

Phenotypic selection on body size in the Great Tit *Parus major* (Niepołomice Forest, Poland)

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Abstract: In 1991–1995 fourteen morphological traits of Great Tits breeding in nest boxes were measured. Their relation to fitness was checked in elements of a tit's biology: survival of young to first reproduction, competition for nesting places, first and second broods, lifetime survival and reproduction. Selection intensity (i) was calculated for principal components of body size. Phenotypic selection evidences were mainly singular. Comparison of body size of individuals recruited to the studied population revealed that males of larger body size were recruited to the population. An experiment showed that individuals with larger bills won competition for nest boxes (i for bill length ranged from 0.05 in males to 0.34 in females). Clutch size depended positively on the measurements of males ($i = 0.07$ and $i = 0.11$ respectively), and negatively on the body measurements of females during the first brood ($i = -0.08$ in 1995). During the second broods there was a positive trend in relation between body size of parents and young condition (for females $i = 0.05$ and $i = 0.02$ respectively, for males $i = 0.08$ in 1992). Intensive selection on body size ($i = -0.34$ for males, $i = -0.61$ for females), due to a catastrophic impact of bad weather was recorded as well. Analysis of lifetime data on the longevity and mean breeding success per year, revealed for 1991 cohort of individuals a strong negative selection on body size in females ($i = -0.46$ with regard to breeding success, $i = -0.16$, longevity) and positive selection on forearm length in males in 1993 ($i = -0.128$, longevity). For 8 cases of selection, its direction in males favoured larger body size (7 cases), whereas in females selection directions were differentiated (3 positive, 3 negative). This pattern was concordant with sexual size dimorphism in the studied population.

Key words: phenotypic selection, body size, sexual size dimorphism, Great Tit *Parus major*

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INTRODUCTION

A phenotypic approach to natural selection assumes that evolutionary change can be measured by combining measurements of selection on phenotypic traits with estimates of heritabilities and genetic covariance. It is based on the quantitative genetics formula: $R = h^2S$, where R is response to selection, h^2 — heritability and S — selection differential (Falconer 1989). The phenotypic approach suggests that field studies can measure selective forces on phenotypes and in this way predict direction of evolutionary

change in traits, provided that there is enough genetic variation.

Although some authors have reported significant short-term selection pressure on morphological traits in the Great Tit (e.g. Lehikoinen 1986, Gosler 1987, Lindén et al. 1992), the general studies based on large longitudinal material do not support this position (Björklund & Lindén 1993). The aim of this study was to find cases of short selection pressures on body size in the Great Tit in selected points of its life cycle. And then to check, if their outcome is concordant with sexual size dimorphism observed in the population studied.

STUDY AREA AND METHODS

The study was carried out in 1991–1995 in Grobelczyk — a part of the Niepołomice Forest (Southern Poland, 20°25'E, 50°68'N). Grobelczyk is a 250 ha area of natural deciduous forest. The predominant tree species are oak *Quercus robur*, hornbeam *Carpinus betulus* and linden *Tilia cordata*. In winter 1991, 350 nest boxes were placed in a grid system (50 m mesh size), 2 m above ground. Nest boxes were inhabited by Great Tit population of average 34 pairs (31–43). Mean breeding success was 8.5 young per brood, their mean recruitment — 3.5%, longevity — 1.19 years for males and 1.12 for females. On average, 16% of pairs raised second broods. Lower numbers of Blue Tit *Parus caeruleus* (mean 26.7 pairs, range 13–40), few pairs of Collared Flycatcher *Ficedula albicollis*, and single pairs of Nuthatch *Sitta europaea* and Starling *Sturnus vulgaris* also occupied nest boxes. In order to determine egg laying date, clutch size and hatching date, the nest boxes were visited weekly during the breeding season. The young were ringed and measured (tarsus length and weight) in the 13th day after hatching. In 1994 and 1995, the population was influenced by experiments, so data from these years are not used in analysis of survival of young to reproduction.

Females were caught mostly during incubation, but both sexes during the feeding of nestling (days 8–10 after hatching). They were ringed, aged and sexed, according to Busse (1984) methods. Fourteen morphological measurements were taken: tarsus length (without intertarsal joint), forearm length (from outer end of radius to inner end of ulna), tail and wing length, bill length (to forehead and to nostrils), its height and width at the nostrils, middle, hind toe and hind claw lengths, breast stripe width, anal patch width and body weight. This large number of measurements was reduced to one or two principal components — PC (Manly 1994), which explained most of the variations and were used as indicators of general body size (PC1, all coefficients in eigenvectors positive) or its proportions (different signs of coefficients in eigenvectors).

Selection analysis was focused on finding relation between fitness and body size during survival of the young to first reproduction, adult winter survival (which gave no significant results due to small number

of wintering birds), during the period of competition for nesting places, first brood and second brood. Each case of selection was also analysed within two episodes of selection (Arnold & Wade 1984): fecundity and young survival. Episodes are multiplicative: number of eggs (first episode) multiplied by proportion of young, which survive (second episode) gives number of fledglings. Also a lifetime selection was estimated in two episodes: longevity and mean breeding success per year, for each cohort of birds found breeding in the studied population. Whenever it was possible, the selection intensity was measured as a standardised selection differential — i (Arnold & Wade 1984). It was calculated according to formula: $i = cov(\bar{w}, Z)/P$, where \bar{w} — relative fitness (number of young divided by the population mean), Z — trait value, P — the trait standard deviation. The significance levels for the i , was for respective Spearman rank correlation (Grant 1985), because some fitness distributions showed deviations from normality.

The role of body size in competition for nest boxes was studied in the field experiment. In 1991, 350 nest boxes were placed in the study area. Assuming overproduction of the population in relation to breeding places, there should be intensive competition for nest places. If body size plays any role in the competition, then winners should be larger than losers, regardless of whether the latter did not breed due to lost conflict for a nest box or if some of them were just late newcomers. In normal situation there is no way to check the body size of losers because it is impossible to catch them. In 1994 168 new nest boxes were erected in an area of the same type of forest, adjacent to the old colony. These nest boxes created new, extra breeding possibilities for birds, which lose the competition.

RESULTS

Young survival

In the years, when the number of nestboxes was unchanged, there was no relation between measured nestling traits and their survival to reproduction (ANOVA, weight: $F_{(2,820)} = 0.085$, ns; tarsus: $F_{(2,808)} = 0.004$, ns). Because sex recognition in fledglings was impossible, the sex effect on survival was not controlled. In 1991, due to bad weather conditions during feeding

period, the body size of young was much smaller than in other years (ANOVA, weight: $F_{(2,820)} = 90$, $p < 10^{-6}$; tarsus: $F_{(2,808)} = 103$, $p < 10^{-6}$). This difference was also reflected in yearling females recorded in the population (ANOVA, PC1: $F_{(4,162)} = 4.6$, $p = 0.001$), whereas in males there were no differences (ANOVA, PC1: $F_{(4,91)} = 1.2$, ns). Taking into account higher survival of males and lower of females, the only explanation is that females were recruited all or at random, whereas in males only the largest individuals, probably winning the conflicts for resources, were recruited. This difference cannot reflect immigration of larger males, as there were no differences in size between birds of local origin and immigrating birds controlled for influence of year (ANOVA PC1: $F_{(2,67)} = 1.67$, ns).

Competition for nest boxes — experiment

There were significant differences in bill dimensions between Great Tits caught in new and old nest box areas. Individuals of both sexes winning the competition for nesting places had larger, stout bills (Table 1).

Reproduction

In 1992, a significant correlation between the number of fledglings and males' PC1 was found ($i = 0.07$, $p = 0.045$, $N = 26$). Analysis of selection episodes re-

vealed that the base for this relation was a correlation of male body size with the number of eggs ($i = 0.046$, $p = 0.012$, $N = 27$; Fig. 1a), with insignificant selection linked with young survival ($i = 0.026$, ns, $N = 27$). There was no relation between female size (PC1) and number of eggs ($r_s = -0.107$, ns, $N = 27$); however, partial correlation coefficient was close to significance, when this correlation was controlled for male size ($R_{ic,m} = -0.39$, $p < 0.1$, $N = 27$).

A similar relation was recorded in 1995, when there was a significant relation between clutch size and male breast stripe width ($i = 0.11$, $p = 0.006$, $N = 11$; Fig. 1b). In this year, there was the highest mean clutch size ever recorded in this population (Fig. 1c), and there were some exceptionally large clutches of 14 and 15 eggs, never recorded before. In this year females' size (PC1) was negatively correlated with clutch size ($i = -0.08$, $p = 0.042$, $N = 11$; Fig. 1d).

Second broods

In a comparison of birds raising second broods with the birds that had only first brood, significant differences in some traits were found (Table 2). There was a positive relation between body size of parents (PC1) and young condition (Fig. 2) in 1992 (males: $i = 0.08$, $p = 0.08$, $N = 7$; females: $i = 0.05$, $p = 0.03$, $N = 12$) and 1993 (males: $r_s = 0.50$, ns.; females: $i = 0.02$, $p = 0.04$, $N = 10$).

Table 1. The traits value compared with ANOVA between nest box area existing for 3 seasons (old) and new nest box area. i — selection intensity, PC — principal components derived from measured morphological traits.

Trait	Males			Females			$F_{(2,820)}$	p
	old	new	i	old	new	i		
Wing	77.2	77.0	–	74.5	73.7	–	0.790	ns
Tail	65.9	65.7	–	62.7	62.7	–	0.025	ns
Bill length	14.06	13.98	0.055	13.94	13.25	0.338	5.124	0.03
Bill height	4.64	4.48	0.258	4.47	4.38	0.205	4.336	0.05
Bill length from nostrils	10.57	10.63	–0.077	10.73	10.02	0.377	5.069	0.03
Bill width	4.31	4.32	–	4.23	4.17	–	0.185	ns
Tarsus	20.36	20.40	–	19.88	19.72	–	0.084	ns
Middle toe	11.13	11.20	–	10.83	10.77	–	0.000	ns
Hind claw	7.29	7.23	–	7.15	7.35	–	0.533	ns
Hind toe	8.75	8.67	–	8.59	5.67	–	0.233	ns
Forearm	23.00	22.97	–	22.23	21.98	–	0.620	ns
Body weight	18.43	18.67	–0.091	18.28	19.33	–0.256	3.060	ns
Breast stripe	11.53	11.40	–	–	–	–	0.005	ns
Anal patch	17.72	16.60	–	–	–	–	0.466	ns
PC 1	1.35	1.02	–	–1.45	–1.93	–	0.526	ns
PC 2	0.102	0.046	0.023	0.567	–1.49	0.352	5.730	0.022
PC 3	–0.381	–0.238	–	0.444	0.100	–	0.056	ns

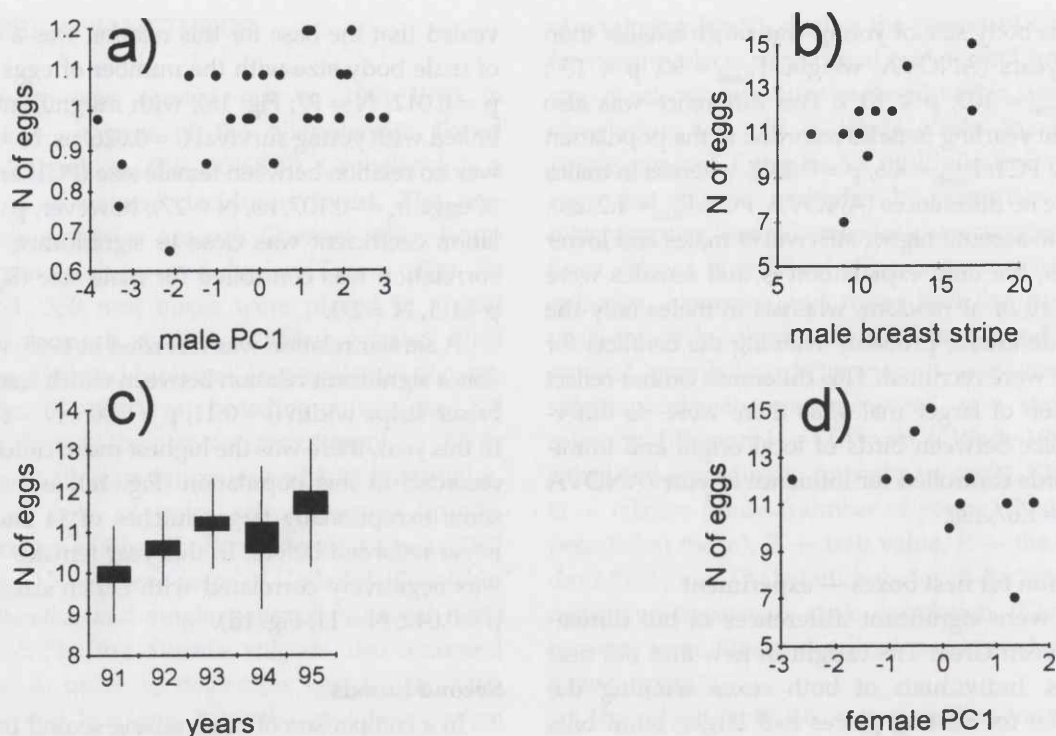


Fig. 1. Correlation between male, or female body size and clutch size. a — male body size (PC1) and clutch size; b — male breast stripe width and clutch size; c — mean clutch size (\pm S.E., S.D.) during the period of the study; d — female body size and clutch size.

Table 2. Comparison of morphological traits of birds raising one versus two broods during the season (ANOVA).

Trait	Mean		F	df	p
	1 brood	2 broods			
Males					
Wing	77.4	75.4	6.72	1, 28	0.015
Claw	7.2	7.5	5.38	1, 28	0.028
Bill length from nostrils	10.3	10.6	5.13	1, 26	0.032
Anal patch	18.8	15.9	4.44	1, 28	0.044
Body weight	18.5	17.9	1.13	1, 26	ns
Females					
Bill length	13.0	14.0	26.9	1, 32	0.00001
Body weight	19.5	17.9	12.1	1, 32	0.0015

Catastrophic events

In 1991 there was a period of heavy rains during nestling feeding (84 mm of rain during 17–19 May, 10°C at noon), 11 (41%) broods died and mean brood size decreased to 5.75 (mean clutch size — 9.44). Nestling mortality was related to general body size of males (their PC1) and body proportions (PC2) in females (Table 3).

Life time data

All cohorts of birds (1991–1995) were checked for relations of body size (PCx) or singular traits with lifetime fitness. Two selection episodes were studied: longevity and mean breeding success. Only for females in 1991 there was a significant selection in both episodes (Table 4) and for males in 1993, showing significant relation between the length of forearms and number of seasons when they

were recorded in the study site ($i = 0.128$, $p = 0.019$, $N = 36$).

Outcome of short selection pressures

Eight cases of phenotypic selection were observed (Table 5). In males seven of them were related to positive selection on body size or body measurements, whereas in females there were only three such cases (Fisher exact test, $p = 0.059$). The difference becomes

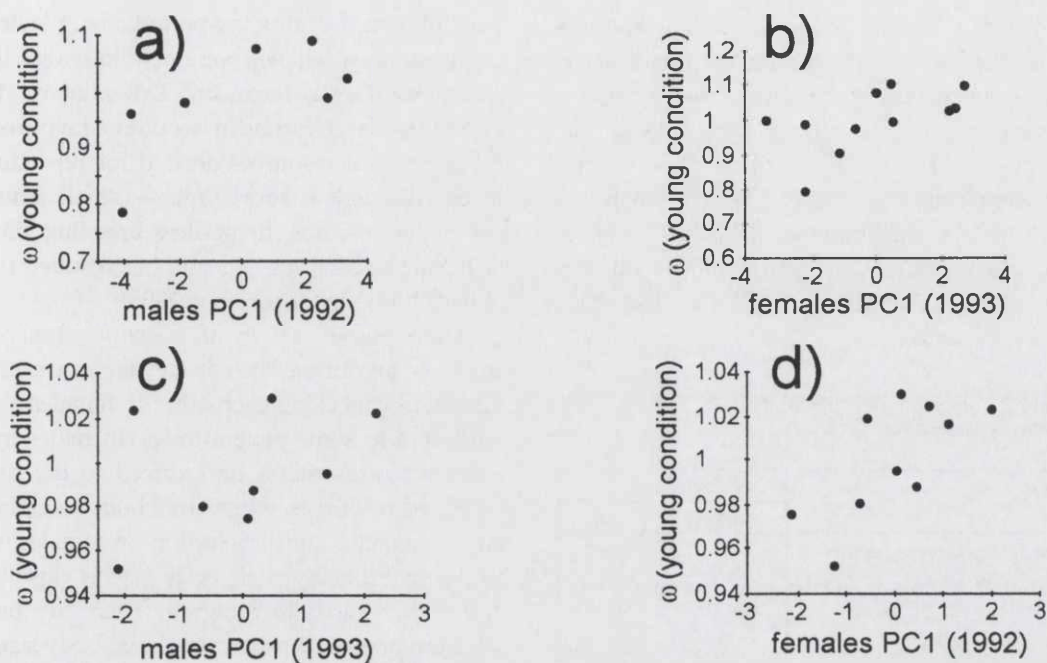


Fig. 2. Relation between body size of parents (PC1) and relative fitness (ω), expressed as the body weight of young during second clutch.

Table 3. Selection episodes for body size of adults, which occurred in the period of the bad weather

Episodes		<i>i</i>	<i>p</i>	N
Males PC1	clutch size	0.02	ns	19
	young survival	-0.34	0.04	19
Females PC2	clutch size	0.002	ns	24
	young survival	-0.61	0.01	27

Table 4. Lifetime data analysis.

1991	Males PC1			Females PC2		
	<i>i</i>	<i>p</i>	N	<i>i</i>	<i>p</i>	N
Fledgings/year	-0.25	ns	24	-0.46	0.029	30
Longevity	0.08	ns	24	-0.16	0.023	30

statistically significant (Fisher exact test, $p = 0.035$) when the influence of catastrophic weather is excluded (as rare and random event).

DISCUSSION

In eight cases of phenotypic selection, its direction differed between sexes: in males larger body size was promoted in all cases, except one (which was caused by

unpredictable, rare climatic event). In females negative and positive selection pressures had equal number, or selection factors acting on males did not caused any effect in females.

Among the described cases, selection related to survival of youngs and recruitment to the breeding population seems to be the most important — all other described mechanisms of selection depend on starting reproduction by the particular bird. Unfortunately, this period of animal life is poorly known, due to the secret way of life of most bird species at this time. Although the relationship between body size/condition of young and their further survival was reported in many studies in Great Tit (e.g. Linden 1990, Tinbergen & Boerlijst 1990, Linden et al. 1992) or other species (Magrath 1991), there were no reports concerning sex specific survival of young birds. Detecting sex-specific survival of the young in relation to their size suggests that body size might be much more important for survival of the young than it has been reported so far.

In hole nesting birds, competition for nesting places is important for reproduction. Experimental exposing of additional nesting places after the onset of breeding showed that individuals with stout bills won the competition. Grant (1985) reported the selection of bill size,

which was related to competition for territories in a population of the Darwin finch *Geospiza conirostris*. Dhondt et al. (1979) interpreted long-term decrease of body size in a population of the Great Tit as a result of releasing competition for breeding sites through surplus of nest boxes. The Great Tit dominates over the Blue Tit in competition for nesting boxes (Dhondt & Eyckerman 1980, Kempeaners & Dhondt 1991), so interference in experiment by competition with Blue Tits, which reach quite high numbers in the study place, seems to be unlikely.

Table 5. Directions of selection pressure on body size during respective cases of phenotypic selection

Selection cases	Selection	
	Male	Female
Survival of fledgings to reproduction	+	0
Competition for nest sites	+	+
Fecundity and body size of males	+	0
Fecundity in optimal season	+	-
Second brood commencing	+	+
Second brood breeding success	+	+
Spell of bad weather	-	-
Longevity	+	-

The rest of the reported cases of selection might be related to availability of resources and/or efficiency in their exploitation. The strongest selection was caused by a catastrophic spell of poor weather, which decreased food availability during feeding period through washing down caterpillars' outbreak from trees and worse foraging conditions. Also selection related to second broods probably reflects restricted food abundance late in the season on territories owned by smaller birds. On the contrary, the selection cases related to female fecundity occurred during periods of food abundance. It means that natural selection operates not only in poor environmental conditions, but also when they are good — it allows full expression of traits (fecundity in this case).

It is interesting that clutch size, which seems to be rather a female trait, depends on male size. Female condition and clutch size depend both on resource availability in the territory she occupies, and feeding by male (Perrins 1965, 1979). During the period of clutch formation, females increase energy requirements by ca 40% (Ricklefs 1974). Thus larger clutches reflect better quality of territories belonging to large males. In 1995 spring was late, but unusually warm and humid,

which caused extra food abundance. First caterpillars were observed during the period of egg laying. In such circumstances, females were able to realise their maximal physiological fecundity. Downhower (1976) suggested that large fecundity would be favoured by natural selection if resources needed for reproduction had to be collected in short time — small females could collect them faster. In poultry breeding programmes artificial selection for egg number resulted in decrease of hens body size (Dickerson 1955).

The general pattern of selection observed in this study — favouring large body size in males, selection directions cancelling each other in females — might be attributed to some general roles. In males most of the observed cases might be reduced to the conflicts for restricted resources, when large body size gives advantage in direct conflict. Selection on females' size is not so direct. Probably their body size is close to optimal one with regards to foraging. There are much more selection pressures promoting large body size in males, so it is disadvantageous for females to lose energy in direct competition with males. They may better survive through a more "effective" way of life.

Data presented in this paper belongs to so called "cross-sectional" data. In opposition to "longitudinal" data, they cannot be related directly to any evolutionary change. On the basis of data from 1991 (Table 4) it can be noticed that in males strong pressure of selection acting in one season was very quickly inflated during the rest of their lives, whereas in females selection pressures were still negative. In males the negative selection in 1991 was inflated probably by numerous episodes of selection promoting large body size in the Great Tit males. On the contrary, in females, negative selection pressures seems to be much more common. Thus, the negative selection observed in the breeding success in 1991 was not changed by selection cases occurring during the rest of bird life.

CONCLUSIONS

Analysed cases of short-term selection on morphological traits of the Great Tit indicate that morphology of this species might be under the influence of current selection pressures. Cases of selection described in this paper may explain the pattern of sexual size dimor-

phism observed in the population with larger males and smaller females. Usually this selection has too low intensity to be detected or measured. Only in cases of strong ecological factors, like rare climatic events, extremely bad or good food conditions, intensifying or releasing competition, the selection can be noticed and/or measured.

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REFERENCES

- Arnold S. J., Wade M. J. 1984. On the measurement of natural and sexual selection: applications. *Evolution* 38: 720–734.
- Björklund M., Lindén M. 1993. Sexual size dimorphism in the Great Tit (*Parus major*) in relation to history and current selection. *J. evol. biol.* 6: 397–415.
- Busse P. 1984. Key to sexing and ageing of European Passerines. *Beitr. Naturk. Niedersachsen* 37, Suppl.
- Dhondt A. A., Eyckerman R. 1980. Competition and the regulation of numbers in Great and Blue Tit. *Ardea* 68: 121–132.
- Dhondt A. A., Eyckerman R., Huble J. 1979. Will Great Tits become Little Tits? *Biol. J. Linn. Soc.* 11: 289–294.
- Dickerson G. E. 1955. Genetic slippage in response to selection for multiple objectives. *Cold Spring Harbor Symposia on Quantitative Biology* 20: 213–224.
- Downhower J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263: 558–563.
- Falconer D. S. 1989. *Introduction to quantitative genetics*. Longman Scientific and Technical, U.K.
- Gosler A. 1987. Sexual dimorphism in the summer bill length of the Great Tit. *Ardea* 75: 91–98.
- Grant P. R. 1985. Selection on bill characters in a population of Darwin's finches: *Geospiza conirostris* on Isla Genovesa, Galapagos. *Evolution* 39: 523–532.
- Kempeaners B., Dhondt A. A. 1991. Competition between Blue and Great Tit for roosting sites in winter: an aviary experiment. *Ornis Scand.* 22: 73–75.
- Lehikoinen E. 1986. Dependence of winter survival on size in the Great Tit *Parus major*. *Ornis Fenn.* 63: 10–16.
- Lindén M. 1990. Reproductive investment and its fitness consequences in the Great Tit *Parus major*. Ph. D. Thesis, Uppsala Univ., Sweden.
- Lindén M., Gustafsson L., Pärt T. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. *Ecology* 73: 336–343.
- Magrath R. D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. *J. Anim. Ecol.* 60: 335–351.
- Manly B. F. J. 1994. *Multivariate statistical methods. A primer*. Chapman & Hall.
- Perrins C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34: 601–647.
- Perrins C. M. 1979. *British Tits*. Collins, London.
- Ricklefs R. E. 1974. Energetic of reproduction in birds. In: Paynter R. A. (ed.). *Avian Energetics*. The Nuttall Ornith. Club No 15, Cambridge Mass.
- Tinbergen J. M., Boerlijst M. C. 1990. Nestling weight and survival in the Great Tits (*Parus major*). *J. Anim. Ecol.* 59: 1113–1127.

STRESZCZENIE

[Fenotypowa selekcja rozmiarów ciała u bogatki]

Praca jest próbą odpowiedzi na pytanie o częstość i charakter występowania w naturalnych populacjach krótkoterminowych nacisków doboru na ilościowe cechy morfologiczne oraz o możliwość wyjaśniania cech morfologii osobnika (wielkości ciała) na podstawie aktualnie działającego doboru.

Badania wykonano w okresie od zimy 1991 do lata 1995. Objęto nimi populację bogatek, zajmujących skrzynki lęgowe w uroczysku „Grobelczyk” (Puszcza Niepołomska, 250 ha lasu grądowego). W czasie badań wykonywano pomiary 14 morfologicznych cech ilościowych. Badano związek z dostosowaniem każdej z nich oraz obliczonych na ich podstawie składowych głównych wielkości ciała, w z góry założonych elementach cyklu życiowego bogatki. Do ilościowego określenia doboru fenotypowego wykorzystywano głównie intensywność doboru (*i*).

Badaną populację stanowiły średnio 34 pary lęgowe. Charakteryzowała się ona niską rekrutacją młodych (ok. 3,5%) i niskim poziomem przeżywalności osobników dorosłych (średnia długość życia samców — 1,19, samic — 1,12 roku).

W czasie badań stwierdzono, że:

- 1) do populacji rozrodczej wchodziły młode samce o większych rozmiarach ciała;
- 2) w konkurencji o miejsca gniazdowe wygrywały osobniki o większych rozmiarach dzioba u obu płci (Tab. 1);
- 3) stwierdzono pozytywną zależność między liczbą znoszonych jaj, jak również liczbą piskląt, a wymiarami ciała samca (Fig. 1a, b);

4) przy bardzo korzystnych warunkach pokarmowych (Fig. 1c) płodność samicy była ujemnie związana z wymiarami jej ciała (Fig. 1d);

5) drugie lęgi charakteryzowały się występowaniem dodatniego doboru na wielkość ciała obu płci, związanego z kondycją ich potomstwa (Fig. 2). Ptaki przystępujące do drugiego lęgu różniły się wymiarami ciała od ptaków wyprowadzających tylko jeden lęg (Tab. 2);

6) analizy doboru związanego z całkowitą długością życia osobników i ich średnim dostosowaniem osiąganym w czasie jednego sezonu, ujawniły dodatni dobór ukierunkowany na długość kości skrzydeł u samców związany z długością życia. U samic stwierdzono silny

negatywny dobór uwzględniający proporcje ciała, związany z obydwoma rozważanymi składowymi dostosowaniami (Tab. 4);

7) załamanie się bazy pokarmowej (na skutek złych warunków atmosferycznych) prowadziło do obniżenia sukcesu rozrodczego, co wywoływało silny, negatywny dobór ukierunkowany na wielkość ciała (Tab. 3).

Stwierdzone przypadki doboru oddziałują pozytywnie na wielkość ciała u samców, podczas gdy u samic kierunki doboru wydają się wzajemnie znosić (Tab. 5). Taki obraz doboru fenotypowego jest zgodny z istniejącym dymorfizmem płciowym wielkości ciała u sikory bogatki.