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URBANIZATION GRADIENT AND GENETIC VARIABILITY OF BIRDS — EXAMPLE OF KESTRELS IN WARSAW

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Abstract. In this paper we hypothesised that Kestrels coming from centre of Warsaw should exhibit lower level of genetic variability as compared to the group from suburbs, where more intensive gene flow from rural population is still taking place and that decrease of genetic variability should appear gradually, in accordance with "ecological" urbanization gradient – from the most diverse suburbs to the less diverse centre. In 2002 the blood samples were collected from Kestrel nestlings at 20 nests localized in Warsaw, in central Poland. From each nest two samples were randomly chosen for further analysis. Among three distinguished groups only slight differences at the level of microsatellite polymorphisms were observed and paired t-tests showed that the differences between groups were not significant. Kestrels from the centre of the city showed the highest mean number of alleles per locus, effective number of alleles, allelic richness and heterozygosity.

Key words: Kestrel, *Falco tinnunculus*, genetic variability, synurbization, microsatellite polymorphisms.

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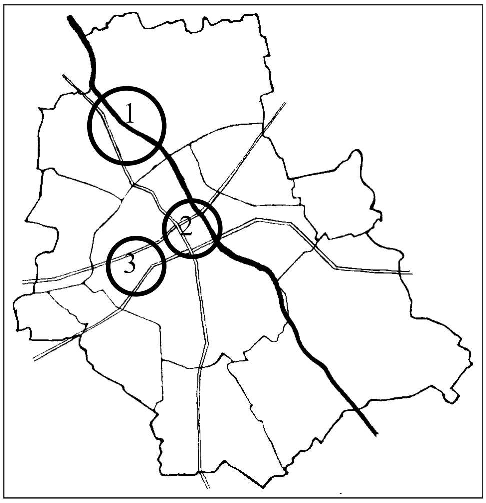
Градиент урбанизации и генетическая изменчивость птиц – пример пустельги в Варшаве. - Р. Рутковский, Л. Рейт, А. Грычиньская-Семянтковская, П. Яголковская. - Беркут. 14 (1). 2005. - Предполагается, что генетическая изменчивость пустельги из центра Варшавы должна быть меньше, чем у птиц из пригородов, имеющих больший приток генов от популяций из окрестных населенных пунктов. Кроме того, снижение изменчивости может проявляться постепенно в соответствии с градиентом урбанизации – от более разнообразных в экологическом плане предместий до менее разнообразного центра города. Для проверки этой гипотезы в 2002 г. были взяты образцы крови у птенцов пустельги из 20 гнезд в Варшаве (Центральная Польша). Из каждого гнезда случайным образом отбирались две пробы для дальнейшего анализа. Среди трех различных групп обнаружены только незначительные различия в уровне микросателлитного полиморфизма, t-критерий показал, что они статистически недостоверны. У пустельг из центра города обнаружено большее количество аллелей на локус, эффективное количество аллелей, выше аллельное богатство и степень гетерозиготности.

INTRODUCTION

For at least two centuries urbanized areas have extended more and more, creating new habitats for animal communities, in most cases destroying natural environment and decreasing heterogeneity of animal word existing there (Luniak, 2004). However, occurrence of wild animals in urban and suburban habitats has been recorded all over the world and a wide range of species has adapted to this man-made environment (e.g. Bird et al., 1996). This process, called synurbization, is connected with some substantial changes in biology of species. Synurbic populations, both mammals and birds, have been known to be either ecologically or ethologically different in comparison with populations inhabiting rural and natural sites. The differences include more sedentary style of life, decreasing proportion of breeding specimens, high re-occupation rate, higher longevity and lowered pressure of natural selection (Andrzejewski et al., 1978; Luniak, 2004). Moreover, it was obvious that urban populations of mammals show lower level of genetic variability and clearly expressed population structure (Wandeler et al., 2003), due to founder effect and/or isolation from rural populations.

In Central Europe the most synurbic diurnal raptors among birds are Kestrels (*Falco tinnunculus*) (Cramp, 1980). Being synurbized for over 150 years, European Kestrels have shown several features characteristic for synurbic species (e.g. Salvati et al., 1999; Rejt, 2001). In Warsaw, Kestrels have been observed from 1970s and nowadays population size in the city is estimated at ca. 70 breeding pairs (Rejt, 2001). Studies carried out in Warsaw showed some ecological and ethological differences between birds breeding in the city centre and suburbs: at least part of the Warsaw population is tended to be resident, the proportion of nest site reoccupation in the city is about 90 % (it suggests occupation of the nest by the same or related specimens), birds ringed as nestling were observed breeding in the city in subsequent years (Rejt, 2001; unpubl. data). It was also found that Kestrels from the city centre tended to started breeding earlier than in the suburbs. We could say that breeding isolation can occur among birds from the centre of Warsaw and birds breeding in outskirts. Moreover, newly founded populations normally consist of few individuals. It was shown that limited number of alleles carried by pioneer individuals, and genetic drift due to small population size, contribute to losses of genetic variation in newly founded populations (Falconer, 1981; Slatkin, 1987). Therefore, we hypothesise that Kestrels from the centre of Warsaw should exhibit lower level of genetic variability as compared to group of the birds from suburbs, where more intensive gene flow from rural population is still taking place. In the preliminary study we failed to show differences in genetic variability among Kestrels inhabiting centre of Warsaw and outskirts of the city (Rejt et al., 2004). However, it should be noted, that the study was based on the small number of genetic markers and polyacrylamide gels genotyping. Hence, we decided to repeat the analysis, employing more of individuals from different parts of Warsaw, more of microsatellite markers and more advanced technique of genotyping, using automatic sequencer. In this paper we also hypothesise that decrease of genetic variability should appear gradually, in accordance with “ecological” urbanization gradient – from the most diverse suburbs to the less diverse centre.



Map of the study site in city of Warsaw.
Расположение участков отбора проб.
1 – Suburb Group (n = 12), 2 – Center Group (n = 20), 3 – Mid-Center Group (n = 8).

MATERIAL AND METHODS

Blood collection

In 2002 the blood samples were collected from Kestrel nestlings at 20 nests localized in Warsaw, in central Poland (21° E, 5°23′ N). From each nest two samples were randomly chosen for further analysis. Blood samples were collected and stored on FTA cards (Whatman BioScience). To avoid loses among chicks (both resulting from blood losses and escaping from nests) all manipulations were done between 10th and 15th day of their lives (according to KE decision No 157/2002). Nests were subdivided into three groups (Fig.), according to the urbanization gradient (see Goszczyński et al., 1993): Centre Group, that is an area in the radius of five kilometres from the geographical centre-point of the city (20 samples, 10 nests); Mid-Centre Group, that is an area in the radius from five to ten kilometres from the geographical centre-point of the city (8 samples, 4 nests) and Suburb Group, that is an area in the radius over ten kilometres from the geographical centre-point of the city (12 samples, 6 nests). It should be noted, that two

Table 1

Number of alleles in locus and size range of identified microsatellite markers in Kestrels from Warsaw area (n = 40)
Число аллелей в локусе и размер диапазона идентифицированных микросателлитных маркеров у пустельг из Варшавы

Locus	No. of alleles	Size range (bp)
NVHfp79–4	9	124–148
NVHfp89	3	115–117
NVHfp13	5	90–98
NVHfp31	5	127–137
NVHfp5	8	101–115

first areas are characterized by similar type of very dense land development, when the third one is significantly less built-up, with numerous open spaces and it is more similar to natural environment inhibited by Kestrels.

DNA Isolation and Amplification of Microsatellite Markers

DNA from blood stored on FTA cards was extracted according to manufacturer protocol. Following isolation process, a little piece of FTA card (c.a. 2 mm in diameter) containing DNA was placed into a tube with 25µl of PCR reaction-mix, containing 12,5µl of Red Taq Ready Mix (Sigma), 10 pmol of each primer and 10µl of water. Forward primers were fluorescently labelled on their 5′ ends with Fam 6 or HEX. PCR conditions were as follows: 3 min. in 94°C; 35 cycles: 1 min. in 94°C; 1 min. in 55°C, 1 min. in 72°C; 5 min. in 72°C. Five microsatellite markers described by Nesje et al. (2000) were amplified: NVHfp79–4; NVHfp13, NVHfp31, NVHfp5 and NVHfp89. The length of amplified fragments was estimated using ABI Prism 3700 automated sequencer. Data were analyzed using GENESCAN 3.1.2 (PE Biosystems).

Statistical Analysis

For each population, relative level of genetic variation were assessed using microsatellite alleles frequency data. GenalEx version 5.04 (Peakall, Smouse, 2001) was used to estimate mean number of alleles per locus (A) in each population, effective number of alleles (N_{ef}) and mean number of private (unique) alleles per locus (P_A). Effective number of alleles enables more significant comparison of allelic diversity to be made across loci with diverse allele frequency distribution (Frankham et al., 2002). Using FSTAT version 2.9.3 (Goudet, 2001) allelic richness (R) (Petit et al., 1998), observed heterozygosity (H_O) and unbiased expected heterozygosity (H_E) (Nei, Roychoudhury, 1974) were evaluated. Allelic richness is a measure of the number of alleles independent of the sample size, and hence it allows to compare this quantity among samples of different sizes (Segelbacher, Storch, 2002). Significance of differences between H_O and H_E was tested using Markov chain method implemented in GENEPOP (Raymond and Rousset, 1995) with 1000 randomization.

Differences between groups in mean values of A, N_{ef}, R, H_O and H_E were tested with paired t-test using SYSTAT 11.

RESULTS

The individual genotypes at 5 microsatellite loci were determined for 40 Kestrels nestlings from Warsaw area. All analyzed loci were polymorphic. The most polymorphic loci were NVHfp79–4 with nine alleles. The smallest number of alleles was found in locus NVHfp89 (3 alleles) (Table 1).

Among three distinguished groups only slight differences in the level of microsatellite polymorphisms were observed and paired t-tests showed that the differences between groups were not significant (Table 2). The highest values of all indicators of genetic variability were observed in Center Group. Kestrels from the center of the city showed the highest mean number of alleles per locus, effective number of alleles, allelic richness and heterozygosity. Although, mean number of private alleles per locus was the highest in Suburbs Group. The lowest mean number of alleles and the lowest heterozygosity were observed in Mid-Center group. However, applying variability of measurements, which took into account differences in sample size between investigated populations (allelic richness) and differences in patterns of allele frequency distribution among analyzed loci (effective number of alleles), showed higher values in this group than in Suburbs. In all groups heterozygote deficiency was observed, however differences between H_O and H_E weren't statistically significant.

Table 2

Genetic variation in analyzed groups, based on microsatellite polymorphisms

Генетическая вариация в анализируемых группах на основе микросателлитного полиморфизма

N – number of birds analyzed, A – mean number of alleles, N_{ef} – effective number of alleles, R – allelic richness, Ho – heterozygosity observed, He – heterozygosity expected, HWE – departure from Hardy–Weinberg equilibrium, Pa – mean number of private alleles.

Group	N	A	N_{ef}	R	Ho	He	HWE	Pa
Mid-Center	8	4	2.92	4	0.5	0.58	ns	**0.00**
Center	20	5	3.35	4.24	0.62	0.67	ns	**0.60**
Suburbs	12	4.4	2.83	3.92	0.58	0.61	ns	**0.80**

DISCUSSION

Genetic variability plays an important role either in functioning of natural population and in evolution of animal and plant species. It is well known, that only by presenting genetic variation a given species is able to respond to environmental pressure, to evolve and to survive in the long run. There is a number of factors reducing genetic variability of natural populations: habitat fragmentation, isolation and random changes connected with small population size (Frankham et al., 2002). Though data are scarce, we supposed that at least some of these factors could appear in populations inhabiting urban environment. For example, due to isolation from conspecifics in natural environment, either because of spatial isolation and breeding isolation created by rising ecological and ethological changes, urban populations could be vulnerable to random factors decreasing genetic variability. Moreover, populations inhibiting urban environment are generally newly founded, thus created by limited pull of individuals (Hansson et al., 2000), therefore "founder's effect" should be observed. Indeed, both of these processes are probably responsible for lower genetic variability among urban foxes in comparison with rural conspecifics (Wandeler et al., 2003). Similar reduced level of genetic variation was also found among urban plant populations (Hollingsworth, Dickson, 1997).

Kestrels inhabiting Warsaw do not make isolated subpopulations and occupy area in continue manner. Their nests are in the center of the city (an area with typical urbanized landscape management), as well as in suburban areas (full of low building and open spaces). Previous studies indicated that birds from suburbs are ecologically and behaviorally more similar to wild populations than Kestrels from central regions of the city. Moreover, preliminary genetic studies (Rejt et al., 2004) indicated significant genetic differentiation between birds inhabiting center of the city and those from outskirts and suggested higher population admixture and migration rates in suburbs of Warsaw. On the contrary this study did not confirm either differences in genetic variability among investigated groups of Kestrels or gradual decrease of genetic variability from suburbs toward the centre. Both allelic diversity and heterozygosity were similar within all studied areas. This fact could indicate that synurbization process, despite observed changes in ecology, didn't affect genetic variability of birds. It is possible that ability to flying does not reduce intensive gene flow, which, in turn, prevents from decrease of genetic variability. However, this hypothesis is in strong opposition to observed biology of synurbic Kestrels. They are ecologically and ethologically different from birds inhabiting natural environments, what was confirmed by several authors (e.g. Salvati et al., 1999). It is very questionable that the species present such plasticity and that such changes turn up so fast that isolation and founder effect could be neglected. Moreover, reproductive isolation between populations may evolve rapidly due to divergent selection regimes and adaptation (Thompson, 1998). There are also some indications that gene flow from natural environment is less intensive in the case of the bird from the central parts of the city than from the suburbs. In this study it was shown that private (unique) alleles are more frequent in Suburb Group than in areas situated deeper in the city. In the Mid-Centre Group private alleles were not found at all, but this group is represented only by eight individuals being studied. Of course, to confirm this observation more detailed studies are needed, employing more individuals and, what is the most important, more samples from natural areas, preferentially surrounding Warsaw. It would enable investigation of migration events and sources of migrants as well as it would confirm or negate existence of genetic structure within analysed population of Kestrels. However, identification of relatively high number of unique alleles for Suburb-Group, despite a small number of individuals analysed, suggests higher population admixture.

If gene flow between natural environment and the centre of Warsaw is really reduced, why did we fail to detect any significant differences in genetic variability among groups under study? To measure genetic variability we relied on polymorphisms of microsatellite markers. Though intensively used in such studies (Girman et al., 2001; Lee et al., 2001; Roeder et al., 2001), reliability of microsatellites in estimation of genetic variability is hotly debated (Schlötterer, Wiehe, 1999; Duarte et al., 2003; Moss et al., 2003). Variation at microsatellite loci seems to be weakly connected with phenotypic variation (Coltman, Slate, 2003) and may or may not fully reflect adaptive genetic variation in natural populations (Moss et al., 2003). However many recent studies have shown their correlation with key components of individual fitness (Coltman et al., 1999; Coulson et al., 1999; Amos et al., 2001). Moreover, extreme decrease of allelic diversity of microsatellite alleles and the level of heterozygosity in microsatellite loci was observed in populations, which experienced the “bottleneck effect”, sever geographical isolation or fragmentation, thus in populations with reduced genetic variability (Rossiter et al., 2000; Whitehouse, Harley, 2001; Martinez-Cruz et al., 2004). Thus, our results seems to be weakly biased due to choice of the genetic marker.

Lack of differences in a level of genetic variability among investigated groups of Kestrels can be explained by two, corelated mechanisms. Kestrels are observed in several cities throughout Europe (Village, 1990). The species seems to express peculiar “willingness” to inhibit cities and easily adapt to this kind of environment. Kestrels are also very frequent in rural areas (e.g. Cramp, 1980), thus multiple founder events or even multiple rural to urban migration cannot be excluded. Thus, in the case of our study, lack of differences in genetic variability might be caused by large genetic pool of founding population in the centre of Warsaw. The factor of time is also essential. Kestrels started inhabiting Warsaw in 1970s. Even if isolation of centre population really exist, it is possible that period of 30 years is to short to observe any decrease in a microsatellite polymorphisms level, especially if multiple founding events took place, as we hypothesised above. Moreover, behavioural and ecological observations indicate that Warsaw Kestrels are in the mid-point of synurbization process — they present some features characteristic for population of the species inhibiting cities for the long time, while others remain typical for rural populations (Rejt, 2001). Therefore, comparison between genetic variability of Warsaw birds with Kestrels from other cities with “older” synurbic populations would be extremely interesting and would enable to test this hypothesis. On the other hand, some studies indicated that with the passage of time genetic variation had increased in recently founded populations (Hansson et al., 2000). The authors analysed microsatellite polymorphisms of great reed warblers (*Acrocephalus arundinaceus*) populations founded in 1978 and connected general increase of genetic variation with increased gene flow among other populations. Hence, it is possible, that the same process took place in the case of Kestrels from Warsaw. Therefore, we can also conclude, that period of 30 years is long enough to reduce differences in a level of genetic variability among distinguished groups.

We documented genetic variability of Kestrels’ population inhibited Warsaw. Our results are out of accordance with the concept of gradual decrease of genetic variability from the outskirts of the city towards the central area. Despite observed ecological and ethological changes, suggesting breeding isolation of a group inhibiting centre of Warsaw, reduction in allelic diversity and heterozygosity was not affirmed. Uncovering factors, which are responsible for securing genetic pool during synurbization process demand further studies, including population from the rural areas and the kestrels from other cities, being on different stages of synurbization.

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