

A long photoperiod overrides non-photoperiodic factors in blue tits' timing of reproduction

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Endocrinological studies have contributed considerably to the development of theory concerning the proximate aspects of the timing of reproduction. In non-domesticated, avian species, the relative importance of the photoperiodic and non-photoperiodic factors influencing later stages of the breeding cycle, such as the onset of egg laying, remains unclear because egg laying is difficult to obtain with captive populations and laboratory experiments of breeding are rarely carried out in the framework of long-term field studies. We set up a special experimental design such that captive Mediterranean blue tits (*Parus caeruleus*) can breed with success in large outdoor aviaries at similar latitudes and altitudes to their wild counterparts. Here we demonstrate experimentally that the non-photoperiodic factors responsible for large and consistent differences in the expression of natural breeding responses between three captive outdoor blue tit populations are ignored during long-day treatment. Based on these findings, an evolutionary explanation is provided for why the relative importance of the non-photoperiodic factors decreases with the progress of the season. The hypothesis can explain observed maladapted breeding dates in free-living populations and could possibly be used to increase the success of breeding programmes with some endangered, captive, non-domesticated, photoperiodic species.

Keywords: blue tit; *Parus caeruleus*; seasonal breeding; captive animals; avian reproduction

1. INTRODUCTION

Seasonally reproducing organisms, such as tits (*Parus* spp.), have evolved proximate responses to a series of environmental cues (photoperiod, climate and food) in order to regulate reproductive function so that their offspring are in the nest during a brief optimal breeding time (e.g. Farner 1961; Murton & Westwood 1977; Wingfield *et al.* 1992; Lambrechts *et al.* 1997; Visser & Lambrechts 1999). In addition, breeding is often inhibited by factors reflecting energetic constraints, such as food abundance, ambient temperature or stress (e.g. Perrins 1970; Clamens & Isenmann 1989; Nager & Van Noordwijk 1995; Silverin 1995; Svensson & Nilsson 1995). Theory predicts that the relative importance of the photoperiodic and non-photoperiodic information used in the regulation of reproductive function changes with latitude and environmental predictability. The photoperiod will regulate reproductive function at high latitudes where the optimal breeding time is highly predictable across years. Photoperiodic in combination with non-photoperiodic factors will regulate reproductive function at lower latitudes where the optimal breeding time is less predictable across years (Cohen 1967; Wingfield *et al.* 1992; Maney *et al.* 1999).

Endocrinological work has contributed much to the construction of a theoretical framework concerning the proximate factors used as predictive information in the timing of reproduction (Wingfield 1980; Wingfield *et al.* 1992; Wingfield & Farner 1993; Sharp 1996). In this context, the relative importance of the photoperiodic and non-photoperiodic factors influencing later stages of the breeding time, such as the onset of egg laying, has rarely been examined experimentally in non-domesticated,

avian species. Ovulation has always been difficult to obtain with captive, non-domesticated, avian species held in standardized indoor conditions, complicating studies of reproduction and breeding programmes for many years (e.g. Kendeigh 1941; Wingfield & Farner 1980; Silverin & Westin 1995; but see, for example, Meijer & Schwabl 1989; Meijer & Langer 1995; Gwinner 1996). Photoperiodic blue tits (*Parus caeruleus*) are one of the rare, non-domesticated birds which can breed with success in captivity using an experimental design with captive populations held in outdoor conditions at similar latitudes and altitudes to the wild populations (Lambrechts *et al.* 1996, 1997, 1999). Unexpectedly, the breeding time of captive outdoor populations does not always match the breeding time of their wild counterparts (Lambrechts *et al.* 1999). In a six-year experiment with independent samples, three study populations of blue tits (mainland southern France, Corsica-Pirio and Corsica-Muro) showed pronounced, consistent differences in their expression of natural behaviour in captivity (Blondel *et al.* 1999; Lambrechts *et al.* 1999). The large differences in the onset of egg laying between the mainland blue tits adapted to a broad-leaved, deciduous habitat and Corsica-Pirio blue tits adapted to an evergreen habitat were attributed to genetic differences in photoresponsiveness during shorter days (Lambrechts *et al.* 1996, 1997). In contrast to the other two study populations, the third, captive, Corsica-Muro population built nests and laid eggs 1.5 months after their wild counterparts adapted to a broad-leaved deciduous habitat (Lambrechts *et al.* 1999), with average laying dates never reported in free-living populations. The very late average breeding time of the captive, Corsica-Muro population could be described as abnormal in the sense that much longer days are required for breeding and can only be attributed to non-photoperiodic

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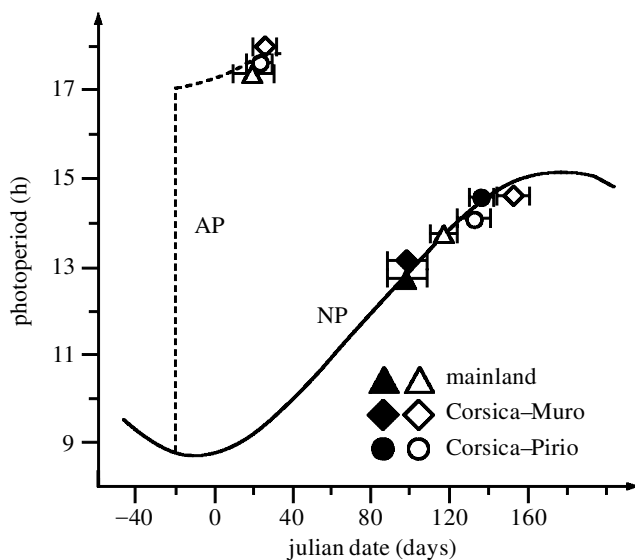


Figure 1. Onset of egg laying (average standard deviation in Julian dates; 1 January = 1 and 1 February = 32) of wild, optimal-habitat blue tits (filled symbols) and captive, outdoor blue tits (open symbols) from three French Mediterranean study sites exposed to two light treatments (natural period (NP) versus artificial period (AP)).

factors retarding their breeding time in captivity (Lambrechts *et al.* 1999).

Here we demonstrate experimentally that the three, captive, blue tit populations exposed to long-day treatment lay eggs at similar dates. During the long-day treatment, blue tits ignored the non-photoperiodic factors responsible for large population differences in the expression of natural behaviour in captivity during shorter days. Based on these findings, a new evolutionary view is presented for why the relative importance of the photoperiodic and non-photoperiodic factors influencing egg laying dates changes with the progress of the season, which also explains maladapted breeding responses in the wild. Long-day treatment could possibly force photoperiodic zoo and/or captive animals to ignore the non-photoperiodic factors causing unnatural breeding responses in captivity.

2. MATERIAL AND METHODS

Captive, outdoor blue tits from all three populations were presented with food *ad libitum* and two light treatments, i.e. a natural increase in day length (natural period (NP), 1986–1998) versus a sudden exposure to long days from 14 December onwards in the same aviaries (artificial period (AP), December 1992 and 1998) (figure 1). All the protocols and methods used are described in detail in Lambrechts *et al.* (1996, 1997, 1999). The samples included data used in former publications (see Lambrechts *et al.* 1997, 1999) and additional breeding data gathered in 1999. All birds exposed to the long-day treatment were at least one year in captivity under natural photoperiodic conditions so that their photoperiodic history (e.g. Sharp 1984) was similar for all the birds tested. Because of the high annual repeatability of individual and average laying dates in captivity, data from different years were combined (cf. Lambrechts *et al.* 1996, 1997). As in former analyses, the effects of light treatment (NP versus AP) and population (mainland versus Muro versus Pirio) and their interactions

on the onset of nest construction and egg laying were tested using two-way ANOVAs (SAS Institute, Inc. 1989)

3. RESULTS

During the long-day treatment, the birds were exposed to photoperiods exceeding those which trigger reproduction in the wild (cf. Lambrechts *et al.* 1996, 1997). If the breeding time with long-day treatment were to be determined proximately by photoperiod in combination with other non-photoperiodic factors, such as stress, food or climate, we would predict winter breeding in all three study populations and that the large differences in breeding time observed during natural days would be preserved with long-day treatment. However, if the average breeding time were to be determined proximately by photoperiod only during the long day-treatment, we would predict similar average winter breeding times for all three study populations.

The results clearly supported the second prediction (figure 1). The three, captive populations exposed to the artificially long photoperiods bred at least three months before the wild and captive populations treated with natural days. The onset of nest building ($F_{1,52} = 1201$ and $p < 0.0001$) and egg laying ($F_{1,46} = 3257$ and $p < 0.0001$) differed highly significantly between the two treatments (NP versus AP). The effects of the interaction between treatment (NP versus AP) and population (mainland versus Muro versus Pirio) on the onset of nest building ($F_{2,52} = 8.12$ and $p < 0.001$) and egg laying ($F_{2,46} = 11.82$ and $p < 0.0001$) were highly significant. All three captive populations had similar nest-construction ($F_{2,16} = 1.19$ and $p > 0.10$) and egg-laying ($F_{2,15} = 1.64$ and $p > 0.10$) dates during the long-day treatment.

4. DISCUSSION

Our aviary experiments with natural and artificial days demonstrated that blue tits are photoperiodic and that the non-photoperiodic factors responsible for the large between-population differences during natural days are ignored during long-day treatment. Our three, captive, outdoor, blue tit populations exposed to artificially long photoperiods started nest building and egg laying at least three months before the captive and wild populations in natural outdoor conditions. Furthermore, breeding was triggered five to six weeks after the start of artificial photostimulation, which is a shorter period than the seven- to eight-week time interval between the start of rapid gonad development and egg laying reported in wild tits (Lebeurier & Rapine 1944; Silverin *et al.* 1989). We obtained winter breeding despite low ambient temperatures (see Lambrechts *et al.* 1997). Thus, the unfavourable climatic conditions did not inhibit breeding during long-day treatment. In addition, our blue tit populations showed large and consistent differences in breeding time with natural days and bred at the same time when suddenly exposed to long days. This has been shown in tits exposed to artificially long photoperiods with natural winter temperatures (Lambrechts *et al.* 1997; this study) and natural long photoperiods with natural summer temperatures (Lambrechts *et al.* 1997).

Our captive outdoor Muro study population exposed to natural days displayed abnormally late breeding in the sense that these breeding dates were never reported in Mediterranean tits. Captives from Muro started breeding more than 1.5 months after their natural counterparts. However, they behaved normally, that is like the other two populations, when exposed to a long-day treatment. Thus, if the bad reproductive performance of the captive Muro population results from population-specific, behavioural problems in coping with an artificial environment (Dawkins 1998; Lambrechts *et al.* 1999), long-day treatment could be a way of forcing blue tits to ignore the factors which trigger these behavioural responses in captivity.

Within a season, parents of late broods produce fewer offspring than parents of early broods (e.g. Dias & Blondel 1996; Verboven & Visser 1998). Late reproduction may therefore increase their fitness costs. However, a late onset of reproduction, that is with a longer photoperiod late in the season, may be adaptive, for instance when few breeding opportunities are available in the following breeding season. Late breeding can happen in late-arriving individuals after migration or in floaters which suddenly acquire a territory (e.g. Lambrechts & Dhondt 1988; Verboven & Visser 1998). In some free-living, blue tit populations, late breeders start egg laying with days exceeding 17 h of light (B. Silverin, personal communication). Based on our findings with captive blue tits, we hypothesize here that, at the adaptive level, the relative importance of the photoperiodic and non-photoperiodic factors influencing the observed breeding time changes within a year as the season progresses. Late-reproducing individuals in a population should proximately use photoperiodic information only because of two potential reasons. First, the adaptive fine-tuning mechanisms and non-photoperiodic factors (see §1) influencing early breeding are not required for late breeding. A response mechanism should therefore be available which allows reproduction in the absence of non-photoperiodic factors. Second, a long photoperiod as an overriding factor perhaps speeds up the reproductive cycle thereby reducing the potential fitness costs associated with a late reproductive attempt. The long-day treatment we used could therefore be considered as a simulation where photoperiodic organisms are suddenly exposed to an advanced breeding season during which non-photoperiodic factors are not used to time reproduction.

A long photoperiod as an overriding factor in the timing of reproduction could explain the maladapted breeding responses of mainland blue tits adapted to an early, broad-leaved, deciduous, oak woodland and breeding in man-introduced, late, evergreen, oak woodland. In southern France, mainland blue tits are confronted with habitat mosaics constituted of both broad-leaved, deciduous and evergreen, oak woodland patches (e.g. Blondel *et al.* 1993; Dias & Blondel 1996; Lambrechts *et al.* 1997). Gene flow between the different woodland types exists (Dias *et al.* 1996). The optimal breeding time, which lasts three weeks, occurs at most one month earlier in broad-leaved, deciduous than in evergreen woodlands (Dias & Blondel 1996; Blondel *et al.* 1999). Mainland blue tits match the brief optimal breeding time in deciduous habitat nicely, but breed in evergreen habitat at least three weeks before the short local optimal breeding time (Dias

& Blondel 1996; Lambrechts *et al.* 1997). Our proximate explanation is that a long photoperiod as an overriding factor is only adapted to deciduous habitat with a short optimal breeding time early in the season. It explains why mainland, evergreen blue tits start reproduction well before the occurrence of the non-photoperiodic cues (e.g. bud burst) (Wingfield 1980; Blondel *et al.* 1993) proximately required to anticipate the late optimal breeding time in evergreen habitat. At the ultimate level, it assumes that landscapes which are dominated by broad-leaved, deciduous habitat and not the local habitat selected the response mechanism (see also Lambrechts *et al.* 1997; Visser & Lambrechts 1999).

Our adaptive explanation also predicts that long-day treatment simulating a late season can help to stimulate reproduction in some photoperiodic, captive and/or zoo animals having problems with breeding. This is because a long-day treatment would proximately force animals to become insensitive to non-photoperiodic factors including captivity stress during shorter days. We therefore do not exclude the possibility that long-day treatment could be a way of increasing the success of breeding programmes with at least some endangered, non-domesticated, photoperiodic animals.

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