# Timing of Hatching and Indirect Selection on Body Size — the Impact of Bad Weather on the Great Tit Parus major in Niepołomice Forest (S Poland)

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# Timing of hatching and indirect selection on body size — the impact of bad weather on the Great Tit *Parus major* in Niepołomice Forest (S Poland)

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**Zając T. 2002. Timing of hatching and indirect selection on body size — the impact of bad weather on the Great Tit *Parus major* in Niepołomice Forest (S Poland). Acta Ornithol. 37: 107–112.**

**Abstract.** This paper reports on the case of selection, due to influence of bad weather on nestling number, acting through different pathways on breeding date and morphological traits in breeding Great Tits. Multiple regression of relative fitness on tarsus length, bill height and forearm length, revealed significant phenotypic selection on male forearm length and female bill height. However, nestling mortality during the bad weather depended on their age, which suggested breeding date as a focal trait for selection. The multiple regression analysis of relative fitness on both body traits and hatching date shows that in males only breeding date was significantly related to fitness, and selection on forearm resulted from correlation of forearm with hatching date. A similar analysis in females shows that both bill height and timing of hatching were equally related to fitness, therefore in this sex both bill height and date of hatching were focal traits for selection.

**Key words:** Great Tit, *Parus major*, phenotypic selection, breeding date, body size

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## INTRODUCTION

Although timing of breeding in birds attracted attention of biologists a long time ago (e.g. Darwin 1913, Fisher 1958), it still brings new areas of interest. A possibility that selection on the breeding date (behavioural trait) may influence evolution of other phenotypic (e.g. morphological) traits, correlated with the breeding date, seems particularly interesting. The problem of such indirect selection, often acting through different pathways, appears to be crucial for explaining significant phenotypic selection cases, occurring together with significant heritability, which did not lead to significant response to selection (e.g. van Noodrwijk et al. 1988, Price et al. 1988, Alatalo et al. 1990).

Few examples have been found where selection outcome depended either on its direct impact on focal trait or on its influence through other traits, through different pathways of selection. The best example comes from Price et al. (1988), who found, that if good nutrition of female, which is a non-heritable trait depending on environment, for instance caused by artificial feeding, simultaneously caused earlier breeding and higher fitness, an apparent negative selection on breeding date was observed. Such a selection brings no evolutionary response, because it acts on a purely environmental trait, correlated, however, both with breeding date and with fitness (Fig. 1A). Price & Liou (1989) or Hőrak et al. (1997) also applied a similar approach to apparent selection on other reproductive traits, whereas Sheldon & Ellegren (1999) used path analysis to partition selection on morphological traits into pathways via female fecundity and male sperm competition.

The selection case described here occurred during a short spell of an extremely bad weather, which resulted in high variance of young numbers, which in turn was related both with parents' body size and their timing of breeding. If body size of parents gives any advantage during the spell of bad weather, then observed selection on morphological traits will be direct. However, if the individuals with larger body size breed earlier (which

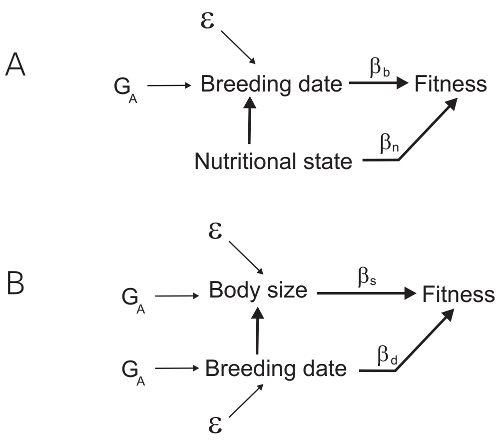

Fig. 1. Two models of relationships between interacting traits and fitness: A — fitness, breeding date and environmentally determined nutritional state during apparent selection, B — fitness and two likely focal traits: body size and breeding date. $\beta_b$ — direct selection on the breeding date, $\beta_n$ — indirect selective force generated by correlation of nutritional state, both with fitness and with breeding date, $\beta_s$ — direct effect of body size on fitness, $\beta_d$ — indirect selective force generated by correlation of breeding date both with fitness and with body size, $G_A$ — additive genetic component, ε — residual nonadditive effect (modified after Price et al. 1988).

might be expected — Krebs 1971, Dhondt et al. 1979, Lemel 1989) and their breeding success is also related to time, then significant indirect relation between body size and fitness should be recorded due to correlation of both body size and fitness to timing of breeding (Fig. 1B). These two options, namely direct vs. indirect selection, were tested in this paper in order to show whether selection may act through separate pathways, influencing body size through a behavioural feature.

## MATERIAL AND METHODS

The study was conducted in "Grobelczyk" — a small, isolated part of the Niepołomice Forest (southern Poland, 20°25′E, 50°08′N) in 1991–1993. Grobelczyk is an 250 ha area of natural deciduous forest, with tree stands of various ages: ranging from small patches of very young stands, to large areas of old-growth forest. The predominant tree species are oak *Quercus robur,* hornbeam *Carpinus betulus* and linden *Tilia cordata.*

The study area comprised 250 nestboxes, placed in the winter 1991. The nest boxes were regularly inspected during the breeding season to determine egg laying date, clutch size, hatching date, number of hatched young and number of fledgings in 13th day after hatching. For three nests the exact hatching date was unknown, thus the sample size is smaller.

Meteorological data were collected by the State Institute of Meteorology and Water Management at the Łazy station, the nearest to the study area (15 km from Grobelczyk). On 17–19 May 1991, when most of the pairs were feeding nestlings, a spell of exceptionally bad weather occurred. During this period inspections of nest boxes were abandoned in order to avoid extra risk to broods and birds. The following week, the nest boxes were additionally inspected to determine mortality of the broods. As a measure of parents' fitness, the number of their nestlings on the 13th day after hatching was used.

### Morphometrics

All females of Great Tits breeding in the study plot (n = 27) were caught, inside the nestbox, during incubation. Their mates were caught in wire traps (which allows a bird to enter a nest box but it prevents the bird from leaving) during nestlings feeding. In order to enable the broods recovery after bad weather catching males were postponed for about a week, which resulted in lower number of caught males. Seven males were not caught due to their absence or very low feeding activity. Adults were ringed, aged, sexed and measured (Svensson 1992). Three morphological measurements were taken: tarsus length which represents pedal locomotor apparatus, was measured from the notch on the back of intertarsal joint to the lower edge of tarsus at the base of toes with accuracy of 0.1 mm; forearm length, which represents flight apparatus, was measured from outer end of radius to inner end of ulna, with 0.1 mm accuracy and bill height, representing feeding apparatus, was measured at the fore edge of the nostrils, with 0.1 mm accuracy. Some traits measured in adults were intercorrelated: in males forearm length was correlated with tarsus length ($r = 0.77$, $n = 20$, $p < 0.001$) and with bill height ($r = 0.47$, $n = 20$, $p = 0.04$); in females only forearm length correlated with tarsus length ($r = 0.50$, $n = 27$, $p = 0.01$). The repeatabilities of measurements for the characters were calculated after Harper (1994), according to the formula:

$$R = \frac{B-W}{B+(N-1)W}$$

where B — the variance between individuals, W — the within individuals variance. For this analysis, I used a set of data from the winters and breeding seasons of 1991–1993 (unpubl. data). The data set contains individuals, which were measured at least twice within less than 3 weeks. The repeatability was the highest for tarsus length ($R = 0.98$, $n = 49$, $p < 0.001$), similarly, it was very high for forearm length ($R = 0.95$, $n = 47$, $p < 0.001$), whereas it was lower for bill height ($R = 0.66$, $n = 60$, $p < 0.001$). None of the characters change significantly with age; they were not affected by wear either (own unpubl. data).

### Selection analysis

After the spell of the bad weather, selection on body characters of adults was analysed. Relative fitness of an adult was estimated as the number of its fledglings which survived to the 13th day after hatching, divided by mean number of young at this age in all studied broods (Arnold & Wade 1984 a, b). The relative fitness and hatching date were transformed into natural logarithms to eliminate skewness.

The presence of a direct relationship between body size and relative fitness was explicitly tested by multiple regression, calculating selection gradients (Endler 1986). A possible influence of hatching date was also tested with multiple regression; this allowed to find out, which of the theoretically possible pathways of selection occurred (Fig. 1B). The path analysis was not used due to low sample size (Conner 1996). When the first path is valid ($\beta_s$ in Fig. 1B), then multiple regression of relative fitness, as a dependent variable, on the rest of variables (morphological traits and hatching date) will show significant relation exclusively between fitness and body traits, with nonsignificant relation with hatching date. When the other model is valid ($\beta_d$ in Fig. 1B), then multiple regression will show no relation between fitness and body traits, whereas it will show significant relation between fitness and hatching date. The co-occurrence of both models is also possible, when body traits will show significant direct relation with fitness and, at the same time, another route will relate fitness with hatching date.

## RESULTS

### Weather conditions and breeding success

Mean date of the first egg laying was 21 April (SD = 4.06, n = 27), with mean clutch size 9.9 eggs (SD = 1.1, n = 27) and mean hatching date 15 May (SD = 3.99, n = 24). Within three days (17–19 May 1991), mean noon temperature decreased to 10.5°C (11.1, 12.0, 8.3°C, respectively; min. temperature dropped to 6°C) with an intensive rain all day (15.7, 37.9, 30.7 mm, respectively; mean 28.1 per day, total 84.3 mm, ca 75% of the month total). The bad weather struck likewise the whole area of southern Poland. In the following days, the weather improved gradually.

The spell of bad weather occurred when 21 nests had hatched (the mean age of nestlings was 5.5 days, SD = 2.01, n = 19) and remaining 6 nests contained eggs. An inspection of the nestboxes in week following the bad weather revealed 11 dead broods. The mean number of dead nestlings was 6.3 (SD = 3.4) per nest, with a maximum of 11 young. The coefficient of variation for the number of nestlings still alive was very high (CV = 40%). Comparison of age between the dead and the live nestlings indicated that the nestlings had died a few days earlier, due to the bad weather. There were only 2 nests in which all nestlings survived; both clutches hatched after the bad weather (on 21 May).

A strong positive relationship was recorded between hatching date and nestling number at the 13th day of life ($r_S = 0.63$, $n = 24$, $p = 0.002$, Fig. 2). The last brood that hatched (on 45th day in the Fig. 2), had low nestling number, due to very low hatching success — the nest contained as many as 7 unhatched eggs.

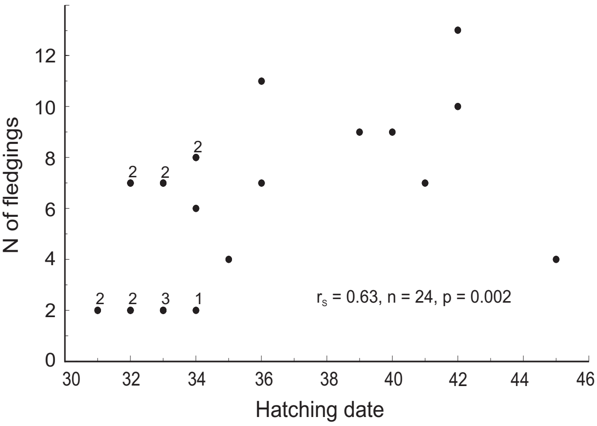

Fig. 2. Relationship between the number of fledglings and hatching date. Points replication indicated by numbers. Day 30 = 10 May, day 46 = 26 May.

### Selection on body size of parents

The direct relationship between measured morphological traits and fitness was analysed by multiple regression (model 1 in Table 1). In males, a strong negative relationship between relative fitness and forearm length was recorded, whereas in females there was a strong negative relationship between relative fitness and bill height.

Male forearm length and female bill height, which were related to fitness in above analysis, also correlated significantly with hatching date ($r_S = -0.70$, $n = 20$, $p = 0.0006$, Fig. 3A and $r_S = -0.41$, $n = 24$, $p = 0.048$, Fig. 3B, respectively).

Table 1. Selection on body size and timing of breeding: Model 1 — results of multiple regression of relative fitness (number of young per nest divided by population mean) on three morphological traits of adults, Model 2 — results of multiple regression of relative fitness on three morphological traits of adults and hatching date of their nestlings. b — raw multiple regression coefficients, reflecting selection gradients (β); relative fitness and hatching dates were transformed into natural logarithms.

| Fitness vs | Males (n = 20) | | | Females (n = 20) | | |
|---|---|---|---|---|---|---|
| | b | t | p | b | t | p |
| Model 1 | | | | | | |
| Tarsus length | 0.08 | 0.28 | 0.276 | -0.24 | 1.33 | 0.197 |
| Bill height | 0.39 | 1.84 | 0.084 | -0.53 | 3.12 | 0.005 |
| Forearm length | -0.80 | 2.64 | 0.018 | 0.10 | 0.53 | 0.598 |
| Model 2 | | | | | | |
| Tarsus length | 0.12 | 0.45 | 0.656 | -0.12 | 0.60 | 0.553 |
| Bill height | 0.22 | 1.12 | 0.282 | -0.42 | 2.38 | 0.028 |
| Forearm length | -0.47 | 1.59 | 0.133 | 0.06 | 0.31 | 0.762 |
| Hatching date | 0.51 | 2.49 | 0.025 | 0.44 | 2.50 | 0.022 |

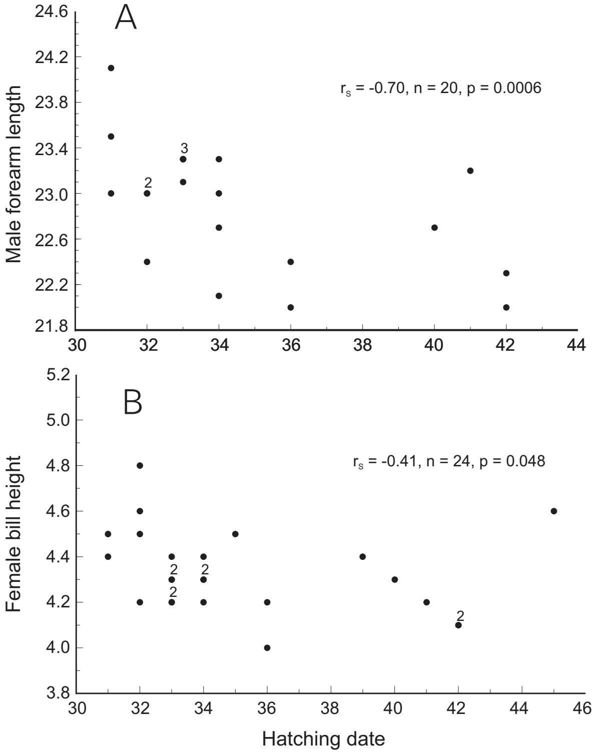

Fig. 3. Relationship between selected body traits of adults and hatching date: A — male forearm length, and B — female bill height; hatching dates — see Fig. 2.

In order to disentangle possible influence of breeding date, multiple regression analysis for fitness, as a dependent variable, and three morphological traits with hatching date, as independent variables was done. It revealed that there was a significant relationship between fitness and hatching date and no significant relation of fitness with body traits in males (model 2 in Table 1). In females, a similar multiple regression analysis showed a significant relationship between fitness and bill height, as well as a significant relationship between fitness and hatching date (model 2 in Table 1).

## DISCUSSION

Two pathways of selection were found in females — the relative fitness was equally related both to bill height and to breeding date. In males, there was only one pathway of selection — the number of fledglings was related to breeding date, whereas selection on forearm length was apparent — it appeared as a consequence of correlation between forearm length and timing of breeding. This indicates, that although morphology can determine behavioural trait — decision to start breeding — the selection influenced mainly behaviour, influencing indirectly morphological trait in males, and partly indirectly, partly directly, morphological trait in females.

In the direct test of selection on body traits with multiple regression, the value of selection coefficient for the male forearm was very high (*b* = -0.80, model 1 in Table 1), whereas in the similar analysis controlled for the breeding date (model 2 in Table 1) the *b* value is lowered by half and does not even reach statistical significance. In females, the second analysis brings considerably smaller decrease in selection coefficient for morphological trait, in comparison to males. This decrease of selection coefficient reflects the degree of indirect selection, which was much smaller in females.

The most probable proximal mechanism of selection were extremely bad conditions for foraging of adults, due to the spell of bad weather (Zając 1995, 1999). Pouring rain washed down outbreaks of caterpillars (mainly oak leaf roller moth *Tortrix viridana* L.). Such outbreaks occur in the Niepołomice Forest yearly, reaching the maximum standing crop in mid-May (Bandoła-Ciołczyk & Witkowski 1976). At the same time, metabolic costs of both nestlings and adults increased, due to low ambient temperature. The weather caused higher mortality among the most advanced, early broods (Fig. 2), because at that time they had the highest absolute energy demands (the highest body mass, development of thermoregulation with poor thermal isolation caused by poor development of feathers — Mertens

1977, Zając 1995). The bad weather had the least impact on the late, youngest broods (incubated or brooded by females). The relation between degree of mortality and nestlings age is responsible for linkage between mortality and timing of breeding — earlier broods were older. Breeding date, in turn, was related to body size — leading in this way to selection on morphology through behavioural trait.

The earlier breeding seems advantageous in usual conditions, when breeding success declines with time within the season (Perrins & McCleery 1989, Hochachka 1990, Verhulst & Tinbergen 1991, Rowe et al. 1994, Wiggins et al. 1994, but see Cichoń & Linden 1995). In such conditions it might be expected that males with longer forearms win conflicts for the best territories and breed early, reaching the highest breeding success. However, in 1991 this mechanism was fatally unmatched to environmental conditions. Probably body size of males could be important in conflicts for restricted resources in winter (Gosler 1987) or for nest sites (Dhondt et al. 1979), both of which could influence timing of breeding. Yet, during the nestling feeding in poor foraging conditions, body size appears to be unimportant.

In females, the relative fitness depends both on breeding date and on size of morphological trait of particular individuals. Contrary to males, female morphology influenced breeding success. As bill height was selected in females, not in males, probably it must have been related with exclusively female function. Taking into account that the nestlings from late broods survived better, probably the relation between bill height and brooding of young was responsible for nestling survival. Morse (1974) suggested that subdominant species should be opportunists, generalising their foraging within a relatively broad niche. If this way of reasoning can be applied to competition between individuals within the species, than it should be expected that subordinated individuals should have less effective, broad foraging niche. Great Tits with higher bills are better off during the winter (Gosler 1987), which suggests that birds with smaller bills should have relatively subordinate social position and broad foraging niche. It may be suspected that during the spell of bad weather, in unusual foraging conditions, broad niche of females with smaller bills enabled them to use more diversified foraging sites, when the main source of food was destroyed; this resulted in higher foraging success. This, in turn, probably enabled females to spend more time on brooding young, thereby protecting them against adverse ambient temperature and loss of energy. Similarly, Grant & Grant (1993) report on the advantage of small bill size for Darwin's finches, when a rare climatic event destroyed the most common food type, to which large-billed individuals were adapted. This way of reasoning suggest again, that morphological trait — bill height — was also selected in close relation with behaviour (foraging and incubating).

The data presented in this paper imply that morphology of individuals might be related to current selection although it may act indirectly, i.e. through behavioural traits. The changes caused by such a selection might be ascribed to causal agents. The case of apparent selection in males shows that the precise estimation of selection strength requires a very broad approach in fieldwork and in analysis (Conner 1996), which ensures the reliable identification of focal traits for selection, and consequently, a proper understanding of relations between behaviour and morphology in terms of current selection pressures.

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## STRESZCZENIE

### [Terminy klucia i pośredni dobór na wielkość ciała — wpływ złej pogody na bogatki w Puszczy Niepołomickiej]

Praca jest szczegółową analizą przypadku niezwykle silnego doboru fenotypowego na wielkość ciała sikor bogatek, który wystąpił w 1991 r., w populacji zamieszkującej skrzynki lęgowe w Puszczy Niepołomickiej.

Jak dotąd, badania mechanizmu działania doboru naturalnego sugerowały istnienie „ścieżek doboru" czyli działania doboru nie tylko wprost na daną cechę, ale również przez interakcje z cechami skorelowanymi. Istnienie takich ścieżek doboru wyjaśniałoby przypadki silnego doboru fenotypowego, który pomimo istotnego stopnia odziedziczalności cech na które działał, nie prowadził do istotnej reakcji na ten dobór w następnych pokoleniach. Najlepszym przykładem tego rodzaju doboru jest stwierdzony przez Price et al. (1988) wpływ kondycji samicy (cechy ściśle środowiskowej, wynikającej ze sztucznego dokarmiania) na datę lęgów i dostosowanie. Ponieważ dobra kondycja samicy powodowała zarówno wzrost dostosowania, jak i wcześniejszą gotowość do lęgów, obserwowano związek daty lęgów z dostosowaniem, podczas gdy w rzeczywistości zależność ta miała pośredni charakter i nie miała podłoża genetycznego (Fig. 1A).

W niniejszej pracy analizowano przypadek związku wielkości ciała sikor bogatek ze zmiennością liczby młodych (Fig. 3A i B), powstałą po okresie bardzo złej pogody. Jeżeli wielkość ciała miała związek z przeżywaniem młodych w czasie złej pogody, to zależność ta będzie miała charakter bezpośredni. Wiadomo jednak, że śmiertelność młodych była związana z czasem przystępowania do lęgów (Fig. 2). Jeżeli również wielkość ciała rodziców wykazuje związek z terminem lęgów, to obserwowany dobór na wielkość ciała może wynikać ze skorelowania zarówno dostosowania, jak i wielkości ciała z jedną zmienną — czasem przystępowania do lęgów (Fig. 1B).

Regresje wielokrotne dostosowania ptaków dorosłych, wyrażonego liczbą młodych, względem trzech podstawowych wymiarów ciała (długości skoku, wysokości dzioba i długości przedramienia) wykazały istotny dobór fenotypowy na wysokość dzioba u samic i długość przedramienia u samców (Tab. 1). Analogiczna regresja wielokrotna powtórzona z uwzględnieniem daty klucia się młodych jako dodatkowej zmiennej wykazała (Tab. 1), że u samców tylko data klucia jest istotnie powiązana z dostosowaniem, a dobór na długość przedramienia staje się nieistotny — zatem musiał być wynikiem skorelowania zarówno wielkości ciała, jak i dostosowania ze wspólną zmienną — czasem klucia się młodych. Podobna analiza u samic (Tab. 1) wykazuje, że zarówno wysokość dzioba, jak i data klucia były jednakowo powiązane z dostosowaniem, stąd można wnosić, że u samic obydwie te cechy były obiektem bezpośredniego działania doboru.