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Selection on laying date in the Blue Tit *Parus caeruleus* and the Great Tit *Parus major* caused by weather conditions

Zajac T. 1995. Selection on laying date in the Blue Tit *Parus caeruleus* and the Great Tit *Parus major* caused by weather conditions. *Acta orn.* 30: 145–151.

Abstract: Three days of heavy rain (15.7, 37.9, 30.7 mm) and low temperature (min. temp. 5.7°C) during the breeding season 1991 caused high brood mortality in the Great Tit (GT) and the Blue Tit (BT), depending on brood advancement — in both species broods which died were older. In GT the mean advancement of dying broods was 5.29 days since hatching, while that of surviving ones 0.54 ($P = 0.0005$). In BT the advancement of broods which died was 7.82 and that of broods which survived — 1.71 ($P = 0.0004$). The mortality was higher in BT than in GT, the former started breeding 4 days earlier on average (mean time of 1st egg laying in BT was 8.09 days, for GT was 11.96 days ($P < 0.0006$)). The calculated standardized selection differentials show very strong selection on the timing of breeding both in GT ($i_{GT} = 0.366$, $P = 0.042$) and BT ($i_{BT} = 1.059$, $P = 0.0003$).

The higher absolute energy demands of older broods in view of limited food resources and vulnerability of young to hypothermia seem to be proximate cause of the mortality in both species. The selection resulted in almost the unification of the time of breeding in both species. The strength of this selection implies that weather could be one of the most important factors determining the timing of breeding.

Key words: Great Tit *Parus major*, Blue Tit *Parus caeruleus*, nestling mortality, breeding biology, timing of broods

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Received — Jan 1995, accepted — July 1995

INTRODUCTION

The timing of breeding is considered as an important factor determining the breeding success in birds (Perrins 1979). It is widely accepted that breeding phenology is adapted to fit the most favorable food conditions in the area (Lack 1954, Lack 1968). This relation is supposed to be a result of weather conditions, but also weather may influence directly both timing of breeding (Nager 1993) and breeding success (e.g. Sasvari & Hegyi 1993, author's data), or finally all these factors may influence breeding success together in relation to time, thus causing selection on the timing of breeding.

Two weather factors, low temperature and rain, are crucial for breeding success by direct (1) and indirect (2) impact:

1) low temperature increase metabolism in homeothermic animals, the cooling effect of low temperature is increased by rain, which raise the moisture of air,

2) low temperature diminishes insects availability by lowering their activity, rain washes away caterpillars from leaves (Szujewski 1980).

The above factors should have a lesser impact on adults which can thermoregulate and look for shelter and food, but these factors should influence young which are vulnerable to hypothermia and depend on extra abundance of food.

If climatic conditions cause selection on the timing of breeding, then an extreme climatic conditions should have a pronounced effect on fitness. The effect should not be random but lead to selection on the timing of breeding. The recent techniques of measuring natural selection in the wild (Endler 1986 for their review) enable to assess a shift in the selected trait (laying date) and to compare selection intensity between species. Such measurements give opportunity to estimate the strength of selection acting in the wild. Due to their extremity these weather conditions give also a clear picture of proximate mechanisms, which selection acts through.

METHODS

In the period 1991–1993 I studied the titmice ecology in the oak-hornbeam deciduous forest named "Grobelczyk" (ca 250ha) where about 400 nest boxes were placed. The area is a part of the Niepołomice Forest (50°68'N, 20°25'E) near Cracow (Kraków) in Southern Poland. Nest boxes were occupied by only two species: the Great Tit and the Blue Tit.

It was an opportunity to test the influence of weather conditions on breeding success directly by observing the results of "natural experiment" that happened in 1991. On 17,18 and 19 May it was cold (mean maximum temperature: 10.5°C, mean minimum daily temperature: 5.7°C) and wet (respectively: 15.7, 37.9, 30.7 mm of daily rain). These values were rather extreme, as shown by the distribution of temperature and precipitation on 17, 18 and 19 of May for 20 years between 1961–1981 (Fig. 1).

On the following days the weather improved. Between 20 and 26 May all the occupied nest boxes were inspected to determine brood mortality. The exact age of broods in the time of the worst weather (assumed as 19 May) was determined as the number of days since the observed laying date of the first egg (in the case of broods with eggs). Age of nestlings on 19 May was determined from the observed hatching date. The term "brood advancement", used in the text, means the number of days since laying the first egg in a given nest, and this measure refers to the nests both with eggs and nestlings. "Brood age" means the age of

nestlings, measured in days since the hatching date — this measure refers only to nests with young.

The calculations of the body weight and metabolism of nestlings were based on their average age, using equations of Mertens (1977). Because the equations were originally constructed for the Great Tit, body weights of Blue Tit nestlings, calculated on the basis of their age, were corrected by the value 0.657, equal to the ratio of the average body weight of Blue Tit young to the average body weight of Great Tit, measured in both species on 13th day of young life.

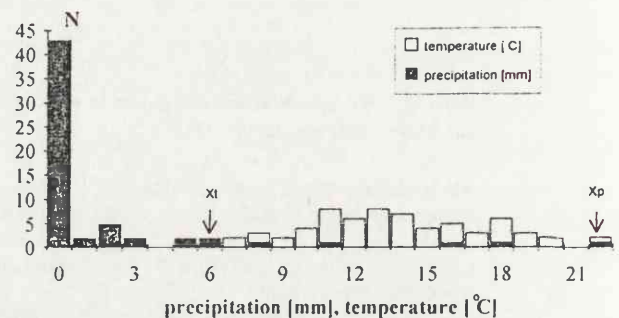


Fig. 1. Distribution (N — number of days) of minimal temperature (t) and daily precipitation (p) in the period 17–19 May 1961–1981. x_t and x_p — mean p and t values for the period of 20 years considered.

[Ryc. 1. Rozkład (N — liczba dni) minimalnej temperatury (t) i dobowych opadów deszczu (p) dla okresu 17–19 maja 1961–1981 x_t i x_p — średnie wartości p i t dla okresu 20 lat.]

Directional selection differential — "S" (Arnold & Wade 1984a,b) is a relation between the value of a selected trait and relative fitness. As the measure of relative fitness I used the number of fledglings from a given breeding attempt divided by the mean number of fledglings for all considered breeding attempts. Directional selection differential ("S", the difference in the character means before and after selection) was calculated as the covariance between relative fitness and laying date, the latter expressed as the number of days between the first egg in a given nest and the first egg laid in the first nest in the area (the same for both species). Directional selection differential was calculated also in standardized form ("i"), which is useful for comparisons because it measures the force of selection in units of phenotypic standard deviation (Arnold & Wade 1984a). Significance levels for this analysis are for Spearman rank correlations of relative

fitness with the character (Grant 1985) because distributions of relative fitness usually depart from normality.

RESULTS

A total of 21 broods of Great Tit died and 24 survived. The mortality in Blue Tit was much higher: 22 broods died and 14 survived. The difference between species was not statistically significant (χ -square test, $X^2 = 1.68$, d.f. = 1, $P = 0.195$, $N = 81$). Most broods which died were the earliest broods in both species (Fig. 2 and 3).

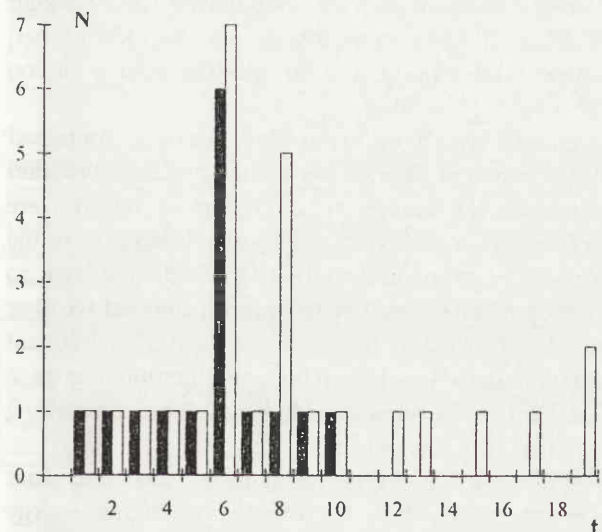


Fig. 2. Blue Tit — the number of broods which died (black bars) on the background of number of all broods (empty bars) against the time of the first egg laying, expressed as number of days since first egg laying in the first nest in population studied.

[Ryc. 2. Sikora modra — liczba martwych lęgów (czarne słupki) na tle liczby wszystkich lęgów (białe słupki) w odniesieniu do czasu złożenia pierwszego jaja, wyrażonego jako liczba dni od zniesienia pierwszego jaja w pierwszym gnieździe w badanej populacji.]

There were statistically significant differences in brood advancement between the dying and surviving broods in both species. In the Great Tit the mean advancement of broods which died was $X_d = 5.29$ ($SD = 2.327$), that of broods which survived $X_s = 0.54$ ($SD = 4.987$; Kruskal-Wallis test, $H = 11.99$, $N = 45$, $P = 0.0005$). In the Blue Tit the mean advancement of broods which died was $X_d = 7.82$ ($SD = 2.403$), while that of survivors $X_s = 1.71$ ($SD = 4.665$; Kruskal-Wallis test, $H = 14.55$, $N = 36$, $P = 0.0004$).

To find out if mortality of broods is related to only nestlings mortality (broods with eggs excluded), the age of dying and surviving broods was compared. The difference was not statistically significant in the case of Great Tit (mean age, respectively, $X_d = 5.29$, $SD = 2.327$; $X_s = 4.08$, $SD = 2.564$; $F = 2.00$, $df = 1,32$, $P = 0.17$) and highly significant in the Blue Tit (mean age, respectively, $X_d = 7.82$, $SD = 2.403$; $X_s = 4.67$, $SD = 2.599$; $F = 10.50$, $df = 1,29$, $P = 0.003$).

The higher mortality of Blue Tit broods may be a result of the earlier onset of breeding in this species. In considered year Blue Tits laid eggs on average 4 days earlier than Great Tit (mean laying time for BT: $X_{BT} = 8.09$ days, $SD = 4.673$; vs mean laying time for

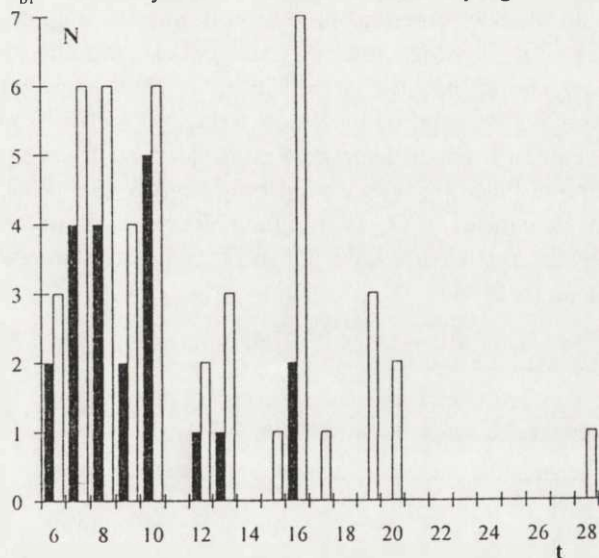


Fig. 3. Great Tit — survival of broods in relation to time. Explanations — see Fig. 2.

[Ryc. 3. Sikora bogatka — przeżywalność lęgów w zależności od czasu. Objaśnienia — patrz ryc. 2.]

GT: $X_{CT} = 11.96$, $SD = 5.060$; $F(1,85) = 12.7$, $P = 0.0006$), so generally the Blue Tits broods were more advanced at the time of bad weather.

Directional selection differential on the laying date was $S_{BT} = 4.95$, ($N = 26$, $P = 0.0003$) for the Blue Tit, and $S_{CT} = 1.86$, ($N = 37$, $P = 0.042$) for Great Tit. Standardized directional selection differential was much higher for the Blue Tit ($i = 1.059$) than for Great Tit ($i = 0.366$), which indicates much stronger selection intensity on the date of laying in the former species.

DISCUSSION

Generally, selection is rarely observed in the wild because individuals are adapted to local, typical conditions. Only if this conditions significantly depart from the norm, it is possible to notice selection towards the new optimum, so as the individuals will fit to new habitat features. If rainy and cold weather in May would become a rule, one could expect very quick selection for late breeding. Its evolutionary rate would be then the product of selection coefficient and heritability of timing of breeding (Arnold & Wade 1984 a).

The selection observed resulted in almost unification of breeding time in both species (Fig. 4.). The Blue Tit which suffered stronger selection, bred 4 days earlier than the Great Tit, but its mean time of breeding was shifted by almost 5 days ($S = 4.95$). The Great Tit bred on average 4 days later, so its mean time of breeding was moved only slightly ($S = 1.86$), the new mean for Great Tit differs by only 1 day (d_2 in Fig. 4.) instead of 4 days (d_1 in Fig. 4.) from the new mean for Blue Tit.

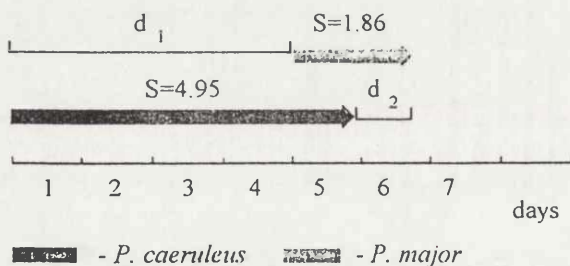


Fig. 4. Results of selection. S — value of selection differential, d_1 — the difference between the species in the onset of breeding before the selection, d_2 — the difference between the species in the onset of breeding after the selection.

[Ryc. 4. Wyniki selekcji. S — wartość różnicy selekcyjnej, d_1 — różnica między gatunkami w terminie przystępowaniu do lęgów przed selekcją, d_2 — różnica między gatunkami w terminie przystępowania do lęgów po selekcji.]

Considering weather conditions, one may speculate that there is the same optimal time for breeding for Great and Blue Tit but other factors, move the mean time of breeding of the Blue Tit to an earlier date. In this way the Blue Tit may avoid competition with Great Tit, feeding on the earlier development stages of caterpillars, which are too small for Great Tit.

There arise question about the proximate mechanisms of selection. Unfavourable weather raises

the energy requirements of homeothermic individuals by decreasing food availability and increasing heat loss. Such conditions are less likely to influence embryos in eggs that are brooded and do not need to be fed, but they affect dependent young which can survive only if their energy requirements do not exceed the amount of energy supplied by parents. The absolute energy requirements of young increase with age, due to an increase in body mass and development of thermoregulation. Young nestlings easily decrease the rate of their metabolism at lower ambient temperatures (Mertens 1977, O'Connor 1975). The higher absolute energy demands of older nestlings, are more likely to exceed the food supply during unfavorable weather. This should lead to the higher mortality of older nestlings in the periods of bad weather, and consequently to selection against the too early onset of breeding.

Broods which survived bad weather contained either incubated eggs or very small nestlings brooded by female, the energy requirements of which were very low. There were no significant differences in the mortality of young in the Great Tit which bred later, so the proportion of nests with eggs during bad weather was higher (0.375) than in the Blue Tit (0.172). In Great Tit young there was not so big age differentiation as in Blue Tit; broods were brooded by female, preventing them from the loss of heat.

When the age of only nestlings is compared, older ones are more likely to die due to higher energy demands, related to body mass. A difference in metabolism between the young which died and the young which survived can be illustrated by calculating metabolism of a model nestling, only on the basis of its age, all other things being equal. Equations published by Mertens (1977) give the maximum metabolism (q_m) of nestlings based on their age, so it is possible to calculate q_m for young classified as dying or surviving. The results (Tab. 1) show that ratio: young of dead broods age/young of surviving broods age; it was 1.6 for the Great Tit and 4.0 for the Blue Tit. The higher metabolism of older Blue Tit nestlings could lead to their death, whereas the 4 times lower metabolism of younger ones could be maintained in bad conditions. In the Blue Tit the mortality was much higher because during unfavourable weather there were many older broods, the metabolism of which exceeded the threshold value.

The costs of thermoregulation can reach 30% of the total metabolized energy (Weathers & Sullivan 1991) and must have a pronounced effect on the viability of nestlings. As nestlings grow they rise their metabolism within the broader range of ambient temperatures in order to maintain body temperature (Mertens 1977, O'Connor 1975). Younger ones lower their metabolism with ambient temperature, so female is not forced to intensify foraging in response to the raised metabolism of their progeny and it has time to warm them (Yom-Tov & Hilborn 1981). By contrast, older nestlings increase the metabolic rate with a decrease in temperature (Mertens 1977, O'Connor 1975). Females have to forage more intensively and stay longer out of the nest, so nestlings have to spend more energy for thermoregulation, which in turn causes an increase in their metabolism.

Table 1. Comparison of presumed metabolism (W=wat) of nestlings which age is equal to the average age of young which survived or died during bad weather.

[Tabela 1. Porównanie zakładanego metabolizmu (W=wat) piskląt, których wiek jest równy średniemu wiekowi młodych, które zdechły bądź przeżyły w czasie złej pogody.]

	<i>Parus major</i>		<i>Parus caeruleus</i>	
	alive	dead	alive	dead
Age (days)	4.1	5.3	4.7	7.8
Weight (g)	7.2	9.3	3.9	8.6
Maximum metabol. (W)	0.12	0.19	0.04	0.16
Ratio of metabolisms	1.56		4.0	

In this case selection through age dependent nestlings mortality caused by bad weather acts in one direction — towards the late timing of breeding (Fig. 5 A). Solid curves show the amount of food required by broods which hatched at two different dates (t_1, t_2). A dashed line shows the amount of food supply. In the case of early broods the amount of food required in the time of bad weather is higher than the food supply, which leads to the death of young. In the case of later broods the amount of food required during adverse weather is lower than the food supply; the broods survive and thus late timing of breeding is favoured. As a result the average time of hatching for the whole of population (X) moves towards the mean date of hatching of successful broods (t_2) by a value equal to the coefficient of selection (S). If the period of bad food supply lasts longer (dotted line) or repeats again, food requirements of young will exceed still small food supply.

The reverse selection acts when unfavorable weather comes too late for early broods (Fig. 5 B). In this case young are raised to independence before food supply is limited, which influence the late broods. It causes selection favouring early breeding, which brings full success, against late breeding which is maladaptive irrespective of the duration of the period of poor food supply. Finally, the average date of hatching (X) moves towards the mean date of hatching of early broods (t_1) by a value equal to the coefficient of selection (S).

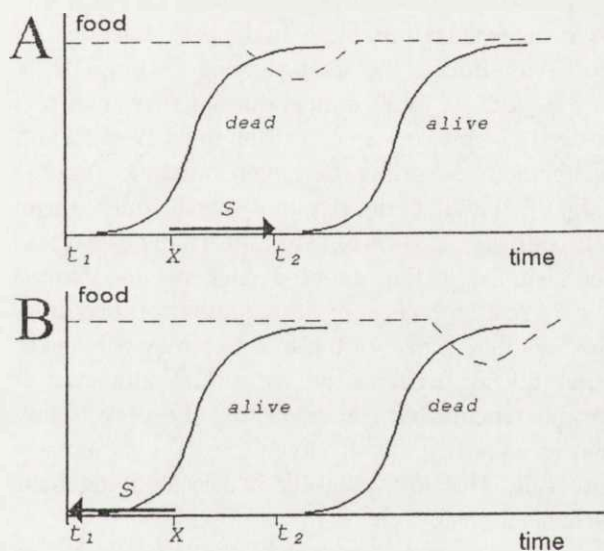


Fig. 5. Selection on breeding date: A — selection for delayed breeding B — selection for early breeding; f — level of food supply, d — prolonged period of bad food supply, c — curve of growth for brood hatched at time t_r , s — selection differential (S) value, X — mean hatching time.

[Ryc. 5. Selekcja na czas przystępowania do lęgów: A — selekcja na opóźnienie lęgów, B — selekcja na wczesne gnieźdzenie się; f — poziom dostępnego pokarmu, d — przedłużony okres niskiej dostępności pokarmu, c — krzywa wzrostu dla lęgu wyklutego w czasie t_r , s — wartość różnicy selekcyjnej S, X — średni termin wykluwania się lęgów.]

These mechanisms — between year variability of food/temperature conditions causing temporal selection — can shift the timing of breeding toward the optimum, where the influence of weather on fitness is minimal.

The problem of the timing of breeding attracts a lot of attention. Many factors are regarded as responsible for timing of breeding, both proximate (e.g. day length — Murton & Westwood 1977, protein accessibility —

Jones & Ward 1976, local environment conditions — Nager 1993) and ultimate — e.g. adjustment to food abundance (Lack 1968), reduced post-fledging reproductive success (Verhulst & Tinbergen 1991). Only measurements of selection caused by each factor would say which of them is important or marginal. The strength of selection recorded here imply that weather conditions may play important role in regulating the timing of breeding. The strength of selective factors was quite high, but they usually occur with small intensity.

Probability of so strong selection as described above seems to be rather low. In the period of 20 years (1961–1981) during the season young feeding (1th of May — 10th of June) temperatures lower than 6°C occurred 21 times (mean 4.71, conf. int. 4.19–5.23) and precipitation exceeding the average value for the studied 3 days (28mm/day) — only 8 times (mean 42.2, conf. int. 25.8–58.6). This means that selection events similar to the observed ones, are too rare to have a real influence on the timing of breeding, especially that impact of those factors may be weaker if they do not occur at the same time. However, it must be remembered that the factors of even very low intensity may operate effectively on the evolutionary time scale. This low intensity makes studying their mechanisms very difficult.

A final question concerns the probability of recruitment of young from the selected broods. The probability of fledged young to become recruited into the breeding population declines over the season (Hochachka 1990), so one would expect the higher fitness of early broods if only at least a few young survived. But unfortunately the studied population was small one and the number of recruited young was very low for both the first (N = 5) and replaced clutches (N = 7).

ACKNOWLEDGMENTS

I thank M. Cichoń, K. Walasz, R.D. Magrath, E. Svensson and J. Tinbergen for their valuable comments on the earlier versions of the manuscript and Małgorzata Juchiewicz for improving the English. Financial support was provided by KBN grant no 4.0168.91.01. and by ZOPiZN PAN.

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STRESZCZENIE

[Selekcja na czas przystępowania do lęgów u sikory modrej i bogatki spowodowana przez warunki atmosferyczne]

W dzikich populacjach zwierząt zazwyczaj nie obserwujemy działania selekcji naturalnej regulującej czas przystępowania do lęgów, gdyż jest on optymalnie dostosowany do lokalnych, typowych warunków.

ków klimatycznych. Jedynie ekstremalne odchylenia od istniejącego optimum wywołują silną selekcję, którą nie tylko można zmierzyć, ale także opisać mechanizm jej działania.

Podstawę do badań związku między warunkami klimatycznymi a czasem przystępowania do lęgów stanowił 3-dniowy okres bardzo złej pogody w maju 1991 r. (śr. min. temp. 5.7°C, śr. opady dobowe 28 mm, są to warunki ekstremalne — ryc. 1), który wywarł znaczący wpływ na lęgi sikory modrej i bogatki. W przypadku pierwszego gatunku z 36 lęgów okres złej pogody przeżyło 14, a w przypadku drugiego z 45 lęgów przeżyło 24.

Prawdopodobieństwo przeżycia złej pogody przez lęg zależało od terminu jego rozpoczęcia — u obu gatunków w czasie złej pogody ginęły lęgi bardziej zaawansowane (ryc. 2 i 3). U bogatki średnie zaawansowanie lęgów, wyrażone w liczbie dni od zniesienia pierwszego jaja, wynosiło w przypadku niepomyślnych lęgów $X_n = 5.29$, a w przypadku pomyślnych było znacznie mniejsze $X_p = 0.54$ ($H = 11.99$, $N = 45$, $P = 0.0005$); u sikory modrej odpowiednio $X_n = 7.82$, i $X_p = 1.71$ ($H = 14.55$, $N = 36$, $P = 0.0004$).

Podobne porównanie wykonane dla wieku piskląt (starsze piskląta mają wyższe bezwzględne zapotrzebowanie pokarmowe co mogło być przyczyną śmiertelności) wykazuje istotne różnice tylko u sikory modrej ($X_n = 7.82$, $X_p = 4.67$, $F = 10.50$, $df = 1,29$, $P = 0.003$), gdyż przystępuje ona do lęgów średnio 4 dni wcześniej niż bogatka ($F(1,85) = 12.7$, $P = 0.0006$), zatem jej piskląta miały o wiele szerszą skalę wieku.

Dla obu gatunków obliczono wskaźnik selekcji kierunkowej — różnicę selekcyjną, wg metodyki Arnolda i Wade'a (1984 a,b; opisuje ona przesunięcie średniej w populacji na skutek działania selekcji, które jest równe współmierności względnego dostosowania i wartości cechy). Różnica selekcyjna dla sikory modrej wynosiła 4.95 ($N = 26$, $P = 0.0003$), dla bogatki 1.86 ($N = 37$, $P = 0.042$), zatem średni czas przystę-

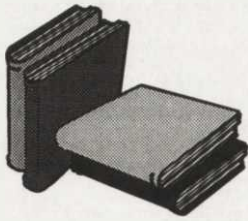
powania do lęgu u sikory modrej został opóźniony przez złą pogodę o prawie 5 dni, podczas gdy u bogatki jedynie o niecałe dwa dni. Zatem selekcja prowadziła do czterokrotnego zmniejszenia różnicy czasu przystępowania do lęgów między gatunkami (d_1 vs d_2 na ryc. 4.).

Mechanizm działania opisanej selekcji jest związany z metabolizmem lęgów. Deszcz i niska temperatura podnosi wymagania energetyczne zwierząt stałocieplnych. Takie warunki nie mają zbyt wielkiego wpływu na embriony wysiadywanych jaj i ogrzewanych piskląt, gdyż są one chronione przez samicę przed wpływem środowiska, a ich metabolizm obniża się lub wzrasta wraz z temperaturą. W przypadku większych piskląt jest inaczej: im są one starsze tym mają wyższe zapotrzebowanie energetyczne związane z masą ciała i rozwojem stałocieplności (O'Connor 1975, Mertens 1977). Jest więc najbardziej prawdopodobne, że podwyższone złą pogodą zapotrzebowanie energetyczne najstarszych piskląt przekrocza poziom zasobów, obniżony z kolei w środowisku na skutek złej pogody. Potwierdzają to obliczenia metabolizmu modelowego pisklącia (tab. 1).

Opisana powyżej selekcja działa zawsze w jednym kierunku — opóźnia przystępowanie do lęgów, chyba, że złe warunki atmosferyczne pojawiają się na tyle późno, że pierwsze lęgi zdążą opuścić gniazdo i usamodzielnic się, a zła pogoda oddziałuje na lęgi najpóźniejsze (ryc. 5).

Nasuwa się pytanie, czy selekcja zdarza się często czy też jest rzadkim zjawiskiem. Na podstawie przeanalizowanych danych meteorologicznych z 20 lat (1961–1981) stwierdzono, że w okresie karmienia piskląt przez rozważane gatunki (1 maja–10 czerwca) warunki równe lub gorsze od średniej obserwowanej w tych badaniach zdarzyły się 21 razy w przypadku temperatury, w przypadku opadów deszczu 8 razy. Oczywiście, czynniki te mogą działać co roku, tyle że z niską intensywnością, trudną do wykrycia.

Redaktor pracy — prof. Maciej Luniak



BOOKS RECEIVED

KORYTARZ EKOLOGICZNY DOLINY WISŁY. STAN, FUNKCJONOWANIE, ZAGROŻENIA

[VISTULA AS AN ECOLOGICAL CORRIDOR. STATE, FUNCTIONING, THREATS]

edited by **Ewa Gacka-Grzesikiewicz, 1995**, IUCN Poland, Warszawa, 198 pp.
English summary

Poland's largest river, the Vistula, is one of the last European rivers that remains its exceptional natural character and richness along the large part of its valley. A debate on the management of the river itself and its valley is still in progress.

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- general characteristics of the Vistula river, its morphology, hydrology, present water quality and hydrotechnical investment
- vegetation along the valley
- avifauna; a total of 325 bird species, 180 breeding ones included, were recorded along the river and its valley (they are listed in the Appendix [Załącznik])
- ichthyofauna of the Vistula and its tributaries
- valorisation of the valley divided into 13 sections

In the conclusions, there are given conditions of protection of the river and pointed possibilities of improvement of the Vistula ecological corridor functioning.

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