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Simultaneous effect of habitat and age on reproductive success of Imperial Eagles *(Aquila heliaca)* in Hungary

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Abstract An unexpected expansion of the Eastern Imperial Eagle *(Aquila heliaca)* population was observed in East Hungary from mountainous habitat into lowlands from 1989 onwards. Here the population markedly increased from 2 to 59 breeding pairs by 2006, while the mountainous population remained more or less stable with 12-17 breeding pairs. At the beginning of the expansion process the nearest neighbour distances between breeding pairs was lower in the mountains than in the lowlands, but presently they are similar, indicating a saturation process in the lowland areas, but no density dependence was revealed on breeding success. During the study period a higher ratio of non-adult pairs was observed in the lowland territories (49%) than in the mountains (22%). We found that both age and habitat influenced breeding success. We also found that age-effect was significant on success rate (i.e. the ratio of pairs that produce at least one chick), while habitat-effect was more evident on fledging success (i.e. the number of fledglings per productive pair). The overall productivity (i.e. number of fledglings per breeding pair) was affected primarily by the age of the pairs, but the interaction term of age x habitat also was significant. We suppose that better feeding possibilities (closer foraging areas and larger prey density) could explain the higher fledging success in the lowlands. We also predicted that pairs inhabiting agricultural areas in the lowlands will have a reduced success rate due to higher human disturbance, together with an age effect of the breeding pairs. Therefore adult pairs probably can habituate to disturbance even if it happens in the close vicinity of their nesting sites.

Keywords: population dynamics, breeding success, territory, raptor

Összefoglalás A parlagi sas kelet-magyarországi elterjedési területe jelentős mértékben kiterjedt az Alföld irányába 1989-től 2006-ig, amely során az alföldi állomány 2-ről 59 párra emelkedett, míg a hegyvidéki állomány viszonylag stabil maradt, és 12-17 pár között változott. A terjeszkedési folyamat elején, a hegyvidéki élőhelyeken kisebb volt a párok közötti legközelebbi szomszéd távolság, mint síkvidéken, azonban ez 2006-ra kiegyenlítődött. Denzitásfüggő hatást egyelőre nem lehet megfigyelni az átlagos költési siker alakulásában. A vizsgálati időszakban, a síkvidéki territóriumokban magasabb volt az átszíneződő fiatal madarak aránya (49%), mint a hegyvidékiekben (22%). A költő madarak korának és az élőhelynek a költési sikerre gyakorolt együttes hatását vizsgáltuk. Azt találtuk, hogy a költő madarak kora inkább a költések sikerességi arányát (sikeres párok/összes költő pár) befolyásolta, míg az élőhely inkább a kirepülési sikerre (kirepült fiókák száma/sikeres pár) volt hatással. Összességében a produktivitást (kirepült fiókák száma/összes költő pár) alapvetően a madarak kora befolyásolta, de a kor és az élőhely interakciója is szignifikáns hatással volt. Az adatok alátámasztják azt a predikciónkat, miszerint a síkvidéki területek jobb táplálkozási lehetőségei (közelebbi táplálkozó területek és nagyobb zsákmány-denzitás) magasabb költési sikert eredményezhetnek. A másik predikciónk, miszerint a síkvidéki párok sikerességi aránya alacsonyabb a jelentősebb emberi zavarás miatt, csak részben igazolódott. Bár ez a trend megfigyelhető volt az adatokban, de csak a párok korával interakcióban volt szignifikáns a különbség. Ezért úgy gondoljuk, hogy a tapasztalt öreg madarak megfelelő mértékben hozzá tudnak szokni az emberi jelenléthez a fészkek közvetlen környezetében is.

Kulcsszavak: populációdinamika, költési siker, territórium, ragadozómadár

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Introduction

Biotic and abiotic environmental variables, like topography, vegetation, prey availability, predators, and competitors, influence habitat selection in birds (Hildén 1965, Cody 1985, Wiens 1989). Habitat selection of larger-sized raptor species typically depends on the availability of nesting sites and feeding areas (Janes 1985, Tapia *et al.* 2008). If raptors choose an optimal nesting habitat, they increase their reproductive success by decreasing the risk of predation (Sergio *et al.* 2007), avoiding competitors (Katzner *et al.* 2003), or human disturbance (López-López *et al.* 2007). Another important component, which is connected to habitat quality and has main effects on raptors' reproductive success, is prey-availability in feeding areas, like density and quality of prey (Penteriani *et al*. 2006, Sergio *et al.* 2006) and distance of foraging areas from nesting sites. Distance between nests and feeding areas play a key role when birds optimize their energy expenditure for maximizing their fitness (Cowie 1977). The quality of nesting sites and feeding areas seems to be important factors, which mainly affect the viability of raptor populations (Krüger *et al.* 2002). Besides the direct and indirect effects of habitat quality, density dependence (Ferrer & Donazar 1996, Ferrer *et al.* 2006, Ferrer & Penteriani 2008) and age of breeding birds (Steenhof *et al.* 1983, Balbontín *et al.* 2003, Ferrer & Bisson 2003, Penteriani *et al.* 2003, Margalida *et al.* 2007) are known to have crucial effects on breeding success. The effect of age can be especially important in instable populations, where the relative frequency of non-adult breeders increases, due to lack of adult breeders in comparison to available habitats (Ferrer *et al.* 2004).

Many of the large-sized raptors are among the threatened birds in the world (Del Hoyo *et al.* 1995). The Eastern Imperial Eagle *(Aquila heliaca)* has a wide distribution area in the forest-steppe zone of the Palearctic region, it breeds from western Austria, Czech Republic, Slovakia and Hungary throughout eastern Europe and Siberia to the Baikal Lake in Russia. Nevertheless its distribution is scattered and the species is globally threatened, as its world population consists only a few thousand breeding pairs (Del Hoyo *et al.* 1995, BirdLife International 2013).

Throughout its distribution area Imperial Eagles are connected to open foraging habitats, where its medium-sized mammal or bird preys are available (Del Hoyo *et al.* 1995). In several regions they are breeding in forested mountains, mostly due to persecution or the lack of suitable trees in the nearby open plain habitats (Petrov *et al.* 1996, Karyakin *et al.* 2008). We have no reliable data about the breeding distribution of Imperial Eagles in Hungary prior to the 1970's, although all early literature since the end of the 19th century mention it as a rare breeder of the Hungarian mountains, and only scarce observations are available from the Great Hungarian Plain (Vasvári 1938). The Hungarian population of the Eastern Imperial Eagle presumably reached its historical minimum with only 15-25 breeding pairs in mountainous forests by the 1980's. During the last two decades an unexpected increase of the population was observed and by 2009 the Hungarian population already exceeded 100 pairs (Horváth *et al.* 2011). In parallel the species also expanded its breeding range from mountain forests to lowland agricultural areas. Two-thirds of Hungary consists of such agricultural habitats, so there is a chance for further area expansion of Imperial Eagles in the near future.

In the present study we investigated the factors affecting reproductive success of the largest subpopulation of Imperial Eagles in Central Europe during its area expansion. As the population is still exponentially increasing and probably is under the saturation point, we predicted that recently there is no significant density dependent effect on productivity. We also hypothesized that both age of the breeding birds and habitat type affect the reproductive success of Imperial Eagles. On one hand we predicted that the probability of successful breeding in the lowland areas is lower than in the mountains, due to a higher level of human disturbance connected to intensive agriculture and higher density of urbanized areas and infrastructure. On the other hand we also predicted that fledging success is higher in lowland areas where Brown Hares *(Lepus europaeus)*, the main prey species of Imperial Eagles (Horváth *et al.* 2010), are more abundant and open foraging areas are closer to the nesting sites.

Methods

Study area

The study was conducted in the central part of the Great Hungarian Plain and adjacent low mountains (46°30'-48°30'N 19°50'-21°40'E, 20 000 km^2). Most parts of the study area are lowlands between 80-100 m a.s.l., like the Jászság, Heves, Borsod, Nagykunság and Békés Plains, which lie in the wide valley of the Tisza River and its tributaries. The Plain is mostly covered by intensive agricultural fields and small remnants of grasslands, which are scattered by small groups of poplars (*Populus* spp.) and black locust trees *(Robinia pseudoacacia)*. The northern border of the Plain is formed by the Mátra, Bükk and Zemplén Mountains (200-1014 m a.s.l.) which are predominantly covered by oak *(Quercus petraea, Q. cerris, Q. pubescens)*, beech *(Fagus sylvatica)* and introduced pine *(Pinus silvestris, P. nigra, Larix decidua)* forests.

Data collection

Breeding territories of the Eastern Imperial Eagle were monitored by a well-trained network of observers, organised by MME BirdLife Hungary and Hungarian national park directorates since 1980 (Haraszthy *et al.* 1996, Bagyura *et al.* 2002, Horváth *et al.* 2011). In the present study we analysed data collected between 1989 and 2006, when monitoring covered all potential breeding territories. At the beginning of each breeding season (February-March) all previously identified territories and their surroundings up to 10 km were visited in order to locate active nests of Imperial Eagle pairs. Afterwards, during the whole breeding season (from April to August) all active nests were controlled for at least once per month to determine breeding success or failure in each breeding stage (incubation, small-, medium- and large-chick and fledging periods). Observations were carried out by spotting scopes (20–60×) from a distance of 0.5-1.5 km to avoid unnecessary disturbance of the birds (González *et al.* 2006a). We checked nest content once during the breeding season to monitor the exact number of alive or dead offspring, when the chicks were 4-7 weeks old (mostly between 10-25 June), or when the breeding failed. Locations of the nests were identified with GPS and stored in a GIS database together with other breeding parameters.

During this 18-year study 645 breeding attempts were monitored in 89 breeding territories. By definition two nests belonged to the same territory if they were closer than 7.3 km to each other (the average nearest neighbour distance in 2006) and not more than one territorial pair used them within the same year (Ferrer & Bisson 2003). Two different breeding habitat types were used by the species in the study area, such as mountainous forests and small patches of trees in open agricultural landscape of the lowlands. The breeding attempts were classified into the two breeding habitat types based on the 200 m contour line. This contour line also separated the open and forested nest sites without any notable overlap, as all (100%) of the 262 'mountainous', but only eight (2.1%) out of the 383 'lowland' breeding attempts were in forested habitats. Subsequent breeding attempts of the same territory were usually within the same habitat type (15 pure mountainous and 67 pure lowland territories). However, in seven territories the pairs switched between the two habitat types. These mixed territories were also classified into that habitat type where more breeding attempts occurred and only the average of these breeding attempts were used for territorial comparisons.

Members of the breeding pairs were categorised during the population monitoring as '*adult*' or '*non-adult*' birds, as these two age classes can be distinguished relatively easily in the field based on plumage characteristics. Similarly to the Spanish Imperial Eagle (Ferrer *et al.* 2004, González *et al.* 2006b) and other large eagles (Steenhof *et al.* 1983, Balbontín *et al.* 2003), Eastern Imperial Eagles regularly breed already in their 3rd-5th calendar year, before they accomplish their moult to the dark brown adult plumage (Katzner *et al.* 2006, authors own data). Nonetheless, the exact age determination of non-adult eagles needs substantial experience (Forsman 1999). A breeding pair was classified as '*non-adult*' if at least one member of the pair was in non-adult plumage, and as '*adult*' if both members were in adult plumage. In 25 cases (4% of breeding attempts) the age class of both birds could not be identified, therefore these were typically excluded from calculations.

Statistical analyses

To avoid pseudoreplication that would arise if each breeding attempt would be included separately, we used territories as sampling units in the comparative analyses (c.f. Steenhof 1987, Ferrer & Bisson 2003, Penteriani *et al.* 2003, Sergio & Newton 2003, Margalida *et al.* 2007), and annual mean values for analysing temporal trends during the study period (Balbontín *et al.* 2003, Ferrer & Bisson 2003). Breeding success was measured with three variables (Steenhof 1987, Balbontín *et al.* 2003), such as the number of fledglings per nesting pair (referred to as *productivity* in the followings), the frequency of nesting pairs that fledged at least one chick (referred to as *success rate* in the followings), and the number of fledglings per successful nesting pairs (referred to as *fledging success* in the followings). For the calculation of mean values for territories we controlled for year effect by subtracting annual means from the original breeding success data (Ferrer & Bisson 2003, Penteriani *et al*. 2003). We excluded those territories from the analyses where less than three breeding attempts occurred. Density dependence was estimated by nearest neighbour distances (NND) (Newton *et al.* 1977, Penteriani *et al.* 2003).

Normal distribution of variables was tested prior applying parametric tests, and in case to significant deviation non-parametric tests were used. Generalized Linear Models were used to test simultaneous effect of habitat type and age of birds on breeding success variables, and the interaction of the two factors were removed from the model, if it had no significant effect. All statistical tests were two-tailed and significance level was set at $P < 0.05$. Data are presented as mean ± SD. Distances were measured by ArcMap© software (ESRI Inc., version 9.0). Analyses were executed by the SPSS programmes package (SPSS Co., ver. 17).

Results

Temporal variation of population parameters

Altogether 79 new territory occupancies (i.e. when a breeding pair appeared in a territory where no breeding attempt was recorded in the previous year) were observed during the study period, with only 12 (15%) located in the mountains, while the rest of the new territories (85%) appeared in the lowland. We identified the age of both breeding birds in 70 cases, from which 57 (81%) new territories were occupied by non-adults. This frequency was significantly different from the 24% value of non-adults, which was observed among the other 550 breeding attempts ($\chi^2 = 123.416$, $P < 0.001$).

Population size increased markedly in the lowland (annually increased by 25%; $F= 281.401$, $df = 1,16$, $P < 0.001$), and also in the mountains, although here the trend was not so sharp and not constant (annually increased by 5%; $F= 5.859$, $df = 1,16$, $P = 0.033$) *(Figure 1a)*. In parallel with the increasing population size the NND decreased in the lowland ($F= 22.445$, $df = 1,16$, $P < 0.001$), but did not change significantly in the mountains ($F = 2.747$, $df = 1,16$, $P = 0.117$) *(Figure 1b)*. The frequency of non-adult pairs in the breeding population increased in the lowlands ($F= 7.401$, $df = 1,16$, $P = 0.015$) and decreased in the mountains ($F= 5.379$, $df = 1,16$, $P = 0.034$) *(Figure 1c)*. None of the breeding success variables showed significant trends in the two habitat types during the study period (productivity: $F = 0.148$, $df = 1,16$, $P = 0.705$ for mountains and $F = 0.108$, $df = 1,16$, $P = 0.747$ for the lowland) *(Figure 2a)*; success rate: $F = 0.401$, $df = 1,16$, $P = 0.535$ for the mountains and $F = 0.613$, $df = 1,16$, $P = 0.445$ for the lowland, *(Figure 2b)*; fledgling success: $F = 0.041$, $df = 1,16$, $P = 0.842$ for the mountains and $F = 0.718$, $df = 1,16$, $P = 0.409$ for the lowland) *(Figure 2c)*.

Density dependence

Territory averages of NND was significantly lower in mountainous than in lowland territories (6.6 ± 3.2 km and 12.7 ± 14.5 km, respectively; Mann-Whitney U-test, Z = -2.728, P = 0.006), although the difference became non-significant, or even reversed by the last years of the study period (8.4 ± 4.8 km and 7.1 ± 4.3 km in 2006, respectively; Mann-Whitney U-test, Z = -0.722, P = 0.470). We did not find any sig-

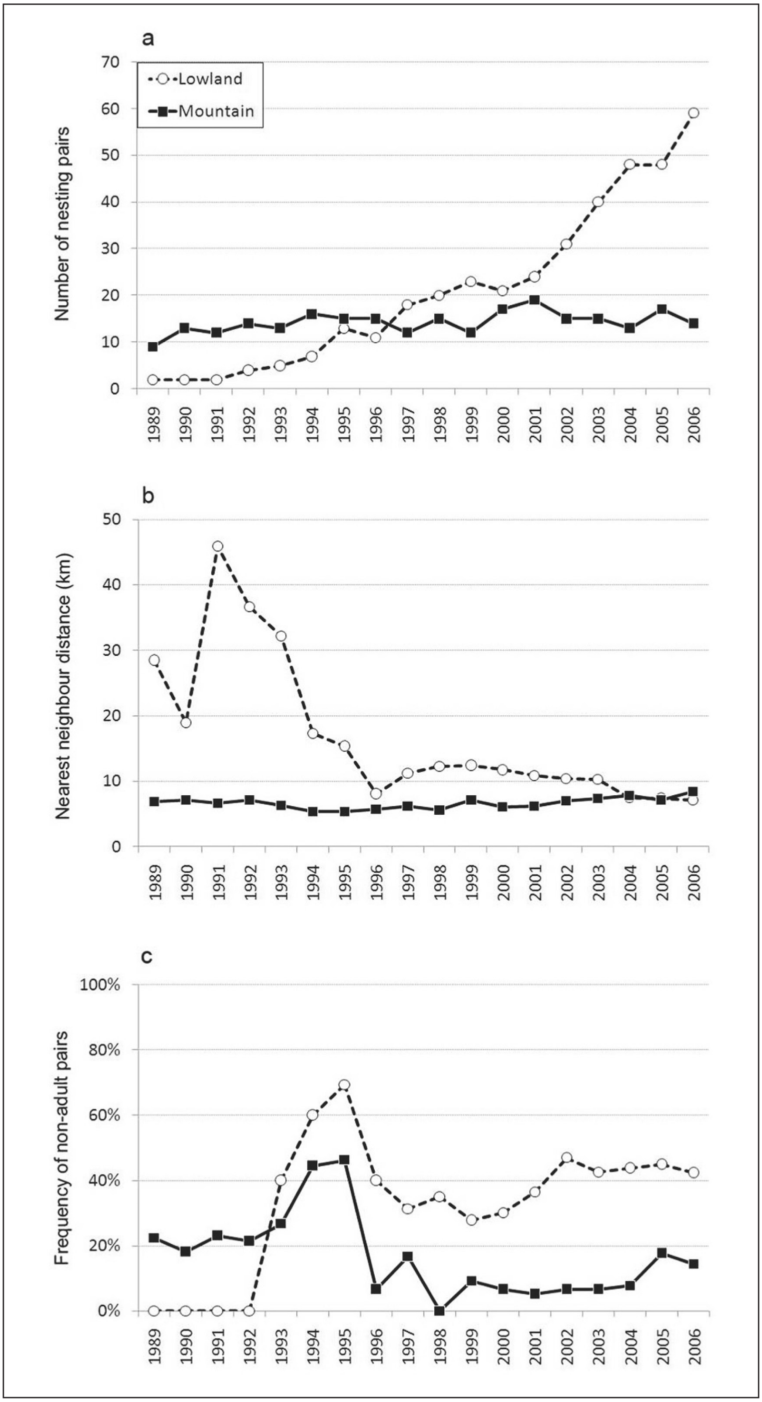

Figure 1. Changes in number of nesting pairs (a), nearest neighbour distance (b) and frequency of non-adult pairs (c) of Eastern Imperial Eagles in lowland and mountain habitats of East-Hungary between 1989 and 2006

1. ábra A fészkelő párok számának (a), a legközelebbi szomszéd távolságnak (b) és a nem-adult párok gyakoriságának (c) változása a kelet-magyarországi parlagi sas állományban a hegyvidéki (fekete négyzet) és síkvidéki (fehér kör) élőhelyeken 1989 és 2006 között

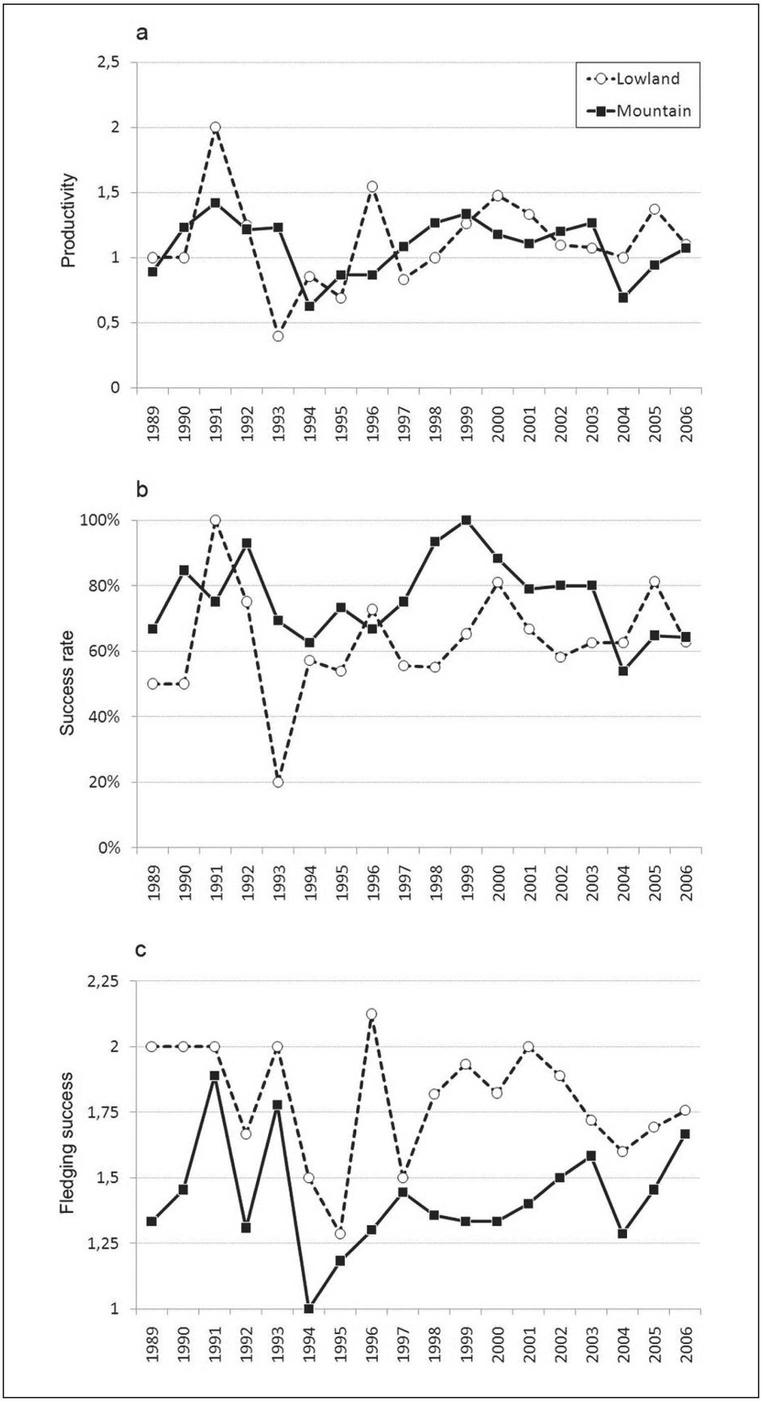

Figure 2. Changes in productivity (a), success rate (b) and fledging success (c) of Eastern Imperial Eagles in lowland and mountain habitats of East-Hungary between 1989 and 2006

2. ábra A produktivitás (a), a sikerességi arány (b) és a kirepülési siker (c) változása a kelet-magyarországi parlagi sas állományban a hegyvidéki (fekete négyzet) és síkvidéki (fehér kör) élőhelyeken 1989 és 2006 között

	Mountain		**Lowland**			
	n	mean ± SD	n	mean ± SD	*t*	*P*
Productivity	20	-0.098 ± 0.371	51	-0.005 ± 0.466	0.805	0.424
Success rate	20	0.006 ± 0.233	51	-0.043 ± 0.210	-0.851	0.398
Fledging success	19	-0.162 ± 0.306	50	0.086 ± 0.390	2.494	0.015*

** significant at P = 0.05 level*

Table 1. Comparison of breeding success variables between the territories of the two habitat types. (Productivity = the number of fledglings per a nesting pair; Success rate = the frequency of nesting pairs that fledged at least one chick; Fledging success = the number of fledglings per successful nesting pairs)

1. táblázat A költési siker változók összehasonlítása a két élőhelyen. (Produktivitás = kirepült fiókák száma / fészkelő párok száma; Sikerességi arány = azon fészkelő párok aránya, amelyek legalább egy fiókát sikeresen kireptettek; Kirepülési siker = kirepült fiókák száma / sikeres párok száma)

	Adult		**Non-adult**			
	n	mean ± SD	n	mean ± SD	*t*	*P*
Productivity	46	0.107 ± 0.602	46	-0.162 ± 0.756	-1.995	0.052
Success rate	46	0.104 ± 0.279	46	-0.115 ± 0.387	-3.257	0.002*
Fledging success	35	-0.079 ± 0.448	35	0.009 ± 0.435	0.903	0.373

** significant at P = 0.05 level*

Table 2. Pairwise comparison of breeding success variables of adult and non-adult pairs within the same territories. (Productivity = the number of fledglings per a nesting pair; Success rate = the frequency of nesting pairs that fledged at least one chick; Fledging success = the number of fledglings per successful nesting pairs)

2. táblázat A költési siker változók páros összehasonlítása az „adult” (két kiszíneződött madárból álló) és „nem-adult” (legalább egy átszíneződő madarat tartalmazó) párok között. (Produktivitás = kirepült fiókák száma / fészkelő párok száma; Sikerességi arány = azon fészkelő párok aránya, amelyek legalább egy fiókát sikeresen kireptettek; Kirepülési siker = kirepült fiókák száma / sikeres párok száma)

nificant correlation between NND and any of the breeding success variables (productivity: r_s = -0.022, P = 0.842; success rate: r_s = -0.056, P = 0.601; fledgling success: r_s = 0.113, P = 0.338). Moreover, as density increased in the lowland habitats during the study period, no changes were observed in any of the breeding success variables (see above). Therefore we assumed that there was no significant density-dependent effect of the studied parameters in the study period.

Simultaneous effect of age and habitat

Breeding success variables showed some difference both regarding habitat type and age of breeding birds in univariate comparisons without considering the possible simultaneous effects (*Table 1* and *Table 2*). We also found significant rank correlations between the frequency of non-adult pairs and each of two breeding success variables of the territories (productivity: r_s = -0.354, P = 0.002; success rate: r_s = -0.337, P = 0.004), although fledgling success did not correlate significantly (r_s = -1.102, P = 0.406). Never-

	Type III Sum of Squares	Mean Square	*F*	*P*
Productivity				
Corrected Model	2.447	0.816	4.895	0.004 *
Intercept	0.617	0.617	3.702	0.059
Habitat	0.002	0.002	0.01	0.922
Age	2.308	2.308	13.853	< 0.001 *
Habitat × Age	0.810	0.81	4.859	0.031 *
Success rate				
Corrected Model	0.767	0.256	6.856	< 0.001 *
Intercept	0.207	0.207	5.547	0.021 *
Habitat	0.152	0.152	4.074	0.048 *
Age	0.725	0.725	19.449	< 0.001 *
Habitat × Age	0.383	0.383	10.275	0.002 *
Fledging success				
Corrected Model	1.379	0.690	5.289	0.007 *
Intercept	0.090	0.090	0.692	0.409
Age	0.531	0.531	4.071	0.048 *
Habitat	1.285	1.285	9.856	0.003 *
Habitat × Age **	-	-	-	-

** significant at P = 0.05 level* *** interaction was not significant, therefore it was removed from the model*

Table 3. Results of the Generalized Linear Models analysing the effects of habitat type and age of the breeding birds on breeding success variables

3. táblázat Az Általánosított Lineáris Modell (GLM) eredménye, amely az élőhely-típus és a költő madarak korának hatását mutatja a költési siker változókra

theless, the frequency of non-adult pairs differed significantly between the two habitat types (22.1 ± 26.3% in the mountains and 49.5 ± 35.1% in lowlands; Mann-Whitney U-test, Z = -2.964, P = 0.003), therefore the possible simultaneous effects were tested in a generalized linear model.

The linear models showed different results for the three breeding success variables *(Table 3)*. We found that overall productivity was affected primarily by the age of the breeding pairs, but also by the interaction between habitat and age effects. Success rate was also primarily affected by the age of the pairs, although the habitat and interaction between the two effects were also significant. Finally habitat showed stronger effect on fledging success, but age of the pairs also had a significant effect.

Discussion

Our results revealed that habitat selection of Imperial Eagles in Hungary changed in the last two decades, causing an unexpected population growth and breeding area expansion. From their mountainous refugees Imperial Eagles expanded their original breeding areas in Hungary to the lowlands, which were most probably abandoned for at least one hundred years. Although presently the new breeding area, the Hungarian Great Plain, with its developed agriculture and dense system of settlements, seems to be suffering from high human disturbances, the reproductive success parameters suggested that this new breeding area offer high-quality breeding sites for the eagles.

Similarly to other studies (Steenhof 1983, Balbontín *et al.* 2003, Ferrer *et al.* 2003) we found a strong effect of age of breeding birds on reproductive success variables, i.e. non-adult pairs bred less successfully. Not surprisingly, in the newly-occupied areas non-adult eagles were more frequent than in the traditional mountainous areas and we found that age and habitat type had simultaneous effects on breeding success variables, as it was also shown on Bonelli's Eagles *(Aquila fasciata)* in Spain (Penteriani *et al.* 2003). We found that age-effect is more significant on success rate (i.e. the ratio of pairs that produce at least one chick), while habitat-effect was more evident on fledging success (i.e. the number of fledglings per productive pair). The overall productivity (i.e. number of fledglings per breeding pair) was affected primarily by the age of the pairs, but the interaction of age and habitat type had also significant effect. We suppose that better feeding possibilities (closer foraging areas and larger prey density) could explain the higher fledging success in the lowlands. We also predicted that pairs inhabiting lowland agricultural areas suffer more from human disturbance resulting in a lower success rate, but even if this trend was observable it had significant effect only in interaction with the age of the pairs. This interaction is probably caused by inexperienced non-adult pairs, which are threatened by the higher level of lowland disturbance, while experienced adult pairs can breed with similar success as in the undisturbed mountains.

Although the exact causes, which started the population expansion in the Imperial Eagles in Hungary are not known, our study revealed that freshly occupied lowland habitats can be more productive than traditional mountainous ones. Such a process is surprising in an expanding population as most studies report that if a population is not saturated the best habitats are occupied first (Newton 1979, Sergio & Newton 2003). Moreover the population size of Brown Hare *(Lepus europaeus)*, the main prey species of Imperial Eagles is Hungary (Horváth *et al.* 2010), has been continuously declining since the 1960's in parallel with the intensification of agriculture (Báldi & Faragó 2007). Therefore the colonization of the lowlands is most probably not caused by any recent increased availability of food supply, but by an increasing population size in the original habitats. After the population in the mountains started to increase and the level of persecution decreased in the lowlands, some eagles tried to settle in these new habitats. The appearance of these first inventory pairs was probably the most important step in the expansion, as the high natal philopatry of the species (González *et al.* 2006b) hinders the sudden colonization of habitats far from the original breeding distribution area. The huge and well visible nests and territorial behaviour of conspecifics indicate, that lowland agricultural areas can be also suitable habitats for them (Newton 1979). During the last two decades these freshly colonized habitats proved to be even more suitable for the species, than the traditional mountainous forests, and since large agricultural regions of the Hungarian Plain are still not inhabited by the species we expect further expansion in the near future.

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