of the control group (Fig. 1, Table 1). In the treatment group, moult started on average when birds were only 33.8 ± 19.5 (mean \pm SD) days old, while the mean age at onset of moult was 58.1 ± 11.7 days in the control group. The two groups differed in the termination of moult by 12 days (control group: 119.0 ± 8.7 days; treatment group: 131.1 ± 13.0 days), whereby early-hatched birds terminated moult later. As experimental birds started moult at an earlier age and completed it when they were older than control birds, the duration of moult was markedly prolonged (control group: 60.9 ± 13.3 days; treatment group: 96.6 ± 26.1 days). The mean age difference in the initiation of autumn migratory activity was small (control group: 111.0 ± 8.8 days; treatment group: 122.1 ± 9.9 days), but significantly different from zero (Table 1).

Table 1 Analysis of variance of age at onset, termination and duration of moult, and age at onset of the main phase of migratory activity

Source of variation	df	SS	F	P	Power
Onset of moult					
Treatment	1	4,128	23.0	<0.001	0.995
Family	5	2,703	3.02	0.037	0.737
Family \times Treatment	5	1,048	1.17	0.361	0.320
Termination of moult					
Treatment	1	1,378	14.8	0.001	0.953
Family	5	1,600	3.45	0.023	0.799
Family \times Treatment	5	136	0.29	0.910	0.105
Duration of moult					
Treatment	1	9,976	31.2	<0.001	>0.999
Family	5	4,462	2.79	0.049	0.697
Family \times treatment	5	1,296	0.81	0.557	0.226
Onset of migratory activity					
Treatment	1	634	6.69	0.020	0.681
Family	5	572	1.21	0.350	0.319
Family \times Treatment	5	270	0.57	0.722	0.162

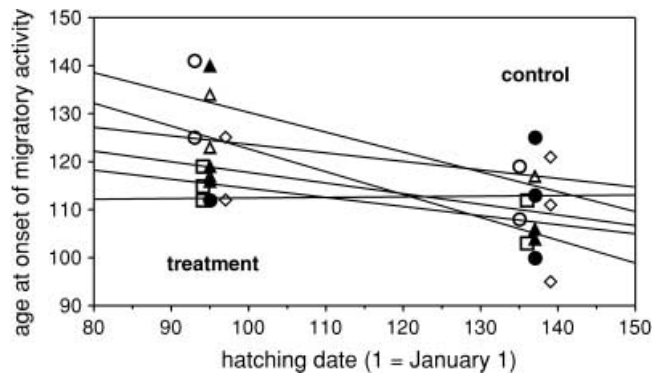


Fig. 2 Reaction norms of the age at onset of the main phase of autumn migratory activity based on the results of the treatment and control in 6 blackcap families. Each family is represented by one symbol and one regression line. Sample size for each family is 5. Regression coefficients vary from $b=-0.50$ to 0.04

In all variables except the age at onset of migration we found significant family effects (Table 1), indicating that there was additive genetic variation to these traits (see also Pulido 2000; Pulido and Berthold 1998). The failure to find significant between-family variance components in the onset of migratory activity was probably due to the low power of the experimental design. Low sample sizes in combination with large variance resulted in low statistical power of the test for family-by-treatment interaction effects (Table 1). Thus, none of the interaction effects were significant at the 5% α -level even though there was considerable variation in the response to the photo-shift treatment among families (for the age at onset of migratory activity, see Fig. 2).

We tested the slope of the mean reaction norm relating the onset of the main phase of migratory activity to hatching date by taking 10,000 random samples (of equal size as the original sample) from the control and the treatment group. For each of these replicate samples, we estimated the linear regression of age at onset of migratory activity on hatching date, obtaining a distribution of 10,000 regression coefficients. The mean regression coefficient of this bootstrap distribution was -0.268 (SD=0.084, CI_{95%} = -0.434 to 0.111 , range = -0.582 to 0.025). The results from the bootstrap analysis of regression coefficients clearly indicate that the slope of the reaction norm was different from 0 and -1 (Fig. 3). However, the mean regression coefficient obtained for very early-hatched birds did not deviate from the mean population reaction norms for southern German blackcaps hatched and reared under natural photoperiodic conditions in 1997–1998 ($n=94$, $b=-0.338$; F. Pulido and P. Berthold, unpublished work) or from the mean slope in the 3 preceding years ($b_{1995-1997}=-0.341$, SE=0.039, $n=158$).

In addition, we found differences in the pattern of migratory activity (Fig. 1). Out of 15 birds of the experimental group 10 had two distinct phases of migratory activity, while only 3 birds of the control group displayed such early nocturnal activity (Fisher's exact test, two-

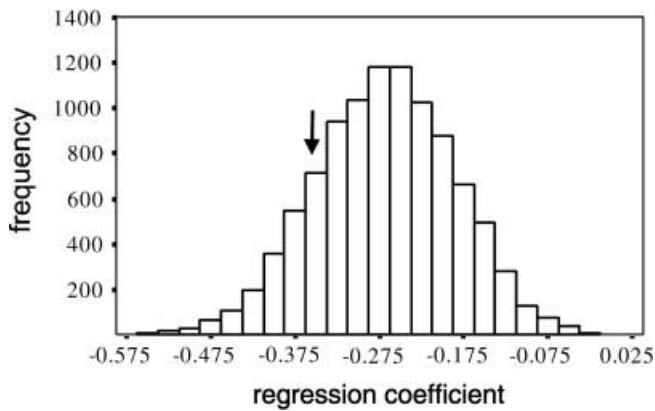


Fig. 3 Frequency distribution of 10,000 bootstrap replications of the regression coefficient (b) for the mean regression of the age at onset of the main phase of migratory activity on hatching date. Each replication was obtained by sampling with replacement from two samples (treatment, and control) of 14 individuals each and estimating a least-square linear regression. The arrow gives the mean regression coefficient for birds hatched in 1997 and 1998 and kept under natural photoperiodic conditions

tailed: $P=0.0139$). This activity was on average initiated at an age of 50 days and terminated at an age of 75 days.

Discussion

The effects of early breeding on the timing of moult and migration

Here, for the first time, we experimentally studied the effects of early breeding on the timing of avian moult and migration. By shifting the phase of the photoperiodic regime, we simulated very early hatching dates that have not yet been found in the blackcap population studied, but which may occur if global warming persists and spring temperatures increase on the breeding grounds. Blackcaps kept under daylengths simulating a hatching date 6 weeks before that of controls started juvenile moult at an earlier age and completed it when they were older; thus the duration of moult was considerably prolonged. The initiation of migration was delayed on average by 11 days in time-shifted birds. If birds had actually hatched on 4 April (simulated hatching date), migration would have started on August 4 – 1 month before the mean onset of migration in birds hatched in mid-May, i.e. in control birds. Thus, taking into account the trend towards earlier breeding caused by global warming (for the blackcap see, for instance, Crick et al. 1997; Crick and Sparks 1999) we should expect an advancement of migration, and can exclude the possibility that in the blackcap a delay in the timing of autumn migration is caused by phenotypic plasticity in response to the photoperiod.

We did not consider the early phase of nocturnal activity which most of the treatment birds exhibited because the amount of activity displayed in this phase was

insignificantly low. Moreover, we do not know whether this early phase of nocturnal activity was just the result of disrupted circannual organisation or reflects true migratory activity, as found, for instance, in 1st-year pied flycatchers and collared flycatchers, *Ficedula hypoleuca* and *F. albicollis* (Gwinner 1989b) and has an adaptive value (Berthold 1988a). However, if we define this activity phase as migratory behaviour we would expect birds that hatch in early April to start migration in mid-June – about 3 months before the actual migration period.

Birds of the treatment group showed a considerable prolongation of juvenile moult and an overlap of moult and the early phase of nocturnal activity. This may seem maladaptive considering that in birds energetically demanding events such as moult and migration are usually separated (cf. Berthold 1996; for an evaluation of the energetic costs of moult see, for instance, Lindström et al. 1993; Murphy 1996). On the other hand, a reduction of moult intensity during the long days around summer solstice – as observed in birds of the treatment group in our experiment – may be advantageous in view of the high costs of intensive moult (see, for instance, Murphy 1996; Hedenström 1999). Under conditions favouring a longer stay on the breeding grounds moult does not need to be completed rapidly, as has been demonstrated in inter- and intra-specific comparative studies in *Sylvia* species where the duration of moult correlates with the degree of migratoriness (Berthold 1988b).

The evolution of the timing of breeding and migration

An improvement of conditions on the breeding grounds due to global warming will lead to earlier breeding and consequently to earlier hatching dates. This may lead to a mismatch between migration schedules and environmental conditions in 1st-year birds because extant response mechanisms are not adapted to the novel photoperiodic conditions. Birds will probably be forced to migrate earlier in the season which could be disadvantageous under conditions favouring a longer stay on the breeding grounds. We assume the timing of autumn migration to be under stabilizing selection, i.e. not only migrating later but also migrating earlier in the season would cause a reduction in fitness. Migrating too early in the season may be disadvantageous with respect to the availability and predictability of specific food resources (berries) used for fat accumulation (Bairlein 1998). Moreover, for juveniles it may be an advantage to stay on the breeding grounds as long as possible as this may enable them to explore future breeding sites and help them find their natal habitat (Baker 1993) and establish territories the following spring (Wegglar 1997). Thus, if environmental changes due to global warming persist, the adaptation of both hatching date and date of onset of migration could be constrained by extant physiological responses to the photoperiod. We therefore expect selection on the photoperiodic response mechanism, i.e. the reaction norm, to occur if populations are exposed to

long-term environmental changes (cf. Visser and Lambrechts 1999).

But do we have any evidence for the evolution of reaction norms? Recently, Visser et al. (1998) found that the timing of reproduction in a great tit (*Parus major*) population in the Netherlands had not changed in a 23-year period, even though there had been increasing selection for earlier breeding. The lack of response of the timing of egg laying to selection has led to a mismatch between the highest need for food and its availability, causing an overall fitness reduction in this population. Visser et al. (1998) considered a change in the “relationship between food availability and a cue used for timing of breeding” as one possible explanation for the lack of adaptive evolution. They concluded that a change in the timing of breeding could only be accomplished if reaction norms responded to selection.

For migration-related traits there is some evidence suggesting that reaction norms may evolve. First, we found significant family effects for the onset, the termination and the duration of moult suggesting that there is additive genetic variation in these traits. Moreover, high heritabilities of the timing and the duration of moult have been found in other passerine species, like the stonechat, *Saxicola torquata* (Helm and Gwinner 1999) and the garden warbler, *Sylvia borin* (Widmer 1999). We therefore expect that in birds with similar hatching date, the timing of moult would readily respond to selection. There is also compelling evidence for the presence of additive genetic variation in migratory traits in the blackcap (Berthold and Pulido 1994; Pulido 2000). For the onset of autumn migration, parent-offspring and full-sib correlations yielded heritability estimates of about 0.4 (Pulido and Berthold 1998; Pulido 2000). We therefore expect rapid evolutionary changes in the timing of moult and migration in response to natural selection within the same “hatching date group”, i.e. a group of birds with the same hatching date. Rapid evolution of the response to the photoperiod is probably constrained by the lack of genetic variation (Pulido et al. 2001). However, reaction norms for the onset of autumn migration could potentially be changed as a by-product of selection on trait means within single “hatching date groups” (Pulido 2000; Pulido et al. 2001).

Moreover, there is experimental evidence for adaptive evolution of reaction norms. Two studies have recently revealed marked differences in the response of the annual routine to the photoperiod in avian populations living in different habitats. Widmer (1999) found differences in the response of the onset of autumn migratory activity to variation in hatching date between a mountain and a lowland population of the garden warbler. Blondel et al. (1999) and Lambrechts et al. (1999) showed that the response of the timing of breeding to day length differed conspicuously between blue tits (*Parus caeruleus*) living in deciduous and evergreen forests on Corsica.

In conclusion, we expect the joint evolution of the timing of reproduction and the timing of moult and migration to be constrained by the extant physiological re-

sponses to the photoperiod, which most probably are maladaptive for birds breeding very early in the season. However, if the current selection regime imposed by a global increase in temperature persists over a longer period of time, we should expect evolutionary changes in the response system used for synchronising annual routines with food availability (see Visser and Lambrechts 1999). We currently do not know whether adaptive evolution of reaction norms will keep track with the rapid ongoing environmental changes. However, if we gain a deeper insight into the genetic architecture of migratory traits and the genetic and environmental control of the annual organisation of birds, we may be able to predict if and to what extent migratory bird species will cope with rapid global environmental changes.

Acknowledgements We are grateful to Lisa Coppack, Barbara Helm and three anonymous reviewers for valuable comments on a previous version of the manuscript.

References

- Bairlein F (1998) The effect of diet composition on migratory fuelling in garden warblers *Sylvia borin*. *J Avian Biol* 29:546–551
- Bairlein F, Berthold P, Querner U, Schlenker R (1980) Die Brutbiologie der Grasmücken *Sylvia atricapilla*, *borin*, *communis* und *curruca* in Mittel- und N-Europa. *J Ornithol* 121:325–369
- Baker RR (1993) the function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. *Ornis Scand* 24:71–79
- Bergmann F (1998) Die Wegzugphänologie von Kleinvögeln in Mitteleuropa – Zugzeiten, Zugmuster, Abhängigkeit von der Witterung und langfristige Trends im Zeitpunkt des Durchzugs. PhD thesis, University of Constance, Germany
- Berthold P (1988a) Unruhe-Aktivität bei Vögeln: eine Übersicht. *Vogelwarte* 34:249–259
- Berthold P (1988b) The control of migration in European warblers. *Acta Congr Int Ornithol* 19:215–249
- Berthold P (1991) Patterns of avian migration in light of current global “greenhouse” effects: a central European perspective. *Acta Congr Int Ornithol* 20:780–786
- Berthold P (1993) Bird migration: a general survey. Oxford University Press, Oxford
- Berthold P (1995) Microevolutionary aspects of bird migration based on experimental results. *Isr J Zool* 41:377–385
- Berthold P (1996) Control of bird migration. Chapman and Hall, London
- Berthold P (1998) Vogelwelt und Klima: gegenwärtige Veränderungen. *Naturwiss Rundsch* 51:337–346
- Berthold P, Pulido F (1994) Heritability of migratory activity in a natural bird population. *Proc R Soc Lond B* 257:311–315
- Berthold P, Gwinner E, Klein H (1970) Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, *Sylvia borin*, und eines weniger ausgeprägten Zugvogels, *S. atricapilla*. *Vogelwarte* 25:297–331
- Berthold P, Querner U, Schlenker R (1990) Die Mönchsgrasmücke: *Sylvia atricapilla*. Ziemsen, Wittenberg Lutherstadt
- Bezzel E, Jetz W (1995) Verschiebung der Wegzugperiode bei der Mönchsgrasmücke (*Sylvia atricapilla*) 1966–1993 – Reaktion auf die Klimaerwärmung? *J Ornithol* 136:83–87
- Blondel J, Dias PC, Perret P, Maistre M, Lambrechts MM (1999) Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* 285:1399–1402
- Brown JL, Li S-H, Bhagabati N (1999) Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc Natl Acad Sci USA* 96:5565–5569

- Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. *Nature* 399:423–424
- Crick HQP, Dudley C, Glue DE, Thompson DL (1997) UK birds are laying eggs earlier. *Nature* 388:526
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proc R Soc Lond B* 266:2487–2490
- Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman and Hall, New York
- Enquist M, Pettersson J (1986) The timing of migration in 104 bird species at Ottenby – an analysis based on 39 years trapping data (in Swedish). *Spec Rep Ottenby Bird Observatory* 8:1–248
- Gatter W (1992) Zugzeiten und Zugmuster im Herbst: Einfluss des Treibhauseffekts auf den Vogelzug? *J Ornithol* 133:427–436
- Gwinner E (1986) Circannual rhythms. Springer, Berlin Heidelberg New York
- Gwinner E (1989a) Photoperiod as a modifying and limiting factor in the expression of avian circannual rhythms. *J Biol Rhythms* 4:237–250
- Gwinner E (1989b) Einfluss der Photoperiode auf das circannual System des Halsbandschnäppers (*Ficedula albicollis*) und des Trauerschnäppers (*F. hypoleuca*). *J Ornithol* 130:1–13
- Gwinner E (1996) Circadian and circannual programmes in avian migration. *J Exp Biol* 199:39–48
- Hedenström A (1999) Aerodynamics of moult in birds: effects of wing gaps on flight performance. *Proc Int Ornithol Congr* 22:536–543
- Helm B, Gwinner E (1999) Timing of postjuvenile molt in African (*Saxicola torquata axillaris*) and European (*Saxicola torquata rubicola*) stonechats: effects of genetic and environmental factors. *Auk* 116:589–603
- Jenni L, Winkler R (1994) Molt and ageing of European passerines. Academic Press, London
- Lambrechts MM, Blondel J, Maistre M, Perret P (1997) A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc Natl Acad Sci USA* 94:5153–5155
- Lambrechts MM, Perret P, Maistre M, Blondel J (1999) Do experiments with captive non-domesticated animals make sense without populational field studies? A case study with blue tits' breeding time. *Proc R Soc Lond B* 266:1311–1315
- Lindström Å, Visser GH, Daan S (1993) The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol Zool* 66:490–510
- Moritz D, Vogel C (1995) Langjährige Änderungen von Zugzeiten auf Helgoland. *Jahresber Inst Vogelforsch* 2:8–9
- Murphy ME (1996) Energetics and nutrition of molt. In: Carey C (ed) *Avian energetics and nutritional ecology*. Chapman and Hall, New York, pp 158–198
- Pulido F (2000) Evolutionary quantitative genetics of migratory restlessness in the blackcap (*Sylvia atricapilla*). Tectum, Marburg
- Pulido F, Berthold P (1998) The microevolution of migratory behaviour in the blackcap: effects of genetic covariances on evolutionary trajectories. In: Spina F, Grattarola A (eds) *Proceedings of the 1st Meeting of the European Ornithologists' Union*, Bologna. *Biol Conserv Fauna* 102:206–211
- Pulido F, Coppack T, Berthold P (2001) Genetic variation and phenotypic plasticity may explain adaptive changes in the timing of autumn migration. In: *Proceedings of the 2nd Meeting of the European Ornithologists' Union*, Gdansk. Ring 22 (in press)
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Visser ME, Lambrechts MM (1999) Information constraints in the timing of reproduction in temperate zone birds: great and blue tits. *Proc Int Ornithol Congr* 22:249–264
- Visser ME, Noordwijk AJ van, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc Lond B* 265:1867–1870
- Weggler MB (1997) Age-related reproductive success and the function of delayed plumage maturation in male black redstarts *Phoenicurus phoenicurus*. PhD thesis, University of Zurich
- Widmer M (1999) Altitudinal variation of migratory traits in the garden warbler *Sylvia borin*. PhD thesis, University of Zurich
- Wingfield JC, Jacobs JD (1999) The interplay of innate and experiential factors regulating the life history cycle of birds. *Proc Int Ornithol Congr* 22:2417–2443
- Wingfield JC, Doak D, Hahn TP (1993) Integration of environmental cues regulating transitions of physiological state, morphology and behaviour. In: Sharp PJ (ed) *Avian endocrinology*. Society for Endocrinology, Bristol, pp 111–122
- Winkel W, Hudde H (1997) Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers *Ficedula hypoleuca*. *J Avian Biol* 28:187–190