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Long-term variability of wing length in a population of the Reed Warbler *Acrocephalus scirpaceus*

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Abstract. 4166 measurements of wing length in Reed Warblers were made during 9 breeding and pre-migratory periods in Central Poland. In the studied population there was significant differentiation in the wing length among seasons in adult and juvenile birds. Multiple regression and path analysis showed that weather factors (temperature and precipitation) during the breeding period determine the long-term variation in the wing length in both adult and young birds. Changes in wing length were explained by natural selection and habitat selection. In breeding and pre-migratory periods, temperature and precipitation influence in food availability, and thus affect optimisation of energetic expenses on feeding. It was revealed that long-winged individuals are best adapted to cold and rainy conditions, the short-winged ones, to warm and dry summers. The weather conditions obtaining when the birds arrive at the breeding grounds could be linked to differentiation in availability of optimal places for establishing territories, thereby influencing cempetition for breeding territories and the effectiveness of their occupation by morphometrically different birds.

Key words: Reed Warbler, *Acrocephalus scirpaceus*, wing length, biometric variability, natural selection

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INTRODUCTION

Long-term variability of metric traits in bird populations have been studied sporadically and mechanisms causing such a differentiation are best known only in the case of sedentary island populations of Darwin's finches *Geospiza* spp. (Grant 1986, 1991). For some widely distributed species, attempts to explain the variation in metric features among years were undertaken by Cowley (1979) and Jones (1987) in the Sand Martin *Riparia riparia*, Dhondt et al. (1979) in the Great Tit *Parus major,* Hogstad (1985) in the Brambling *Fringilla montifringilla* and Wojciechowski (1992) in Swallow *Hirundo rustica.* Among-year variation in wing length was also shown in Song Sparrow *Melospiza melodia* (Schluter & Smith 1986); in Brown-headed Cowbird *Molothrus ater* (Fleischer & Rothstein 1988); in the Goldcrest *Regulus regulus*, the Great Tit *Parus major*, the Robin *Erithacus rubecula* and the Chaffinch *Fringilla coelebs* (Busse 1976), however these authors did not explain this phenomenon.

Cowley (1979) interpreted changes in the wing length in the Sand Martin returning from African wintering quarters as a result of poor feeding conditions affecting the length negatively. The association between the feeding factor and the wing length was also suggested by Van Balen (1967). He linked the longer wing and the higher body weight of Great Tits inhabiting broadleaved forests, to larger food abundance than in dry coniferous forests. Another reason of such variation was shown by Hogstad (1985) who tried to explain the characteristics of metric parameters of the Brambling by spatial differentiation within the population and by directional movements of individuals.

Some authors drew attention to a changing pressure of natural selection as an explanation of variation in morphometric traits among years — in Darwin's finches (Boag & Grant 1981, Price & Grant 1984, Grant 1986, 1991), in the Great Tit (Dhondt et al. 1979), in the Sand Martin (Jones 1987), in the Black-bellied Seedcracker *Phyrenestes ostrimus* (Smith 1990) and in Swallow (Wojciechowski 1992).

Natural selection can also explain the evolution and maintenance of the geographical variation in the House Sparrow *Passer domesticus* in North America (Johnston & Selander 1973, Fleischer & Johnston 1982, 1984).

Amongst many environmental factors, weather conditions are considered as one of the most important, moulding food availability for insectivorous birds (Finlay 1971, Turner 1984, Stocek 1986) and remarkably influencing time of arrival at breeding grounds (Pikulski 1986) and the timing of breeding (Kuźniak 1991). It was also shown that weather conditions may affect the egg size (Pikulski 1986), the time of hatching (Kendeigh 1941), variation in body mass of hatchlings and the rate of their growth (Bryant 1978, Orell 1983, Järvinen & Ylimaunu 1986), nestling mortality (Bryant 1978, Erlinger 1986, Kuźniak 1991) and mortality of adult birds (Perrins 1965, Lack 1966, van Balen 1980, Winkel 1981).

In populations of vertebrates weather conditions were recognised also as causing directional adaptive changes. In birds they explain directional selection in the bill height in the Ground Darwin's finch *Geospiza fortis* (Grant 1986, 1991). During droughts on Galapagos Islands natural selection favoured birds with high bills, which more efficiently cracked large seeds — the main food at this time. The selection was caused by distinctly higher mortality of birds with lower bills worse fitted to these conditions. Wojciechowski (1992) proved that weather conditions explain changes in the wing length in a population of the Barn Swallow, which was connected with different fitness of morphometrically different individuals. Weather conditions which influence directly food availability and abundance may determine phenotype-dependent survival, and as a result some pattern of relation between phenotype features and the intensity of such environmental factor can be expected.

Studies on flight bioenergetics and field metabolism using methods based on marking birds with heavy water (D_2O^{18}) revealed a significant relation among some metric parameters, sexual differentiation and the amount of energy used during flight (Ettinger & King 1980, Bryant & Westerterp 1982, 1983, Westerterp & Bryant 1984, Williams 1988). Thus, it may be supposed that the size of these features may undergo selection.

The aim of this paper is to describe among-year variation in wing length in the population of Reed Warbler and to explain it in terms of natural selection.

STUDY AREA

The study was conducted in fish-ponds Okręt (52°02′N, 19°51′E) and Rydwan (52°03′N, 19°49′E) in the region of Łowicz, Central Poland.

The area of the Okręt fish-pond is 160.0 ha, and Rydwan fish-pond — 110.0 ha, and their mean depth — ca 1.3 m. The level of filling of fish-ponds with water changed in relation to weather conditions. The littoral zone of the surface of the fish-ponds was covered in ca 20–40% by rush vegetation. Rush on the Okręt fish-pond was dominated by Reed *Phragmites australis*, Reed Mace *Typha latifolia*, Manna Grass *Glyceria maximae* and Bulrush *Scirpus lacustris*. In the area of Rydwan fish-pond, besides *Phragmition* communities characteristic for the Okręt fish-pond, occurred also communities of Horsetail *Equisetum limosi*, Dock *Rumex hydrolapathum* and Sweet Rush *Acoretum calami*.

METHODS

Methods of fieldwork

The material was collected in years 1972–1980 during 701 days of catching in total, resulting in 4166 birds ringed (Table 1). Birds were trapped in ca 30 stylon 7.5 m long mist-nets which were fixed in rows deep into the rush, every year in the same places. Standard methods of the Operation Baltic were used in catching and in measurements (Busse 1983). The sex of birds was determined only in adults of the basis of the incubation path occurrence (Svensson 1970).

Data analysis

Data obtained from long-term retraps (measurements of own-ringed birds recaptured after several years) were treated equally to the data collected from birds ringed in a given year.

In the case of studies connected with analysis of metric features there is a possibility to make two basic independent errors: sample error and method error, which jointly give a total error (Blalock 1960). Taking into account a possibility of making measurement mistakes (Ewins 1985, Barret et al. 1989), the error of the measurement method was estimated by comparing the values of measurements in adult birds recaptured within the same season (short-term retraps) in which seasonal changes connected with feather growth were not expected. For the comparison the paired-samples t-test was used (Sokal & Rohlf 1981). Differences between measurements of the analysed metric trait were non-signifi-

Table 1. Numbers of birds caught in Okręt and Rydwan fishponds; ad. — adults, juv. — juveniles.

Periods	Days	Numbers of birds		Short–term retraps		Long–term retraps	
		ad.	juv.	ad.	juv	ad.	juv.
2 VII–1 VIII 1972	31	118	58	29	16	–	–
7 VII–27 IX 1973	83	113	392	35	91	6	3
6 VII–8 X 1974	95	187	677	36	123	3	7
5 VII–22 IX 1975	80	89	154	20	17	7	5
3 VII–28 IX 1976	88	236	620	43	95	8	8
2 VII–29 IX 1977	90	173	256	32	42	15	17
2 VII–29 IX 1978	90	159	304	34	29	12	6
3 VII–24 IX 1979	84	113	183	26	14	6	10
2 VII–9 IX 1980	60	87	247	17	23	5	4
Total	701	1275	2891	272	450	62	60

cant ($t^0 = 0.08$, $r = 0.93$, $df = 253$, ns), thus the possibility the measurement error did not modify results of the analysis.

Wing length distribution in all samples fitted the normal distribution (K–S test) which allowed for using parametric tests.

Changes in mean wing lengths among years were tested using the fixed-effect model of the one-way analysis of variance (Lindman 1992). Significant differences among values the means for subsequent years were compared by the Tukey's test for samples of different size (Lindman 1992).

To assess the influence of environmental factors on the variation in wing length among years, multiple regression models were constructed and, on their basis, models of path analysis (Sokal & Rohlf 1981). Quantitative models of the path analysis including the effect of correlations among the studied independent variables lead to the determination of the most important factors affecting the variation in mean wing lengths among years.

The following variables describing weather conditions for subsequent months of the stay at the breeding ground were used as independent variables in the model: monthly mean 24-hour temperature (in °C) and monthly sum of precipitation (in mm of water column). The second variable was log-transformed. Weather data were calculated from recordings made by a field meteorological station localised in Topola-Błonie (ca 20 km from the study area). Data from year 1972 were excluded from the analysis because of shorter period of catching birds (Table 1).

Relations of the fat score and with wing length, subsequent years, days in a year and time of a day were tested using the logistic multiple regression (Afifi & Clark 1990). In the nominal variable two levels were established: lean birds ($T \leq 1$) and fat birds ($T \geq 2$), as determined according to the Operation Baltic procedure (Busse 1983).

Long-term repeatability of wing length (the proportion of interindividual component of variance in total variation) in population was conducted by the comparison of measurements of long-term retraps following Żuk (1979). Repeatability of wing length was measured as the angular coefficient of regression of first measurements on the mean of measurements of the same individuals caught in subsequent years (Żuk 1979).

All the calculations were done using the SPSS PC+ statistic software.

RESULTS

Long-term variation in the wing length

Distinct changes in the mean value of the wing length in the subsequent years of the study were found (Fig. 1). The course of these changes were similar in both age groups in the population ($r = 0.95$, $n = 9$, $p < 0.001$). Tukey's test allowed to distinguish in the population groups of years with significantly different mean wing lengths (Table 2). Generally, in adults and young birds in years 1972–1975 wing length was significantly shorter in comparison with years 1976–1980.

Multiple regression and path models showed that weather factors influenced mean wing length of adult birds, as temperature and precipitation during the breeding and pre-migratory periods had

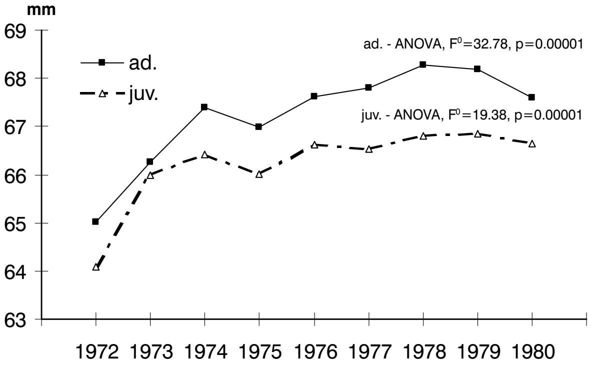

Fig. 1. Changes in the mean wing length in the Reed Warbler population in 1972–1980 years.

Table 2. Comparison of mean wing-length between the years using the multiple range Tukey test, HA — two–tailed, lines — means not significantly differs.

Adults	1972	1973	1975	1974	1980	1976	1977	1979	1978
x̄	65.02	66.26	66.99	67.39	67.60	67.62	67.80	68.18	68.28
n	91	95	84	168	85	207	170	113	154

Juveniles	1972	1973	1975	1974	1977	1976	1980	1978	1979
x̄	64.09	65.98	66.01	66.41	66.53	66.62	66.64	66.81	66.85
n	43	371	142	545	249	578	234	266	175

significant effects (Table 3, Fig. 2). Moreover, the model of path analysis showed that mean monthly temperatures (June–August), correlated negatively with mean wing length, moulded the variation quantitatively more distinctly than the positively correlated temperature of May. The remaining variables (precipitation in May and June) were less important in shaping this variation (Fig. 2).

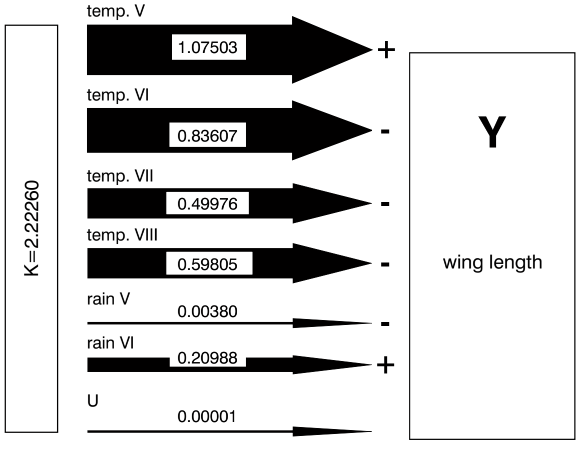

Fig. 2. Path analysis model of the influence of factors on long-term variability in wing length in adult birds. U — unknown variable, K — sum of colinearity effect between dependent variables.

Relations between mean wing length and the analysed weather factors in the group of young birds were similar to these in the adults, with the influence of July and August temperatures being most significant factors determining the among-year variation (Table 3, Fig. 3).

During the study period, weather conditions (temperature, precipitation) influencing food availability were clearly more favourable in years 1972–1975 than in the subsequent years. This resulted in the remarkably higher proportion of fat birds (U-test, p = 0.002) as well as by the higher mean fat score in the first period (Student-t test, p = 0.0001).

Logistic regression for relations between fat score and wing length, controlling for the year of studies, the day of a year and the time of the day,

Table 3. Backward multiple regression models of analysis of relations between wing-length and mean temperature and logarithm of rain sum of month (log s.r.). R^2 — Adjusted R Square, b — regression coefficient, SEb — standard error of b. * — $R^2 = 0.99$, Durbin Watson test — 2.543, $\alpha > 0.05$; ** — $R^2 = 0.99$; Durbin Watson test — 2.643, $\alpha > 0.05$.

Variable	b	SEb	t°	p
Adults*				
temp. V	0.4629	0.0008	593.67	0.0001
temp. VI	-0.3821	0.0009	-440.50	0.0222
temp. VII	-0.3055	0.0005	-584.58	0.0001
temp. VIII	-0.4503	0.0006	-700.39	0.0009
log s.r. V	-0.1833	0.0037	-48.95	0.013
log s.r. VI	1.5365	0.0049	314.18	0.002
Juveniles**				
temp. V	0.0177	0.0004	49.36	0.0129
temp. VII	-0.1278	0.0003	-468.97	0.0014
temp. VIII	-0.1810	0.0003	-565.19	0.0011
log s.r. V	-0.4524	0.0018	-250.51	0.0025
log s.r. VI	-0.0499	0.0020	-25.34	0.0251
log s.r. VII	-0.0036	0.00001	-198.51	0.0032

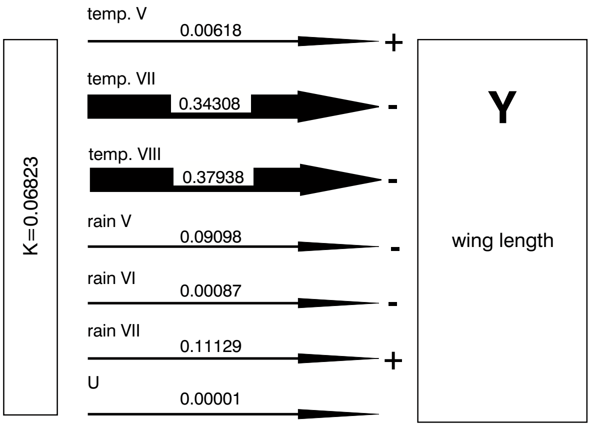

Fig. 3. Path analysis model of the influence of factors on long-term variability in wing length in juveniles birds. U and K — see Fig. 2.

showed the existence of different relations in different periods. In rainy years with relatively low temperature, a positive correlation between the fat score and the wing length was shown in both adult and young birds (Table 4). Oppositely, in warm years with moderate precipitation the relation between the fat score and the wing length showed a reverse direction. In the group of adult birds the fat score was significantly connected with short wing, while in the group of young birds the regression coefficient for the wing length was statistically non-significant, but the direction of relation was opposite to the case of cold and rainy years (Table 5).

Table 4. Relationship between fat contents of birds and wing length in 1976-1980 years in logistic multiple regression models with controlled years, days in the season, and time of the day. b — regression coefficient, SEb — standard error of b, W° — Wald statistic.

Variable	b	SEb	W°	p
Adults				
Wing length	0.1828	0.0863	4.483	0.0342
Day	0.1081	0.0115	87.706	0.00001
Juveniles				
Wing length	0.1184	0.0339	12.182	0.0005
Day	0.0289	0.003	92.098	0.00001
Time of day	0.2487	0.0215	133.752	0.00001

Table 5. Relationship between fat contents of birds and wing length in 1973–1975 years in logistic multiple regression models with controlled years, days in the season, and time of the day. b, SEb and W° — see Table 4.

Variable	b	SEb	W°	p
Adults				
Wing length	-0.1869	0.07	4.483	0.0076
Day	0.0517	0.0123	17.576	0.00001
Time of day	0.0939	0.0488	3.702	0.0544
Juveniles				
Wing length	-0.0805	0.07	1.325	0.24980
Day	0.0627	0.012	27.167	0.00001
Time of day	0.1004	0.0466	4.639	0.0313
Year	-0.5521	0.1655	11.126	0.0009

Long-term repeatability of the wing length

In the studied population of the Reed Warbler the coefficient of repeatability of the wing length measurement was relatively high ($r_{(b)}$ = 0.736, F° = 72.25, p = 0.00001), suggesting the important role of individual characteristics in forming this trait.

DISCUSSION

Significant relations between the mean wing length and the mean monthly temperature during the breeding and pre-migratory periods and with the logarithm of the sum of precipitation, existing in both age groups, and also quantitative proportions among the path coefficients, suggest that the temperature is the most important factor determining the among-year variation in wing length (Table 3, Fig. 2 and 3). The negative correlations of independent variables (the mean temperature of June, July and August) with the mean wing length in the subsequent years, with the high value of the coefficient of repeatability for this trait ($r_{(b)}$ = 0.736), suggested a selection-based mechanism causing the differentiation, where the selective pressure for a longer wing would operate.

The following mechanism seems probable: in cold year, characterised by feeding conditions unfavourable for the Reed Warbler (reduced availability of food) the selective pressure favouring long-winged individuals could take place. In favour of this hypothesis would be relations between the fat score and the wing length in years different with respect to weather. The mechanism of such a selective pressure could be based on higher efficiency of food searching of long-winged individuals in the weather-unfavourable periods in comparison with the short-winged ones. The result of this adaptation could be the more effective energy management of the long-winged birds causing the intra-population differentiation in survival of morphometrically different individuals. Reduced amount of insects caught or increased energy expenses on preying and food searching might increase mortality of short-winged birds, or make it difficult to store energy resources needed for migration, and thus also influence their survival during migration.

Mechanism of selection in wing length

Selection of wing by weather conditions treated as factors influencing food availability is highly probable. It is known that low temperature (especially below 13°C) causes a rapid decline in the number of flying insects (Stocek 1986), and that large insects react very quickly to temperature changes (Turner 1984). Food composition of Reed Warblers (Green & Davies 1972, Bussmann 1979, Cardenas et al. 1983, Bibby & Thomas 1985) shows that insects which can quickly response to changes in weather conditions constitute a remarkable percent of their diet, which changes in dependence from the availability of insects of the habitat (Bibby & Thomas 1985). A remarkable part of the Reed Warbler diet are relatively large insects, mainly Dipterans, which are very sensitive to precipitation and temperature. The size of Reed Warbler prey ranges from 3.2 mm to 6.6 mm (after Schulze-Hagen & Flinks 1989), and the largest caught insects are over 35 mm-long (Dyrcz 1979).

The method of Reed Warbler feeding suggests that during bad weather conditions the birds may have difficulties in getting the food (Davies & Green 1976, Bibby & Thomas 1985, own observations). Davies & Green (1976) showed that Reed Warblers prey on active insects which move, and Bibby & Thomas (1985) claimed that ca 36–40% of feeding places are tree-crowns and the tendency to visit them changes with respect to their distance from the breeding territory. The majority of foraging places in this species is localised near the nest, but often outside the breeding territory (Catchpole 1972, Borowiec 1983, Król 1984, own observation). In the study area Red Warblers were also often picking food from bushes growing near a dyke or were flying away to feed at the edge of the nearby forest. Król (1984) showed partial exclusion of feeding places within a breeding pair and between pairs and also aggressive behaviour among males collecting food outside their breeding territories. This would support the concept of a limiting effect of the feeding factor in the breeding period, even under favourable weather conditions. Under unfavourable conditions, the limiting influence of the feeding factor can be even much stronger.

In adverse weather conditions, birds may starve as they use much more energy to search and prey on insects than in periods of favourable weather. A support for the above idea is provided by the results of the logistic regression explaining the relation between fatness and wing length in years differing with regard to weather conditions, and also by preliminary studies of the food composition of birds from the genus *Acrocephalus* in cold and wet days (Nowakowski & Lewandowski 1995). Birds which died in a period of long-lasting rains and intensive colds during supplementary studies on populations of the Reed Warbler and the Sedge Warbler *Acrocephalus schoenobaenus* conducted in the Ławki Marshes (the Biebrza river valley) in 1989–1993, it was shown that over 50% of birds had digestive systems completely empty, and ca 30% only partly filled (less than $^{1}/_{3}$ of the stomach capacity). It was also noted that long-lasting periods of rain and cold (more than 12 hour of almost constant precipitation) are connected with higher mortality of short-winged birds. In the species studied in the Biebrza valley it was revealed that birds which died had significantly shorter wing in comparison with survivors (Table 6). It was also found that mortality was higher in the case of young birds, the proportion of which reached 85% in the group of dead birds (J. J. Nowakowski — unpubl. data). Higher mortality of short-winged birds during rains and colds suggests that they are worse at feeding during adverse weather and have to bear higher energetic expenses on searching for food.

Wing length is involved in the energy management of flight throughout its relation with wing surface. Tucker (1973) concluded from theoretical considerations that the flight speed in which the energetic expense of transport is the lowest is described by the equation $U = 14.6M^{0.20}$ where U is flight speed (in m/s), M — body mass (in kg) and value 14.6 in the proportionality coefficient. The author suggested that this coefficient

Table 6. Comparison of mean of wing length between dead and living individuals for the Reed and Sedge Warblers population in Biebrza Marshes in 1989–1993. $\bar{x}$ ± SD — mean and standard deviation of wing length for both living and dead birds.

	$\bar{x}$ ± SD (n)		t°	p
	living	dead		
Reed Warbler				
Juv.	66.80 ± 1.65 (182)	65.13 ± 2.03 (8)	2.30	< 0.001
Ad.	67.68 ± 1.25 (19)	65 (1)	2.09	< 0.002
Sedge Warbler				
Juv. (1993)	66.47 ± 2.01 (263)	64.00 ± 1.41 (2)	2.45	0.005
Juv. (1989–1993)	66.69 ± 1.80 (2259)	65.84 ± 1.34 (49)	4.34	0.0001
Ad. (1989–1993)	67.58 ± 1.73 (540)	66.58 ± 1.39 (9)	1.70	0.064

diminished markedly with a stable body mass when the wing span increased. Furthermore, Schmidt-Nielsen (1991) showed that the lifting force of the wing, which balanced the body weight during flight, is proportional among others also to the wing surface. A comparison of the body mass and wing length in 6 species from the genus *Acrocephalus* conducted by Aidley & Wilkinson (1987) displayed an interrelation of both the variables. Palearctic migrants (*A. scirpaceus, A schoenobaenus, A. arundinaceus*) had a remarkably lower proportion of body mass to the cube of the wing-length in comparison with sedentary species from the Western Africa (*A. baeticus, A. rufescens, A. gracilirostris*). Thus, it may be concluded that the wing length is an important adaptive feature in birds (also in the Reed Warbler) influencing energetic expenses on flight. As a consequence, in changing trophic conditions wing length may undergo selection optimising energetic budgets, as shown for different birds and mammals by McNab (1980, 1988).

It seems that short-winged Reed Warblers, whose flight can be less economic, are also worse at exploiting limited food. Therefore, individuals with a relatively shorter wing may be subject to increased mortality or less efficiently accumulate fat reserves needed for autumn migration. The strongest, negative, relations between the mean wing length and temperature in the group of adults occurred when birds had the most constrained energetic budget (June — expenditure on raising nestlings, August — preparation for migration). These relations explain ca two-third of the observed variation in the wing length (Fig. 2).

The influence of temperature on the determination of the long-term variation in wing length of young birds seems to be stronger than in adults (Fig. 3). Temperature, causing food shortage, indeed appears to most heavily affect young birds. This can be associated with their lack of experience in using food resources and also with incompletely developed mechanisms of thermoregulation. It is known that the tolerance of the Passerines to cold is higher when they take more food, while in case of food deprivation they limited heat production and it was mainly the stored fat which was then metabolised (Sturkie 1965). In the Passerines, the lowest value of the respiration quotient RQ was observed as soon as after three hours of starving (Sturkie 1965). It was also demonstrated experimentally that higher heat production was higher in thermoneutral temperature and that in low temperature metabolism of poorly feathered birds increases faster than in birds with normal plumage. In young birds plumage can be incompletely developed (Sturkie 1965).

Mechanism of habitat selection

In adult Reed Warblers, besides the negative correlation with the mean temperature of June, July and August, the among-year variation in wing length was remarkably connected with the logarithm of the sum of precipitation in May, which was accompanied by the positive correlation with the mean temperature of this month. The relations in juvenile birds were similar to those in adults, although the quantitative effect was smaller (Fig. 2 and 3).

Precipitation and temperature conditions in May (the period when the reed rush of the littoral zone develops) changing from year to year can contribute to variation of microhabitats of the rush area, which can mould their attractiveness for birds arriving from wintering grounds. Population studies conducted on Reed Warbler showed that this species establishes territories most often in reedbeds with water (Erlinger 1986, Borowiec & Dąbrowska 1991) or very wet (Anselin & Meire 1989). Such areas of reed rush with well developed dense vegetation are the optimal habitat for this species (Leisler 1981, Anselin & Meire 1989, Schulze-Hagen & Sennert 1990). Some studies on *Acrocephalus* species showed that optimal territories of highest quality are occupied by birds arriving earlier (Anselin & Meire 1989) which have longer wings than the birds arriving later.

It may be supposed that low precipitation in May accompanied by high temperature can negatively influence the water level in the littoral zone of waterbodies or change humidity in reedbeds during their formation. Differentiation in the attractiveness of habitats and a decrease in the area suitable for birds would intensify competition among males. The limitation of attractiveness of rush zone habitats could cause habitat selection and occupation of optimal areas by long-winged individuals which arrive early. Short-winged birds which come later would have to occupy suboptimal areas or would be excluded from breeding. Taillandier (1990) showed that earlier arriving males of the Reed Warbler had higher breeding success and M. Kupczyk (unpublished data) revealed that pairs breeding in optimal habitats produced more youngs than pairs inhabiting edge parts of reedbed. Also Catchpole (1974) showed higher breeding success of the Reed Warbled in homogeneous reed rush than in habitats with mixed vegetation, which was connected with higher humidity of the environment and larger amount of insects from the genus *Chironomus*. The usually extended in time and weakly synchronised arrival of the Reed Warbler (Borowiec 1983, Schulze-Hagen & Sennert 1990, Taillandier 1990) induces differences in choosing breeding places. Thus, with enhanced competition for breeding territories, the more effective choice of habitats by long-winged individuals would increase their frequency in population, explaining at the same time relations between weather conditions of May and the wing length of adult birds.

In the case of young birds analogous relations can occur only by inheritance because in spring juveniles do not exist yet and thus the direct influence of weather conditions on their wing length is not possible. In the above description of the influence of May weather on wing length of adult birds a hypothesis was put forward that the May weather induces the differentiation of habitats, causing intensification of competition for breeding places of the optimal quality. Pairs inhabiting optimal habitats have higher breeding success and their offspring should be better recruited to the breeding population. Because birds occupying optimal habitats have longer wings, this feature can appear in their offspring due to genotypic component in wing length.

The conclusion of this paper is that in the Reed Warbler the main mechanism shaping the population variation in the wing length among years is changing pressure and direction of natural selection that favours long-winged birds in cold and rainy years, which concurs with a mechanism based on habitat selection taking place after birds' arrival at the breeding area.

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STRESZCZENIE

[Wieloletnia zmienność długości skrzydła w populacji trzcinniczka]

Analiza przyczyn wywołujących długoterminową zmienność cech metrycznych w populacji ptaków podejmowana była sporadycznie. Badania prowadzono na stawach rybnych Okręt i Rydwan, koło Łowicza w latach 1972–1980, przy użyciu standardowych metod stosowanych podczas Akcji Bałtyckiej (Busse 1983). Materiał obejmował pomiary 4166 ptaków (Tab. 1). Zróżnicowanie długości skrzydła między latami testowane w modelach analizy wariancji było istotne zarówno wśród ptaków dorosłych jak i młodych (Fig. 1). Przeprowadzone porównanie istotności zróżnicowania średnich testem wielokrotnego rozstępu Tukey'a pozwoliło na wyróżnienie grup średnich istotnie różniących się od siebie (Tab. 2). Kierunki zmian wartości średniej długości skrzydła miedzy latami wykazywały taki sam przebieg w obu wyróżnionych grupach wiekowych populacji ($r = 0.95$, $n = 9$, $p < 0.01$). W latach 1972–1975 w badanej populacji stwierdzono mniejszą średnią długość skrzydła w porównaniu do lat 1976–1980. Istotnymi zmiennymi skorelowanymi ze zmianami średniej długości skrzydła miedzy latami okazały się czynniki pogodowe okresu lęgowego i przedwędrówkowego: logarytm sumy opadów atmosferycznych i średnia temperatura dobowa dla poszczególnych miesięcy (Tab. 3, Fig. 2 i 3). Długość skrzydła była dodatnio skorelowana z temperaturą maja i opadem czerwca, zaś ujemnie z pozostałymi zmiennymi w grupie ptaków dorosłych, przy czym ilościowo czynnik temperaturowy odgrywał najistotniejsza role w kształtowaniu zmienności (Fig. 2). W grupie ptaków młodych zależności te były bardzo podobne. W modelu zmienności długości skrzydła w tej grupie wiekowej najistotniejszą role odgrywały suma opadów lipca i sierpnia (Fig. 3). W okresie lat chłodnych i deszczowych (1976–1980), a więc niekorzystnych dla ptaków, populacja charakteryzowała się dłuższym skrzydłem, a ptaki długoskrzydłe efektywniej odkładały zapasowe materiały lipidowe potrzebne do odbycia wędrówki (Tab. 4). W okresie lat ciepłych z relatywnie niewielkimi opadami (1972–1975) populacja miała mniejszą średnią długość skrzydła, zaś efektywniej odkładały związki lipidowe ptaki krótkoskrzydłe (Tab. 5).

Czynniki pogodowe znane są jako warunkujące zmienność szeregu parametrów populacyjnych, a ich wpływ na zróżnicowanie długości skrzydła w badanej populacji trzcinniczka może wiązać się z kilkoma rodzajami oddziaływań. Niska temperatura i opady istotnie, negatywnie wpływają na zagęszczenie niektórych owadów w powietrzu (Turner 1984, Stocek 1986), zaś skład diety trzcinniczka (m.in. Bussmann 1979, Cardenas et al. 1983, Bibby & Thomas 1985) pozwala przypuszczać, iż w okresie takich niekorzystnych warunków pogodowych w środowisku obniża się dla niego ilość pokarmu dostępnego. Niska temperatura i opady wydają się jednocześnie istotnie oddziaływać na gospodarkę energetyczną ptaków. U wielu badanych gatunków stwierdzono, że niska temperatura i brak pokarmu powoduje szybkie spalanie materiałów zapasowych dla zachowania prawidłowych procesów termoregulacyjnych. U ptaków wróblowatych istotny spadek RQ następuje już po trzech godzinach głodzenia (Sturkie 1965). Ograniczenie dostępności pokarmu i niekorzystne czynniki pogodowe przy napiętym wówczas budżecie energetycznym wydają się być czynnikami selekcji kierunkowej, faworyzującej ptaki długoskrzydłe. Świadczy o tym stwierdzona w takim okresie dodatnia zależność między długością skrzydła a stopniem otłuszczenia ptaków, jak również fakt najprawdopodobniej relatywnie większej śmiertelności w grupie ptaków krótkoskrzydłych. Zależność taką stwierdzono w populacji biebrzańskiej tego gatunku i mimo odmiennych warunków siedliskowych w obu miejscach, wydaje się, że stwierdzona zależność mogła dotyczyć również omawianej populacji. Porównanie długości skrzydła ptaków, które zginęły ze średnią tej cechy dla ptaków, które przeżyły okres silnych, długotrwałych opadów wskazało na nielosową śmiertelność różnych morfometrycznie ptaków w populacji (Tab. 6).

Natomiast dodatnie związki temperatury z długością skrzydła i ujemne z log sumy opadów w maju mogą wynikać ze zróżnicowanego czasu przylotu osobników długoskrzydłych i krótkoskrzydłych w latach różniących się warunkami pogodowymi i selekcją siedlisk. Warunki pogodowe maja (niska suma opadów i wysoka temperatura) mogą wiązać się różnicowaniem wilgotności siedliska podczas formowania się szuwaru trzcinowego, wpływając na ograniczenie powierzchni atrakcyjnych dla ptaków, powodując tym samym nasilenie konkurencji o przestrzeń. W wielu badaniach (m.in. Erlinger 1986, Anselin & Meire 1989, Taillandier 1990) wykazano zajmowanie przez trzcinniczka terytoriów w szuwarze trzcinowym zalanym wodą lub silnie wilgotnym oraz wyższy sukces lęgowy par zajmujących takie optymalne siedliska. U trzcinniczka optymalne siedliska zajmują na ogół ptaki przylatujące wcześniej (Anselin & Meire 1989), a najwcześniej przylatują ptaki starsze i długoskrzydłe, przez co wzrasta wartość średniej długości skrzydła w populacji. Niska temperatura w maju może natomiast opóźniać i synchronizować czas przylotu różnych morfometrycznie grup ptaków, które zasiedlając jednocześnie środowisko, mogą tym samym wpływać na obniżenie średniej. Efekt takich zależności, stwierdzony w niewielkim ilościowo udziale u ptaków młodych, można więc wiązać się z genetycznym przekazywaniem cechy na potomstwo. Współczynnik powtarzalności długości skrzydła dla badanej populacji był dość wysoki ($r_{(b)} = 0.736$, $F^{\circ} = 72.25$, $p < 0.01$), wskazując pośrednio na istotny udział komponentu genotypowego oraz stałych czynników środowiskowych w kształtowaniu tej cechy.