

Factors Affecting the Between-Season Divorce Rate in the Urban Populations of the European Blackbird *Turdus merula* in North-Western Poland

Author: Wysocki, Dariusz

Source: *Acta Ornithologica*, 41(1) : 71-78

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: <https://doi.org/10.3161/068.041.0101>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Factors affecting the between-season divorce rate in the urban populations of the European Blackbird *Turdus merula* in north-western Poland

Dariusz WYSOCKI

Department of Vertebrate Anatomy and Zoology, University of Szczecin, Wąska 13, 71-412 Szczecin, POLAND, e-mail address: darekw@univ.szczecin.pl

Wysocki D. 2006. Factors affecting the between-season divorce rate in the urban populations of the European Blackbird *Turdus merula* in north-western Poland. *Acta Ornithol.* 41: 71–78.

Abstract. The between-season divorce rate of the European Blackbird was studied in 1997–2003 in two city parks in northwest Poland. Within the population studied, 52 and 51% of pairs in each park were observed to divorce. Of the eight parameters included in the analysis, the divorce rate was found to depend on marriage training and the time of territory acquisition. Territory quality, breeding success, synchrony in territory acquisition, age and size of the partners were unimportant. 19.5% of pairs with marriage training were observed to divorce, whereas 65.5% of pairs without marriage training did so. Birds acquiring their territories earlier divorced their partners significantly less frequently than those acquiring a territory at a later date. During the first post-divorce breeding season, young males that stayed in the park started breeding earlier than in the preceding year; old males started breeding later, whereas the difference was not significant in young or old females. Regardless of their age, the divorced birds showed a reduced number of fledglings raised with a new partner. The reduced breeding success may be a result of poor adaptation to increased pressure from predators. Similar divorce rates in pairs with and without breeding success and the rarer divorces among pairs claiming their territories earlier strongly support the habitat-mediated hypothesis. However, the more frequent desertion of poor territories by females, as well as differences found between older males and females in the timing of the onset of breeding before and after divorce, indicate that an individual may choose divorce to maximize fitness.

Key words: European Blackbird, *Turdus merula*, between-season divorce rate, mating

Received — Nov. 2005, accepted — May 2006

INTRODUCTION

Despite the large number of studies on avian mating systems and a substantial increase in the amount of relevant information, we lack a full understanding of the factors that determine whether pair bonds are maintained or severed. In birds, divorce is defined as the separation of pair mates with re-mating of at least one of the pair partners, and eight hypotheses have been proposed to explain the phenomenon of between-season divorce in monogamous species (Choudhury 1995, Ens et al. 1996). According to Heg et al. (2003) the hypotheses can be grouped into four categories based on the ultimate causes of between-season divorces. All other hypotheses can all be considered as proximate variations of these four ultimate explanations. Two adaptive

views on divorce predict a negative relationship between divorce and breeding success.

The “incompatibility hypothesis” suggests that the two members of a pair may not be intrinsically of poor quality, but when together, their combined qualities result in reduced fitness. It predicts that pairs with a low breeding success will more likely divorce, and after divorce, both birds should increase their reproductive success with the new mate (Coulson 1972, Rowley 1983).

The “better option hypothesis” predicts that one partner will benefit from divorce, leaving its former mate as a victim, so an individual’s reproductive success expected in the future should be higher with the new than with the old mate, irrespective of the degree of the previous success (Ens et al. 1993). Nevertheless, the low prior breeding success can in many cases increase the probability

of improvement. The divorce rate should also increase with a greater availability of unpaired individuals in the population, for example at a higher mortality rate; increasing numbers of widowed birds; and higher recruitment rate of the juveniles (Choudhury 1995). As opposed to these two hypotheses, the next two has been considered non-adaptive.

The "forced divorce hypothesis" (Ens et al. 1993, Taborsky & Taborsky 1999) states that where one of the partners is chased out by an usurper, only the usurper is expected to benefit. According to the "habitat-mediated hypothesis" (Owen et al. 1988, Desrochers & Magrath 1993), an external event other than usurpation destroys the basis of the partnership leading to divorce. According this hypothesis the reproductive success will not influence divorce rate and will not increase after divorce. Other hypotheses can all be considered as proximate variations of these four ultimate explanations. For example, according to Heg et al. (2003), the musical chair hypothesis (Dhondt & Adriaensen 1994) and the asynchronous arrival hypothesis (Gonzalez-Solis et al. 1999) might be variants of incompatibility hypothesis (early- and late-arriving individuals reproduce equally well, but pair members arriving at different times on the breeding grounds do worse) or of the better option hypothesis (early arrivers do best; late arrivers are in a poorer condition and are less fit; early arriving birds can better pair with birds that also arrive early).

A model by McNamara & Forslund (1996) suggested that divorce frequency depends on longevity, variation in quality between mates, and the costs of divorce and mate retention. The model predicted that due to increased costs of waiting for a partner that has not survived the winter, divorces should be more frequent in short-lived bird species. One of the exceptions are species that spend the whole year within their territories or form flocks and therefore have complete knowledge on the mate's survival, so the costs of mate death do not apply to them (Rowley 1983, Freed 1987).

In the present study I have tested factors affecting the between-season divorce rate of blackbird occurring in Central Europe.

Although the European Blackbird is one of the best known European birds, most long-term population studies in which the majority of individuals were colour-ringed have been conducted in Western Europe where numerous ecological variables (e.g. density and the migratory status of a

population) differ from those observed in Central Europe (Snow 1988, Desrochers & Magrath 1996, Streif & Rasa 2001). Both the German population and the populations studied in the UK are stationary and winter in their breeding territories or in their immediate vicinity (Snow 1988, Desrochers & Magrath 1996, Streif & Rasa 2001), while as little as 10–20% of the studied population spends the winter near its territory (D. Wysocki, unpubl.).

The population studied in this paper is mostly monogamous (Wysocki 2004b) and despite its low density (Wysocki et al. 2004) there is strong competition for optimal nest sites (Wysocki 2004c, Wysocki & Walasz 2004).

METHODS

The observations were made in 1997–2004 in two city parks of Szczecin: the Żeromski Park (Park Z, 21.9 ha) and the Kownas Park (Park K, 16 ha). In each park, observers (1–3 persons) recorded bird behaviour every other day from dawn until the afternoon (6–8 h per day). From 70% (in 1997) to more than 90% (after 1999) individuals in both parks were colour-ringed. Park Z, located centrally in the city, is subjected to constant human intrusion, and is surrounded by buildings and streets. The annual return rates to the park were 73 and 67% for males and females, respectively. The coefficient of correlation between male and female ages was $r = 0.30$ ($n = 291$, $p < 0.05$).

Park K is a part of a large green that grades into suburban woodlands. The intensity of pedestrian traffic is much lower. The annual return rates were 59% and 48% for males and females, respectively. The coefficient of correlation between member of the pair ages was $r = 0.34$ ($n = 135$, $p < 0.05$). The study area has been described in detail by Wysocki et al. (2004); the most important ecological parameters of the studied population were given by Wysocki (2005c).

The timing of territory occupation and wintering behaviour were determined from observations made at 3- to 7-day intervals during winter (until the end of February) and at 1- to 2-day intervals later from March–July. If an individual was at least once encountered in a park and its vicinity, the bird was assumed to have spent the month of encounter in the park; if the bird was not observed, it was assumed to have spent the month outside the park. It was also assumed that the time when the mate moved in was the time of the territory acquisition by the pair (e.g. if the

male had occupied the territory since pentad 5 on and the female moved in pentad 10, that pentad was the time of territory acquisition). In winter when the pair mates were observed in the same fragment of the park (usually the same patch of the bushes — there were six different patches in park Z) or of a housing estate (there were four different estates in the vicinity of park Z) it was assumed that the pair was spending the winter together. If the pair members were seen in different locations on the same day, it was assumed that the pair was spending the winter separately.

When breeding dates were compared, the date of finding the first egg in a park was assumed to mark the beginning of the reproductive season in a given year (if the first egg was laid on 1 April, pentad 1 of the breeding season extended from 1 until 5 April). To avoid pseudoreplication, only the first year was taken into account when comparing the time of first breeding of those females that formed a bond with their partners for a number of consecutive years. The tarsus length was measured with callipers to the nearest 0.05 mm (Svensson 1992). If the difference between the right tarsi of a male and a female were lower than or equal to 1 mm, the two individuals were assumed to be similar in size; if the difference was higher than 1 mm, the two birds were assumed to differ in size. An individual's age was determined from contrast in wing plumage (Svensson 1992). Because most of the birds were ringed as nestlings, fledglings, or in their second year of life, the exact age structure of the population studied is well known (Wysocki 2004a).

Data processing and analysis

I defined divorce as occurring if both members of a pair were individually marked in one year and survived to the next without reuniting. In Park Z, 239 out of 314 pairs observed in the seven years of study were colour-ringed. In Park K data on 94 colour-ringed pairs out of 164 observed pairs were collected (see Table 1). In addition, for pairs that divorced during the breeding season, the between-season divorce rate analysis included only the most recent partner of a given individual. To determine effects of territory quality on divorce rate, the park was divided into 100 m quadrants. In each quadrant, the number of fledglings raised during a given season was determined. A quadrant was classified as good if more than 30 fledglings were raised from 1997–2003 (mean 54.5 ± 18.0 , $n = 8$), intermediate for 15–30 fledglings

(23.5 ± 4.3 , $n = 8$), or poor with less than 15 fledglings (7.3 ± 4.3 , $n = 22$). From September until the end of February at least once week, the park and its immediate surroundings (the most important feeding places within the radius of about 500 m) were checked to determine wintering sites of individuals.

The logistic regression was used to identify the most important factors affecting divorce rate in the study sites. In the model, the occurrence (or otherwise) of divorce was the dependent variable and fixed factors included the explanatory variables: male and female age, marriage training (the pairs staying together in the previous breeding season were assumed as marriage-trained, i.e., forming pairs for two consecutive breeding seasons at least; the pairs that bonded up in a given year were non-marriage-trained), differences between tarsus length of mates, time of territory occupation by both partners, synchrony of territory occupation, territory quality, and breeding success in the previous breeding season. For the purpose of data analysis, the time of territory acquisition was divided into three periods: I — pentads 1–10 (early pairs), II — pentads 11–20 (intermediate pairs), and III — the last pentad 20 (late pairs). It was further assumed that, if a male and a female acquired their territory during one or two pentads, they showed high synchrony; if the timing extended to 3–5 pentads, the synchrony was assumed to be intermediate; and if the timing of territory acquisition by a male and a female differed by more than 5 pentads, the synchrony was low. Because Park K is a part of a large green area with scattered houses and gardens, wintering mode of the blackbird could be precisely determined for Park Z only; with respect to Park K in most cases we only know the time of territory acquisition.

The statistical treatment of data was based on pentads (five-day long intervals, for example, pentad 1 proceeded from 1 to 5 January, pentad 2 from 6 to 10 January, etc.).

Presented data contain mean \pm SD. Student's *t* test was used to compare divorce rate in relation to the timing of territory acquisition, while Wilcoxon's pair sequence test was used to compare the number of nestlings before and after divorce (compliance to the normal distribution was tested with the Kolmogorov-Smirnov test); χ^2 test was used to test for significance of differences in divorce rate and territory change. The statistics were performed with the STATISTICA software package.

RESULTS

Divorce rate

Mate change due to a partner's disappearance accounted for an average of 43.1% of changes in Park Z and 59.6% in Park K (Table 1). Among the birds whose survival during the winter was known, the between-season divorce rate was similar in both parks ($\chi^2 = 0.04$, $df = 1$, $p = 0.84$) and showed no differences between years (for both parks combined: $\chi^2 = 13.04$, $df = 13$, $p = 0.44$). The mean divorce rate was 52% in Park Z ($\chi^2 = 15.65$, $df = 13$, $p < 0.27$) and 51% in Park K ($\chi^2 = 3.75$, $df = 13$, $p < 0.99$) (Table 2).

Because I found no differences in the divorce rates between the parks, data were pooled for all subsequent analyses.

Table 1. Mate change due to partner's disappearance (%) in 1997–2003. N — sample size.

Year	Park Z	N	Park K	N
1997	33.3	9	57.1	7
1998	30.8	13	50.0	8
1999	27.3	22	55.6	9
2000	42.1	38	60.0	20
2001	34.0	47	42.1	19
2002	58.5	53	66.7	15
2003	47.4	57	81.2	16
All years	43.1	239	59.6	94

Table 2. Between-season divorce rate (%) in 1997–2003. N — sample size.

Year	Park Z	N	Park K	N
1997	16.7	6	33.3	3
1998	30.0	10	25.0	4
1999	52.9	17	66.7	3
2000	65.2	23	50.0	8
2001	54.8	31	54.5	11
2002	31.8	22	80.0	5
2003	73.3	30	33.3	3
All years	43.1	139	51.3	37

Table 3. Logistic regression coefficients (B), their standard errors (SE) and probabilities (p) for individual predictors of between-season divorces of European Blackbirds. Overall Model Fit: $\chi^2 = 29.89$, $df = 8$, $p = 0.0002$.

Factor	B	SE	p
Difference between mates in the tarsus length	-0.41	0.40	0.30
Breeding success in the previous breeding season	0.06	0.43	0.88
Male's age	0.18	0.25	0.46
Female's age	0.19	0.34	0.57
Territory quality	0.06	0.26	0.82
Marriage training	1.24	0.57	0.029
Time of territory acquisition	-0.87	0.37	0.018
Synchrony in territory acquisition	-0.03	0.28	0.92

Factors affecting divorce rate

Of the eight parameters in the model the divorce rate in the population studied was found to depend on marriage training and time of territory acquisition (Table 3).

Among pairs with marriage training, 19.5% of the pairs ($n = 41$) were observed to divorce, while the divorce rate among those pairs without marriage training was 65.5% ($n = 116$) ($\chi^2 = 25.77$, $df = 1$, $p < 0.0001$). No differences in divorce rate between pairs with 1 ($n = 26$), 2 ($n = 9$), and 2+ ($n = 6$) years of marriage training were found ($\chi^2 = 2.50$, $df = 5$, $p = 0.78$).

Those birds which acquired their territories earlier, divorced their partners significantly less frequently than those which acquired a territory at a later date (males: permanent bonds, pentad 11 ± 6 ; divorced, pentad 16 ± 7 ; $t = 4.38$, $p < 0.0001$; females: 12 ± 7 and 18 ± 7 , respectively; $t = 5.40$, $p < 0.0001$). The wintering site in December and January of partners nesting in Park Z bore no relationship to the pair bond stability in the next breeding season, while those pairs staying at the same places in February divorced less frequently (Table 4). When birds that had already claimed their breeding territories by that time are excluded from the analysis; there is no statistical difference (36 out of 38 divorced pairs and 21 out of 25 stable pairs overwintered separately in February, Fisher's exact test, $p = 0.16$).

Divorces are usually accompanied by a change in territory [males: 22% of the divorced individuals ($n = 71$) and 85% of those staying in a stable bond with their previous year's mate ($n = 101$) remained in their territories; $\chi^2 = 67.72$, $df = 1$, $p < 0.001$; females 16% ($n = 83$) and 83% ($n = 87$), respectively; $\chi^2 = 76.49$, $df = 1$, $p < 0.001$].

No relationship between the probability of a given pair divorcing in the subsequent year and breeding success [50% pairs that had raised at least one fledgling ($n = 99$) and 56% that lost all the clutches ($n = 73$) were observed to divorce; $\chi^2 = 0.54$, $df = 1$, $p = 0.46$] was observed. Nor was

Table 4. Number of divorces in relation to the wintering site of mates.

Wintering		Divorced	Stable pairs	χ^2	p
December	together	15	12	0.50	0.48
	separately	26	29		
January	together	23	32	2.52	0.11
	separately	26	19		
February	together	24	36	7.11	0.008
	separately	31	16		

the relationship between territory quality in the previous year and divorce rate significant [60% pairs in the good territories ($n = 71$), 37% in the average quality territory ($n = 41$), and 56% in the worst territories ($n = 24$) were observed to divorce; $\chi^2 = 5.99$, $df = 5$, $p = 0.31$].

Between-sex differences were found in the rate of territory abandonment in poorer-quality fragments of the parks (the lowest fledgling production). Males that had occupied poor territories moved out less frequently than did the females; 31% and 58%, respectively. The differences were not significant in good and intermediate quality territories (Table 5).

Table 5. The frequency of the male and female territory abandonment (%) in different quality fragments of the park (defined by fledglings' number). * — $p < 0.001$, N — sample size.

Fledgling production	Males (N)	Females (N)
Low	31 (51)	58 (59)*
Intermediate	29 (35)	40 (35)
High	45 (77)	49 (77)

Consequences of divorce

Regardless of age, divorced birds showed a reduced number of fledglings raised with a new partner (Table 6). Because differences between young and old individuals were not statistically significant, data for the two categories were pooled for testing. Pairs that stayed together in the subsequent breeding season showed an increased breeding success, although the difference was not significant (Table 6).

During the first post-divorce breeding season, young males (in their second breeding season) that stayed in the park started breeding earlier than in the preceding year, old males started breeding later, and the difference was not significant for young and old females (Table 7 - pairs which moved into the park after pentad 12 were not included in analysis).

The young females in Park Z that stayed with their mates for the subsequent breeding season began breeding earlier (season N : pentad 6.3 ± 2.9 , season $N+1$: pentad 4.2 ± 1.8 , $n = 9$, Student's t -test for pairs, $t = 2.30$, $p = 0.05$), and old females did not change their timing (pentads 3.6 ± 1.8 and 3.6 ± 1.7 , respectively, $n = 32$, Student's t -test for pairs, $t = 0.10$, $p = 0.92$).

There are differences in the time of territory occupation between birds maintaining a stable pair bond; the widowed birds staying in the same territory they occupied in the previous year; the divorced birds staying in the same territory as in the previous year; and divorced birds changing their territory (Table 8), but the differences between stable pairs and widowed birds were not significant (for males as well as for females the post hoc Turkey test $p > 0.05$). Thus the earlier territory occupation by birds maintaining stable pair bond is not only the consequence of a greater ability of those birds to acquire the territory.

Among the divorced pair members, 32% of males ($n = 71$) and 31% of females ($n = 71$) re-paired with a mate that was younger than their original one (differences non-significant: $\chi^2 = 0.03$, $df = 1$, $p = 0.86$). Only 4 males failed to find a new mate the following year.

Table 6. Breeding success of divorced pairs (in the breeding season before and after divorce; Wilcoxon's pair sequence test) and of faithful pairs in their first and second breeding season (Student's t -test for pairs). N — sample size.

	Season N	Season $N + 1$	Statistic (N)	p
Divorced				
Males	2.1 ± 2.3	1.6 ± 2.2	$Z = -1.76$ (73)	0.08
Females	2.0 ± 2.3	1.4 ± 1.7	$Z = -2.00$ (71)	0.045
Faithful	2.1 ± 2.0	3.0 ± 2.7	$t = 1.79$ (35)	0.08

Table 7. The start of the breeding season (pentad \pm SD) before and after divorce (Student's t-test for pairs). N — sample size.

	Before	After	N	t	p
Young male	6.1 \pm 2.2	3.6 \pm 1.7	22	4.58	0.0001
Old male	3.7 \pm 2.1	4.8 \pm 2.1	38	-2.33	0.026
Young female	4.8 \pm 2.1	4.2 \pm 2.6	13	0.71	0.49
Old female	4.5 \pm 2.2	3.9 \pm 2.0	44	1.32	0.19

DISCUSSION

Significant differences are found in comparing the between season divorce rate in Szczecin with the data from England (Desrochers & Magrath 1996), and Germany (Streif & Rasa 2001); 52.3%, $n = 176$; 31.7%, $n = 183$, and 19.3%, $n = 57$ respectively; $\chi^2 = 26.50$, $df = 5$, $p < 0.0001$. Snow (1988) reported for England an 11% rate of the between-season divorces, however because of the small number of pairs he had observed ($n = 18$), these data were not included in analysis. Moreover, in the population studied in Western Europe (Desrochers & Magrath 1996, Streif & Rasa 2001), pairs that subsequently divorced produced fewer fledglings prior to divorce than birds in stable pair bonds. This pattern was found not only in young females that showed increased breeding success from one breeding season to the next regardless of the partner quality (Desrochers & Magrath 1993; see Seather 1990 for review), but also among experienced females (Desrochers & Magrath 1996). Despite increased parental competence of young females gained from experience (Desrochers & Magrath 1993, Wysocki et al. 2004), young and old females taken together showed a reduction in breeding success after divorce. Unlike the UK population (Desrochers & Magrath 1996), no quadrant quality-dependent difference in divorce rate was observed. However, the lack of relationship between quadrant quality and divorce rate can result from the different causes of divorce. Analysis of within-season divorce rate in this population (Wysocki 2004d) showed usurpation to be the predominant cause of divorces in good quadrants with desertion being much more prevalent on poor territories. The much higher rate of poor territory desertion by females, which are usually the divorcing sex in the European Blackbird (Desrochers & Magrath 1996, Wysocki 2004d), shows that territory quality was an important factor for divorce rate in our study population as well.

As opposed to the English population (Desrochers & Magrath 1996), in Szczecin the divorce rate depended on the duration of the

Table 8. The mean time of territory acquisition (\pm SD) by birds maintaining the same territory and a stable pair bond (FAITH-ST); widowed birds staying in the same territory as in the previous year (WID-ST); divorced birds staying in the same territory as in the previous year (DIV-ST); and divorced birds changing their territory (DIV-CHT). N — sample size.

	Males	N	Females	N
FAITH-ST	9.7 \pm 1.0	41	10.7 \pm 1.0	41
WID-ST	12.6 \pm 1.1	30	12.9 \pm 1.4	24
DIV-ST	14.2 \pm 0.9	48	16.8 \pm 1.3	26
DIV-CHT	19.1 \pm 1.3	23	18.7 \pm 1.0	45

$F_{3,138} = 12.09$, $p < 0.0001$ $F_{3,132} = 15.6$, $p < 0.0001$

pair bond. Three times higher divorce rate of the pairs without the marriage training support the better option hypothesis (Heg et al. 2003), and especially the incompatibility hypothesis (Coulson 1972). The better option hypothesis is also supported by the more frequent desertion of poor territories by females as well as the differences found between old males and females in the timing of the onset of breeding before and after divorce. In blackbirds the later start of the breeding season leads to its shortening and a lower number of the brood (Desrochers 1992) hence the costs of divorce for old males are higher than for old females. The differences between males and females are most likely a result of an individual having a choice of new mates after divorce. The population under study is markedly dominated by males; consequently, their potential for finding a new mate is limited, and the differences in timing of the onset of breeding are statistically significant. The females have a much higher potential choice of mate, thus the time they start breeding depends more upon a individual female's condition (Desrochers 1992).

The reduced breeding success after divorce contradicts the predictions of a better option and the incompatibility hypothesis which assumes that the divorce is a strategy for an individual to increase its reproductive success (Choudhury 1995). However, the reduced breeding success may be a result of poor adaptation for the population studied to recently observed increase in predator pressure in city centers (Marchant et al. 1990, Wysocki 2005b). In a city park with a very simple vegetation structure, the sites preferred by the Blackbird for the highest nest concealment (conifers) are often an ecological trap because they are selectively searched by corvids (Wysocki et al. 2004, Wysocki 2005c). Therefore, a change in partner and territory usually results in reduced breeding success, while fidelity to the previous partner

(which is usually associated with remaining in the same well known territory) is more frequently observed to increase breeding success.

The very low frequency of divorces among pairs that claim their territories earlier, strongly support the habitat-mediated hypothesis (especially “musical chairs” hypothesis (Dhondt & Adriaensen 1994). The hypothesis assumes that in species in which individuals exercise choice for territory rather than for mate quality and settlement depends upon arrival sequence from migration, divorce may be a side effect of differential arrival of the sexes. In such populations, divorce rates should be high but without low reproductive success in the previous breeding season and without a measurable gain in reproductive success in the successive season, which was demonstrated for my population. On the other hand, this hypothesis does not predict the impact of the marriage training on the stability of pair bonds. Because some birds of the studied population do migrate, the impact of accidental events on the divorce rate (Owen et al. 1988) should not be rejected. The earlier territory occupation theoretically might be a side effect of stable pair bonds (stable pair do not have to spend time and energy on pair formation); however the lack of differences in the time of territory occupation between stable pairs and widowed birds suggests that in this case the time of territory occupation is important *per se*.

The difference between this population and those in Germany (Streif & Rasa 2001) and UK (Desrochers & Magrath 1996) stems most likely from different overwintering strategies. In Western Europe, the Blackbirds basically stay near their future breeding territories throughout the year, while 10–20% of the population in this study is regularly observed in the two parks during winter, while 60% appear there sporadically, and 10–20% birds are never found in or near the parks between 1 December and 1 March. Differences between divorce rate of Polish, English and German populations are in agreement with the model of McNamara & Forslund (1996) and Rowley’s (1983) suggestion that costs of mate death, reduced reproductive success due to waiting for a previous mate that has died over the winter, dramatically increases divorce rate in short-lived females. Consequently, in those populations the members of which have a detailed knowledge on a partner’s survival (western European populations overwintering near their breeding territories), divorces should be observed less frequently compared to populations in which that

knowledge is incomplete, such as my study population that has higher winter dispersal.

Similar divorce rates in the pairs with and without breeding success and the rarer and rarer divorces among pairs that claim their territories earlier, strongly support the habitat-mediated hypothesis. On the other hand, the dependence of the divorce rate on the duration of the pair bond is inconsistent with this hypothesis but it (as well as more frequent desertion of poor territories by females and the differences found between old males and females in the timing of the onset of breeding before and after divorce) supports the better option hypothesis. The results obtained in this study show that the costs of waiting for a partner and of changing the territory are very high in this population and the birds can only afford to search for a better option in suitable circumstances.

ACKNOWLEDGEMENTS

I would like to thank Robert Magrath and two anonymous reviewers for constructive criticism of an early draft of the manuscript, B. J. Ens for his kindness, Sebastian Guenzel, Anna Durka, and Marta Górecka for helping in the field. I appreciate the improvements in English usage made by Kent McFarland through the Association of Field Ornithologists’ program of editorial assistance.

REFERENCES

- Choudhury S. 1995. Divorce in birds: a review of the hypotheses. *Anim. Behav.* 50: 413–429.
- Coulson J. C. 1972. The significance of the pair-bond in the Kittiwake. *Proc. Int. Ornithol. Congr.* 25: 424–433.
- Desrochers A. 1992. Age-related differences in reproduction by European blackbirds: restraint or constraint. *Ecology* 73: 1128–1131.
- Desrochers A., Magrath R. D. 1993. Age-specific fecundity in European blackbirds (*Turdus merula*): Individual and population trends. *Auk* 110: 255–263.
- Desrochers A., Magrath R. D. 1996. Divorce in the European blackbird: seeking greener pastures. In: Black J. M. (ed.). *Partnerships in birds: the study of monogamy*. Oxford Univ. Press.
- Dhondt A. A., Adriaensen F. 1994. Causes and effects of divorce in the blue tit *Parus caeruleus*. *J. Anim. Ecol.* 63: 979–987.
- Ens B. J., Choudhury S., Black J. M. 1996. Mate fidelity and divorce in monogamous birds. In: Black J. M. (ed.). *Partnerships in birds: the study of monogamy*. Oxford Univ. Press.
- Freed L. A. 1987. The long-term pair bond of tropical house wrens: advantage or constraint? *Am. Nat.* 130: 507–525.
- Heg D., Bruinzeel L. W., Ens B. J. 2003. Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. *Anim. Behav.* 66: 175–184.

- Marchant J., Hudson R., Carter S. P., Whittington P. A. 1990. Population trends of British breeding birds. BTO, Tring.
- McNamara J. M., Forslund P. 1996. Divorce rates in birds: predictions from an optimization model. *Am. Nat.* 147: 609–640.
- Mulsow R., Tomiałojć L. 1997. Blackbird. In: Hagemeyer W. J. M., Blair M. J. (eds). *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*, T & AD Poyser, London, pp. 544–545.
- Owen M., Black J. M., Liber H. 1988. Pair bond duration and the timing of its formation in barnacle geese. In: Weller M. W. (ed.). *Wildfowl in winter*. Univ. Minnesota Press, Minneapolis.
- Rowley I. 1983. Re-mating in birds. In: Bateson P. (ed.). *Mate choice*. Cambridge Univ. Press.
- Saether B. E. 1990. Age-specific variation in reproductive performance of birds. *Curr. Ornithol.* 7: 251–283.
- Snow D. W. 1988. *A study of Blackbirds*, 2nd ed. British Museum (Natural History), London.
- Streif M., Rasa O. A. E. 2001. Divorce and its consequences in the Common Blackbird *Turdus merula*. *Ibis* 143: 554–560.
- Svensson L. 1992. *Identification Guide to European Passerines*. Stockholm.
- Tomiałojć L. 1993. Breeding ecology of the Blackbird *Turdus merula* studied in the primaeval forest of Białowieża (Poland). Part 1. Breeding numbers, distribution and nest sites. *Acta Ornithol.* 27: 131–157.
- Wysocki D. 2004a. Age structure of urban population of Blackbird (*Turdus merula*) in Szczecin (NW Poland). *Zoologica Poloniae* 49: 219–227.
- Wysocki D. 2004b. Alternative mating strategies in the urban population of European Blackbird (*Turdus merula*) in Szczecin (NW Poland). *Ardea* 92: 103–112.
- Wysocki D. 2004c. Nest reusing in Blackbirds — the way for the safe breeding? *Acta Ornithol.* 39: 164–168.
- Wysocki D. 2004d. Within-season divorce rate in urban population of European blackbird *Turdus merula*. *Ardea* 92: 219–228.
- Wysocki D. 2005a. Does corvid abundance affect the breeding success of urban populations of European Blackbird *Turdus merula*? In: Jerzak L., Kavanagh B. P., Tryjanowski P. (eds). *Corvids of Poland*. Bogucki Wyd. Nauk. Poznań, pp. 181–187.
- Wysocki D. 2005b. Nest site selection in the urban population of Blackbird (*Turdus merula*) in Szczecin (NW Poland). *Acta Ornithol.* 40: 61–69.
- Wysocki D., Adamowicz J., Kościów R., Śmietana P. 2004. Breeding territory in urban population of European blackbird *Turdus merula*. *Ornis Fennica* 81: 1–12.
- Wysocki D., Walasz K. 2004. Two Blackbird females sharing the same nest. *Acta Ornithol.* 39: 47–49.

STRESZCZENIE

[Czynniki wpływające na rozwody w miejskiej populacji kosa]

W latach 1997–2003 w dwóch parkach Szczecina badano częstotliwość rozwodów miejskiej populacji kosa. Stwierdzono, że w parku Z 43%, a w parku K 60% zmian partnera jest spowodowanych jego zniknięciem (Tab. 1). Wśród par, które przeżyły do następnego sezonu częstotliwość rozwodów wynosiła 52% w parku Z i 51% w

parku K (Tab. 2). Spośród ośmiu analizowanych parametrów, częstotliwość rozwodów zależała stażu małżeńskiego i czasu zajęcia terytorium (Tab. 3). Wśród par ze stażem małżeńskim rozwodziło się 19.5%, natomiast wśród par bez stażu 65.5%. Ptaki, które zajmowały terytoria szybciej rozwodziły się rzadziej od ptaków, które zajmowały terytoria później. Nie stwierdzono zależności między miejscem zimowania danej pary w grudniu i styczniu, a częstotliwością rozwodów. Istotna zależność w lutym wynika z wcześniejszego powrotu danej pary w terytorium lęgowe w porównaniu do par, które się rozwiodły (Tab. 4). Stwierdzono, że samice częściej niż samce porzucają terytoria gorszej jakości (Tab. 5). W przeciwieństwie do populacji badanych w Anglii i Niemczech nie stwierdzono zależności między częstotliwością rozwodów, a sukcesem lęgowym czy też jakością terytorium danej pary w poprzednim sezonie lęgowym. Bez względu na wiek i płeć ptaki rozwiedzione miały niższy sukces lęgowy z nowym partnerem (Tab. 6). W czasie pierwszego sezonu lęgowego po rozwodzie młode samce (w 3 r.) przystępowały do lęgów szybciej niż w poprzednim sezonie lęgowym, natomiast stare samce przystępowały do lęgów później. W przypadku samic różnice te nie były istotne statystycznie (Tab. 7). Stwierdzono różnice w terminie zajęcia terytorium między ptakami, które zachowały poprzedniego partnera i terytorium, wdowcami, którzy zajmowali te same terytoria jak w poprzednim roku oraz ptakami rozwiedzionymi, które zachowały te same terytoria i które zmieniły terytorium. Jednakże brak różnic między parami stałymi i wdowcami wskazuje, że wcześniejsze zajęcie terytorium przez kosa mające tego samego partnera nie wynika z większych możliwości pary ptaków do obrony tego terytorium. Zmniejszenie się sukcesu lęgowego rozwodników może być efektem słabego przystosowania się tej populacji do wzrastającej presji drapieżników. Podobna częstotliwość rozwodów wśród par które wyprzewodziły pisklęta i które straciły wszystkie lęgi oraz rzadsze rozwody par, które zajmują swoje terytoria wcześniej są zgodne z przewidywaniami hipotezy wpływu środowiska zewnętrznego (the habitat-mediated hypothesis), jednakże częstsze porzucanie gorszych terytoriów przez samice i różnice stwierdzone między starymi samcami i samicami w terminie przystąpienia do lęgu przed i po rozwodzie wskazują na ptaki mogą również rozwodzić się gdy pojawia się możliwość znalezienia lepszej opcji (the better option hypothesis).