Estimates of Energy Expenditures for Reproduction in the Pied Flycatcher *Ficedula hypoleuca* Pall. in an Industrially Polluted Environment

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Abstract—Energy expenditures for reproduction in local populations of the pied flycatcher in the environs of the Middle Urals Copper Smelter (Revda, Sverdlovsk oblast) have been estimated on the basis of the results of long-term studies (1989–2008). It is shown that the total energy expenditures per fledgling over the nesting period are 1.2 times higher than in the background area, which is explained by increased energy losses (by a factor of 4.1) resulting from partial mortality of the progeny (eggs or nestlings). Variation in the average energy "cost" of one fledgling in the heavily polluted zone is also higher, compared to the background area. Average energy expenditures per fledgling increase in years with cold weather, and the same is observed when the birds lay larger clutches.

Keywords: reproduction, reproduction cost, populations, pied flycatcher, industrial pollution, heavy metals, Middle Urals.

Studies on bird energetics have been rapidly developing over the last few decades. Modern instrumental methods and computation of time and energy budgets make it possible to successfully perform such studies under natural conditions. The amounts of energy expended for different forms of reproductive behavior and at different stages of the nesting cycle have been determined in a number of species. Allometric dependencies have been obtained for the relationships between reproductive energy expenditures and body mass (Dolnik, 1992, 1995, 1996; Kendeigh, 1970; Kendeigh et al., 1977). The energy-based approach to the estimation of expenditures for reproduction has an advantage over traditional censuses of offspring number. The reproductive parameters (nests, eggs and nestlings) and the efforts required from the parents differ between stages of the nesting cycle. Using the number of individuals alone, it is difficult to compare the losses at different stages of nesting (abandoned clutches, mortality of embryos and nestlings) and the expenditures of different pairs and local populations living under different environmental conditions. Such a comparison becomes possible if made in terms of energy, the universal equivalent of biological processes (Ricklefs, 1979).

Data on energy expenditures for reproduction can be used to analyze the reproductive strategies of different bird species and different conspecific populations (Dolnik, 1995). The energy costs of the offspring have been determined for the chaffinch *Fringilla coelebs* (*Populyatsionnaya ekologiya...*, 1982) and a number of waterfowl and other coastal bird species (Dolnik, 1995; Nakul, 2006). However, the expenditures of reproductive energy estimated for particular pairs do not fully reflect the population expenditures for reproduction, because unsuccessful reproductive attempts are not taken into account. In addition, the interpopulation variation of expenditures for reproduction remains poorly studied (Dolnik, 1995; Sanz et al., 1998). At the same time, local conditions (weather, biotopes, food resources) affect the demographic parameters of different populations, including the efficiency of reproduction. Increasing mortality in local populations as a result of shortage of resources is typical of pessimal habitats (Payevsky, 1985). Areas affected by industrial pollution can be included in this category. They are characterized by simplification of the structure of phytocenoses, decreased biological production at all trophic levels, and reduced ecological capacity of habitats for the majority of species (Vorobeichik et al., 1994; Chernen'kova, 2002; Kozlov et al., 2009). Considerable reproductive losses have been observed in birds that live under such conditions, including reduction of clutch size and an increase in the proportion of abandoned clutches and in egg and nestling mortality (Bel'skii et al., 1995a, 1995b, 2005; Nyholm, 1994; Eeva and Lehikoinen, 1995, 1996). These losses have to be reflected in increased energy expenditures of the local population on reproduction.

The aim of this study was to estimate pollution-related changes in energy expenditures for rearing one fledgling in local populations of the pied flycatcher in the Middle Urals. Calculations were based on the authors' own data on changes in reproduction and mortality parameters of this species along the pollution gradient and on published estimates of energy expenditures at different stages of the nesting cycle (Dolnik, 1995; Dolnik and Dolnik, 1981; Moreno and Carlson, 1989; Moreno and Sanz, 1994; Moreno et al., 1997). Traditional calculations of expenditures per breeding pair are complicated under natural conditions, since not all pairs that abandon their nest build a new one, and it is impossible to determine whether the nest is the second one of an older pair or the first one of a new late-breeding pair. The method we used for calculating the average "cost" of one fledgling for a local population makes it possible to bypass the uncertainty caused by the impossibility to determine the exact number of breeding birds.

MATERIAL AND METHODS

Long-term studies of the reproduction of pied flycatchers in nestboxes were performed in Nizhnie Sergi, Pervoural'sk, and Revda districts of Sverdlovsk oblast. The Middle Urals Copper Smelter, located in the environs of Revda, is a strong source of environmental pollution with polymetallic dust and sulfur dioxide, and the whole range of transition from almost undisturbed forest communities to the extreme stages of their degradation to industrial barren can be observed in this area (Vorobeichik et al., 1994). Three distinct zones of toxic load have been distinguished along the pollution gradient: the impact zone (heavy pollution; up to 3 km from the plant); the buffer zone (moderate pollution; 3–15 km from the plant); and background zone (pollution at the regional background level; more than 15 km westward from the plant, opposite to the prevailing wind direction). These zones were distinguished with regard to the state of forest phytocenoses and the contents of heavy metals in the soil (horizon A1, extraction with 5% HNO_3). The average concentrations of Cu ($\pm$ SE, µg/g air-dry soil) were 86.9 ± 7.6 ($n = 32$) in the background zone, 862.4 ± 63.9 ($n = 42$) in the buffer zone, and 3769.6 ± 151.9 ($n = 47$) in the impact zone; the concentrations of Pb were 67.3 ± 4.9, 283.2 ± 14.1, and 639.1 ± 43.2 µg/g, respectively (Bel'skii et al., 2005).

In each zone, three or four plots with nestboxes were established (a total of 11 plots). The nestboxes were occupied mainly by the pied flycatcher. This species is migratory; in the Middle Urals, it arrives to its nesting areas in early May and has one reproduction cycle per season. The birds start to lay eggs during the second half of May. Most nestlings fledge during the last ten days of June; in late nests, sometimes as late as mid-July. After fledging, the broods begin to migrate and leave their nesting areas.

Regular censuses of the occupied nestboxes were taken annually from 1989 to 2008, recording the number of eggs and the numbers of nestlings after hatching and before fledging. In cases of nestling mortality, the age at death was estimated. The mass of the nest material was determined by weighing some nests ($n = 129$) after the nesting season (feces and food remains were removed prior to weighing).

The energy expenditures of animals can be expressed either in absolute units (kJ/day) or in the relative units of basal metabolism (BM) (Dolnik, 1995). Basal metabolism is the minimum amount of energy required to maintain fundamental physiological processes in an organism at complete rest, in the absence of food digestion and expenditures for thermoregulation and biological production (growth, reproduction, molting). Expressing the expenditures in BM units is convenient for extrapolations between species, since activities of the same type (flight, running, etc.) have the same dependence on the BM value in all birds (Dolnik, 1995). The value of one BM unit—basal metabolic rate (BMR)—in the pied flycatcher under natural conditions was calculated on the basis of its oxygen consumption 2.92 mL O_2/g body weight per hour, determined by the method of doubly labeled water (Moreno and Carlson, 1989; Moreno and Sanz, 1994). Since the consumption of 1 L O_2 is accompanied by the release of 20 kJ energy (Schmidt-Nielsen, 1990), then, taking into account the average body weight of female and male pied flycatchers in the Middle Urals (13.45 and 12.59 g, respectively), the respective BMR values are 18.85 and 17.64 kJ/day, averaging 18.25 kJ/day for both sexes. The rate of bird metabolism probably does not depend on the level of pollution in their environment (Eeva et al., 2003). Therefore, we used the same BMR value for birds in all toxic load zones. There are other estimates of BMR value (Gavrilov et al., 1996; Bushuev, 2009), but their authors did not measure some other parameters relevant to this study.

The nests of the pied flycatcher where at least one egg was laid, including those with abandoned eggs, were included in the calculations. For each nest, the energy expended for rearing the offspring—which includes nest-building, production and incubation of the eggs, and feeding of the nestlings—was calculated. The first three items are energy expenditures of the female alone, while the last item includes the expenditures of both parents. The total expenditures of the local population (all nests in each particular zone of pollution) were divided by the total number of fledglings. The resulting value was the average energy cost of one fledgling (kJ):

$$C_{fl} = \frac{\sum PE_{nest} + \sum PE_{egg}N_{egg} + \sum PE_{inc} + \sum PE_{fl}N_{fl} + \sum PE_d N_d}{\sum N_{fl}},$$

where C_{fl} is the sum of productive energy expenditures for one fledgling in a given population; PE_{nest}, productive energy for building the nest; PE_{egg}, productive energy for synthesizing one egg; N_{egg}, number of eggs in the clutch; PE_{inc}, productive energy for incubating the clutch; PE_{fl}, productive energy for feeding one nestling until it leaves the nest; N_{fl}, the number of fledglings in the nest; PE_d, productive energy of rearing one nestling until the day of its death; and N_d, number of dead nestlings.

The productive energy for reproduction in the pied flycatcher was calculated in the following order:

(1) **Nest-building.** The average nest mass (M_{nest}) was 44.3 ± 1.8 g ($n = 46$) in the background zone, 27.3 ± 2.2 g (20) in the buffer zone, and 35.7 ± 1.7 g (63) in the impact zone. The average energy expenditures for building 1 g of the nest in passerines are 0.09 BMR (Dolnik, 1995), i.e., 1.64 kJ for the pied flycatcher in the study area. Therefore, the total productive energy for building the nest $PE_{nest} = 1.64 \times M_{nest}$.

(2) **Egg production.** The amount of energy in one pied flycatcher egg was calculated as the product of its mass and its specific energy content, 4.98 kJ/g wet mass, including the shell (Ojanen, 1983). The average mass of one egg was calculated from the average egg volume in each zone of pollution (Bel'skii et al., 1995a) and average egg density (including the shell), 1.06 g/cm^3 (Rahn and Paganelli, 1989). The results were 1.71 ± 0.01 g in the background zone; 1.76 ± 0.02 g in the buffer zone; and 1.66 ± 0.02 g in the impact zone. Since the efficiency of egg production is 70% (King, 1973), the average productive energy for synthesizing one egg PE_{egg} is 12.16 ± 0.04 kJ in the background zone, 12.49 ± 0.11 kJ in the buffer zone, and 11.80 ± 0.12 kJ in the impact zone.

(3) **Egg incubation.** The expenditures for incubating the clutch and for self-maintenance (DEE_{inc}, kJ/day) in female pied flycatchers, measured by the doubly labeled water method, are

$$DEE_{inc} = 15.38 + 9.32 \times N_{egg}$$

(Moreno and Sanz, 1994).

The average expenditures for self-maintenance in the course of incubation in female flycatchers (calculated for *Empidonax minimus* and *E. trailii*, Tyrannidae) are 1.74 BMR (Dolnik, 1995); i.e., for pied flycatchers in the study area, 32.7 kJ/day. Since the energy of incubation alone was calculated, we subtracted the energy of self-maintenance from DEE_{inc}. The total productive energy for incubating the clutch PE_{inc} was calculated taken the average incubation period to be 14 days.

(4) **Feeding the nestlings.** The energy costs of feeding pied flycatcher nestlings were determined in Spain by the doubly labeled water method (Moreno et al., 1997). In broods (4.2–4.6 nestlings) aged 13 days, parents' energy expenditures for feeding one nestling with an average body mass of 12.83 g amount to 14.73 kJ/day (without expenditures for self-maintenance), or 0.87 BMR (for the Spanish population of the pied flycatcher, 1 BMR = 16.95 kJ/day; Moreno et al., 1997). Therefore, the expenditures for feeding one nestling in the Middle Urals in our case are 15.86 kJ/day. The energy expenditures on feeding one nestling depend on the age of the nestling in the common kestrel *Falco tinnunculus* (Deerenberg et al., 1995) and common starling *Sturnus vulgaris* (Ricklefs and Williams, 1984), but not in the great tit *Parus major* (Sanz and Tinbergen, 1999), northern wheatear *Oenanthe oenanthe* (Moreno, 1989), and pied flycatcher (Moreno et al., 1997). Taking the average nestling period to be 15 days, the expenditures of the parents for rearing one nestling until it fledges (PE_{fl}) are 237.8 kJ. The expenditures for one dead nestling (PE_d) are 15.86 kJ/day multiplied by its age at death.

Calculating the distribution of losses by stages of the nesting cycle, we took into account the fact that egg mortality renders useless not only the expenditures for incubation but also the expenditures for egg production and, if the whole clutch is lost, also the expenditures for building the nest. Similarly, the losses at the feeding stage included not only the expenditures for feeding the nestlings until their death but also the expenditures for synthesizing and incubating the eggs from which they hatched.

The significance of differences between the three pollution zones was estimated with the Kruskal–Wallis and Mann–Whitney tests. The distributions of energy expenditures over the nesting stages in different zones were compared using the χ^2 test. The relationships between variables were determined using Pearson's linear correlation. The average values of the parameters for a certain year in each particular zone of pollution were used in analysis as replications. The dependence of energy expenditures on several variables was estimated by stepwise linear regression.

RESULTS

We studied two parameters: (1) total energy expenditures per fledgling in the local population (combined expenditures for the surviving and perished offspring) and (2) energy loss of the population resulting from partial offspring mortality (abandoned nests with eggs, production and incubation of eggs with perished embryos, feeding nestlings that did not survive to leave the nest).

The calculations have shown a significant change in the total productive energy expenditures per fledg-

Expenditures of productive energy per fledgling in local populations of pied flycatchers in different pollution zones in the Middle Urals and distribution of total expenditures and energy losses by stages of the nesting cycle (average ± SE)

Parameter, stage of nesting cycle	Pollution zone (observation period, years)		
	background (20)	buffer (18)	impact (19)
Productive energy expenditures per fledgling, kJ/season			
Total expenditures	384.1 ± 5.5	395.8 ± 9.0	465.0 ± 21.3**
Energy losses	28.5 ± 5.2	46.2 ± 8.7*	116.7 ± 20.1**
Distribution of total expenditures by stages of nesting cycle, %			
Nest-building	3.7 ± 0.1	2.7 ± 0.1	7.2 ± 1.0
Egg production	3.8 ± 0.1	4.2 ± 0.1	5.5 ± 0.5
Egg incubation	28.2 ± 0.3	29.8 ± 0.6	28.8 ± 0.9
Feeding the nestlings	64.3 ± 0.5	63.3 ± 0.7	58.5 ± 0.9
Distribution of energy losses by stages of nesting cycle, %			
Nest-building and egg-laying	5.6 ± 1.4	2.3 ± 0.8	10.5 ± 3.3
Egg incubation	42.6 ± 3.3	51.2 ± 6.1	51.0 ± 4.9
Feeding the nestlings	51.8 ± 3.7	46.5 ± 6.2	38.5 ± 5.8

Note: Differences from the background value are significant at $*p < 0.05$ or $**p < 0.001$ (Mann−Whitney test).

ling along the pollution gradient (Kruskal−Wallis test $H = 24.66$, $df = 2$, $n = 57$, $p < 0.001$) (table). These expenditures increased by a factor of 1.2 in the impact zone, compared to the background zone (Mann−Whitney test $U = 29$, $df = 38$, $p < 0.001$) and the buffer zone ($U = 48$, $df = 36$, $p < 0.001$), but did not differ between the buffer and background zones ($U = 128$, $df = 37$, $p = 0.13$). The effect of industrial pollution was more clearly manifested in the values of energy loss. The total losses per fledgling differed significantly between the pollution zones ($H = 31.41$, $df = 2$, $n = 57$, $p < 0.001$), being 1.6 times higher in the buffer zone and 4.1 times higher in the impact zone than in the background zone (table; $U = 100$, $df = 37$, $p = 0.019$ and $U = 12$, $df = 38$, $p < 0.001$, respectively). The losses in the buffer and impact zones differed by a factor of 2.5 ($U = 36$, $df = 36$, $p < 0.001$).

Analysis of the distribution of productive energy expenditures by stages of the nesting cycle has shown that the highest expenditures were those for feeding the nestlings, about half as much energy was expended for egg incubation, and the smallest proportion of energy was required for egg production and nest building (table). In a strongly polluted environment, the relative expenditures for building the nest and for synthesizing the eggs increased by factors of 1.9 and 1.4, respectively, compared to the control, while the proportion of energy expended for feeding the nestlings slightly decreased (by a factor of 1.1). Nevertheless, the distribution of energy expenditures by stages of the nesting cycle did not differ between the background and impact zones: $\chi^2 = 2.77$, $df = 3$, $p = 0.43$.

The distribution of energy losses by stages of the nesting cycle differed from the distribution of total expenditures (table): in the background zone, $\chi^2 = 10.27$, $df = 2$, $p = 0.006$; in the buffer zone, $\chi^2 = 22.97$, $p < 0.001$; in the impact zone, $\chi^2 = 24.09$, $p < 0.001$. While the total expenditures for incubation were no higher than 30% of the energy expended for rearing the offspring, the losses at the incubation stage reached 40−50% of the total losses. In the background zone, the losses at the stage of feeding the nestlings were higher than during the incubation period, while these two parameters in the buffer zone were approximately equal. In the impact zone, the energy lost as a result of egg mortality was higher than that lost with perished nestlings. The losses due to nest desertion by females at the egg-laying stage were also higher in the impact zone, compared to the other zones (table). Changes in the structure of losses along the pollution gradient were statistically significant ($\chi^2 = 8.24$, $df = 2$, $p = 0.016$).

If the structure of losses is calculated from the numbers of dead individuals (eggs and nestlings), it will be different from that described above. In the background zone, 19.7% of offsprings perished at the stage of egg-laying; 50.7%, at the stage of incubation; and 29.6%, at the nestling stage. At the same time, the relative losses of energy were especially high at the last stage of the cycle (table). The proportion of energy losses due to nestling mortality in the other zones was also higher than losses estimated from offspring number.

Analysis of interannual variation in the total energy expenditures per fledgling over the 20 years of study has revealed a considerable increase in their range in the impact zone, compared to the other zones (figure). The maximum values of energy expenditures reached 804.6 kJ/in the impact zone, 524.9 kJ/season in the buffer zone, and 476.2 kJ/season in the background zone, with the minimum values being comparable in all three zones (348−387 kJ/season). The average coefficient of variation (±SE) for this parameter in the impact zone (20.0 ± 3.5%) was also higher, compared to the buffer zone (9.6 ± 1.7%) and background zone (6.3 ± 1.0%). The interannual dynamics of the total expenditures was similar in the background and buffer

Expenditures per fledgling, kJ/season
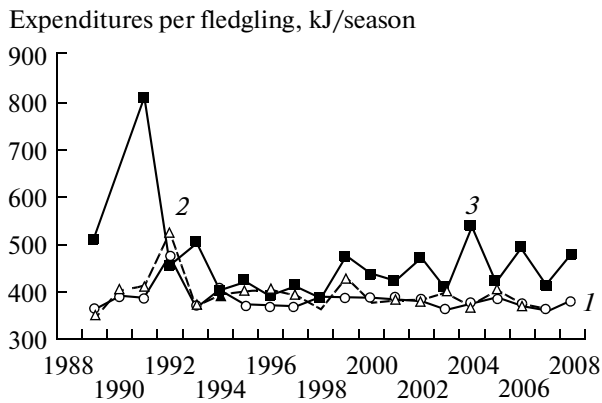
Interannual variation of average energy expenditures per fledgling in the pied flycatcher (1) in the background, (2) buffer, and (3) impact zones.

zones: linear correlation coefficient $r = 0.83 \pm 0.14$, $p < 0.001$. The expenditures in the impact and buffer zones were not correlated ($r = 0.03 \pm 0.26$), as well as those in the impact and background zones ($r = -0.004 \pm 0.243$). The dynamics of energy expenditures displayed no cyclicity (figure).

Long-term data on each pollution zone were used to analyze the dependence of the total energy expenditures and losses per fledgling on (1) clutch size, (2) phenology of reproduction (median date of the start of egg laying), and (3) average temperature of May and June (the period of mass nesting). The average parameters for a particular year in each zone were used for as replications. Since the clutch size correlated with the starting date of egg laying (linear correlation coefficient $r = -0.65$, $n = 56$, $p < 0.001$), the latter parameter was excluded from the model. Stepwise multiple regression analysis showed that the value of total energy expenditures per fledgling in the background zone had a negative dependence on the temperature of May and June (standardized regression coefficient $\beta = -0.48 \pm 0.21$, $p = 0.03$) and, at a tendency level, on the clutch size ($\beta = 0.44 \pm 0.21$, $p = 0.053$). These two factors explained, respectively, 24% and 21% of variance in the dependent variable (squared partial correlation). In the buffer zone, the expenditures of the birds correlated, at a tendency level, only with the temperature of the nesting season ($\beta = -0.44 \pm 0.22$, $p = 0.067$), which explained 19% of the variance. In the impact zone, the expenditures of the birds also showed correlation with the average temperature of May and June ($\beta = 0.49 \pm 0.21$, $p = 0.033$; 26% of the variance). The value of energy losses in the background zone showed a negative dependence on the temperature of May and June ($\beta = -0.48 \pm 0.21$, $p = 0.036$; 23% of the variance) and, at a tendency level, on the clutch size ($\beta = 0.41 \pm 0.21$, $p = 0.069$). In the impact zone, the value of losses positively correlated with the temperature of the nesting season ($\beta = 0.49 \pm 0.21$, $p = 0.033$; 25% of the variance).

DISCUSSION

The distribution of productive energy expenditures by stages of the nesting cycle shows that the highest expenditures fall on the period of feeding the nestlings (table). This is explained by the highest level of locomotor activity of the adult birds during this period. The relative decrease in the expenditures for feeding the nestlings in the impact zone, compared to the background zone, is due to the smaller number of nestlings per nest. By contrast, the expenditures for synthesizing the eggs and, especially, for building the nests are higher in the impact than in the background zone. This redistribution of energy expenditures results from the increased proportion of abandoned, incomplete clutches in the impact zone: $18.5 \pm 2.3\%$ ($n = 276$ nests), compared to $5.2 \pm 0.7\%$ ($n = 911$) in the background zone (Bel'skii, 2010). This fact shows that the structure of energy losses in polluted environment changes due to increasing expenditures for nest-building and egg production.

The total energy expenditures per fledgling in the pied flycatcher increase with an increase in pollution level due to higher energy losses. Importantly, if we did not take into account abandoned nests and perished eggs and nestlings, energy expenditures per fledgling would be similar in all three zones: 345–353 kJ/season. This value, approximately equal to 19 BMR, is likely the species-specific minimum energy cost of one fledgling under the conditions of the Middle Urals. It is higher than the cost of one fledgling in the chaffinch, 9.1 BMR (Dolnik, 1992). The differences between species are probably explained by their specific ecological features. The species feeding on highly mobile (e.g., flying) prey, such as flycatchers, expend more energy for feeding the nestlings, compared to the gatherer species (such as the chaffinch).

The conclusion that birds in the zone of industrial impact expend more energy for reproduction is not unexpected and agrees with previous data on offspring mortality in chemically polluted environments (Nyholm, 1994; Eeva et al., 1995, 1996; Bel'skii et al., 1995a, 1995b, 2005). The approach used in this study, with diverse parameters being converted into their energy equivalents, provided for a correct comparison of reproductive efforts and allowed us to reveal subtle differences between local populations of pied flycatchers. Thus, their average reproductive parameters such as clutch and brood sizes (Bel'skii et al., 1995a, 1995b, 2005) and the average expenditures per fledgling in the buffer zone do not differ from those in the background zone, but energy losses in the buffer zone are significantly higher. This fact illustrates that offspring mortality in the pied flycatcher increases at the intermediate levels of toxic load considered in this study.

Another novelty in the proposed approach is that the losses at different stages of the nesting cycle are compared more correctly. Traditionally, ornithologists express the mortality of eggs and nestlings in their numbers or percentage of the number of eggs laid (Payevsky, 1985), thereby unintentionally equating parental expenditures for egg production and incubation to those for care of nestlings. The approach used in this study is aimed at taking into account all energy expended per member of the offspring from the start of nesting. For an egg with a perished embryo, this energy equals the expenditures for egg production and incubation, while for a perished nestling it additionally includes the expenditures for its feeding prior to death. Thus, taking into account the progressive increase in the energy cost of one member of the offspring during its development, we can more adequately assess the dynamics of reproductive losses during the entire nesting cycle.

The increased variation in the energy cost of one nestling in the impact zone may indicate destabilization of environmental conditions under technogenic impact. The increased average value and variation of expenditures for reproduction allow us to characterize the impact areas as pessimal for a number of bird species.

Analysis of the dependence of pied flycatcher's expenditures for reproduction on several variables has shown that the strongest effect on the energy cost of one fledgling is that of the weather. The negative correlation between the average cost and the temperature of the nesting period in the background zone reflects the effect of air temperature on physiological processes in the birds and the state of their food supply. When temperature drops, causing a decrease in the activity of invertebrates (prey for the birds), more energy is expended for foraging. As a result, reproduction-related expenditures and losses are higher in colder years. The opposite trend observed in the impact zone (higher expenditures and losses in warmer years) probably reflects local specificity of phenological conditions. On the one hand, polluted areas are typically characterized by earlier snow melting in spring and earlier start of plant growth (Kozlov et al., 2007), which should lead to shifts in the phenology of phytophagous insects, which make up most of the pied flycatcher's diet. Despite this fact the reproduction of pied flycatchers in the impact zone starts later than in the background zone: the difference varied from year to year between 1 and 12 days, averaging 5.8 ± 0.7 days (Bel'skii, 2010). Under normal conditions, the period of maximum food demand in insectivorous birds coincides with a peak in the abundance of phytophagous insects. In the polluted zone, the pied flycatcher's reproduction period appears to be delayed relative to the peak of food abundance. In warmer years, the development of the larvae of phytophagous insects is accelerated, and the time gap between the period of the maximum demand for food and the period of its highest abundance increases. As a result,

the reproduction-related losses of the pied flycatcher in the highly polluted zone are increased. Such desynchronization between the reproduction of migratory birds and the development of their food supply in a warming climate has led to a decrease in the reproductive success and abundance of some passerine species in Western Europe (Visser et al., 2006; Both et al., 2010).

The positive correlation of reproductive energy expenditures and clutch size in the background area complies with the well-known fact that the clutches producing the largest numbers of fledglings are usually those of modal size (or slightly larger), rather than of the maximum size. The increase in clutch size beyond the optimal level leads to higher nestling mortality, especially under unfavorable environmental conditions (Klomp, 1970; Payevsky, 1985; Zimin, 1988).

Thus, the high energy cost of pied flycatcher offspring in polluted areas reflects the generally unfavorable conditions for the existence of this species and limits the possibility of self-maintenance for its local populations. The low reproductive efficiency of the pied flycatcher in impact zones (Bel'skii et al., 1995b, 2005) suggests that the long-term existence of this species in disturbed habitats is impossible without a regular inflow of immigrants.

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