Microevolution of the Barn Owl (Tyto alba Scop. 1769) in Europe

Ph.D Thesis

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The first owls (Strigiformes) appeared in the Paleocene (65-60 million years ago, MYA) whereas their adaptive radiation happened in the Eocene or slightly earlier (60-55 MYA). Barn owls (Tytonidae) are the most ancestral branch among the recent owls. The most primaeval fossil representative of tytonid owls is *Nocturnavis incerta* from the late Eocene (34-40 MYA). During the Oligocene and early Miocene (35-20 MYA) barn owls were a very diverse group and they practically disappeared toward the end of early
Miocene (20-15 MYA). Since the strigid owls first appeared in the early Miocene as well (both in North America and Europe), with a high probability the true owls began to supersede the tytonids at that time (23-15 MYA). The most feasible cause for this is the diversification of small mammals in the early-middle Tertiary, which accelerated a new adaptive radiation of owls. In the lower Miocene the strigid owls diversificated, producing many species. From the middle Miocene on the tytonids returned with the modern *Tyto* genus (ca. 15 MYA) and since then only this genus is known in Europe. In the Quaternary (early Pleistocene) the *Tyto alba* appears (ca. 1.6 MYA). Today only two genera of tytonid owls survive: *Tyto* and *Phodilus*, the latter being represented by one species *Ph. badius*. Both the neoendemic disjunct areal and the morphological characters of this species point in the direction, that it is closer to the Paleogene owls than *Tyto*.

Three of the 7 subspecies of the barn owl described in the Western Palearctic are insular endemisms, one does not live in Europe and a further one has a limited area. Two subspecies, the *T. a. alba* and the *T. a. guttata* live on the great majority of the European distribution. The most accepted hypothesis says that the afore mentioned subspecies were evolved during the last ice age. The recent distribution is explained by the postglacial areal expansion from two different refugia in SW and SE Europe. Following this hypothesis, the *T. a. alba* phenotype (subspecies) reached the British Isles through Western Europe from the SW European refugium, and the *T. a. guttata* phenotype expanded along the northern side of the Alps to the Channel from the SE European refugium. Data in the literature indicated a relatively narrow transition zone.
Since my field observations seemed to contradict this conception, I first tried to discover the location of the transition zone. Then I investigated the pairing system of the both phenotypes in the zone. With the description of the directions of movements, and the barriers affecting them, I obtained data on gene flow and with help of the genetic data I quantified them. I investigated a sample from the middle of the zone (Switzerland) and another one from the eastern side of it (Hungary) with the RAPD method. Between the genetic substructuring and differentiation of the populations there are differences to be expected since after the last ice age both subspecies differentially admixed on the investigated areas. Furthermore the difference in the dispersal distances of the sexes affects the within- and among populations differentiation. My dissertation studies the pairing system and the effects of time passed since the last ice age, barriers and differential dispersal distances on the genetic constitution of the populations.

Most important results included in the dissertation:

1. Transition zone and pairing system

1.1 Results got in the investigated areas indicate that the whole European distribution of the barn owl became a part of the transition zone.

1.2 On the eastern side of the zone the *guttata* subspecies reaches a proportion of more than 84% of the population. During the relatively short period of study (3 years) this percentage seemed to be stable ($\chi^2=1,595$, df=4, p>0.7).
1.3 Sexual dimorphism with respect to the colouration of plumage could not be found ($\chi^2 = 1.4$, df=2, p=0.50).

1.4 The pairing of the phenotypes is random (the mean colouration of the male and female individuals of breeding pairs does not correlate; Spearman correlation: $r_S$=0.06, n=64, p>0.50).

2. Gene flow and barriers

2.1 All barn owls ringed in the outland and recaptured in Hungary came from N-NW-W i.e. from the direction of the transition zone (n=29, $\chi^2$=39.14, p<0.001).

2.2 Contrary to this, there is no prevailing direction of emigration from Hungary (n=198, $\chi^2$ = 5.92, NS).

2.3 The dispersal directions are sex-independent (n1=43, n2=16, $\chi^2$=7.35, NS).

2.4 In Hungary the time of fledging (early or late) does not influence the direction of movement (n1=157, n2=61, $\chi^2$=4.93, NS).

2.5 The reported breedings of immigrants confirm that gene flow occurs (immigrants breed, genetic data support the result as well).

2.6 The overall trend shows a significantly greater emigration from, than immigration in Hungary (i.e. the population is rather „source”-featured; n1=124 001, n2=9061, Fisher’s p<10^-8).

3. Genetic structure of populations
3.1 Within populations the genetic differentiation of females is greater than that of males.

3.2 Among populations male genetic differentiation is greater than female.

3.3 In the Swiss population (middle of the transition zone) the genetic differentiation is greater than in the Hungarian (eastern side of the zone).

3.4 In the Swiss population (middle of the transition zone) the sexual differentiation is also greater than in the Hungarian one (eastern side of the zone).

3.5 Between the Hungarian and Swiss populations the number of migrant individuals/generation reaches ca. 1. If calculated separately for the sexes, then 0.525 for males and ca. 1 for females. This means a low amount of gene flow.

3.6 The among sexes differentiation of the species detectable with RAPD lies between 7.04% and 14.24%.

3.7 The genetic substructuring of the populations of the species – in comparison to other species - is substantial.

3.8 Caused by the frequent bottlenecks, drift plays an important role in the microevolution of the species. This can be seen in the amount of gene flow as well.

The results show that the two subspecies - evolved during the last glacial period – did not differentiate to that an extent that, with the draw back of ice, they would be reproductively isolated from each other. The individuals, showing no preference in connection with the subspecific feature (plumage colouration) in the last ca. 10 000 years, admixed with each other so that both phenotypes and all intermediate forms can be found on the whole European area. However the admixture did not reach
the level, where a clin would be no more detectable – even phenotypically. This could have several reasons from which the most important is the low extent of gene flow explained by barriers, monogamous pairing system and resident character of the species. From the low level of gene flow follows that the populations exhibit a substantial genetic substructuring. The gene flow in the direction of the middle of the transition zone is more remarkable than in the opposite direction. This is not surprising if we assume that on the edges of the distribution of a species the habitats are not of as good quality as in the middle of it. Furthermore the differences in the dispersal strategies of the sexes generate a higher level of sexual differentiation in the middle of the zone versus in the edge of it. From the genetic point of view this could be advantageous, since it increases heterozygosity. Drift plays an important role in the microevolution of the species. The barn owl is a species adapted to warm climate. Considering Europe’s unbalanced winter periods the populations frequently go through bottlenecks.