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Migration and wintering of Finches (Fringillidae) in the Carpathian Basin based on ringing recoveries

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The study is based on the foreign related recoveries (longer than 100 km) of the Databank of the Hungarian Ornithological and Nature Conservation Society – BirdLife Hungary Ringing Centre until the end of 1997. The most common finch species with more than 10 foreign recoveries were included in the study: Linnet (*Acanthis cannabina*), Goldfinch (*Carduelis carduelis*), Greenfinch (*C. chloris*), Siskin (*C. spinus*), Hawfinch (*Coccothraustes coccothraustes*), Chaffinch (*Fringilla coelebs*), Brambling (*F. montifringilla*), and Bullfinch (*Pyrrhula pyrrhula*). All of these species are partial migrants with different irruptive tendencies. The Hungarian - related recoveries of the Brambling and Siskin, which are the most irruptive species, connect these birds to those wintering in W Europe, but the other species use different, more eastern wintering areas. While those spend the winter in western parts of the Mediterranean area, particularly on the Iberian Peninsula, the Hungarian related Chaffinch, Bullfinch, Linnet and Hawfinch populations spend the winter on the Apennine Peninsula, while the Greenfinch and Goldfinch on the Balkan Peninsula. The three large Mediterranean peninsulas served as refuges for the finch populations in the glacial period. According to the observable pattern today, the role of the peninsulas were not significantly different, as finches use all three areas for wintering. The differences are on the population level, which possibly means that the populations survived on the different peninsulas, and when expanded to north occupied different breeding areas in Europe.

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1. Introduction

Thirty-five species of finches (Fringillidae) occur in the Western Palearctic (Cramp & Perrins 1994, Beaman 1996). In Hungary, nine of these breed regularly, and 8 are present only during migration /wintering or as rare visitors (Keve 1984, Magyar *et al.* 1998). Finches can be classified as residents, partial migrants, or irruptive species. The distinction between these categories is not

entirely sharp, and different populations of the same species can have different migratory behaviour.

For the species studied, the most important wintering sites are in the British Isles, the Atlantic zone, and in the Mediterranean. Some species can stay north to the 70° in winter (Cramp & Perrins 1994).

In the present study the data of birds recovered in Hungary or ringed in Hungary and recovered abroad are used to find out the origin of birds migrating

Tab. 1. Summary of the ringing and recovery statistics for finches in Hungary. The totals ringed is from Varga & Simon (1997).

Species	Total numbers ringed in Hungary	Recovered		Total
		same season	after >1 year	
Linnet	11159	21	3	24
Goldfinch	31105	37	13	50
Greenfinch	78866	50	7	57
Siskin	51748	191	27	218
Hawfinch	19486	112	10	122
Chaffinch	28938	87		87
Brambling	16568	18	8	26
Bullfinch	11490	9	10	19
All	249360	525	78	603

through or wintering in, and the wintering sites of the birds breeding in or migrating through Hungary.

2. Material and methods

We used data available in the Databank of the Hungarian Ornithological and Nature Conservation Society - BirdLife Hungary at the end of 1997 (Tab. 1), but only species with more than 10 foreign recoveries were analysed. These foreign recoveries



Fig. 1. Hungarian related recoveries of the Linnet in Europe. Solid squares: foreign location, either of ringing or recovery, when recovery was from the same migration season. Solid circle: foreign location, either of ringing or of recovery, when recovery was from a different migration season or one year or more passed between the ringing and the recovery. The Hungarian site is not marked.

ies span the period between 1908 and 1997 and are summarised in the Appendix. Where possible, we distinguished between same-year recoveries and those found later than the year of ringing. We could not separate by age or sex, because these categories have been distinguished in the last decades only.

Two different recovery groups were separated:

- (A) The ringed specimen was recovered in the same migration period as ringed.
- (B) One year or more passed between the ringing and the recovery.

The recovery numbers of these categories are referred in the text as A, B respectively, between brackets after the name of the country or area (where it is not mentioned other way in the text).



Fig. 2. Hungarian related recoveries of the Goldfinch in Europe. See the legend of Fig. 1.



Fig. 3. Hungarian related recoveries of the Greenfinch in Europe. See the legend of Fig. 1.



Fig. 4. Hungarian related recoveries of the Siskin in Europe. See the legend of Fig. 1.

3. Results

3.1. Linnet (Fig. 1)

The recoveries fall in a very narrow stripe. One bird ringed in Poland was recovered in Hungary during autumn migration. One bird each, ringed during winter in Hungary was recovered in Finland, Poland and Lithuanian spring and in later years birds were recovered in Poland (0,2). The southern recoveries were mainly from Northern and Central Italy (0,4) and Malta (6,6). This migration direction was also supported by two additional recoveries ringed in Italy and subsequently found in Hungary.

3.2. Goldfinch (Fig. 2)

The recoveries show a narrow migration passage in northwest-southeast direction. The birds arrived from the Northwest, mainly from Germany, Poland, Slovakia and the Czech Republic. The main destinations of the birds migrating from and through Hungary are on the Balkan Peninsula: Croatia (4,6), Yugoslavia (2,8), Albania (1,0), Greece (4,0), and Bulgaria (1,1). A few specimens were recovered in

winter in Italy (1,2). One bird ringed in Croatia was recovered in Hungary, and 1-1 bird ringed in Hungary moved to the Czech Republic and Poland on spring migration. Specimens ringed in Croatia (2), Yugoslavia (1), Bulgaria (1), Czech Republic (2), Slovakia (1) and Poland (1) were recovered in other years in Hungary.

3.3. Greenfinch (Fig. 3)

All recoveries of birds from the north were ringed in Hungary and recovered later in countries to the north-northeast. The most northerly of these countries was Lithuania (0,1); others were recovered in Poland (0,8), Czech Republic (0,1) and Slovakia (0,4). The main wintering area of this species seemed to be in Greece (9,7). Recoveries along this route were from the former Yugoslavia (2,2), Albania (0,1), Bulgaria (0,1) and Turkey (0,1). A smaller number of birds migrated to the SW, demonstrated by recoveries from the Croatian seashore (5,1), northern and southern Italy (2,2), and Malta (0,2). One bird ringed in Italy was recovered on spring migration, and birds ringed in Yugoslavia (1), the Czech Republic (1) and Slovakia (3) were recovered in other years in Hungary.



Fig. 5. Hungarian related recoveries of the Hawfinch in Europe. See the legend of Fig. 1.

3.4. Siskin (Fig. 4)

The large number of recoveries showed very diffuse migratory directions. The birds arriving from north originate mainly from the Baltic States: Lithuania (3,1), Latvia (1,0) and Estonia (0,1), Finland (1,1), Sweden (0,1) and Russia (3,2). Birds ringed in Hungary move to wintering grounds principally in Northern Italy (86,26), and during the winter they reach southern parts of Italy. A few specimens were recovered on the northern parts of the Balkan Peninsula in Slovenia (4,1), Croatia (4,0), Yugoslavia (2,1), and Bosnia (0,3) on their way to Italy. Some birds tended to move to different parts of the Mediterranean, from Greece (3,0), Bulgaria (5,0) and Cyprus (0,1) on the east to France (2,0) and Spain (1,1) in the west. A smaller number seem to have changed migratory direction: either ringed in Hungary and recovered in Austria (2,7), Germany (0,6), and Belgium (1,4), or viceversa: ringed in Austria (0,2), Germany (2,0), the Netherlands (0,1) and recovered in Hungary.



Fig. 6. Hungarian related recoveries of the Chaffinch in Europe. See the legend of Fig. 1.

3.5. Hawfinch (Fig. 5)

The small number of northern birds recovered in Hungary originated from Sweden (0,1), Slovakia (1,1) and Germany. Northern recoveries of Hungarian-ringed birds were from Estonia (0,2), the Ukraine (0,1), Slovakia (0,1), and Poland (0,1). Birds ringed in Hungary were recovered in high numbers on the wintering sites, mostly in Northern Italy (27,63), a few birds on the Croatian seashore (1,6), Bosnia (2,0) and in South France (3,1), and 1-1 in Sicily, Sardinia and Tunisia. The birds recovered on autumn migration and on wintering showed migration along a nar-



Fig. 7. Hungarian related recoveries of the Brambling in Europe. See the legend of Fig. 1.



Fig. 8. Hungarian related recoveries of the Bullfinch in Europe. See the legend of Fig. 1.

row line. One bird ringed in Yugoslavia was recovered in Hungary, and 1-1 Hungarian ringed bird was recovered in Poland and Slovakia during spring migration.

3.6. Chaffinch (Fig. 6)

According to recoveries, there were no birds arriving from the north to Hungary. Only 2 birds ringed in Hungary were recovered after more than a year in Ukraine and Belarus. The wintering sites of birds ringed in Hungary migrated almost exclusively to the Apennine Peninsula (34 recovered in Italy on autumn migration and 46 as captured). Three specimens were recovered at the Dalmatian seashore on migration. The most important wintering areas within the Apennine Peninsula are North and Central Italy, but a few birds were recovered in southern Italy. A few birds covered longer distances: 2 were recovered in Sicily, 2 in Sardinia and one in South France. One bird crossed the Mediterranean Sea and was recovered in Algeria (not indicated on the map).

3.7. Brambling (Fig. 7)

Most of the birds were recovered after more than one year west of Hungary: in Germany (0,1), southern France (0,2) Spain (0,1) and the greatest number in northern Italy (1,8). Two birds were recovered to south direction in Yugoslavia (0,2) and 1-1 to far east in the Caucasus Mountains in Georgia and in the Ural Mountains in Russia (3223 km). Birds ringed in Germany (0,2), France (0,1), Italy (0,1) and Yugoslavia (0,1) were recovered in Hungary. One bird each was recovered within the same migration period in Italy on autumn migration and in Norway on spring migration.

3.8. Bullfinch (Fig. 8)

The few birds recovered in Hungary were ringed in Sweden (2,0), Finland (1,2), Estonia (1,0), Poland (0,1) and Slovakia (1,2). Birds ringed in Hungary were recovered in later years in Russia (0,3), Ukraine (0,1), Latvia (0,1), Norway (0,1), and Poland (0,1). Birds migrating through Hungary to southern wintering areas were recovered in Croatia (2,0) and North-Italy (1,0).

4. Discussion

The formation of migration patterns relates to geographical and evolutionary causes. The formation of migration routes was determined by the in- and/or back settlement after the last glacial period. The recent wintering areas correspond to the breeding areas under the glacial period. If a species survived in a small area during the glacial period today can be wide-

spread, but all populations spend the winter at the ancient areas. Those species, which survived the glacial period in a bigger area, can have different migration routes and wintering areas today. These migration routes evolved according to the geographical barriers, which make migration more difficult. The high mountains lying in a West-East direction played this role in Europe (Busse 1987, Csörgô & Ujhelyi 1991). These principles appear most clearly in the migration routes of long-distance migrants.

In case of partial migrants and irruptive species the picture is more difficult. The migration routes are not well defined and the migration speed is very slow (Hilden & Saurola 1982, Ellegren 1993). These species change from animal to plant diet for the winter. This change results in the possibility to survive at northern latitudes and in worse weather conditions. The movement of these species is almost entirely controlled by the quantity of available food (Svårdson 1957, Berthold 1984, Jenni 1987, Alerstam 1990). In the continental areas of the temperate zone the characteristics of winters can not be predicted, thus it is not possible to predict the quantity of accessible food. Wintering site fidelity would be senseless for species adapted to these fluctuating conditions (Schlenker 1976, Yunick 1983, Csörgô & Molnár 1991).

According to the facts above, the studied species differ from each other. They can spend the winter in the Carpathian Basin according to the actual weather conditions on a scale varying by species. The species differ in the origin and destination of the birds passing through Hungary.

The Linnet is a partial migrant. The birds breeding in West Europe migrate to

the Iberian Peninsula on a narrow front, while from south Europe to North Africa (Cramp & Perrins 1994). From the areas between Finland through Poland to Hungary the birds migrate to the Apennine peninsula and Malta on a very narrow migration passage. The birds breeding in the more eastern parts of Europe spend the winter on the Balkan Peninsula and Asia Minor.

The Goldfinch is also a partial migrant. The European populations spend the winter at different parts of the Mediterranean area (Cramp & Perrins 1994). The birds breeding on the British Isles, in France and Germany migrate to the Iberian Peninsula. A minority of the western European birds crosses the Strait of Gibraltar and migrates to African wintering grounds (Asensio 1986). There is a migratory divide at 10° E (Zink 1995). Birds breeding east of this line migrate on a broad front in a S-SW direction to the Balkan where this species is very common in winter from the Dalmatian coast to the southern islands (Cramp & Perrins 1994, Zink 1995). This is the typical wintering area of the Hungarian birds as well. Only a small number of birds winter on the Apennine peninsula. There were a low number of captures compared to other finches in the Lombardian bird-capturing gardens (Schubert *et al.* 1986).

The Greenfinch is a partial migrant in most of its breeding range. There are resident individuals even in the northernmost Scandinavian populations, but only the southernmost populations are fully resident (Cramp & Perrins 1994). The migration is going on a broad front, and the species are wintering on all the three large Mediterranean peninsulas. The birds from Scandinavia and the Baltic states move

SW on fairly narrow front and spend the winter along the northern coasts of Europe to Iberia in the south. The western populations migrate in SW direction to the Iberian Peninsula. The birds breeding in Switzerland and Germany spread over a wide area from the Iberian Peninsula to Northern Italy during the winter, but the majority migrates to the Apennine Peninsula. The birds breeding in the north-east migrate to the Baltic areas, while from southern areas to the Balkan Peninsula (Cramp & Perrins 1994). Most of the birds ringed in Hungary were recovered on the Balkan Peninsula, with a few recoveries from the Apennine peninsula.

The northern populations of the Siskin are migratory while the southern ones are resident (Cramp & Perrins 1994). Individual birds can follow different wintering strategies: one part of the population shows nomadic behaviour throughout the winter, while others are faithful to the wintering site (Senar *et al.* 1990, 1992). Some individuals spend the subsequent winters in areas far from each other, while others show wintering site fidelity. The European migration routes of the species cannot be clearly defined, only some tendencies can be observed. The Norwegian birds usually spend the winter more to the west than the Finnish ones (Eriksson 1970b). The majority of the birds migrating through the Baltic areas arrive from South Finland and beside the west European wintering grounds in France, and the Iberian Peninsula (Asensio 1985) spend the winter in large numbers in Northern Italy (Payevsky 1994). The Hungarian recoveries fall in this migration group. A large number of these recoveries show connection with the SW directed migration route of Scandinavian birds

(Germany, Belgium, Switzerland, France), but there are no recoveries from the typical wintering grounds (Iberian Peninsula, British Isles) of these populations except one from Mallorca.

The Hawfinch is mostly resident in West Europe, only a small part of the population is migratory and even those cover only short distances. The North and Central European populations are partial migrants with a typical S-SW direction of migration (Cramp & Perrins 1994). Some of the Central European birds can reach North Africa during the winter, but the most important wintering areas are the Iberian Peninsula, southern France and northern Italy (Asensio 1990, Cramp & Perrins 1994). This is true for Hungarian breeders, as well. A few birds from the direction of Poland are passing through Hungary. The centre of wintering areas of the European populations is in the western basin of the Mediterranean region. More eastern populations spend the winter in Ukraine, Crimea and Caucasus (Dementiev & Gladkov 1954).

The southern populations of the Chaffinch are residents; the different populations northward and eastward become more migratory (Cramp & Perrins 1994). The direction of migration changes between west and south. The standard direction of north and west European populations is SW (Pedreck 1970, Hecke & Verstuyft 1972) The Scandinavian birds spend the winter in an area spanning from Denmark and Germany to the British Isles. The southernmost occurrence in winter is at the Iberian Peninsula. The Russian population is wintering on the Baltic Coast. Birds breeding in Germany and Switzerland migrate to the western Mediterranean area, while east-European

birds spend the winter in northern-Italy (Cramp & Perrins 1994, Zink 1995). The wintering areas possibly differ between very close breeding populations. The breeding population of the Czech Basin winters in the south of France, while the Slovakian population spends the winter in northern Italy (Hajek & Basová 1960, Cramp & Perrins 1994). This is the typical wintering area of the Hungarian population too, so the Slovakian and Hungarian birds may use the same wintering area. However, according to Savigni & Massa (1983) and the data presented here. The birds from Slovakia and the Baltic States arrive to the wintering grounds via the Alps and the Po lowland in northern Italy, while Hungarian birds migrated through the northern Adriatic.

The Brambling is breeding only in the northernmost areas of Europe. Every population is migratory and their wintering areas lie between the British Isles and the Caucasus (Cramp & Perrins 1994). The wintering strategies can be different. Part of the population spends the winter as north as the weather permits, other birds migrate to wintering areas separated by the origin of birds. In France, the Norwegian birds spend the winter in the western, the Swedish in the middle while the Finnish and Russian birds in the eastern areas (Yeatman-Berthelot 1991). Another migration route starts from north Europe, the birds migrate on this one to wintering areas in Northern Italy (Eriksson 1970a). There is no clear separation between the two groups. Other birds following a third strategy have no favoured migration route, the same bird can change wintering areas year by year, can spend subsequent winters on the British Isles and in the Caucasus

(Alerstam 1990). The irruptive tendency of the Brambling is the highest among the studied species, which is in direct relation with the winter food, first of all with the beech mast (Jenni 1987). The males spend the winter farther north than the females, which is a typical pattern of partial migration (Eriksson 1970a, Jenni 1982). The migration route in spring can differ from the one in autumn. The few Hungarian related recoveries belong to those migrating from north Europe to North-Italy, but a part probably changed wintering areas to west Europe or spent the subsequent winter far east in the Caucasus.

The populations of the Bullfinch are usually partial migrants, although in some areas they are residents. There are resident individuals in the northernmost populations also. The migratory specimens cover only short distances, and the wintering areas are inside the breeding area of the species (Cramp & Perrins 1994). The Scandinavian birds reach the latitude of Belgium-Switzerland-Romania dispersing SSW-SSE direction (Saurola 1979 in Cramp & Perrins 1994). Birds migrating through Southern Germany typically move to SW direction to Southern France (Barlein 1979). The direction of migration of the more eastern breeding populations is SW (Cramp & Perrins 1994), a part of the birds recovered in Hungary are related to them. The recoveries show a migration route from Scandinavia and the Baltic states through Poland and Hungary to Northern Italy and the Dalmatian seashore.

The role and importance of the Carpathian Basin for European finches is very different among species. The lack of recoveries and the well-known migration route of the north-eastern population of

the chaffinch indicate that this species is not migrating through Hungary in significant numbers. The Greenfinch and Goldfinch populations breeding north of Hungary in the region of Poland partly wintering, partly migrating through Hungary to southern areas. Other species migrate to and through Hungary from Scandinavia and NE Europe as well.

The Hungarian - related recoveries of the Brambling and Siskin, which are the most irruptive species, connect these birds to those wintering in W Europe, but the other species use different, more eastern wintering areas. While those spend the winter in western parts of the Mediterranean area, particularly on the Iberian peninsula, the Hungarian related Chaffinch, Linnet and Hawfinch populations spend the winter on the Apennine peninsula, while the Greenfinch and Goldfinch on the Balkan peninsula.

The three large Mediterranean peninsulas served as refuges for the finch populations in the glacial period. According to the observable pattern today, the role of the peninsulas were not significantly different, as finches use all three areas for wintering. The differences are on a population level, which possibly means that the populations survived on the different peninsulas, and when expanded to north occupied different breeding areas in Europe.

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Összefoglalás

A pintyfélék (Fringillidae) vonulása és telelése a Kárpát-medencében a külföldi visszafogások alapján

Vizsgálatainkat a Magyar Madártani és Természetvédelmi Egyesület Gyűrűző és Vonuláskutató Szakosztály Adatbankjának külföldi vonatkozású, 100 km-nél hosszabb távú visszafogásai alapján végeztük. Az 1997 végéig összegyűlt összesen 603 visszafogási adatot térképen ábrázolva elemeztük. A vizsgált 8 gyakori faj (erdei pinty - *Fringilla coelebs*, fenyőpinty - *F. montifringilla*, zöldike - *Carduelis chloris*, tengelic - *C. carduelis*, csíz - *C. spinus*, kenderike - *Acanthis cannabina*, süvöltő - *Pyrrhula pyrrhula*, meggyvágó - *Coccothraustes coccothraustes*) parciális vonuló, különböző mértékű inváziós hajlammal. Vonulásukat erősen befolyásolja az időjárás és a táplálék elérhetőség évenkénti változékony-sága. A parciálisan vonuló fajokra általában nem jellemző a vonulási út és telelőterület hűség, ezért a megkerülések nagy egyedi és évenkénti változatosságot mutatnak. A nyolc faj átvonuló egyedei különböző helyről származnak, és telelő területük is különböző. A Kárpát-medencének megfelelő szélességen nagyrészt magas hegyek terülnek el, ezért az észak felől a Mediterráneum felé tartó magevő madaraknak fontos átvonulási területe. Innen fajoként különböző irányba, az Appenin- vagy a Balkán-félsziget felé haladnak tovább, míg az inváziós fajok Európa nagy területén szétszóródnak. A leginváziósabb hajlamú fenyőpinty és csíz hazai vonatkozású visszafogásai a Ny-Európában telelőkhöz kapcsolják az itt átvonulókat is, de a többi faj eltérő, keletebbi telelő területeket használ. Míg azok általában az Ibériai félszigeten vagy legalábbis a Mediterráneum nyugati medencéjében telelnek, a magyar vonatkozású madarak közül az erdei pinty, a süvöltő, a kenderike és a meggyvágó az Appenin félszigeten, a zöldike és a tengelic a Balkán félszigeten telel. A jégkorszakban a három nagy mediterrán félsziget az északról délre szoruló pintyfélék refugiumaként is szolgálhatott. A mai képző szerepük a vizsgált fajok esetében nem különbözhetett lényegesen, mivel ma mindhárom terület telelőhelyként szolgál. A különbségek populációs szintűek, ami azt jelenti, hogy a felmelegedéssel észak felé terjedő fajok a félszigetektől kiindulva Európa különböző területeit foglalták el.

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Appendix continued.

	Haw finch						Chaffinch						Brambling						Bullfinch					
	I.			II.			I.			II.			I.			II.			I.			II.		
	A1	A2	B	A1	A2	B	A1	A2	B	A1	A2	B	A1	A2	B	A1	A2	B	A1	A2	B	A1	A2	B
Austria			1																					
Switzerland																								
Germany						1								1			2							
Belgium																								
Holland																								
France		3	1						1					2		1								
Spain														1										
Portugal																								
Algeria									1					1	8		3							
Italy		27	63			5		34	46												1			
Malta																								
Slovene																								
Croatia		1	6						3					2		1				2				
Bosnia		2																						
Yugoslavia				1																				
Albania																								
Greece																								
Turkey			1																					
Cyprus																								
Bulgaria																								
Romania																								
Czech Rep.																	1						1	2
Slovakia	1		1		1	1																		
Ukraine			1						1													1		
Georgia														1										
Russia														1								3	1	
Belarus									1															
Estonia			2																			1		
Lithuania																								
Latvia																								
Poland	1		1																	1				1
Finland																							1	2
Sweden						1																		2
Norway													1								1			

Mating pattern and mate choice in the Lapwing *Vanellus vanellus*

A. Liker and T. Székely

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We investigated the mating behaviour of Lapwings in a Hungarian grassland between 1992 and 1994. 80% of males were monogamous and 20% were polygynous (n=59 males). Polygynous males acquired two females (primary, secondary) that laid one clutch each on the males' territory. Monogamous males, that became polygynous later, spent more time on song-flight (7.5 ± 1.6 (s.e.)%) than the ones which remained monogamous (1.6 ± 0.7 %). Polygynous males tended to have more successful nests on their territories (1.0 ± 0.3) than monogamous males (0.5 ± 0.1). All females out of 104 had one social mate in a breeding season, except one female mated to two males (sequential polyandry). Secondary females laid their nests 8.4 ± 1.2 days after the primary females completed their nests and at that time several males were still unmated. We found no indication that secondary females were 'inferior' to monogamous and primary females, because body condition, clutch volume and nest survival were not different among monogamous, primary and secondary females. Our results suggest that polygyny was not forced on females by the lack of unmated territorial males; rather secondary females preferred already mated males to unmated ones.

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1. Introduction

Shorebirds (infraorder Charadriides) are ideal subjects to investigate questions about avian breeding systems, since they have an extraordinary variety of mating patterns including monogamy, polygyny and polyandry (Pitelka *et al.* 1974, Erckmann 1983). The Lapwing *Vanellus vanellus* is one of the most common shorebirds in Europe and until recently it has been considered a typically monogamous species (Cramp & Simmons 1983). Recent studies on individually marked birds

showed, however, that the Lapwings' mating behaviour is more flexible than it was previously thought. For example, it turned out that social polygyny is common in many populations and 30-50% of males are mated to several females simultaneously (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Some of the polygynous males are polyterritorial and they defend separate territories for each of their mates (Byrkjedal *et al.* 1997, Parish *et al.* 1997). In addition, female Lapwings appeared to mate with a single male in a breeding season, although recently both double-clutching and sequential polyandry

have been reported (Blomqvist & Johansson 1994, Parish *et al.* 1997). Studies also suggest that variation in male reproductive success may be explained by female choice (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997), although female preference for particular males may be counteracted by the aggressive interactions among females (Liker & Székely 1997a).

In this study we investigate three aspects of mating behaviour in Lapwings. First, we investigate their mating patterns in a Hungarian alkaline grassland ('puszta'). Although several studies have been published on the mating patterns of Lapwings (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997), these studies were carried out in Northern and Western Europe where the Lapwings often breed in arable land or cultivated grassland. Second, we investigate the reproductive success of males and females in various pair-bonds. In particular, we compare the reproductive success of polygynous and monogamous males, since a previous study by Grønstedt (1996) suggested that more eggs hatch on the territories of polygynous males than on the territory of monogamous ones. We also compare the nest survival of monogamous and polygynous females. Finally, we investigate why do some females mate with an already mated male. Previous studies suggested that neither the lack of unmated males (Byrkjedal *et al.* 1997, Parish *et al.* 1997) nor the random settlement of females provide a sufficient explanation for the polygyny in the Lapwing (Byrkjedal *et al.* 1997). Thus some females seem to prefer already mated males over unmated males. This preference may relate to the quality of males' displays (song-flights), the age

of the males, their territory size, or to the abundance of food on their territory (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997). However, the relative importance of the males' characteristics (or that of their territories) has remained controversial (Byrkjedal *et al.* 1997). In this paper we examine several potential mate choice cues such as the conspicuous song-flight display of males, a possible honest indicator of male quality (Andersson 1994), and the attributes of their territories such as size and abundance of food. We studied mating pattern and reproductive success between 1992 and 1994, whereas mate choice was investigated in 1994. The latter study involved a subset of closely monitored males.

2. Study area and methods

2.1. Study site

We studied the Lapwings in Miklapuszta, Central Hungary (46° 40' N, 19° 10' E) between 1992 and 1994. Miklapuszta (2000 ha) consists of alkaline grasslands, temporary and permanent wetlands and plateaus formed of loess, where 200-300 Lapwings bred during the study. We investigated an area of approximately 700 ha each year. Halophytic plants such as *Festuca pseudovina*, *Puccinellia limosa*, *Artemisia maritima*, *Lepidium cartilagineum* and *Camphorosma annua* grew in patches of the alkaline grassland (Székely *et al.* 1994). The loess plateaus were 0.5-4 m high and they rose steeply from the surrounding flat alkaline grassland. These plateaus were covered by *Muscari racemosum*, *Verbascum phoeniceum*, *Filipendula vulgaris* and

Orchis morio. Lapwings bred mainly on the flat alkaline grassland, although they often fed on the plateaus. In March 1994 we estimated the densities of earthworms in some loess plateaus and flat alkaline grasslands by using the formalin method (Raw 1959). The abundance of earthworms was about 90 times higher on the loess plateaus (8.9 ± 2.5 (s.e.) earthworms $\times 0.5 \text{ m}^{-2}$, $n=14$ samples) than on the flat alkaline grassland (0.1 ± 0.1 earthworms $\times 0.5 \text{ m}^{-2}$, $n=23$ samples; Mann-Whitney U test, $z=5.217$, $P<0.0001$).

2.2. Field work

Field work was carried out between the first week of April and the last week of June except in 1994, when it was started in the second week of March. Laying dates were known for clutches found during egg-laying. For clutches found during incubation, the egg-laying dates were estimated by floating the eggs in water (A. Liker unpublished data, see also van Paassen *et al.* 1984) or by calculating them from the date of hatching by assuming 26 days of incubation (A. Liker & G. Noszály, unpublished data). Laying dates refer to the laying of the last egg in a clutch which coincides with the start of incubation (Cramp & Simmons 1983). In each clutch we measured breadth and length of eggs to the nearest 0.1 mm and estimated egg volumes by using 0.457 as the volume constant (see Galbraith 1988). Clutch volumes were estimated for each clutch by multiplying mean egg volumes by clutch size. Nests were visited every second or fourth days. Successful nests (i. e. those that hatched at least one chick) were identified by the presence of chicks or by the occurrence of eggshell frag-

ments in the nest lining. Location of each nest was recorded on a map of 1:10 000 scale.

2.3. Identification of adults and determination of mating patterns

We used two methods to identify Lapwings. First, adults were captured on their nest by a funnel trap and they were ringed with a metal ring and an unique combination of colour rings ($n=9$ males and 92 females). Captured adults were also weighed to the nearest 1.0 g and their tarsus length were measured to the nearest 0.1 mm. Second, we used individual plumage characteristics to recognise adults within a breeding season ($n=50$ males and 12 females). We made a drawing chart for each individual by sketching facial markings, white markings on their black breast stripe and length of their crest. Plumage variation among individuals has often been used to identify Lapwings (e.g. Berg 1993, Blomqvist & Johansson 1994, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Our charts were reliable to identify individuals within a breeding season as evidenced by three colour ringed males which we repeatedly identified solely by using their chart. Pair-bonds were determined during nest checks and behavioural observations (see Liker & Székely 1999). One female bred on the territory of each monogamous male. Polygynous males had simultaneous pair-bonds with two females on their territories. Female that laid the first clutch on the territory of a polygynous male was termed primary female, whereas female that laid her clutch second was termed secondary female. This notation does not imply any dominance relation between females.

2.4. Observations of male behaviour and territory size

We observed the behaviour of 17 males between 15 March and 30 March in 1994. The observations were carried out between 06:00-10:00 and 15:00-18:00 from a hide or a car about 100 m away. Three observations of 60 minutes each were collected from each male with 5.3 ± 0.3 (s.e.) days between successive observations. For each male the day of observation was randomly chosen and we also randomised the observations among males in a day. Behaviour of males, such as song-flight and ground-display, was recorded at every minute by instantaneous sampling. The ground-display included rocking-display, scraping-ceremony and mating-ceremony (see Cramp & Simmons 1983 for definitions). We recorded the position of the male on a map of 1: 6 500 scale at every five minutes when the male was on the ground. All observations were carried out by A. L.

2.5. Data processing and statistical testing

Each clutch or individual was used once in each analysis. Some males were polygynous in one breeding attempt although they bred monogamously in other breeding attempt(s) e.g. initiated a new nest after the failure of their first nest or bred in a different year. We include these males as polygynous in the analyses. Daily probabilities of nest survival were estimated by the Mayfield method (1975), and their standard errors and tests were calculated by following Hensler & Nichols (1981). Display behaviour of males was analysed as percentages of total observation time

during which the focal male was in view. Territory size was estimated by drawing a maximum convex polygon around the position of males during each 60 minute observation period. We took the mean area of these three polygons. We also mapped the loess plateaus onto the territory maps, and the size of loess plateaus within each territory was estimated from these maps. Date of egg-laying was the number of days since 1st March. Body condition of incubating females was estimated as residuals of body mass regressed on tarsus length i.e. $\text{BODY MASS (ln(g))} = 2.855 + 0.650 \times \text{TARSUS LENGTH (ln(mm))}$ ($r^2 = 0.149$, $P < 0.001$, $n = 91$ females). The number of days incubated at the time of weighing were not different between monogamous (14.5 ± 0.8 (s.e.) days, $n = 23$), primary (20.3 ± 2.4 days, $n = 6$) and secondary females (15.1 ± 2.3 days, $n = 6$; Kruskal-Wallis test, $\chi^2 = 4.695$, d.f. = 2, $P > 0.05$). As we had few cases of polygyny we pooled the data from all three years. Non-parametric tests were used such as Spearman rank correlations (r_s) since the normality or the homoscedasticity assumptions of parametric tests were often violated. Partial correlations were performed on ranked data as suggested by Daniel (1990). In multiple independent comparisons the critical level of significance was corrected as suggested by Motulsky (1995). Statistical analyses were carried out by SPSS 4.0 for the Macintosh. Mean \pm s.e. and two-tailed probabilities are given.

Tab. 1. Mating pattern of male Lapwings in 1992-1994. Each male was included once in each year and once in the 'all years' category. One male had a monogamous pair-bond and a polygynous pair-bond in two breeding attempts in 1994; his polygynous pair-bond is included.

Year	Mating pattern of males	
	Monogamous (%)	Polygynous (%)
1992	4 (100.0)	0 (0)
1993	23 (92.0)	2 (8.0)
1994	23 (69.7)	10 (30.3)
All years	47 (79.7)	12 (20.3)

3. Results

3.1. Mating patterns

3.1.1. Males

80 nests were laid on the territories of 59 males. 56 nests were laid on the territories of monogamous males ($n=49$ males), and 24 nests were laid on the territories of polygynous males ($n=12$ males; two males had both a monogamous and a polygynous pair-bond, see below). Thus 20.3% of the 59 males were polygynous at least in one breeding attempt (Tab. 1). Six males out of 59 were involved in more than one breeding attempt. The mating pattern of two individually marked males changed within or between years. One male (H97) was monogamous in 1992, but he had both a polygynous and a monogamous pair-bond

in 1994. The other male (H214) was polygynous in 1993 and monogamous in 1994. Both of these males changed their mates between years, but we do not know whether H97 changed his mate between successive nesting attempts in 1994. On the other hand, four males mated only monogamously. Two males (HP58, HP53) bred twice monogamously in 1994 and one male (HP42) bred three times monogamously in 1994. One male (H44) mated monogamously twice in 1992 and once in 1994. HP58 kept the same mate for both of his breeding attempts although we do not know whether the other three males (HP53, HP42, H44) changed their mates between successive pair-bonds.

3.1.2. Females

122 clutches were laid by 104 females. All females had a social pair-bond with one male at a time. 17 females out of 104 laid more than one clutch (16 females laid two clutches each and one female laid three clutches) and we identified the mate of two such females. One of these females (T366) laid both of her clutches for the same male (HP58, see above). The other female (T379) laid one clutch each for a polygynous and monogamous male in 1994 and she changed mates between the two nests (sequential polyandry). Four

Tab. 2. Hatching success of Lapwing nests. Daily probabilities of nest survival and their standard errors were estimated by the Mayfield method (see 'Methods'). Daily probabilities of nest survival were not different between nests of polygynous females (primary and secondary females combined: 0.9728 ± 0.0077) and monogamous females ($z=0.778$, $P>0.4$).

	Mating pattern of females		
	Monogamous	Primary	Secondary
Daily probability of nest survival (mean \pm s.e.)	0.9650 ± 0.0063	0.9779 ± 0.0098	0.9674 ± 0.0121
No. of nests found	55	11	12
No. of nests lost	30	5	7
Exposure (no. of days)	858	226	215

Tab. 3. Body condition, clutch volume and date of egg-laying in female Lapwings, mean \pm s.e. (no. of females). Condition of incubating females is given as residuals of a linear regression of $\ln(\text{body mass})$ on $\ln(\text{tarsus length})$ (see 'Methods'). Laying dates are the no. of days after 1st March. To correct for the four independent comparisons at 5% significance level we identify $P=0.0127$ as corrected critical significance level. χ^2 values and uncorrected probabilities of Kruskal-Wallis tests are given.

	Mating pattern of females			χ^2	P
	Monogamous	Primary	Secondary		
Female					
condition ($\ln(g) \times 10^{-2}$)	1.9 \pm 1.2 (23)	-0.8 \pm 0.9 (6)	0.2 \pm 2.6 (6)	2.257	>0.3
tarsus length (mm)	48.1 \pm 0.4 (23)	48.0 \pm 0.5 (6)	48.1 \pm 0.7 (6)	0.016	>0.9
Clutch volume (cm ³)	87.3 \pm 2.1 (56)	86.9 \pm 2.6 (12)	93.8 \pm 2.9 (12)	1.794	>0.4
Laying date (day)	50.0 \pm 2.9 (55)	38.1 \pm 6.9 (11)	46.1 \pm 6.3 (12)	3.353	>0.1

females deserted their clutch or brood, although none of these females remated or re-nested after desertion (Liker & Székely 1999).

3.2. Reproductive success

3.2.1. Males

3.81 \pm 0.09 and 7.58 \pm 0.36 eggs were laid on the territories of monogamous ($n=47$ males) and polygynous males ($n=12$ males), respectively (Mann-Whitney U test, $z=5.862$, $P<0.001$). Since daily survival was not different between monogamous and polygynous nests (Tab. 2), polygynous males tended to have more successful nests on their territories (1.0 \pm 0.3, $n=11$ males) than monogamous males (0.5 \pm 0.1, $n=46$ males; Mann-Whitney U test, $z=1.707$, $P=0.088$).

3.2.2. Females

Females settled on the territories of already mated males throughout the breeding season (Fig. 1). Several females chose mated males when unmated males were still available since laying dates were not different between monogamous, primary and secondary females (Tab. 3).

Secondary females laid their nest 8.4 \pm 1.2 days after the primary ones on the same territory. It took 5 days to lay the modal clutch size of four eggs (A. Liker & G. Noszály, unpublished data), thus secondary females started to lay their eggs on average three days after the primary females completed theirs. The difference

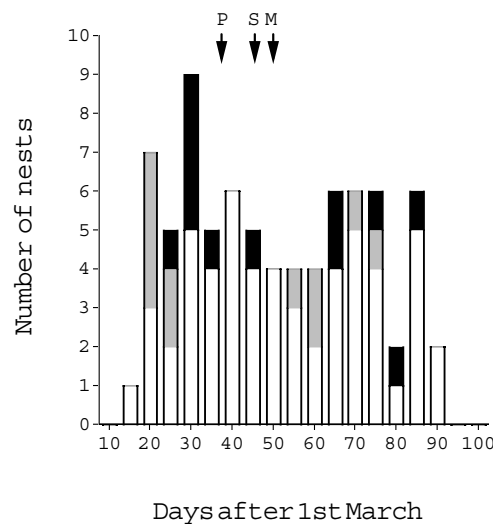


Fig. 1. Distribution of egg-laying dates of monogamous (M), primary (P) and secondary (S) female Lapwings (white, hatched and black bars, respectively). Nests laid over each five-day periods are pooled from 1992, 1993 and 1994 ($n=78$ nests). Arrows indicate mean dates of egg-laying.

between laying dates of primary and secondary females was unrelated to the date of egg-laying of the primary female ($r_s = -0.339$, $P > 0.3$, $n = 11$ territories). The distance between the nests of primary and secondary females was 95.9 ± 8.8 m ($n = 12$ territories).

We found no indication that secondary females were of lower 'quality' than primary and monogamous ones, since monogamous, primary and secondary females were not different in body condition, tarsus length and clutch volume (Tab. 3). Finally, the daily survival of nests was not different between monogamous and polygamous females (Tab. 2).

3.3. Mate choice

Six males attracted two females each, nine males attracted one female each and two males remained unmated in March 1994. Polygynous, monogamous and unmated males often defended neighbouring territories, thus females were able to sample these males before they settled (Fig. 2). We investigated whether the display behaviour of males, the size of their territories, or the area of abundant food in their territories influenced mate choice of females.

3.3.1. Display behaviour

Initially, we found a negative relation between display behaviour of males and

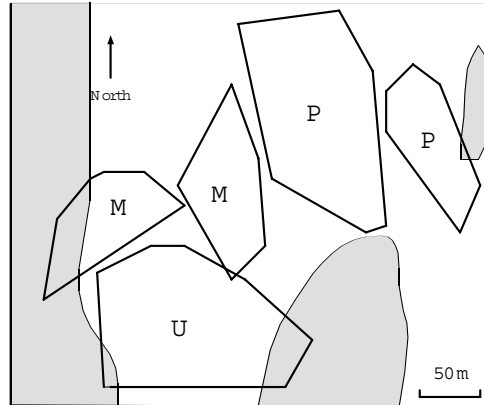


Fig. 2. An example of five male territories in Lapwing. The males were unmated (U), monogamous (M) or polygynous (P) at 30 March 1994. Loess plateaus are dotted.

number of females they attracted (ground-display: $r_s = -0.491$, $P < 0.05$, song-flight: $r_s = -0.468$, $P = 0.058$, $n = 17$ males). This may be because already mated males reduced their display behaviour; perhaps they were occupied with nest-building or incubation. We therefore re-analysed the relation between display behaviour and mating success by dividing males into two groups: (1) unmated and monogamous males which obtained a new mate after the observations of display behaviour and became monogamous or polygamous, respectively (successful males) and (2) males which did not obtain a new mate after the observations and remained unmated or monogamous, respectively (unsuccessful males). We found that before obtaining a mate all males spent a

Tab. 4. Territory size and area of loess plateau in territories of male Lapwings (mean \pm s.e.). χ^2 values and probabilities of Kruskal-Wallis tests are given.

	Mating pattern of males			χ^2	P
	Unmated (n=2)	Monogamous (n=9)	Polygynous (n=6)		
Territory size (ha)	0.48 \pm 0.15	0.43 \pm 0.14	0.47 \pm 0.06	0.985	>0.6
Area of loess plateau (ha)	0.01 \pm 0.01	0.07 \pm 0.03	0.11 \pm 0.05	1.307	>0.5

high proportion of their time on song-flight displays, regardless their subsequent success (no difference between unmated successful and unmated unsuccessful males, Fig. 3). This pattern changed, however, after the settlement of the first female on the male's territory: six males out of fifteen monogamous ones that eventually attracted a secondary female spent significantly more time on song-flight ($7.5 \pm 1.6\%$) than the nine monogamous males which did not attract an additional mate ($1.6 \pm 0.7\%$, Mann-Whitney U test, $z=2.520$, $P<0.02$, Fig. 3; this result remains significant at $P=0.05$ when we control for the two comparisons by sequential Bonferroni correction). After obtaining a second mate polygynous males decreased their display to that of the level of unsuccessful monogamous males (Fig. 3). The time spent on ground-displays was not related to male mating success: we found no difference between monogamous males that attracted a new female ($8.2 \pm 3.7\%$, $n=6$ males) and the ones that did not ($10.2 \pm 5.4\%$, $n=9$ males, Mann-Whitney U test, $z=0.354$, $P>0.7$).

3.3.2. Territory size

We found no evidence that territory size or the area of abundant food in the males' territory ('loess plateaus') were important in female choice, because neither territory size nor area of loess plateaus were different among unmated, monogamous and polygynous males (Tab. 4). The area of loess plateaus remained unrelated to the number of mates when we controlled for territory size by partial correlation ($r_s=0.271$, $d.f.=14$, $P>0.3$). Also, laying date of the first clutch on a male's territory was unrelated to territory size

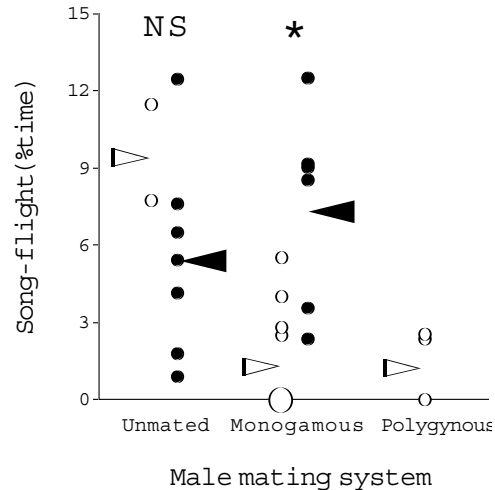


Fig. 3. Time spent on song-flights in relation to the number of mates at the time of the observations ($n=17$ males). Successful males attracted a new mate after the behavioural observations (filled dots, mean: black arrow), whereas unsuccessful males did not (circles, mean: white arrow). The large circle includes five males. Mann-Whitney U tests between successful and unsuccessful unmated males ($P>0.1$), and between successful and unsuccessful monogamous males ($P<0.02$).

($r_s=0.305$, $P>0.2$, $n=14$ males) and to the area of loess plateaus ($r_s=0.178$, $P>0.5$, $n=14$ males).

Since display behaviour tended to decrease with the number of mates (see above), we analysed the relations between display behaviour and territory size by controlling for the number of mates at the time of observation. Nevertheless, territory size was unrelated both to the time spent on song-flights (partial correlation by controlling for the number of mates, $r_s=0.395$, $d.f.=13$, $P>0.1$) and to the time spent on ground-display ($r_s=0.205$, $d.f.=13$, $P>0.4$).

4. Discussion

4.1. Mating pattern

We found that polygyny was a common mating behaviour of Lapwings in a Hungarian grassland, although the frequency of polygyny appeared to be lower (20% of males) than in Western Europe, where 30%-50% of male Lapwings were polygynous (Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). Furthermore, males paired with at most two females in Hungary, whereas in other populations males pair with up to three or four females (Kelly 1989, Berg 1993, Byrkjedal *et al.* 1997, Parish *et al.* 1997). We offer three explanations for the differences among these populations. First, abundance of food may be higher in cultivated habitats in Western Europe than in alkaline grasslands, which may facilitate the aggregation of the females in the former habitat type. Concentration of females probably increases the ability of males to monopolise a number of females. In line with this argument, density of earthworms was about 20 times and 15 times higher in England and in Norway, respectively, than in our study site (Baines 1990, Grønstedt 1996). Second, Lapwings often breed at high densities presumably to defend their nest from predators (Berg *et al.* 1992). This predicts that clumped breeding and thus higher potential for polygyny should be more prevalent at sites where nest predation is high. This argument, however, is unlikely since nest predation was about 60% and 15% in England and Sweden, respectively, whereas nest predation was about 60% in our site (Baines 1990, Berg *et al.* 1992, Liker & Székely 1997b).

Third, aggressive behaviour of females against other females may also influence the frequency of polygyny. In particular, we found that female Lapwings were very aggressive towards a female intruder, especially at the beginning of incubation (Liker & Székely 1997a). The pattern of such aggressiveness suggests that resident females attempt to constrain their males' attempt to attract a new female in order to monopolise the full paternal care of their mate (Slagsvold & Lifjeld 1994). The significance of male help for the survival of the young may vary among populations (Lyon *et al.* 1987, Dunn & Robertson 1992, Gowaty 1996), therefore the intensity of female-female aggression for male care is also expected to vary. The latter argument predicts that female-female aggression will be less intensive in such populations where polygyny is common. Behavioural data are required from other populations of Lapwings to evaluate fully the significance of female-female aggression in their mating system. Nevertheless, these arguments demonstrate the validity of Davies (1989) warnings that to understand mating patterns of a given sex (e.g. males) we need to investigate the behaviour of both sexes, because the observed mating pattern (e.g. polygyny) may be the result of different interests of males and females ('sexual conflict').

Genetic relatedness between offspring and their putative parents may indicate deviation from the observed pattern of social polygamy. In particular, extra-pair copulations (EPCs) have been reported in Lapwing (Cramp & Simmons 1983, Parish *et al.* 1997). EPCs also occur in Hungary, since we observed twelve copulations among individually identified Lapwings, of which one copulation was an extra-pair

copulation and eleven were within-pair copulations (A. Liker unpublished data). These observations suggest that a proper quantification of reproductive success of each mating pattern requires genetic studies of the relatedness between offspring and parents.

4.2. Reproductive success

Our study suggests that polygyny is advantageous for males. We suggest that secondary females do not pay a cost (in terms of reduced reproductive success) at least during incubation. However, we consider both results preliminary. First, our data refer only to one component of reproductive success: the hatching success. Clearly, one needs to take into account subsequent stages of offspring development such as survival of chicks until fledging and the probability that the young are recruited into the breeding population. Given the mobile nature of the precocial chicks and the high dispersal of juvenile Lapwings (Thompson *et al.* 1994), estimating such values seems to be a formidable task. Second, we do not have data on the full costs of polygyny for male and female Lapwings. Polygynous males may achieve higher reproductive success in a given year, but this benefit may be negated if territorial fights or displays incur costs in survival or future reproduction. Similarly, secondary females may have lower survival prospects or may be handicapped in future breeding attempts.

4.3. Mate choice

Why do some females mate with an already mated male? We showed that polygyny was not forced on females by the

lack of unmated males. Another possibility is that random settlement of females produced the observed variation in male mating success (Hartley & Shepherd 1995). The latter explanation, however, is unlikely for Lapwing, since we found that female settlement was not random in relation to male behaviour and females preferred those males which spent a lot of their time on song-flights. Deception of females about the mating status of males (as proposed by Lundberg & Alatalo 1992) is also unlikely, since secondary females laid their eggs on the same territory as primary females so they must have been aware of the presence of the primary females. Thus it seems to us that some males (or their territories) were genuinely more attractive to females than others.

Recent studies suggest that female Lapwings use either the characteristics of the males or that of their territory in mate choice (Berg 1993, Grønstedt 1996, Byrkjedal *et al.* 1997, Parish *et al.* 1997). For instance, Grønstedt (1996) observed that male Lapwings with a large roll angle in song-flights were preferred by females. We suggest that the time spent on song-flights may also be important. Aerial displays such as song-flights are energetically costly, therefore they may signal the condition, health or overall quality of the males (Andersson 1994, Buchanan & Catchpole 1997). In a line with this argument Blomqvist *et al.* (1997) suggested that song-flight in male Dunlins *Calidris alpina* serves primarily mating advertisement. It is also possible that display behaviour varies over the age of males. For example, old males may be better at displaying than young ones simply because they are able to spend more time on displaying or they may be able to per-

form more sophisticated aerial manoeuvres. Indeed, male age and experience seem to be important, since old male Lapwings are more likely to become polygynous than young ones (Parish *et al.* 1997).

Song-flights may also signal the ability of males to fight against other males (Dabelsteen 1978). For instance, males that spend large amount of time on song-flights may obtain the best territories, and females may in fact choose their territory - and not the males *per se*. However, the importance of territory in mate choice is controversial in the Lapwing. On the one hand the observations of both Grønstedt (1996) and Parish *et al.* (1997) suggest that territory quality did not influence the mating success of males. On the other hand Berg (1993) showed that polygynous male Lapwings defended larger territories than monogamous ones, and that the large territories possessed larger foraging areas (flooded fields) than the small ones. Finally, Byrkjedal *et al.* (1997) found that male mating success was related to territory size in some years, but not in others. This controversy may be settled in two ways. First, by assessing the abundance of food on both breeding and feeding territories and estimating how significant is the territory in provisioning of the adults and their young. Thus choosing a territory with abundant food may be more important in such a population, where the Lapwings spend most of their time feeding on their territory. For example, Lapwings spend over 90% of their time on their territory in Sweden and they usually fed there (Berg 1993), whereas in Hungary they spend 70-80% of their time on the territory and they feed mostly off-territory (A. Liker, unpublished data). However, if food is

uniformly superabundant in all territories then females should find another a cue which may be used to discriminate among males (Grønstedt 1996, Byrkjedal *et al.* 1997, D. M. B. Parish pers. com.). Second, experimental studies would be invaluable to separate the significance of males' characteristics from that of their territories in mate choice. For example, experimental manipulations of the ability of males to display acrobatic displays or the amount of earthworms on some territories would test unequivocally the significance of display behaviour and food abundance, respectively.

In conclusion, we showed that 20% of male Lapwings were polygynous whereas the rest bred monogamously in Hungary. Females that settle second on the territory of mated males do not seem to pay a cost, at least not until their eggs hatch. Polygynous males spent more time on song-flight than monogamous ones, supporting the idea that sexual selection (either by female choice or by male-male competition) has influenced the evolution of this display. We point out that further investigations are required on the long-term costs and benefits of each mating patterns by estimating the genetic relatedness between the offspring and their putative parents. Finally, we call for experimental manipulations to tease apart the various hypothesised cues in the mating behaviour of Lapwings.

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Összefoglalás

A bíbicek *Vanellus vanellus* párzási rendszere és párválasztása

Bíbicek párzási viselkedését vizsgáltuk 1992-1994 között Miklapusztán. A párt kapott hímek 80%-a monogám, 20%-a poligin párzási rendszerben költött ($n=59$ hím). A poligin hímek territóriumán egyidőben két tojó fészkel. Nem találtunk különbséget a monogám és poligin hímek között a territóriumok méretében és táplálék-ellátottságában, viszont különbözött a hímek udvarlási viselkedése: párválasztás idején a poligin hímek több időt töltöttek a territórium fölötti csapongó repüléssel (7.5 ± 1.6 (s.e.) %), mint a monogám hímek ($1.6 \pm 0.7\%$). A poligin hímek szaporodási sikere feltehetőleg nagyobb a monogám hímek szaporodási sikerénél, mivel több sikeres fészkelési kísérlet volt a poligin hímek territóriumán (1.0 ± 0.3), mint a monogám hímekén (0.5 ± 0.1). A tojók egyetlen szociális partnerrel álltak párba a fészkelési időszak során ($n=104$ tojó), kivéve egy tojót, amely két hímmel rakott fészket egy szaporodási időszakon belül (szekvenciális poliandria). Poliginiában az egy territóriumon fészkelő tojók tojásrakása között 8.4 ± 1.2 nap különbség volt, a másodiknak megtelepedő tojók fészkerakása idején a populációban még jelen voltak párnélküli hímek is. Nem találtunk különbséget a monogám, az elsőnek megtelepedő valamint a másodikként megtelepedő poligin tojók kondíciója, fészkealmérete és fészkeik kelési sikerre között, ami arra utal, hogy nincs különbség a különböző párkapcsolatban fészkelő tojók "minőségében". Az eredmények azt mutatják, hogy a bíbiceknél a poligin párzási rendszer nem a párnélküli hímek hiányának, hanem a tojók párválasztásának a következménye. A poligin tojók számára a jó minőségű partner választása indirekt nyereséggel (pl. előnyös genetikai tulajdonságú utódok) vagy közvetlen nyereséggel (pl. utódgondozás) egyaránt járhat, a párválasztásból származó előny tisztázása azonban további kutatást igényel.

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Breeding ecology of the Great Crested Grebe *Podiceps cristatus* in northeastern Slovenia

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The paper presents the results of breeding ecology of the Great Crested Grebe (*Podiceps cristatus*) on Dravsko polje in northeastern Slovenia. Up to 44 pairs breed on Dravsko polje, mainly in the Raški ribniki-Požeg Landscape Park. This represents about 15% of the entire breeding population in Slovenia. The highest breeding density was 7 pairs/10 ha. There were significant differences in breeding densities between localities. Correlation between the lower nest diameter and the nest-height was significant, whereas correlation between the upper nest-diameter and nest-height was not significant. The relationship between breeding pairs of the Little Grebe *Tachybaptus ruficollis* and the Great Crested Grebe was positive but not significant.

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1. Introduction

The Great Crested Grebe (*Podiceps cristatus*) is distributed throughout Europe, however, it is the most common in the northern part of Europe (Cramp & Simmons 1977, Fjeldsa & Lammi 1997). It breeds on various inland waters. Studies about breeding biology and ecology of the Great Crested Grebe are numerous from those regions (e.g. Cramp & Simmons 1977, Glutz von Blotzheim *et al.* 1987 and references therein). On the other hand the data from other regions are scarce, especially for more southern localities (e.g. Sarrocco 1986).

The aim of this paper is to provide information on the breeding ecology of the Great Crested Grebe from the southern part of its distribution.

2. Study area

The work was done on Dravsko polje in northeastern Slovenia (46°27'N, 15°41'E). This is a plain of about 210 km², between 240 and 270 m a.s.l., consisting of agricultural areas, forests, mainly small settlements and various waterbodies. The climate is continental, with about 1000 mm of precipitation, concentrated mainly in spring and autumn (Furlan 1990). The area belongs to the sub-Pannonic phytogeographical area (Marinèek 1987).

The most important waterbodies for breeding of the Great Crested Grebe are Raèe ponds, reservoirs Požeg and Medvedce, gravel pit Hoèe, clay pits Pragersko and Gaj. Raèe ponds and reservoir Požeg are parts of the Landscape Park Raški ribniki - Požeg. Raèe ponds (fish-ponds complex) consist of three ponds,

cover 33 ha and are managed for semi-intensive fish-farming. The emergent vegetation consists mainly of *Typha angustifolia* and runs mostly along the northern shore of Veliki ribnik. The other dominant plant species are *Nymphoides peltata*, *Polygonum amphibium* and *Trapa natans*. Reservoir Požeg covers 35 ha and includes 3 islands. The western part of the shoreline is overgrown with *Typha angustifolia*, *Phragmites australis*, *Juncus* spp. and *Carex* spp. Reservoir Medvedce is the biggest waterbody on the Dravsko polje and covers 155 ha. It was filled with water in 1993 (Vogrin 1996, Vogrin & Vogrin 1999). Most of the shoreline is covered by a narrow belt of *Carex* spp. and *Juncus* spp. Inside of the reservoir there was also a lot of dead trees and bushes. Gravel pit Hoèe, clay pits Pragersko and Gaj are the deepest waterbodies on Dravsko polje, with depths between 4 and 10 m. Water vegetation is absent on these localities.

Raèe ponds, reservoirs Medvedce and Požeg are managed for semi-intensive fish-farming. Gravel pit Hoèe, clay pits Pragersko and Gaj are used for a variety of recreational activities, e.g. recreational fishing, windsurfing, swimming.

3. Methods

This paper is based on studies of numbers, breeding, distribution and breeding biology of the Great Crested Grebe, in the period between 1986 and 1997 (except years 1988-1989 and 1994). In order to detect pairs and breeding attempts, waterbodies on Dravsko polje were monitored from May to September. During this period all waterbodies suitable for breeding of Great Crested Grebes were visited at 5-15 day

intervals. Breeding was considered to have taken place if nests, incubating birds, eggs or young were detected.

Searching for nests was performed only on Raèe ponds and was carried out 2-5 times in a breeding season (May-July). Attempts were made to find all nests, by carrying out a systematic search of the vegetation throughout the ponds (see also Vogrin 1999).

Nests were measured to the nearest 0.5 cm. Lower nest diameter was measured at the water level and the water depth was measured near the nest.

Data (nest measurements) were log-transformed to normalise their distribution for parametric analyses (Pearson's correlation). Kruskal-Wallis test was performed on non-transformed data. Statistical analyses were carried out using the SPSS statistical package and according to Sokal & Rohlf (1995).

4. Results and discussion

4.1. Breeding densities

Breeding population of the Great Crested Grebe on Dravsko polje is increasing (Fig.

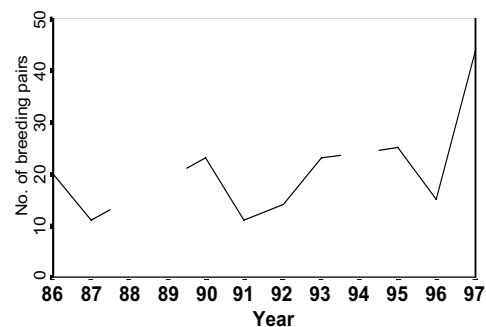


Fig. 1. The number of breeding pairs of the Great Crested Grebe on the Dravsko polje, NE Slovenia between 1986-1997.

1). According to data from Geister (1995) and taking into account that increase in breeding density occurs elsewhere, about 15% of Slovenian population of the Great Crested Grebe breeds on Dravsko polje.

An increase of breeding populations of the Great Crested Grebe was found elsewhere (e.g. Cramp & Simmons 1977, Sarrocco 1986, Walravens *et al.* 1990, Dvorak *et al.* 1993, Fjeldsa & Lammi 1997), however in some areas, the number of breeding pairs decreased (Musil 1995). The main reason of their increase is prohibition of hunting, eutrophication of water and creations of new waterbodies (Cramp & Simmons 1977, Goc 1986).

The number of breeding pairs fluctuates from year to year (Fig. 1). The same pattern was found also by Stanevičius (1994) on Lithuanian lakes. Since in all years the fish stock in all waterbodies were about the same, food supply could not be the reason for such fluctuations. The main reasons, at least in my study area, are probably cutting of vegetation, increasing of recreational activities and empty ponds during breeding seasons. Moreover, on Raèe ponds breeding sometimes being delayed by unfavourable environmental conditions, mainly by the absence of water.

The highest densities I found during the study were 6.6 pairs/10 ha in 1987 on clay pit Gaj and 7 pairs/10 ha in 1997 on the Veliki ribnik - Raèe ponds. These breeding densities approached values reported by Ławniczak (1982), Cempulik (1985), Jermaczek and Jermaczek (1987), Kupezyk (1987), Dvorak *et al.* (1993), Mackowicz and Krajewski (1993), Trnka (1995), Witkowski *et al.* (1995).

The smallest water body where the Great Crested Grebe breed measured 4 ha

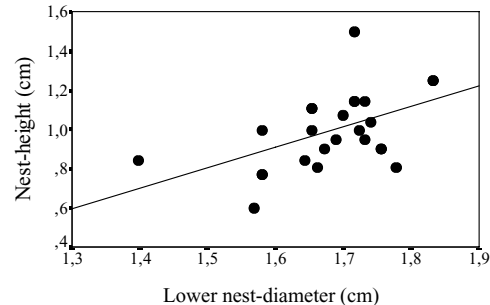


Fig. 2. The relationship between the lower nest-diameter and the nest-height in the Great Crested Grebe *Podiceps cristatus* on the Dravsko polje (logarithmic value).

(gravel pit). According to data from literature (Cramp & Simmons 1997, Fuchs 1978), the Great Crested Grebe could breed also on a water surface measured about 1 ha.

Breeding density varied greatly among localities. I compared three localities, where the Great Crested Grebe breeds regularly. Differences among localities were highly significant (Kruskal-Wallis test, Chi-square=9.42, df=2, $P < 0.001$).

Breeding density of the Great Crested Grebe on Dravsko polje was not dependent on the size of the area ($r=0.67$, $P > 0.05$, $n=7$), that is in contradiction with the results of Goc (1986). Such differences can be hardly explained, however the small sample size could be one of the reasons. The other reason could be the presence of people (fishermen) at smaller waters, which could affect the breeding densities of waterbirds (Bossert 1992, Keller 1992a, Ingold *et al.* 1992).

In 1995 and in 1997 I found that some pairs did not breed on Raèe ponds. Those specimens were probably young birds, mainly males (Cramp & Simmons 1977). Compared with data obtained in Northern and in Central Europe (e.g. Ławniczak

1982, Goc 1986, Moskal & Marsa³ek 1986, Stanevičius 1994, and references therein) colonial nesting was very rare and occurred only once (Vogrin 1989).

4.2. Nest - measurements

During the investigation 32 nests were measured (Tab. 1). The water depth near the nests was similar to those in Poland ponds (Ławniczak 1982). The correlation between the log-transformed data of lower nest-diameter and nest-height was significant ($r=0.51$, $P<0.05$, $n=25$; Fig. 2), whereas correlation between the upper diameter and nest-height was not significant ($r=-0.14$, $P>0.05$, $n=25$). Since nest-height is important to prevent egg losses (Keller 1992a), lower nest-diameter must be broader to secure safety building. Compared with data from Switzerland (Keller 1992b) nests of the Great Crested Grebe are broader and higher in my study area.

4.3. Inter-specific relationship

It is well known that Great Crested Grebes tend to nest in the neighbourhood of Coots (*Fulica atra*), mainly to increase antipredator protection (see Goc 1986, Stanevičius 1994 and references therein). According to this hypothesis, I tested the relationship between the densities of species. The correlation coefficient was positive but not significant ($r=0.36$, $P>0.05$, $n=8$). However, it would be much better to compare breeding success of Great Crested Grebes near and away from Coot nests (see for example Goc 1986). On the other hand, we must also take into account the predation by Coots on grebe eggs (Goc 1986).

Tab. 1. Size of the nest and water-depth in cm at the nest of the Great Crested Grebe *Podiceps cristatus* on the Dravsko polje.

	Lower diameter	Upper diameter	Nest-height	Water-depth
Mean	47.5	26.5	11.5	50.0
SD	9.2	4.8	5.8	7.8
Min.	25.0	17.0	4.0	38.0
Max.	68.0	32.0	32.0	61.0
N	32	27	26	29

I also compared the relationship between densities of the Great Crested Grebe and the Little Grebe (*Tachybaptus ruficollis*). Both species are syntopic on most of waterbodies on the study area. After Cramp & Simmons (1977), Glutz von Blotzheim et al. (1987) the Little Grebe is a zoophagous bird, it feeds mainly on insects and larvae, crustaceans, amphibian larvae and small fish, whereas the Great Crested Grebe is mainly insectivorous. We can assume competition between the two species both for food and for nest sites. Surprisingly, the relationship between both grebes are even positive but not significant ($r=0.62$, $P>0.05$, $n=8$). As already Newton (1998) pointed out, it seems that similar species responds in similar way to the same environmental factors.

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Összefoglalás

A búbos vöcsök *Podiceps cristatus* költés- ökológiája ÉK Szlovéniában

Az ÉK Szlovéniai Dravsko síkságon (210 km²) egyes években 44 pár búbos vöcsök fészkel, elsősorban a Raèki ribniki-Požeg Tájvédelmi Parkban, ami a szlovén állomány mintegy 15%-t teszi ki. A legnagyobb sűrűség 7 költő pár/10 ha volt. Az egyes területeken a költő párok denzitása eltérő volt. A fészkek magassága és alsó átmérője között szignifikáns korreláció volt, a fészkek magassága és felső átmérője között viszont nem. A kisvöcsök (*Tachybaptus ruficollis*) és búbos vöcsök költő párjainak a száma között nem szignifikáns, pozitív korreláció volt.

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The Great White Egret *Egretta alba* during autumn and winter on Dravsko polje in northeastern Slovenia

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Distribution and abundance of the Great White Egret (*Egretta alba*) wintering on Dravsko polje in northeastern Slovenia were studied during 1985-1996. The wintering population of Great White Egret increased in the last years. About 30% (up to 50 individuals) of the entire Slovene wintering Great White Egret population was on Dravsko polje. Great White Egrets preferred waters and avoided arable lands during all studied months (October-March). They foraged in small groups. Feeding flocks were mobile and reformed after disturbance in new areas of the study site. The number of Great White Egrets and Grey Herons (*Ardea cinerea*) correlated in the study area.

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1. Introduction

The Great White Egret (*Egretta alba*) is cosmopolitan species. In Europe it occurs mainly in the Eastern and Southeastern parts of the continent (e.g. Bauer & Glutz von Blotzheim 1966, Cramp & Simmons 1977, Voisin 1991). In Europe its breed first of all in Ukraine, Hungary, Austria and Romania (Kárpáti *et al.* 1986, Voisin 1991, Monteanu & Ranner 1997). According to Voisin (1991) and Monteanu & Ranner (1997) European population winters chiefly in Mediterranean area and in North Africa, whereas in last years the numbers of Great White Egret wintering in Central Europe is increasing.

In Slovenia the Great White Egret is a common visitor, especially in NE Slovenia during spring and autumn migration (pers. obs.). The nearest breeding colonies is in

Hungary at Kis-Balaton marshland where there are 140 breeding pairs (Kárpáti *et al.* 1986) and in Austria in the reed belt of lake Neusiedl, where there are more than 400 breeding pairs (e.g. Dvorak *et al.* 1993, Winkler *et al.* 1994). During the last few winters in Slovenia the Great White Egret occurred along river Drava and in the Seèovlje Salina (Sovinc 1994, Škornik *et al.* 1992).

Nevertheless, the distribution of wintering Great White Egrets in Central Europe and the relationship with other herons are still poorly known (see Voisin 1991 and references therein). The purposes of this paper are to present numbers and occurrence of the Great White Egret on Dravsko polje in northeastern Slovenia during autumn and winter and to present the relationship between the number of Great White Egrets and the Grey Herons (*Ardea cinerea*).

2. Material and methods

Dravsko polje - Drava field (46°25'N, 15°45'E) is an alluvial plain, situated in northeastern Slovenia between river Drava and Mt. Pohorje on altitude from 238 m to 270 m. Dravsko polje belongs to the sub-Pannonic phytogeographical area (Marinèek 1987). Fishpond complex Racki ribniki and reservoir Medvedce are the most important wintering sites of the Great White Egrets. Detailed description of the whole area, fishpond complex and reservoir are given in earlier papers (Vogrin & Šorgo 1995, Vogrin 1996, 1997, 1999, Vogrin & Vogrin 1998).

Field observations were carried out between 1985 and 1996 (except 1988) during October and March. Observations from river Drava were not included in this analysis. Observations were divided into two groups for further statistical analyses: individuals observed near water (reservoirs, ponds, gravel pits) and on arable lands (fields, mown meadows and pastures).

Statistical analyses were performed with non-parametric tests (Chi-square, Kruskal-Wallis 1-Way Anova test), since data were not normally distributed and with Spearman correlation coefficient (Sokal & Rohlf 1995). Data were analysed using the SPSS 6.0 statistical programs.

3. Results and discussion

Altogether 285 individuals of the Great White Egret were observed in the study area. The mean number of individuals per check was 5.4. The highest average number of individuals per check was observed

in November (Fig. 1). The largest flocks with 36 individuals were observed in 1995 and 1996.

Great White Egrets preferred water, and avoided arable lands. The percentage of observations near water were: October 95%, November 98%, December 99%, January 22%, February 80%, March 91%, respectively. The differences between specimens per check among months were not significant (Kruskal-Wallis 1-Way Anova test, Chi-square=5.5, df=5, $P>0.05$), whereas the differences among years were highly significant (Kruskal-Wallis 1-Way Anova test, Chi-square=21.14, df=7, $P<0.005$). From Fig. 2 it is obvious that numbers of the Great White Egret on Dravsko polje is increasing.

The reason for the increasing number of the Great White Egret after 1994 is probably the new habitats provided by reservoir Medvedce, which was first filled with water in 1993. Reservoir Medvedce is 155 ha large and is intended for intensive fish rearing (Vogrin 1996). Since then reservoir was regularly drought in autumn (October-November) till late winter or early spring. In the bottom of the discharged reservoir remains a lot of fishes (pers. obs.) which could serve as food for

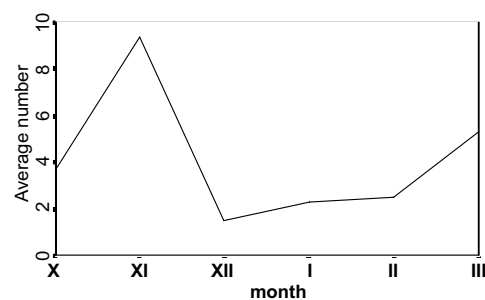


Fig. 1. Average number of Great White Egrets on Dravsko polje in northeastern Slovenia, 1985-1996.

herons. According to e.g. Newton (1980) the availability of food seems to be by far the most important factor in determining the numbers of birds and this is probably valid also for wintering Great White Egrets.

First winter data from northeastern Slovenia for the Great White Egret was given by Lukaè (1983) for Ormož reservoir on river Drava. Since then the Great White Egret regularly wintering on river Drava (Janžekoviè 1986), up to 20 specimens (Sovinc 1994, pers. obs.).

However, until now Dravsko polje was not known as a wintering place for the Great White Egret in Central Europe. In the last two years (1995-1996) on average 30-50 individuals were wintering on Dravsko polje, mainly in drought reservoir Medvedce and fishponds Raèe (Landscape Park Raèki ribniki - Požeg). According to this data and data from Sovinc (1994), about 30% of entire Slovene wintering population of Great White Egret occurs on Dravsko polje.

Wintering population of the Great White Egret on Dravsko polje is important also in Central Europe if we compare data from Monteanu & Ranner (1997). It seems that some important wintering populations exist also in Croatia, mainly along river Sava and the nearest fishponds. Nevertheless, Ern (1990) and Schneider (1989) for example present only data from autumn migration (but see Monteanu & Ranner 1997).

Great White Egrets usually forage alone (e.g. Voisin 1991), whereas this was not true on Dravsko polje during autumn and winter (Chi-square=1.47, df=1, $P>0.05$). For example, during this study Great White Egrets were encountered forage in average flock of 5.4 individuals

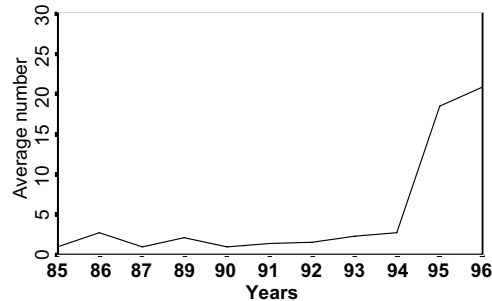


Fig. 2. Average number of Great White Egrets on Dravsko polje in northeastern Slovenia, 1985-1996.

(see also above). Feeding flocks were mobile and reformed after disturbance in new areas of the study site (Chi-square=4.17, df=1, $P<0.05$), suggesting that the flocks were not simply temporary responses to a local food supply.

Great White Egrets feeds mainly with fish but catch also small mammals, birds, amphibians and insects (Cramp & Simmons 1977, Voisin 1991), whereas Grey Herons feeds mainly with fish (e.g. Bauer & Glutz von Blotzheim 1966, Fasola *et al.* 1993, Peris *et al.* 1994) and small mammals (e.g. Exnerova & Bohaè 1991). According to these data interspecific competition has been suspected to occur in competition for food, and, in particular, it is expected to be more effective when food is limited (Pianka 1974), e.g. during winter. This assumption is confirmed by observations of aggressive interactions between both herons in reservoir Medvedce during wintering. We can expect that relationship between these two species is negative. However, the number of Great White Egrets increased significantly with increasing numbers of Grey Herons (Fig. 3, $r_s=0.46$, $P<0.005$, $n=33$). It may be assumed that Great White Egrets tend to form heterospecific

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A fészekaljpredáció jelentősége, valamint kísérletes vizsgálatának előnyei, hátrányai és módszertana

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Báldi, A. 1999. The use of artificial nests for estimating rates of nest survival. – *Ornis Hung.* 8-9: 39-55.



Nest predation is one of the most important factors influencing reproductive success and community composition of birds. Recent studies also showed that nest predation increases after habitat fragmentation. Therefore, there is a strong interest of conservation biologists to describe and understand patterns of nest predation. However, studying nest predation have some problems, such as observer's disturbance, habitat destruction, and methodological problems. The conduction of nest predation experiments with artificial nests has no such problems, but there are several other ones. The most important of such difficulties is the relation between nest predation rates of actual and dummy nests. A recent concensus seems to be that artificial nests are useful to compare nest predation rates between areas or experimental treatments, but they are inappropriate to estimate absolute predation rate. A cheap and easy way of constructing a nest is to form it using chicken wire, and line it with dead vegetation. Quail eggs are used most commonly in these experiments, although quail eggs are larger than the eggs of most passerines. This could potentially bias predation rates, since predators with small gapes are unlikely to take these eggs. The identification of the predators requires an automatic camera systems, imprint eggs, or other devices to record tracks or feather/hair of the predators. To evaluate whether there are any differences between two or more areas, or treatments, a test of homogeneity is recommended, such as the G-test. A common shortcoming of nest predation experiments is the spatial scale of studies, which are usually within the home range of only a few potential predators. Therefore, local effects may significantly influences the results, which makes generalisation difficult.

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1. Bevezetés

1.1. A fészekaljpredáció jelentősége

Az ornitológiának mindig is az egyik fő kutatási területe volt a madarak reprodukciójának a vizsgálata. A legnagyobb múlttal a fészkeléshez kötődő tanulmányok rendelkeznek, hiszen ide olyan viszonylag könnyen megfigyelhető és mérhető paraméterek tartoznak, mint a költés kezdete, fészekaljméret, fióka szám, kirepült fió-

kák száma stb. Nem véletlen, hogy már évtizedekkel ezelőtt kimutatták, és azóta egyre több igazolást nyert, hogy a költés-siker egyik legfontosabb befolyásoló faktora a fészekaljpredáció (innentől FAP-nak rövidítve) (pl. Skutch 1949, Ricklefs 1969, Martin 1995, Shaeter 1996, Yanes & Suárez 1997). Valóban, az irodalomból példának bemutatott néhány adat általában igen jelentős FAP-t mutat, bár lényeges eltérések vannak fajok, élőhelyek, és tanulmányok között (1. táblázat). Az adatok, és

1. táblázat. Természetes madárfészkek pusztulásának mértéke, nyitott fészkekkel rendelkező fajoknál. A pusztulás minden esetben predációt jelent, de nem feltétlenül azonos időszakra vonatkozik (kotlás, fiókanevelés, vagy a kettő együtt). Az áttekintő cikkek esetében a cikkben szereplő fajok pusztulási rátájának átlagát adtam meg. Több helyen zárójelben feltüntettem a fészkelési mikrohabitatot is.

Tab. 1. Nest loss due to nest predation in various open nesting birds (the examined period i.e., laying, hatching, or nestling, may not be the same). Predation rates from review papers were averaged for all species. The nesting microhabitat is noted in paranthesis for some cases.

Hely/Site	Faj/Species	%	Forrás/Reference
USA	Σ 21 faj	~ 35	Gates & Gysel 1978
USA	Σ 6 faj	72-79 (talaj)	Martin 1988
		58-86 (cserje)	
		44-53 (korona)	
USA	Σ 3 faj	31 (erdő, talaj)	Martin 1993
	Σ 11 faj	46 (erdő, cserje)	
	Σ 17 faj	35 (erdő, korona)	
	Σ 24 faj	49 (mező, talaj)	
	Σ 22 faj	40 (mező, bokor)	
Puerto Rico	Puerto-ricoi vireo (<i>Vireo latimeri</i>)	70	Woodworth 1997
Európa / Europe	Σ 32 faj	28	Martin & Clobert 1996
Svédország	fenyőrigó (<i>Turdus pilaris</i>)	17	Meilvang <i>et al.</i> 1997
/ Sweden	szőlőrigó (<i>Turdus iliacus</i>)	55	
Spanyolország	déli szikipacsirta (<i>Calandrella rufescens</i>)	45-95	Suárez <i>et al.</i> 1993
/ Spain	kövi pacsirta (<i>Galerida theklae</i>)	83-89	
	mezei pacsirta (<i>Alauda arvensis</i>)	79	
	sziki pacsirta (<i>Calandrella brachydactyla</i>)	70	
	réti pityer (<i>Anthus pratensis</i>)	72	
Anglia / England	fekete rigó (<i>Turdus merula</i>)	78-92	Cresswell 1997
Lengyelország			
/ Poland	foltos nádiposzáta (<i>Acrocephalus schoenobaenus</i>)	11	Halupka 1996
Magyarország			
/ Hungary	tövisszűrő gébics (<i>Lanius collurio</i>)	31	Farkas <i>et al.</i> 1997
Magyarország			
/ Hungary	széki lile (<i>Charadrius alexandrinus</i>)	50-94	Székely 1992

a cikk további része is elsősorban a nyitott fészkekkel rendelkező fajokra vonatkozik.

Közismert, hogy a táplálékkeresés során a rendelkezésre álló forrásokat a madarak felosztják a kompetíció csökkentése érdekében (MacArthur 1958), így egy közösségben azonos mikrohabitatban táplálkozó fajok általában együtt nem fordulnak elő. A FAP a költő madárközösségek szerveződésére is hatással van, mint azt Martin (1988) és Sieving & Willson (1998) kimutatta. T. Martin saját megfigyelései és irodalmi adatok alapján igazolta, hogy a FAP sűrűségfüggő, és a predátorok specializálódhatnak adott típusú fészkek keresésére. Tehát a

szelekció előnyben részesíti azon fajok koegzisztenciáját, amelyek más mikrohabitatban (talaj, bokor, vagy lombkorona) fészkelnek, mivel emiatt egy adott fészektípus keresésére specializálódott predátor a tényleges fészeksűrűségnek csak kis részét keresi. Martin egy későbbi tanulmányában (Martin 1996) 2400 mesterséges fészkek és 1408 valódi fészkek adatainak a feldolgozása alapján megerősíti, hogy a koegzisztens madárfajok fészkekének mikrohabitatja különböző, és átfedés esetén megnő a FAP. Sieving & Willson (1998) kimutatta a predációs ráta és egyes közösségszerkezeti paraméterek korrelációját.

A FAP a természetvédelem számára is lényeges. Egyfelől a ritka, veszélyeztetett, vagy zavarásra érzékeny fajoknál a FAP mértékének ismerete, a predátorok azonosítása a védelem számára alapvető információ, ezek alapján lehet a hatékony védelmi intézkedéseket megtenni. Például Székely (1997) szerint a hazai széki lile (*Charadrius alexandrinus*) állomány egyik fő veszélyeztető tényezője (az élőhelyének eltűnés mellett) a FAP. A fészkek dróthálóval történő körülkerítése a fészkek kelési sikerét növelte, mert a drótháló megakadályozta a predátorokat a fészkek elérésében.

A FAP vizsgálatok másik fontos alkalmazott vonatkozása a tájszerkezet átalakításának, a földhasználatnak vagy a területkezelés hatásainak az értékelése, ideértve például az élőhelyszegélyeket és élőhelyfragmentációt (Báldi 1996). Gates & Gysel (1978) 21 faj 194 fészkeinek sorsát követték nyomon, és azt találták, hogy a predáció szignifikánsan magasabb volt a szegélyekben. Ezt részben a nagyobb fészeksűrűség miatt megnövekedett predátor aktivitással magyarázták. Így alakulhat ki tehát a szegélyekben az ökológiai csapda (ecological trap), amikor a vegetáció kedvező szerkezete miatt nagy a madárfészeksűrűség, ami viszont megnöveli a predációt. Mivel Gates és Gysel másodlagos, emberi tevékenység nyomán kialakult szegélyeket vizsgált, eredményük alapján az élőhelyfragmentáció előrehaladtával a megnövekedő predáció hatásai akár kontinentális léptékben is mutatkozhatnak.

1.2. A fészkek aljpredációs kutatások problémái

A FAP tehát mind a közösségökológia, szaporodásbiológia, tájökológia és kon-

zervációbiológia számára fontos tényező, így vizsgálata, értelmezése lényeges feladat. Csakhogy legalább öt lényeges problémával találkozunk magunkat szemben, ha nekivágunk egy FAP-s vizsgálatnak: (1) zavarásra érzékeny fajok elhagyhatják a megfigyelő által megtalált fészket, (2) a fészekkeresés közben jelentős élőhelyrombolást okozhat a megfigyelő, például nádasban, vagy más érzékeny élőhelyen, (3) a költés során korán predált, de később megtalált (üres) fészkeknél nem észlelhetjük a predációt, (4) nem találunk meg minden fészket, így megfigyeléseink torzítottak lehetnek, végül (5) gyakran nehéz anynyi fészket olyan térbeli elrendezésben találni, hogy következtetéseink megalapozottak és statisztikailag kiértékelhetőek legyenek.

2. A természetes fészkek vizsgálatának egy lehetséges alternatívája: műfészkek készítése

A FAP-s kutatások számos problémájára megoldást jelenthet a mesterséges (artificial nest), vagy mű (dummy nest) fészkekkel (továbbiakban MF) végrehajtott kísérletek. Igaz, számos új probléma vette át a régiékat helyét. Ennek ellenére sok témát vizsgáltak már MF révén kísérletes úton (lásd a 2. táblázatban a felsorolást a fő témákról). Az alábbiakban röviden áttekin-tem ezen vizsgálatokat.

A FAP közösségszerkezetet befolyásoló hatásának számos vonatkozását vizsgálták. Például Marini (1997) kimutatta a FAP denzitásfüggésének térszála-, Sasvári *et al.* (1995) az élőhelytípus-, Chamberlain *et al.* (1995) pedig az élőhely-struktúrára függését. Hoi & Winkler (1994) és Marini & Weale (1997) igazolta, hogy

adott faj FAP-ja nem csak a saját denzitásától, hanem a közösség más fajainak fészekdenzitásától is függ. Martin (1993) az eltérő élőhelytípusban illetve vegetációszinten levő fészkek predációs rátáját elemezte valódi és MF segítségével. Szerinte nem igaz az a régóta elfogadott feltevés, hogy a talajon levő fészkek predációs rátája nagyobb, legalábbis erdőkben. Lengyel & Székely (in press) a fészkekanyag rejtő és hőszigetelő szerepét vizsgálta.

Számos vizsgálat született különböző konzervációbiológiai problémák kutatására. Ammon & Stacey (1997) a legeltetett területeken levő nagyobb FAP-t mutatta ki. A pusztuló ürömfajd (*Centrocerus urophasianus*) állománya esetében a megfelelő takarást biztosító élőhelykezelés fontosságát hangsúlyozta DeLong *et al.* (1995). A talajon levő fészkek takartságának, azaz rejtettségének fontosságát iga-

zolta Mankin & Warner (1992) is, míg D'Eon (1997) a fészkek rejtettségét nem találta lényeges faktornak egy rokon faj, a fenyőfajd (*Dendragapus canadensis*) valódi fészkeinél. A mocsári madárközösségek reprodukciós sikerének a növeléséhez Jobin & Picman (1997a) és Honza *et al.* (1998) a magas vízszintet tartja szükségesnek, mivel így a predátorok egy része számára a terület megközelíthetatlenné válik.

A legtöbb vizsgálat az élőhelyszegélyek és különböző méretű élőhelyfoltok predációs rátáinak összehasonlítására irányult. Gates & Gysel (1978) klasszikus munkája után Wilcove (1985) 10 különböző méretű erdőbe (3,8 ha - 100 000 ha) helyezett ki mesterséges fészkeket az USA K-i részén, és azt találta, hogy a kisebb foltokban nagyobb a predációs ráta (1. ábra). A kis mintaszám ellenére levonta azt az azóta számos helyen citált következte-

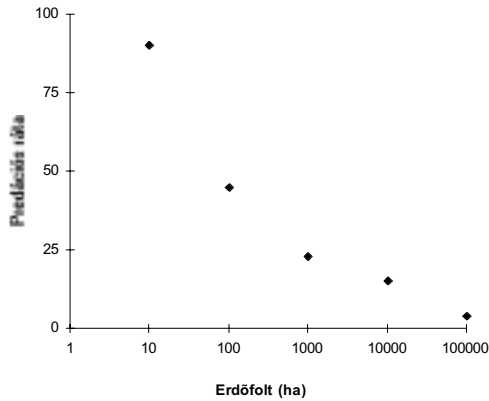
2. táblázat. Néhány jelentősebb téma, melyet a fészkekajpredációs kísérletekkel vizsgáltak. Tab. 2. List of some of the studies in which artificial nests were used.

Konzervációbiológia (conservation biology):

- élőhelyek, elsősorban erdők fragmentálódásának a hatása a költéssikerre (effect of habitat, mainly forest, fragmentation on breeding success),
- élőhelyszegélyek és belső élőhelyek fészkekajpredációs rátájának összehasonlítása (comparison of predation rates in edge and interior habitats),
- erdők életkorának a hatása a fészkekajpredációra (effect of forest age on nest predation),
- érintetlen illetve kezelt erdők fészkekajpredációs rátájának összehasonlítása (comparison of nest predation in pristine and managed forests),
- erdőtípusok fészkekajpredációs rátáinak összehasonlítása (comparison of nest predation rates in different forest types),
- emberi zavarás hatása a fészkekajpredációra (effect of human disturbance on nest predation),
- mezőgazdasági területek földhasználatának hatása a fészkekajpredációra (effect of land use on nest predation),
- közutak melletti füves padka milyenségének és a fészkekajpredációnak a kapcsolata (effect of roadside management on nest predation).

Ökológia és tájökológia:

- apparent kompetíció kimutatása (evidence of apparent competition),
 - a fészkek láthatóságának és a fészkekajpredációjának kapcsolata (relationship between nest visibility and predation),
 - a fészkekanyag szerepe a tojások elrejtésében és hőszigetelésében (role of nest material in concealment and insulation of eggs),
 - élőhely struktúra hatása a fészkekajpredációs rátára (effect of vegetation structure on nest predation),
 - vízmélység hatása a fészkekajpredációra (effect of water depth on nest predation),
 - tájszerkezet hatása a fészkekajpredációs rátára (effect of landscape structure on nest predation rate).
-



1. ábra. A fészkek-alj-predációs ráta függése a vizsgált erdőfolt méretének függvényében (Wilcove 1985 alapján).

Fig. 1. The relation between nest predation rate and forest size (after Wilcove 1985).

tést, hogy a neotropikus vonuló énekesfajok kontinentális léptékű csökkenésének oka részben a fragmentáció miatt meg-növekedett FAP lehet. Ezzel rokon érveléssel Brittingham & Temple (1983) a gulyajáró (*Molothus* spp.) fészekparazitizmusát tette felelőssé a neotropikus vonuló énekesfajok pusztulásáért.

A FAP kísérletek túlnyomó részét nyitott fészkek (open cup nests) használatával végezték. Ennek fő oka, hogy a témakör elsősorban az ilyen típusú fészket rakó madarakra vonatkozik. Sandström (1991) azonban kimutatta, hogy természetes fészekodvakba rakott fürjtojások esetén a szegélyben (0-20 m) nagyobb volt a predációs ráta, mint a szegélytől távolabb (>20 m). Ugyanakkor Pöysä et al. (1997) nem talált szegélyfüggést nagyméretű deszkaodúba rakott tyúktojás predációjában.

2.1. A műfészkekkel végzett kísérletek előnyei

A mesterséges fészkekkel végzett kísérletek mellett számos elméleti, etikai és gya-

korlati érv szól, többek között a valódi fészkek kutatásánál leírt problémák megoldása. Így a kísérleti célnak megfelelő elrendezést lehet létrehozni (erdősáv, erdőszegély, erdő belső FAP-nak különbsége, naponta és hetente látogatott fészkek FAP-nak eltérése, stb.), továbbá minden fészkenél egyszerre kezdődik a kísérlet, így a más korú fészkekből származó variancia eliminálható. Nagy mintaszámot lehet elérni. A kísérletek reprodukálhatóak és megismételhetőek, így a változó környezet hatásaira lehet következtetni. És végül, de nem utolsósorban, e módszer révén a valódi fészkeket és a kótló madarakat nem zavarjuk.

2.2. A műfészkekkel végzett kísérletek korlátai

A MF-vel végzett kísérleteknek számos hátránya van. A fő probléma, hogy általában nem tudjuk, mennyire közelít a valódi predációs rátához a MF FAP-ja. Major & Kendal (1996) áttekintő munkája szerint a nagyszámú MF FAP kísérletek túlnyomó részénél nem történt természetes fészkek vizsgálata, így a MF révén kapott adatok és a valódi fészkek predációjának viszonya nem ismert. A néhány komparatív vizsgálat ellentmondó eredményeket kapott, van ahol a MF predációja, van ahol a természetes fészkek predációja volt a nagyobb, mások pedig nem találtak különbséget (Major & Kendal 1996). Major és munkatársa az adatok újraszámolása után a MF predációját az esetek 70%-ban nagyobbak találta a természetes fészkek predációjánál. Ezt újabb vizsgálatok is alátámasztják (Wilson et al. 1998)

Az eredmények sokszínűségére néhány példát mutatok be. Berg (1996) a nagyplóling (*Numenius arquata*) és bíbic (*Vanellus*

vanellus) fészkek predációját hasonlította össze MF predációjával. A MF-t a vizsgált fajok fészkeihez hasonlóan alakította ki a talajon. A MF-ek predációja négyszer nagyobb volt a természetes fészkek predáltságánál, tehát a predációs ráta közvetlen becslésére nem alkalmas a MF végzett vizsgálat. Különböző élőhelyek közötti összehasonlításra viszont alkalmasnak találta, tehát a FAP relatív térbeli eloszlását a valódi fészkek predáltságának megfelelően tükrözte. Észak-amerikai *Anas* és *Aythya* récék fészkeinek predációjának vizsgálatokor Guyn és Clark (1997) nem talált korrelációt valódi és műfészkek predációja között sem térben sem időben, de egy jóval nagyobb mintaszámú tanulmányban (953 MF és 1318 természetes fészkek) Butler & Rotella (1998) a mű és természetes fészkek sikerességének gyengén szignifikáns pozitív korrelációját mutatta ki. Pöysä *et al.* (1997) szintén nem talált különbséget a predációs rátában természetes fészkekben és deszkaodúkban költő kerцерécék (*Bucephala clangula*) között.

Általánosságban azonban a kevés forrás alapján a MF nagyobb predációs rátáját mutatták ki (Major & Kendal 1996). Mi lehet a nagyobb MF predáció oka? Egyrészt a predátor megtanulhatja a kísérletezőt, a MF-t, vagy a mintavételi területet a táplálékkal összekapcsolni. Csakhogy számos pro és kontra megfigyelés látott napvilágot. Régóta vitatott kérdés, hogy akár mű, akár valódi fészkek ellenőrzése növeli-e a fészkek predációját. Valódi fészkeken végzett nagyszabású vizsgálatok alapján Mayer-Gross *et al.* (1997) nem talált általánosítható szabályt, a rigófélék és a rovarévők fészkeinek predációja csökkent, a pintyféléké nőtt. Götmark (1992) áttekintő munkája szerint sem általános a zavarás predációnövelő hatása valódi fész-

keknél, bár jelentős a variancia a rendek között. MF esetében a fészkekellenőrzések számának növelése általában nem növelte a predációs rátát (Götmark 1992).

Másrészt, a műfészkek elhelyezése valószínűleg különbözik a természetes fészkekétől. Például a szülők olyan helyet választhatnak, ahol kicsi a predációs veszély, vagy ellenkezőleg, rosszul becsülik fel a várható predációt (Székely 1992).

Harmadrészt, a MF és a valódi fészkek eltérő FAP rátáját a szülő madarak és a fiókák hiánya is okozhatja. A szülők ugyanis a legtöbb fajnál aktívan védik a fészket, így számos predátort elkergethetnek (pl. Berg 1996). Ugyanakkor a fiókák hívogató és eleségkérő hangja a fészkekből nyomra vezetheti a predátorokat.

A FAP-ráta a fészkek típusától függhet. Martin (1987) szerint a MF-nek használt fonott kosárcák predációja alacsonyabb volt, mint a fészkekanyaggal bélelt és kívülről borított kosárcáké, illetve az előző évi valódi fészkeké. Egy olaszországi vizsgálatban sem találtak különbséget a fészkekanyaggal bélelt drótfonat, és az előző évi valódi fészkek predációs rátája között (Matessi & Bogliani 1999).

2.3. Műfészkek készítése

Hogyan készítsünk el egy MF-t? Milyen faktorokat kell figyelembe venni, hogy minél jobban hasonlítsanak a MF a természetes fészkekre? A 3. táblázatban számos példát láthatunk az eddigi vizsgálatokban alkalmazott MF-re és a tojásokra. MF-t általában a vizsgálat során megcélzott faj fészkehez hasonlóan kell készíteni. Két fő típus van, a talajon levő, és a talaj feletti (bokor és lombkoronában, 1-2 m magasan) fészkek. A legegyszerűbb a talajfészkek készítése. Sekély mélyedést kell kiala-

kítani, esetleg bélelni száraz növényekkel, amire azután a tojás(ok) kerül(nek). Más fészektípusoknál valamilyen vázra van szükség. A szakirodalomban a boltokban kapható kanári fészek (fonott kosárka) szerepel általában, amit jobb esetben a kihelyezés helyén gyűjtött fűvel, vagy más megfelelő fészekanyaggal bélelnek, néha még kívülről is borítanak. A legegyszerűbb és legolcsóbb, az általam is használt módszer esetén kislyukú dróthálóból (csirkehálóból) négyzeteket vágunk ki, azokat fészekformájúra alakítjuk, majd béleljük. A fészek bokorra vagy más helyre történő rögzítése a dróthálóból kiálló drótok segítségével végezhető. E típusnak meg van az a korábban írt előnye (2.2. fejezet), hogy predációs rátája valószínűleg nem különbözik a valódi fészekétől.

2.4. A tojások

Ideális esetben a vizsgálandó faj, vagy fajok tojásához hasonló méretű és színű tojást kell használni. Csak hogy ilyenek nagy mennyiségben történő beszerzése gyakorlati nehézségekbe ütközik. Nagytetű madarak esetében a tyúktojás a legmegfelelőbb, főként ha meg is van festve. A számos énekesmadarat megcélzó vizsgálat során általában fürjtojást használtak (kivéve Sasvári *et al.* 1995). Az énekesmadár tojások azonban jelentősen kisebbek a fürjtojásnál. Például DeGraaf & Maier (1996) a fehérmancsú amerikaieger (*Peromyscus leucopus*) táplálkozását vizsgálta. A rágsálók a zebrapinty (*Poephila guttata*) tojását megették, de a fürjtojást nem bírták feltörni. Ez azért jelentős probléma, mert a rágsálók jelentős predátorok lehetnek (Bures 1997). A probléma kiküszöbölésére javasolja Picman *et al.* (1988), hogy a fürjtojást ecetsavval kell kezelni,

hogy a tojáshéj a kisszájú és gyengébb predátoroknak is áttörhető legyen.

A tojás színének hatását igazolta Yahner & Mahan (1996), akik szerint a barna színű tyúktojás predációja szignifikánsan kisebb volt a fehér színű tojásnál. Jobin & Picman (1997b) viszont nem talált különbséget a kétféle tyúktojás predációja között. Davies (1992) elhagyott énekesrigó (*Turdus philomelos*) és fekete-rigó (*T. merula*) fészkekbe rakott különböző színű tojásokat, és szintén nem talált különbséget a predációs rátában. Javaslom, hogy a valódi tojásokhoz minél hasonlóbb színű és méretű tojásokat tegyünk a MF-be. Az átszínezést számos módon lehet megoldani, spray-vel lefújni, teába áztatni, filctollal pettyezni, festeni, stb.

Egy tanulmányban (Nour *et al.* 1993) valódi tojást nem is tettek a fészkekbe. E kivételtől eltekintve legalább egy, de gyakran több valódi tojás is kerül a fészkekbe (3. táblázat). A gyurmatojásokat a predátorok azonosítása miatt szokták a fészkekbe rakni, azaz a fog és csőrnyomok megőrzése miatt. Éppen ezért célszerű a fészkekben rögzíteni, hogy a predátor ne tudja elvinni.

2.5. A műfészkek kihelyezése

A műfészkek kihelyezésénél a szabály az, hogy a vizsgálandó faj vagy fajok által használt helyekre és módon kell a fészket tenni. Igaz, Yahner & Voytko (1989) énekesmadárfészkeket részben az előző évi tényleges madárfészkek helyére, részben véletlenszerűen helyeztek ki, és nem találtak különbséget a predációs rátákban. Annak érdekében, hogy a MF-en minél kevésbé érződjön a "mesterségesség", számos módszert alkalmaztak, bár ezeknek a hatékonyságát még nem tesztelték. Az

3. táblázat. Fészkealjpredációs kísérletek során használt tojás és fészektípusok, valamint elhelyezések eljárások felsorolása. A felsorolás a fészkealjpredációs irodalom szerteágazósága és gyors fejlődése miatt nem tekinthető teljesnek.

Tab. 3. Some of the experiments which used artificial nests.

Tojás/Egg	Db. /No	Fészkek / Nest	Elhelyezés / Nest site	Forrás / Source
fűrj+gyurma / quail+plasticine	2+1	elhagyott és áthelyezett feketeterigó fészkek/abandoned and relocated blackbird nest	bokor/fa / schrub/tree	Chamberlain et al. 1995
mezei veréb / tree sparrow	3	kosárka / basket	talaj + bokor/fa / ground + shrub/tree	Sasvári et al. 1995
fűrj+gyurma / quail+plasticine	1+1	fűvel bélelt drótháló / wire lined with dry grasses	talaj + bokor/fa / ground + shrub/tree	Ammon & Stacey 1997
fűrj / quail	1	kanári fészkek / canary nest	bokor/fa	Marini & Weale 1997
fűrj / quail	2	5 énekesfaj előző évi fészkei/real passerine nests	bokor/fa	Marini 1997
tyúk (féhér+barna) / brown and white chicken	1	elhullott növényekből fészkekformájúra préselve / nest form pressed from dry vegetation	talaj / ground	Jobin & Picman 1997b
tyúk (barna) / brown chicken	2	fűvel bélelt csirkeháló / chicken wire lined with grasses	bokor/fa, valódi fészkek helyére / shrub/tree, on real nest' sites	Yahner & Voytko 1989
fűrj / quail	2	fűvel bélelt kosárka / wicker nest lined with grasses	talaj / ground	Whelan et al. 1994
fűrj / quail	2	elhagyott, helyén hagyott feketeterigó fészkek / abandoned black bird nests without relocation	bokor/fa / shrub/tree	Cresswell 1997
white clay / fehér agyag	1	semmi (?) / nothing (?)	talaj / ground	Haskell 1995
gyurma / plasticine	3	száraz növényekből formált fészkek / nest formed from dry vegetation	talaj / ground	Møller 1989
kék mű kanári+gyurma / blue dummy canary+plasticine	2+1	kanári fészkek / canary nest	talaj + bokor/fa / ground + shrub/tree	Nour et al. 1993
fűrj / quail	2	kanári fészkek / canary nest	talaj / ground	Fenske-Crawford & Niemi 1997
fűrj / quail	2	helyi fűvel, mohával bélelt és burkolt kanári fészkek / lined canary nest with mosses on it	talaj + bokor/fa / ground + shrub/tree	Santos & Telleria 1992
fűrj / quail	2	helyi fűvel, mohával bélelt és burkolt kanári fészkek / lined canary nest with mosses on it	talaj + bokor/fa / ground + shrub/tree	Arango-Vélez & Kattan 1997
tyúk (barna) / brown chicken	2	helyi fűvel bélelt csirkeháló / chicken wire with grass lining	talaj + bokor/fa / ground + shrub/tree	Yahner et al. 1989
fűrj / quail	1	száraz fű összeragasztva / glued dry grass	sűrű gyékény / dense cattail	Picman et al. 1993
tyúk+viasszal töltött kifűjt tyúk / chicken+chicken filled with wax	7+2	helyi fűvel bélelt mélyedés/ground depression with grass lining	talaj / ground	Pasitschniak-Arts & Messier 1996
tyúk (barna) / brown chicken	1	helyi fűből formált mélyedés / depression with grass lining	talaj / ground	Jobin & Picman 1997b
fűrj / quail	1	száraz fű összeragasztva / glued dry grass	mocsári vegetáció / marsh vegetation	Jobin & Picman 1997a
virginiai fogasfűrj / northern bobwhite	2	helyi növényekkel bélelt mélyedés / ground depression with grass lining	talaj / ground	Leimgruber et al. 1994
tyúk / chicken	2	40*40cm-es, homokkal beszórt tábla / 40 by 40cm board with sand	talaj? / ground (?)	Andrén 1992
fűrj / quail	1	kanári fészkek / canary nest	talaj / ground	Burger et al. 1994
fűrj / quail	1	kanári fészkek / canary nest	bokor / shrub	Langen et al. 1991
tyúk (barna) / brown chicken	2	40*40cm-es, homokkal beszórt tábla / 40 by 40cm board with sand	talaj? / ground (?)	Huhta et al. 1996
fűrj / quail	3	kanári fészkek / canary nest	talaj / ground	Small & Hunter 1988
tyúk / chicken	1	odú / nest box	fa / tree	Pöysä et al. 1997
fűrj / quail	2	növényzetből formált / formed from vegetation	talaj / ground	Bergin et al. 1997
fűrj / quail	2	fűvel bélelt kosárka / basket lined with grasses	talaj+bokor+fa / ground+shrub+tree	Sloan et al. 1998
virginiai fogasfűrj / northern bobwhite	3	fűből és levelekből formált fészkek / nest formed from grasses and leaves	talaj / ground	Niemuth & Boyce 1997
fűrj / quail	1	semmi / nothing	talaj / ground	Telleria & Santos 1992

3. táblázat folytatása / Tab. 3. continued.

Tojás/Egg	Db. /No	Fészkek / Nest	Elhelyezés / Nest site	Forrás / Source
fácán és/vagy tyúk (barna) / pheasant or/and brown chicken	2-4	mélyedés / depression	talaj / ground	Mankin & Warner 1992
fűj+gyurma / quail+plasticine	2+1	zuzmóval bélelt csirkeháló / chicken wire lines with lichens	fa / tree	Darveau et al. 1997
fűj+gyurma / quail+plasticine	2+1	mohával bélelt mélyedés / depression lined with mosses	talaj / ground	Darveau et al. 1997
tyúk / chicken	1	talajba rejtett 8*8cm-es fadarab / 8 by 8cm hidden wood	talaj / ground	DeGraaf 1995
tyúk / chicken	1	levelekkel bélelt kanári fészkek / canary nest lined with leaves	bokor / shrub	DeGraaf 1995
tyúk (barna) / brown chicken	2	30*30cm-es homokkal beszórt tábla / 30 by 30cm board with sand	talaj / ground	DeGraaf & Angelstam 1993
tyúk (barna) / brown chicken	2	semmi / nothing	talaj / ground	DeGraaf & Angelstam 1993
tyúk (barna) / brown chicken	2	levelekkel bélelt kanári fészkek / canary nest lined with leaves	fa / tree	DeGraaf & Angelstam 1993
fűj / quail	1	természetes odúk / natural holes	fa / tree	Sandström 1991
fűj / quail	3	fűvel bélelt kanári fészkek / canary nest lined with grasses	talaj+bokor/fa / ground+shrub/tree	Wilcove 1985
fűj+gyurma / quail+plasticine	1+1	száraz növényekkel bélelt kanári fészkek / canary nest lined with dry plants	talaj+bokor / ground+shrub	Bayne et al. 1997
10cm-es agyagkorong/fácán / 10cm clay/pheasant	1/3	semmi / nothing	talaj / ground	Paine et al. 1997
fűj / quail	2	fűvel bélelt kanári fészkek / canary nest lined with grasses	bokor / shrub	Martin 1987
fűj / quail	2	fűvel bélelt, mohával borított kanári fészkek / canary nests lined with grasses and covered by mosses	bokor / shrub	Martin 1987
fűj / quail	2	elhagyott valódi fészkek / abandoned actual nests	bokor / shrub	Martin 1987
barna / fehér tyúk/virginiai fogasfűj / brown or white chicken or northern bobwhite	3	sekély mélyedés az avarban / shallow depression in the litter	talaj / ground	Yahner & Mahan 1996
fűj+gyurma / quail+plasticine	1+1	kosárka / basket	talaj+bokor / ground+shrub	Bayne & Hobson 1997
fűj / quail	1	száraz fűből formált / formed from dry grasses	bokor / shrub	Picman & Schriml 1994
fűj / quail	2	sekély mélyedés / shallow depression	talaj / ground	Berg 1996
fűj / quail	1	semmi / nothing	talaj / ground	Rönkä & Koivula 1997
tyúk / chicken	1	sekély mélyedés / shallow depression	talaj / ground	Butler & Rotella 1998
tyúk+viaszal töltött kifűjt tyúk / chicken+chicken filled with wax	7+1	száraz fűvel bélelt mélyedés / depression lined with dry grasses	talaj / ground	Guyn & Clark 1997
gyurma/viasz / plasticine/wax	2	énekes sármány eredeti fészkei / real nests of Song sparrow	fűcsomó / grass tussock	Rogers et al. 1997
tyúk+viaszal töltött kifűjt tyúk / chicken+chicken filled with wax	7+2	száraz növényekkel bélelt sekély mélyedés / shallow depression lined with dry plants	talaj / ground	Pasitschniak-Arts & Messier 1995
fűj / quail	2	kosárka (csésze szerű + zárt, bebújó nyílásos) / baskets (cup form + closed with entrance hole)	nád, talaj / reed, ground	Hoi & Winkler 1994
fűj / quail	2	semmi / nothing	talaj / ground	Berg et al. 1992
fűj / quail	2	száraz fűvel és levelekkel bélelt kosárka / basket lined with dry grasses and leaves	talaj+bokor/fa / ground+shrub/tree	Vander Haegen & DeGraaf 1996

egyik kivétel Báldi (2000) munkája, ami-
ben a kihelyezés időpontjának a hatását
mutattam ki. A napközben kirakott fészkek
nagyobb arányban predálódtak, mint a

szürkületkor kirakottak, feltehetőleg ami-
att, hogy jó látási viszonyok mellett a vi-
zuális predátorok már a kísérletező tev-
kenységére felfigyeltek. A kísérletek leírá-

sakor gyakran találkozni az emberi szaganyagok eliminálására irányuló gumicsizma és gumikesztyű viselettel. Itt említhető a MF lemosása forró vízben, terepen történő levegőztetése, általában 5 napon át, vagy a "kézmosás" helyi avarban és talajban a MF készítése és kezelése előtt. A valódi fészkek szaganyagának rekonstruálása érdekében madártollakat, vagy kereskedelemben kapható réceszagot alkalmaztak, ez utóbbit, értelemszerűen, récefészkek-nél. Ezeknek az elrendezéseknek az alapjául lényegében csak Whelan *et al.* (1994) munkája szolgál, akik egy kísérletben mesterséges szaganyagokkal igazolták, hogy a kísérletező szagnyomai vonzzák a szaglás alapján vadászó predátorokat. Általánosságban azonban a kísérletező határsárol megoszlanak a vélemények. Az idézett cikkekben azon túl, hogy leírják a gumicsizma, vagy gumikesztyű használatát, a helyi tóvízzel történt lemosást, vagy a tóban történt festést, nem történt meg e módszerek hatásának tesztelése, de a szerzők saját "alaposságukat" legalább illusztrálták.

3. A predátor azonosítása

Lehetséges, hogy egyes FAP kísérleteknek elsődleges célja a fő fészkepredátorok azonosítása, de minden más esetben is alapvető információt jelent a predátorok ismerete (Hernandez *et al.* 1997a). Ez azonban nem könnyű feladat, hiszen gyakran nem marad héjmaradvány sem, ami megkönnyíthetné az azonosítást. Szinte minden állatfaj, ami képes "áthatalni" a tojásbélyen potenciális predátor: például osztrák Duna menti ligeterdőkben a nagy tarkaharkály (*Dendrocopos major*) volt a fő fészkepredátor (Christine Kurzman,

Konrad Lorenz Institut, pers. comm.). Egy észak-amerikai vizsgálatban a predátorok között volt a kanadai vörösmókus (*Tamiasciurus hudsonicus*) és a hócipősnyúl (*Lepus americanus*) is (DeGraaf 1995). Reitsma *et al.* (1990) az általuk gyanított fő predátorokat eltávolították a vizsgálati területről, azonban a predációs ráta mégsem változott.

Talajon levő fészkek esetén lehetséges a tojásokat elsimított homokot tartalmazó tálcára helyezni, amiben a nyomok megmaradnak (3. táblázat). Saját próbálkozásaim alapján, amikor tálcákra homokot tettem, és középre egy fűrjtojtást, általában nem tudtam a predátort azonosítani, mert vagy nedves lett, utána "beton" keménységre szilárdult a homok, vagy tálcástól felborult, vagy azonosíthatatlanul szét lett túrva.

A legolcsóbb és legegyszerűbb, ha a fészkekbe olyan anyagból készült műtojást teszünk, amiben a csőr illetve fognyomok megmaradnak. A nyomokat múzeumi vagy más kitömött példányok csőr és fognyomaihoz lehet hasonlítani, így azután a predátorok azonosíthatóak. Guyn & Clark (1997) a mesterséges réce fészkekbe tyűtojást tett, és az egyiket kifűjték, majd vissza töltötték meg. Legtöbb vizsgálatban azonban gyurmát szoktak használni. A gyurmának ugyan jellegzetes szaga van, ennek ellenére kísérleteim során gyurmatojáson találtam több vízicikány (*Neomys* sp.) és róka (*Vulpes vulpes*) fognyomot is. Madarakra a gyurma szagának valószínűleg elhanyagolható a hatása.

A predátor azonosításának legbiztosabb módja, ha lefényképezzük őket. Több nagy fényképezőgép gyártó cégnek vannak automata, infraérzékelős gépei, azonban ezekből a drága gépekből legalább 10-t be kellene szerezni, és napokra kinthagy-

ni a terepen. Hazai viszonyok között ez az út nemigen járható. Kompletts felszerelést meg lehet rendelni több cégnél is, például a Trailmaster kamerákat (Hernandez *et al.* 1997b), vagy Magyarországon a Nature Observer műszereket (Hód-mezőgazda RT., Hódmezővásárhely). Ezen berendezések általában infrásugárral és infraérzékelővel működnek (lásd Carthew & Slater (1991) cikkét egy infraérzékelős automata kamerarendszer összeállításáról), és igen drágák. Ennél viszonylag egyszerűbb, amikor elektronikus mikrokapcsolót alkalmaznak az áramkör megszakítására (pl. Ball *et al.* 1994). Talán a legolcsóbb, ám ezzel együtt a legrázósabb, ha saját magunk állítunk össze egy felszerelést. Útmutatót ad például Picman (1987) és Danielson *et al.* (1996). Problémát jelent, hogy mire a cikkek hozzáférhetőek számunkra, a technika haladása miatt a leírt olcsó kompakt-kamerákat már nem lehet beszerezni, csak módosított változataikat. Végsősoron szükség van egy elektronikusan exponáló kompakt-kamerára, lehetőleg vakus, automata filmtovábbítás, és dátumozós hátlapú legyen. Ezenkívül egy mikrokapcsoló, és drót szükséges. A kamera elektronikus elsütőrendszerébe be kell iktatni a mikrokapcsolót, a mikrokapcsolóhoz pedig rögzíteni kell (például pillanatragasztóval) a tojást. Elméletben tehát a tojás megmozdításakor a mikrokapcsoló kapcsol, a kamera exponál. Saját próbálkozásaink során a fő problémát az jelentette, hogy a kamerák vakujának a kondenzátora bekapcsolt állapotban egy órán belül elvesztette a töltését, emiatt a kamera nem exponált, csak ha ki- majd bekapcsoltuk. Ez a probléma megfelelő kameratípus választásával orvosolható.

Az ideális FAP kísérlethez tehát kellenek a műfészkek és tojások, énekesmada-

rakra vonatkozó vizsgálatnál javasolt egy fűrj és egy kisméretű gyurma tojás fészkek behelyezése. A kísérleti elrendezésen túl, további fészkek szükségesek automatikus kamerával ellátva a predátorok, és nyomai-
knak az azonosítására. A gyurmatojás megfelelő méretű legyen, azaz a megcélzott faj tojásméretére hasonlítson.

4. Néhány alapismeret az adatfeldolgozáshoz

Mit kezdjek, ha van egy briliánsan végrehajtott kísérletem? A jelenlegi tudományos gyakorlat szerint az adatok önmagukban nem publikálhatók. Egy jó tanulmányhoz adatfeldolgozás és alapos értékelés is kell. Ezen feladatok vázolója számos könyv alapját képezik (angolul alapfokon Fowler & Cohen (1995), jóval bővebben Sokal & Rohlf (1981), magyarul Précsényi *et al.* (1995)). A következőkben egy egyszerű tesztet ismertetek, amelyet számos szegélyhatás vizsgálat elemzésében használtak. Ez a G homogenitás teszt.

Tegyük fel, hogy 10 MF-t helyeztem ki egy erdő szegélyébe, 10 MF-t a szegélytől 10 m-re, és 10 MF-t a szegélytől 50 m-re. A szegélyben 8 fészkek predálódott, a 10 m-re levő mintában 5, az 50 m-re levőben pedig 6. Azaz:

	Szegély	10m	50m	Összesen
Predált fészkek száma (megfigyelt érték):	8	5	6	19
Kihelyezett fészkek száma:	10	10	10	30
Homogén eloszlás esetén várt érték:	6,3	6,3	6,3	

A homogén eloszlás esetén várt értéket úgy számítjuk ki, hogy az összes bekövetkezett predációs eseményt (19-t), a három kategória (szegély, 10 m, 50 m) között ho-

mogén módon, egyenletesen "osztok el".
A várt érték tehát: $19/3=6,3$.

Kérdésünk, hogy a háromféle élőhelyen eltérő volt-e a predációs ráta?

A G érték számolása:

$$G=2 \times \sum \text{megfigyelt érték} \times \ln(\text{megfigyelt érték/várt érték}),$$

ahol Σ az összes kategóriában számolt 'megfigyelt érték $\times \ln$ (megfigyelt érték/várt érték)' eredményének összegzését jelenti, 'ln' pedig a természetes alapú logaritmust.

Esetünkben tehát:

1. lépés:

$$8 \times \ln(8/6,3) + 5 \times \ln(5/6,3) + 6 \times \ln(6/6,3) = 1,911 + (-1,156) + (-0,293) = 0,462$$

2. lépés: $2 \times 0,462 = 0,924 = G$

3. lépés: Williams féle korrekció számolása, melyet egyutas összevetéseknél (pl. esetünkben), és 2×2 -es kontingencia táblázatnál javasolt elvégezni. A korrekciós faktor (KF):

$$KF = 1 + (a^2 - 1) / (6 \times n \times v),$$

ahol a a kategóriák száma, n az összes esemény száma, v a szabadsági fokok száma, azaz $a-1$.

$$KF = 1 + (3^2 - 1) / (6 \times 19 \times 2) = 1 + 8 / 228 = 1,035$$

4. lépés: $G_{\text{kor}} = G / KF = 0,924 / 1,035 = 0,893$

5. lépés: az így kapott G_{kor} értéket a szabadsági foknak megfelelő helyen összehasonlítjuk a χ^2 eloszlás kritikus értékeivel, és megnézzük milyen szignifikancia szint tartozik hozzá. Ilyen szignifikancia értékeket számos módszertani könyvben közölnek (lásd a fejezet elején a hivatkozásokat). Esetünkben ahhoz, hogy statisztikailag igazolható, azaz szignifikáns különbséget mutassunk ki a FAP szegélyfüggésében, a G_{kor} -nak 5,99-nél nagyobbnak kellene lennie. Mivel ez nem igaz, a

FAP szegélyfüggését adataink alapján nem tudtuk igazolni. (Megjegyzés: a teszt elvégzésének több előfeltétele van, például a mintavételi egységek egymástól függetlenek legyenek. Azonkívül a tesztet az eredeti értékek alapján kell elvégezni, származtatott, például százalékosan kifejezett adatok esetében nem megengedett az alkalmazása stb. A fent citált statisztikai könyvekben részletes útmutatók olvashatóak.)

Tegyük fel, hogy ugyanezt a kísérletet, 100-100-100 MF-kel végeztük volna el, de a pusztulás aránya azonos lett volna (80-50-60). Ekkor már erősen szignifikáns különbség jött volna ki ($G_{\text{kor}} = 9,224$, $P < 0,01$). Tehát a megfelelő méretű mintaszám minden kísérlet egyik alapvető feltétele! Ez a példa illusztrálja a MF-kel végzett kísérletek népszerűségét is, hiszen 300 darab, a szegélytől adott távolságokban levő valódi fészket találni, szinte megoldhatatlan feladat.

5. A valódi és műfészkek predációs vizsgálatainak kritikája, és további kutatási irányzatok

A fészkepredációs tanulmányok egy fő problémája, hogy a vizsgálatok jelentős része csak lokális skálán értelmezhető, hiszen a vizsgálati terület gyakran csak egyik két predátor vadászterületére esik (kivételem például Robinson *et al.* (1995) 5 USA tagállamot felölelő vizsgálata). Tehát sok esetben megalapozatlan azt a következtést levonni, hogy például az egyik élőhelyen nagyobb volt a FAP, mint a másikon, mert lehetséges, hogy mindössze éppen a vizsgálat évében, azon a néhány hektáros területen nem voltak fészkepredátorok. A

Kis-Balaton II. tározóján kihelyezett 10-10, egy tyúk és egy gyurmatojást tartalmazó fészkek esetében egy nap után az egyik minta mind a 10 fészke érintetlen maradt, a másikonál csak kettő. Ez utóbbinál három szürkevarjú "bogarászott" a gátoldal fűvében, majd repült el a fészkek ellenőrzésekor. Több tojást már kilyukasztva, de még hiánytalanul találtunk (Báldi 1999). Feltehető, hogy a szakirodalomban talált sokféle ellentmondó eredmény is annak köszönhető, hogy a lokális hatások dominálnak a vizsgálatokban. A fészkepredáció végül is számunkra nem más, mint mintavétel a helyi predátorokból. Így rögtön számon kérhetjük a mintavételre vonatkozó szabályok érvényesülését, például a megfelelő mintaelemszámot, a minták függetlenségét. Amennyiben a mintavételi területünk a fő predátor egy, vagy néhány átlagos vadászterülete méretű, a mintáink nem függetlenek, azaz az eredmények alapján általánosítani nem szabad. A publikációkat tehát mindig annak a fényében kell vizsgálni, hogy mennyire befolyásolhatta az eredményt a helyi predátor "egyénisége", tapasztalata, vagy egyáltalán a jelenléte.

Véleményem szerint tehát olyan nagyleptékű kísérleteket kell végezni, amikben a helyi predátorok okozta hatás csökkenthető. Ha a fő predátor például valamelyik varjúféle, ahol a territórium durván 100 hektár, akkor úgy kell a kísérletet megtervezni, hogy számos potenciális territóriumot magába foglaljon a mintavételi terület. Ez azonban sok esetben gyakorlatilag nem megvalósítható. Ha például kicsi a vizsgáló terület, pl. egy park vagy egy nádas, akkor egyszerűen nem lehetséges olyan számú ismétlést csinálni, hogy biztosan több potenciális predátor territóriumát lefedjék. Ilyen esetekben a predátor azonosítása révén lehetséges e hibaforrást

vizsgálni, ha azonos fajú a predátor, akkor lehetséges, hogy egy egyed, vagy pár "ráállt" a MF keresésre. Mindenesetre nem szabad e problémáról megfeledkezni az adatok kiértékelésekor. Egy megfelelő kísérleti elrendezést használt Hoi & Winkler (1994) a Fertő-tó nádasaiban, akik 10 MF tettek ki egy transzektbe, és 10-10, egymástól távolabb elhelyezett transzekt részesült azonos "kezelésben". Ezzel az elrendezéssel a helyi adottságokból, például szürkevarjú fészkek vagy gémtelep közelségéből adódó "zaj" csökkenthető.

A mű és a valódi fészkek predációjának a kapcsolata továbbra is az egyik fő kérdés, létezik-e egyáltalán valamilyen trend, vagy törvényszerűség. A kapott eredmények automatikus általánosításának néhány buktatóját Haskell mutatta ki (Haskell 1995a, b). Mint fentebb volt róla szó, elsőnek Wilcove (1985) írta le, hogy a kis erdőfoltokban nagyobb a neotropikus vonulók FAP-ja, mint nagy foltokban. Csakhogy a neotropikus vonulók tojásmérete jóval kisebb a kísérletekben használt fűrjtojás méreténél, körülbelül a fele, kétharmada (Haskell 1995a). Ez a méretkülönbség a kistermetű, kisebb szájnnyílású predátorok esetében már a predációt gátolhatja. Valóban, Haskell (1995b) kimutatta, hogy a nagyobb erdőfoltokban a kisszájú predátorok dominálnak, akik a fűrjtojást már nem tudják predálni. E probléma elkerülésére legjobb módszer az énekesmadár méretű tojások használata, vagy legalább a fűrjtojás mellé rakott gyurmatojás megfelelően kicsi méretűre készítése.

Köszönetnyilvánítás. Köszönöm Székely Tamás konstruktív bírálatát a kéziratról. A tanulmány elkészítését, és a terepi vizsgálatok kivitelezését az OTKA F/19737 pályázat támogatta.

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Short communications - Rövid közlemények

Visual deception of a Great White Egret by shiny plastic sheets

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Several years after the end of the Gulf War in 1991 many crude oil lakes still existed in the desert of Kuwait (Pearce 1995). These lakes were formed when oil wells and pipelines were blasted and the resulting spills were subsequently accumulated in more than 900 oil ponds. These oil lakes trapped thousands of birds, especially those species that are associated with water (Pilcher & Sexton 1993, Horváth & Zeil 1996). Similar phenomenon was observed in the waste oil lake in Budapest, Hungary (Horváth *et al.* 1998).

At warm weather the surface of these lakes is flat and shiny and it acts as an efficient reflector, like a water surface. It is pertinent to suppose that the deceiving capability and attractiveness of these oil lakes may be explained by their shiny surface. Birds may be deceived by the reflected light which may imitate the glitter of a water surface. Thus, we hypothesized, the birds might mistake the oil for water.

Our hypothesis was that water birds may be attracted to the oil lakes by the bright reflection of light. Such smooth, shiny surfaces may mimic water and thus attract water birds. The optical cue of these shiny surfaces may be so strong that birds are visually compelled to remain in the immediate vicinity of the lakes in spite

of the fact that other senses signal that these are not water.

To test this hypothesis, we performed a choice experiment with a Great White Egret (*Egretta alba*) in the field. We imitated a crude oil lake or a wet muddy surface by means of a huge shiny black plastic sheet laid onto the ground, while a brighter water was mimicked by a shiny white plastic sheet. We observed the reactions of an egret to these plastic sheets. Our main aim was to learn whether an egret, as a typical bird associated with water, can be deceived by and lured to such plastic sheets in its natural habitat. If yes, which sheet is preferred by it, and how does it respond to these dummies.

From 2 to 14 August 1997 a choice experiment was performed in the field at Kunfehértó (46° 23' N, 19° 24' E), a village in the southern part of the Hungarian Great Plane. Two huge plastic (polyethylene) sheets measuring 20 m x 30 m were laid on the ground in a large alkaline field at about 500 m from a lake where a Great White Egret (*Egretta alba*) lived. Such plastic sheets are commonly used in agriculture. One of the sheets was black and the other milky translucent. Due to the greenhouse effect the lower surface of the latter dimmed in some minutes following

Tab. 1. The behaviour of a Great White Egret (*Egretta alba*) at the white and black plastic sheets during the choice experiment from 2 to 14 August 1997.

BEHAVIOUR OF THE EGRET ON THE PLASTIC SHEETS	TIME (day, hour:minute)	WEATHER
landing next to the white plastic at a distance of 3 m ; flying away in a few minutes	05,17:39	sunny, calm , clear sky
landing beside the white plastic; approaching it at a distance of 1 m ; flying away	06,09:07	sunny, calm , clear sky
landing next to the white plastic; walking to it; stepping onto its edge; flying away in some minutes	07,17:00	sunny, breeze, clouded sky
TRANSPOSITION OF THE PLASTIC SHEETS	08	
17:36 - landing next to the white plastic and stepping onto it; walking about; striking off with the bill; looking for prey; fishing; gazing at the plastic bowed down; looking around with head high up	09,17:36- 17:58	sunny, breeze, clouded sky
17:46 - reaching the edge of the white plastic; crossing the grass between the plastics; walking to the black plastic		
17:48 - stepping onto the black plastic; walking about; neck and head being usually high up; crossing fast the plastic		
17:51 - reaching the edge of the black plastic; standing about on the grass; plucking; looking around		
17:58 - flying away		
18:03 - landing next to the white plastic and stepping onto it; walking about; picking the plastic with the bill; standing about; watching; plucking; resting	11,18:03- 19:32	sunny, calm , clear sky
18:33 - sitting down; standing up; standing about; defecating		
19:25 - flying to the black plastic; walking about; picking the plastic with the bill		
19:32 - flying away		

unfolding. Because the billions of tiny water drops (vapour) scattered the incident light diffusely the plastic sheet became brilliant white.

The distance between the plastic sheets was 30 m. In the first half of the choice experiment the white plastic sheet was closer to the lake, and in the second half of the experiment the two sheets were transposed with each other. The vegetation beneath the sheets was mown. The sheets were stretched out horizontally as tight as possible, and they were pinned down by bricks at the edges. Because of wind-generated wrinkles and thermal dilatation in sunshine the surface of the sheets became sometimes uneven, which was compensated by repeated spanning of the sheets at sunrise, noon and sunset. This spanning did not disturb the observed bird, because it always rested at these hours in the surrounding vegetation.

During the experiment we observed a Great White Egret attracted to the plastic sheets from a hide at a distance of 30 m from both sheets. This distance was large enough not to trouble the observed bird, and small enough to ensure the visual inspection of possible prey animals on the plastic sheets. Although we did not mark the observed bird, we were convinced that always the same egret landed on the plastic sheets, because during our choice experiment only a single Great White Egret stayed in the habitat. The observation lasted every day from 05:00 to 20:00 hours by changing the observers over at noon. Using a telescope (Kowa TSN, x60 zoom), we checked both plastic sheets continuously looking for possible preys (e.g. insects, lizards or frogs) available for egrets. We could observe that there were not any such animals on the plastics during the time the egret walked

on them. From 40-50 m with our telescope we could observe any object not smaller than about 1 cm on the plastic sheets.

In earlier studies, the optical characteristics (brightness, colour, degree and direction of polarization) of the black and white plastic sheets (Horváth & Pomozi 1997, Horváth *et al.* 1998, Kriska *et al.* 1998) used in the choice experiment were measured and compared with those of crude oil lakes (Horváth & Zeil 1996, Horváth *et al.* 1998) and natural water bodies (Schwind & Horváth 1993, Horváth 1995, Horváth & Varjú 1997, Horváth *et al.* 1998, Kriska *et al.* 1998). On the basis of these measurements we could establish the following: (1) The optical characteristics of the shiny black plastic sheet are practically the same as those of (i) wet, marshy soil; (ii) dark, deep water bodies; or (iii) black crude oil surfaces. (2) The optical characteristics of the shiny white plastic sheet are very similar to those of (iv) bright-bottomed shallow clear water bodies; or (v) turbid white (e.g. alkaline) water. Hence, the white plastic sheet used in our choice experiment mimicked clear water with bright bottom or white and turbid water, while the black plastic sheet imitated some kind of black and wet mud, or black crude oil surfaces.

We observed a Great White Egret to return five times to the white plastic sheet and land three times on it whereas it stepped and walked on the black sheet twice. The reactions of the egret to the plastic sheets are summarized in Tab. 1. The egret always flew to the white plastic sheet. After landing at the edge of the white plastic, it stepped onto the sheet, where it stood or walked about, frequently picked the plastic or stroke off with its

bill, plumed itself, rested, watched, sought for prey, "fished", gazed at the white surface with its neck bowed down, looked around, defecated, or even sat down. In spite of any tactile, olfactorial or thermal experience the egret behaved quite similarly on both of the plastics as at real water surfaces (Hancock & Elliott, 1978; Hancock & Kushlan, 1984).

The egret was apparently deceived, because we heard and saw that it pecked at the plastic sheet. Once, "fishing" on the white plastic and reaching its edge the egret took a short cut across the field between the plastic sheets towards the black plastic and stepped onto it. It walked about on the black plastic for some minutes while gazed at the dark surface, sometimes stroke off or "fished", however, it crossed the plastic rather quickly. When the bird reached the edge of the black plastic sheet it began to preen on the grass, and finally flew away.

After transposing the black and white plastic sheets, the egret landed twice again first on the white plastic sheet. It is remarkable that once the bird stayed for 1.5 hours on the white plastic, and showed the same reactions and behaviour elements as earlier. Thereafter the bird visited the black plastic sheet for some minutes, and then flew away (Table 1).

Since we did not see any prey animal on the plastic sheets during the time the egret walked on them, the attractiveness of the plastics can be explained only by visual cues. The reactions to the plastic sheets of the egret might be explained in such a way that egrets often forage in shallow water where they can fish and catch prey. Shallow waters are usually brighter than deeper ones. Wading birds rarely fish in deeper, that is, darker waters (Hancock &

Elliott, 1978; Hancock & Kushlan, 1984). The five visits of the egret at the plastic sheets, especially its sojourn of 90 minutes in one of the five occasions on the white plastic convinced us of its keen interest aroused and captivated by the plastics. The behaviour of the egret demonstrated that the bird was probably deceived by the water-imitating optical cues of the white plastic sheet, and the bird undoubtedly mistaked the white plastic sheet for water in spite of the fact that the other characteristics (temperature, smell, mechanical properties, etc.) were quite different from those of real water.

Because only the optical characteristics of the plastic sheets were approximately common with those of real water, the egret was probably attracted to the plastic by the reflection of light. This optical cue was strong enough to strain the egret to react upon the plastic dummies quite similarly as upon natural waters (Hancock & Elliott, 1978; Hancock & Kushlan, 1984). This observation is important, because it may explain how crude oil lakes attract egrets and other wading birds. We propose that the deceiving capability and attractiveness of these oil lakes to egrets (and other water-seeking birds) may be explained by the shiny appearance of their surface. These birds might be deceived by the reflected light, which may imitate them the glitter of a water surface.

The egret observed in our choice experiment seemed to prefer the white plastic sheet against the black one. From this we may conclude that the water-specific behaviour might have been elicited in the observed bird by phototaxis. In our opinion, the light reflected from the flat surface of oil lakes and tar seeps could

deceive and lure water-seeking birds similarly. These birds may mistake the shiny oil surfaces for water or wet mud. We suggest that after landing at an oil lake and probing the oil birds may recognize that the warm, black, non-transparent, sticky and smelly oil is not water, however, the light reflected by the oil surface is a so strong visual cue that it elicits water-specific responses.

It would be important to investigate further the visual ecologic impacts of oil lakes to the avifauna in detail, because only on the basis of such studies can be explained the enigmatic attractiveness of oil reservoirs to birds. These studies are the basis of the necessary environmental protective measures that should be urgently taken in order to eliminate any natural tar seeps or man-made oil spills which are so dangerous to birds, especially to those associated with water.

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Összefoglalás

Hogyan tévesztett meg egy nagykócsagot egy fekete és egy fehér csillogó műanyag fólia?

Tanulmányunkban arról számolunk be, hogy miként tévesztett meg vizuálisan egy nagykócsagot (*Egretta alba*) egy fehér és egy fekete, 20 m x 30 m-es műanyag fólia, amelyeket 1997 augusztusában terítettünk ki egy mezőre a dél-alföldi Kunfehértó kiszáradt szikes tavának egykori medrében. A nagykócsagot a fóliák többször is magukhoz vonzották. A madár viselkedése igen hasonlított a nagykócsagok valódi vizeknél mutatott viselkedéséhez. A madár a fehér fóliát részesítette előnyben a feketével szemben. Értelmezésünk szerint miután a madár leszállt a fóliákhoz és rájuk ment, észlelhette, hogy nem vízzel van dolga, de a fényes, sima felszínű fóliák által visszavert fény olyan erős vizuális jelnek számíthatott, hogy a madárból vízspecifikus viselkedési elemeket váltott ki.

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