

# The method of running-averages in the study of breeding parameters: an example of the Blackbirds (*Turdus merula*)

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Vanicsek, L. and Ludvig, É. 1992. The method of running-averages in the study of breeding parameters: an example of the blackbirds (*Turdus merula*). — *Ornis Hung.* 2: 1-10.

The seasonal variation of breeding parameters is usually described by calculating the averages of parameters in non-overlapping intervals. This method has two disadvantages: (1) the improper choice of the interval-length makes it impossible to detect either the seasonality or the correlation between parameters in some cases, and (2) even if the interval-length is correct, the detection of seasonality depends on the starting point of the first interval. These problems are discussed in relation to our data collected in an urban Blackbird population during four successive breeding seasons from 1986 to 1989. The method of calculating running-averages is recommended which offsets the above mentioned disadvantages. However this method raises some new problems which are also discussed.

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## 1. Introduction

As in other open-nesters, Blackbirds (*Turdus merula*) usually lay two or three (or more) clutches during a breeding season. Consequently their breeding season lasts three to four months. This makes it possible to study the effect of changes in the environment on the breeding parameters during a season.

The seasonality of breeding parameters or their relationships are usually determined by sorting data into non-overlapping intervals and calculating their averages and the correlation between the different parameters. The interval-length depends on the amount of data, authors usually calculate monthly (Snow 1955, 1969, Saemann 1979), half-monthly (Snow 1958, Ribaut 1964), 10-day (Havlin 1963), weekly (Perez et al. 1979), or 5-day averages (Havlin 1963,

Dyrcz 1969). If we have only few data and we use short intervals, the effect of the seasonality can be hidden by random fluctuations. On the other hand if we use too long intervals, the seasonality of parameters cannot be detected either. This is because in this case data from breeding attempts under quite different circumstances are drawn together. An extreme example is when the interval-length equals with the length of the whole breeding season.

Another, usually neglected problem is defining the starting-point of the first interval. The finer the arrangement of intervals (in the case of a large data-set shorter intervals can be used), the less important the problem is. However if the interval-length exceeds the 15-20% of the length of the breeding season, the improper marking of the starting point of the first interval may cause serious problems, and it can be a mat-

ter of chance whether the seasonality or the relationship between the parameters appear or not.

This paper uses the well-known method of calculating running averages to avoid or resolve these problems in the examination of seasonality of breeding parameters in an urban blackbird population.

## 2. Material and methods

Data were collected during a long-term study of the breeding of an urban blackbird population from 1986 to 1989. Our study area, the Vérmező is a 13 ha park in the middle of Budapest. It consists of large areas of lawn with a great variety of scattered bushes and trees. About 60-70 pairs of blackbirds breed in the area and lay about 150-200 clutches in a year. During the four years, 447 nests were examined from which 365 were considered complete. Only breeding data from these nests were involved in further analysis.

In theory running averages can be calculated in two ways. In the first method the daily averages are calculated first, then the running-averages of intervals from the first, second etc. days are calculated from these averages. In case of a small data-set the number of data per day may be very variable and perhaps there may be days without any data. Consequently it is better if we calculate the running averages from rough data. This method is in fact nothing else than the extension of calculating the averages of non-overlapping periods for each possible case according to the following process:

Let us choose a possible interval-length ( $L$ ) and a starting-point ( $t$ ). Let us calculate the average of the chosen parameter ( $a_1$ ) from data of nests started in the  $/t, t+L-1/$  interval. In the following steps let us calculate the averages of parameters ( $a_2, a_3..a_x$ ) in the  $/t+1, t+1+L-1/, /t+2, t+2+L-1/ .....$

$/t+x, t+x+L-1/$  intervals. Calculating the averages following each other we get the average of the interval  $/t+L, t+2L-1/$  which is the first interval which does not overlap with our first interval  $(/t, t+L-1/)$ . If the calculation of averages is carried out in non-overlapping intervals

$$/(t+m)+yL, (t+m)+(y+1)L-1/ \quad (1)$$

- where  $m$  is the number of days with which the original starting-point ( $t$ ) is modified and  $y$  is the serial number of non-overlapping intervals - then a series of averages of non-overlapping intervals can be calculated for each possible case of  $y$  at a constant value of  $m$ . By increasing  $m$  by one we get the next series of non-overlapping intervals etc. In this way we get the method used up to now with the difference that each possible series was calculated. If the interval-length is  $L$ , then  $L$  kinds of series of non-overlapping periods can be produced. If we do not specify the value of  $y$  and the averages are calculated in intervals

$$/t+x, t+x+L-1/ \quad (2)$$

- then producing all kinds of possible averages, the series of series of non-overlapping intervals (1) are calculated. In this case each interval overlaps with  $L-1$  other intervals. It is important to mention that in the case of the first and the last few intervals there are fewer data so their averages are not reliable.

## 3. The choice of interval-length

### Example 1: the number of nests

The number of nests started in different periods of the breeding season is quite variable. During the field-work it seemed that many of nests began simultaneously at the beginning of the breeding season, later we

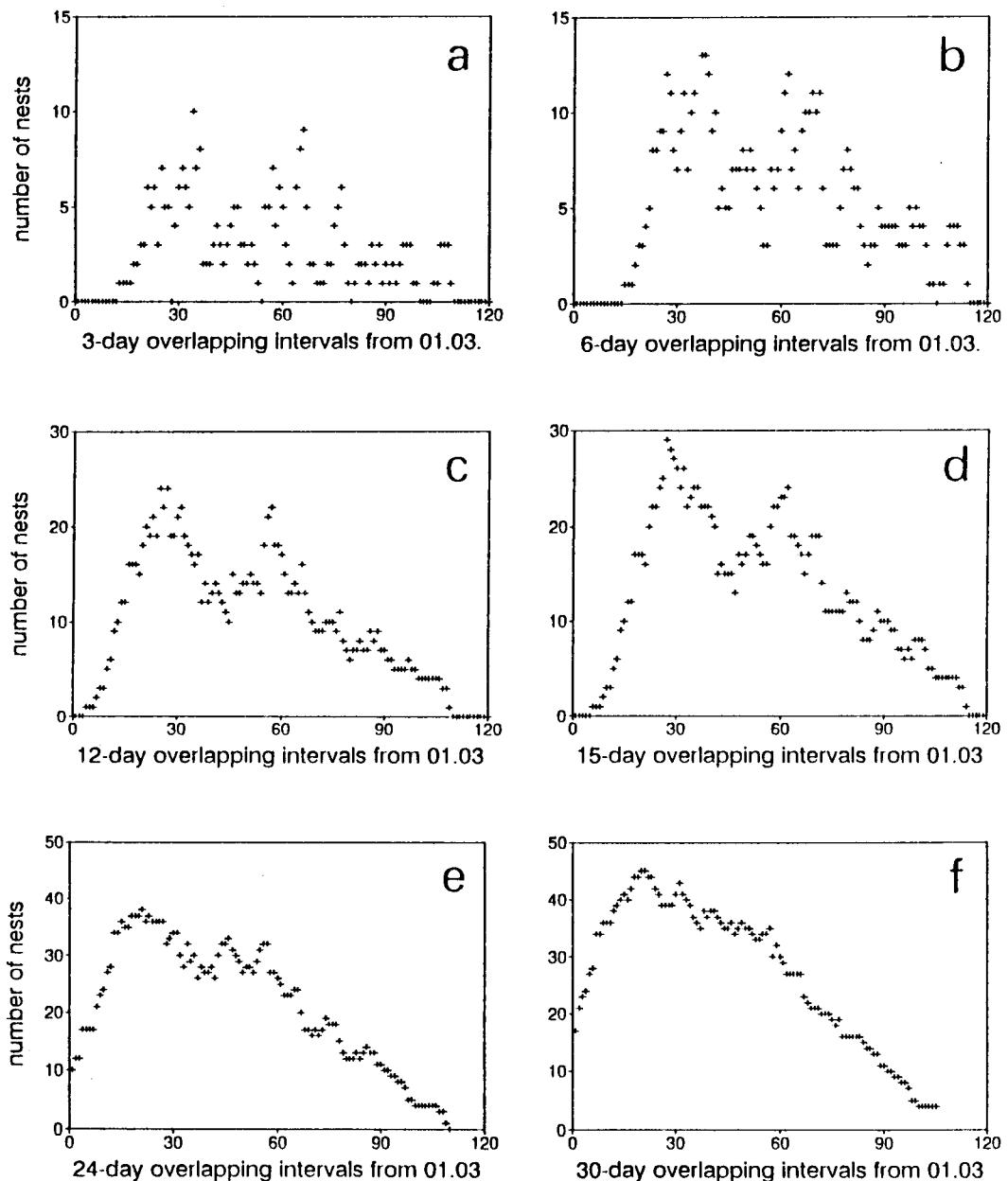


Fig. 1. The number of nests in 3-day (a), 12-day (c), 15-day (d), 24-day (e) and 30-day (f) overlapping intervals in 1988.

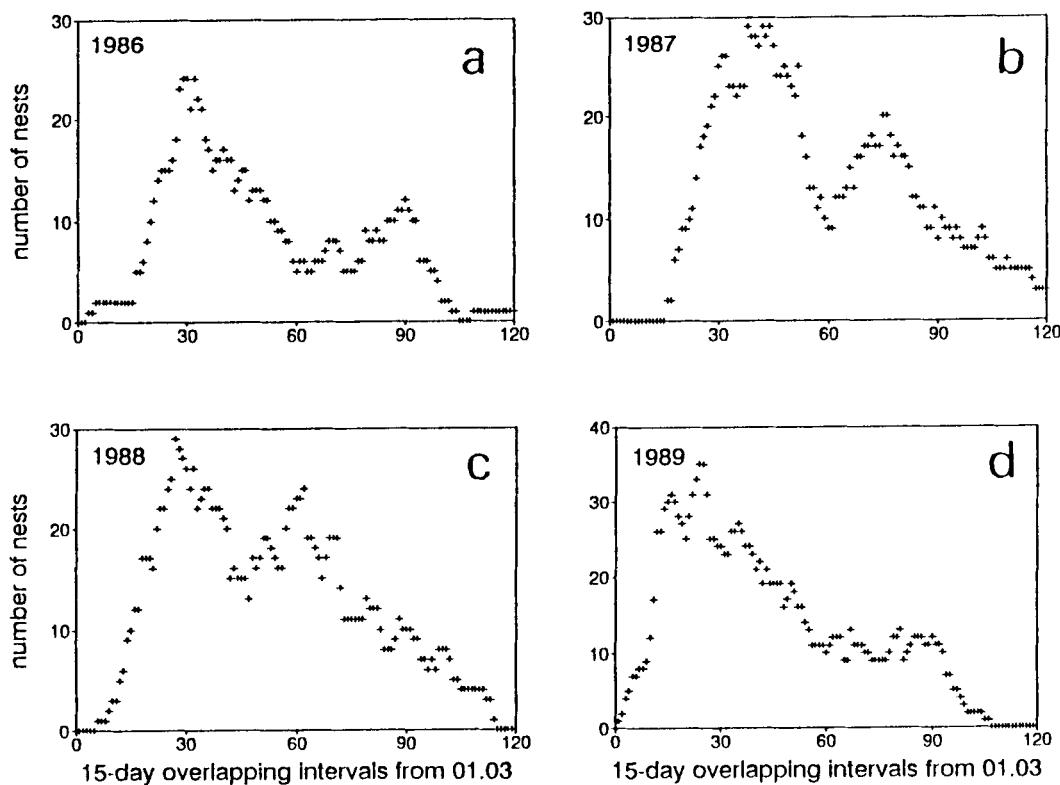


Fig. 2. The number of nests in 15-day overlapping intervals in 1986 (a), 1987 (b), 1988 (c) and 1989 (d).

found fewer nests, while in the middle of the season the number of nests increased again and finally decreased. The question is which interval-length can display this tendency. Let us demonstrate it on data from 1988.

First let us calculate the averages according to (2) in the case of different interval-lengths and let us represent them as a function of the serial number of overlapping periods ( $x$ ) (Fig. 1) In the case of low values of  $L$  (Fig. 1a, b) the change in the number of nests does not appear, and in the case of large values of  $L$  (Fig. 1e, f) the change becomes smooth. In the case of medium values of  $L$  (Fig. 1c, d) both peaks in the number of nests are expressed. Breeding

began on different dates in different years according to the weather (mainly the temperature). However at the appropriate interval-length the slopes of the first peaks seem to be similar in each year (Fig. 2) This characteristic feature of appearance of nests was used to synchronize the four years when their data were compiled.

#### **Example 2: the seasonal pattern of breeding success**

Many papers have described the seasonal pattern of breeding success (which is usually given as the proportion of successful nests in a given interval) in blackbirds.

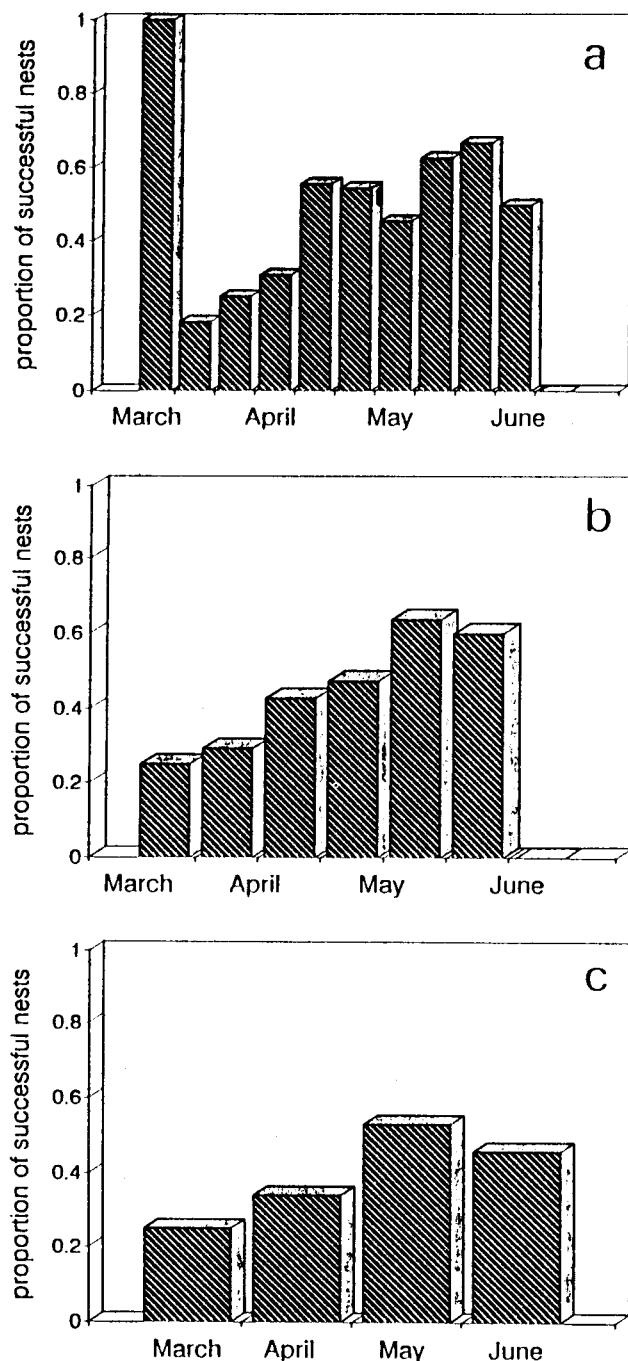


Fig. 3. The proportions of successful nests in 10-day (a), 15 day (b) and 30-day (c) non-overlapping intervals is 1988.

Some authors found that breeding success increased continuously throughout the season (Snow 1955, Havlin 1963, Baum 1968), while others detected an early maximum as well (Ribaut 1964, Dyracz 1969). One paper described a seasonal pattern with a maximum in the middle of the season (Koródi-Gál 1967), finally Snow (1969) and Saemann (1979) revealed both an early and a middle maximum in the seasonal pattern.

The differences in the results of these authors are caused by the different arrangement of data. In the following we will demonstrate that these patterns can be produced from the same data-set by modifying both the interval-length and the starting point of the first interval. Figure 3a, b and c show the proportions of successful nests started in 10-day, 15-day and 30-day non-overlapping intervals in 1988, respectively. These kinds of arrangements of intervals can be found in similar studies (e.g., Havlin 1963, Ribaut 1964 and Snow 1969). If the interval-length is quite short (e.g., 10 days, Fig. 3a) then the first few nests - which are usually successful, because predators have not begun to plunder the nests - are sorted into the first interval, consequently their breeding success will be higher than those of the following intervals. However, if we choose a longer interval-length (e.g., 15-days, Fig. 3b) then the first interval will contain more nests than in the previous case, thus the proportion of successful nests will be much lower and the first maximum in the seasonal pattern of breeding success will disappear, although the final decrease is still well-expressed. If we choose a quite long interval-length (30 days, Fig. 3c) then the characteristic seasonal pattern of the breeding success found by using 10-day intervals is lost entirely: the early maximum disappears and the final decline in the breeding success is not so expressed, the seasonal pattern tends to be increasing throughout the season.

#### 4. The choice of starting point of the intervals

If we calculate averages in non-overlapping intervals with interval-length L (method 1), we can get L kinds of series by varying the value of  $m$  from 0 to L-1. If the change of the parameter is quick at least in a short period of the season, then the series of averages could be quite different.

#### Example 3: correlations between breeding parameters

Most of the papers which described the seasonal pattern of breeding success, attributed it to the seasonal changes in the rate of predation (Snow 1955, 1969, Koródi-Gál 1967, Dyracz 1969). Only Ribaut (1964) found the proportion of predated nests similar throughout the season. To settle the question, correlations should be calculated between the proportions of successful and predated nests and between the proportions of successful and deserted nests. However correlations can be calculated only between proportions from non-overlapping periods, otherwise the number of our pairs of points would be artificially multiplied and thus the degree of freedom of the correlation would be seriously violated. Consequently for example if we have the proportions of successful and predated nests in all series of non-overlapping periods (the number of series equals with the interval-length (L)), then L kinds of correlations can be calculated between the two breeding parameters. In the following example we will show that in some cases it depends on the starting point of the first interval ( $m$ ) whether the correlation between the two proportions is significant or not.

Fig. 4a shows the proportions of successful (filled triangles), predated (asterisks) and deserted nests (empty squares) during

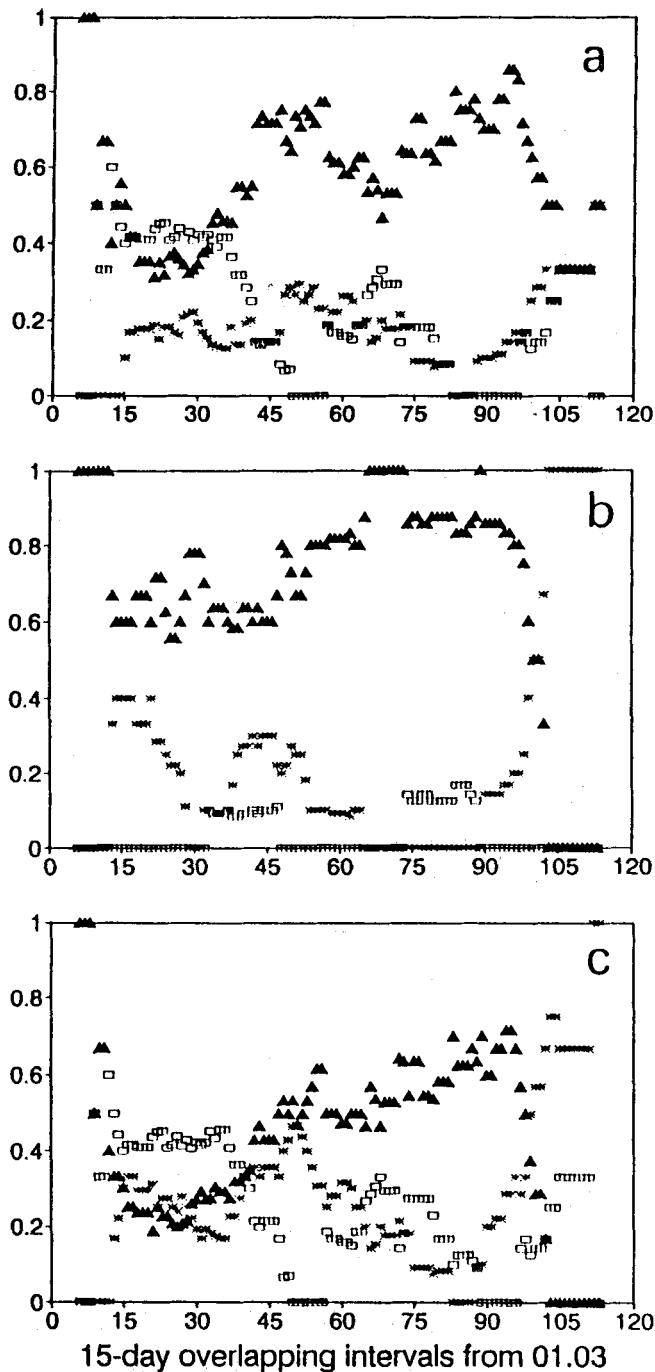


Fig. 4. The proportions of successful (filled triangles), predated (asterisks) and deserted nests (open squares) in 15-day overlapping intervals in 1988 during the incubation periods (a), during the nestling stages (b) and during the whole breeding attempts (c).

the incubation periods in all 15-day overlapping periods, Fig. 4b shows the same proportions during the nestling stage while Fig. 4c shows these proportions during the whole breeding attempt. Consequently Fig. 4a refers to the hatching success, b to the fledging success and c to the breeding success, and if we want to find the causes of their seasonal patterns, we should correlate the proportions of nests in series from non-overlapping intervals. In the case of 15-day intervals, 15 kinds of correlations can be calculated between each pair of parameters. The correlation coefficients are shown in Fig. 5. In the case of hatching success it is always the proportion of deserted nests which correlates significantly negatively with the proportions of successful nests, although the correlations with the proportions of predated nests are also negative but not significant except one case (Fig. 5a). On the other hand in the case of fledging success it is the rate of predation which causes the seasonal pattern: all correlation coefficients but one are significant and most of the correlations with the proportions of deserted nests are positive instead of being negative (Fig. 5b). However in the case of breeding success the result is quite ambiguous (Fig. 6c). As the pattern of breeding success is caused by the factors shaping the patterns of hatching success as well as the factors shaping the pattern of fledging success, if the causes are different as in our case, then the pattern of breeding success can be attributed to both predation and desertion. However, it depends on the modification of the starting point ( $m$ ), whether the correlations with the rate of predation or desertions are significant. This example points out that if we analyse the cause of some seasonal pattern or the correlation between two seasonally changing parameters, then the choice of only one series of non-overlapping intervals can lead to false or ambiguous results.

**Acknowledgements.** The authors thank J. Török for his help in the field work and comments. R. Alatalo, A. Gosler, J. Jacobs, E. Pásztor, and J. Garay also made very useful comments.

## Összefoglalás

### A mozgó-átlagok módszere a feketerigó (*Turdus merula*) költési paramétereinek vizsgálatában

A költési paraméterek szezonálitásának kimutatására általánosan alkalmazott módszer, hogy a paraméterek értékeit egymásra következő, nem átfedő intervallumokban átlagolják, és ennek alapján vizsgálják a szezonálitást, illetve állítják a paramétereket egymással szembe. Ez a megoldás több hibalehetőséget tartalmaz: (1) Az időintervallumok hosszának rossz megválasztása nem minden esetben teszi lehetővé az egyébként létező szezonálitás, vagy a paraméterek közötti összefüggés kimutatását; (2) még megfelelő intervallumhossz esetén is, a kimutathatóság függ attól, hogy az első intervallum kezdőpontját hol jelöl ki. A feketerigó egy városi parkban költő populációjának (Vérmező, Budapest 1986-89) költésfenológiai vizsgálatából származó adatokon mutatjuk be ezeket a problémákat. Megoldásként javasoljuk a mozgó-átlagok számításának módszerét, amelynek segítségével az (1) és (2) során jelentkező hiba csökkenthető, illetve amelyen keresztül a nem-átfedő intervallumok átlagainak számításával kapcsolatban újabb nehézségek mutathatók ki.

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*Received 18 September 1991, revised 25 November 1991,  
accepted 5 December 1991*

# The delivery of surplus prey to the nest by a pair of Bee-eaters (*Merops apiaster*)

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Horváth, G., Fischer, M. H. and T. Székely. 1992. The delivery of surplus prey to the nest by a pair of Bee-eaters (*Merops apiaster*). — *Ornis Hung.* 2: 11-16.



Observations are presented on the delivery of surplus food to the nest of a pair of Bee-eaters, including the quantity and species composition and size of surplus food items. The delivery of surplus food may be explained by (1) the death of young, (2) the arrival of helpers, (3) increased success of prey capture because of the discovery of a rich food supply nearby, or (4) an aversion of the nestlings to venomous bumble-bees which are fed when other food for the nestlings is unavailable. The delivery of surplus food suggests that the adjustment of food delivery to the nest is not a quick process, and that the adults need a few days to adjust their effort to the requirements of the nestling.

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## 1. Introduction

Bee-eaters (*Merops apiaster*) are colonial breeders and feed their young with insects (Cramp 1985). Although previous studies reported the composition of nestlings' diet (Korodi-Gál & Libus 1968, Cramp 1985), rate of feeding (Tapfer 1957, Dyer & Demeter 1981) and amount of food delivered (Korodi-Gál & Libus 1968), the delivery of surplus food to the nest, which we describe here, has not been reported before.

In this work we present observations on the delivery of surplus food to the nest of pair of Bee-eaters, including the species composition and size of surplus food items. We suggest some possible hypotheses for explanation of the odd behaviour of one pair studied. The delivery of surplus food suggests that the adjustment of food delivery to the nest is not a quick process, and that the adults need a few days to adjust

their effort to the requirements of the nestlings.

## 2. Material and methods

A single nest was observed for a week in late July of 1984 near the town Kiskunhalas, in southern Hungary. The nest was excavated about 30 cm from the top of an almost vertical dune of firm sand. There were 8 other burrows in the proximity (ca 1-10 m), but only the one studied was inhabited at the time of observation. In previous years all holes had been occupied. Other groups of nest-holes occurred 150-200 m away.

The breeding site was surrounded by farmlands with pastures, orchards, lucerne and clover fields, sunflower and maize fields, and with dunes covered by pines, locust-tree and poplar groves. At the time of observation there were no beehives in the area.

Taxon time	<i>Bombus terrestris</i>	<i>Bombus lapidarius</i>	<i>Bombus agrorum</i>	<i>Apis mellifera</i>	<i>Vespa spp.</i>	<i>Melolonthioae</i>	<i>Calliph-tamus italicus</i>	<i>Hete-rop-tera</i>	Total
day 1	60*	3*	2*	3*	2*	3**	4**	2**	79
day 2	22	1	1	—	—	—	—	—	24
day 3	8	1	—	—	—	—	—	—	9
day 4	3	—	—	—	—	—	—	—	3
day 5	1	—	—	—	—	—	—	—	1
day 6	2	—	—	—	—	—	—	—	2
day 7	—	—	—	—	—	—	—	—	0

Tab. 1. The number and composition of surplus prey delivered to the nest by Bee-eaters as a function of time. On the first day fresh and old items were indistinguishable (\*), except for some definitely old items (\*\*). The number of items declined during the week (Spearman rank correlation with day one excluded  $r=0.943$ ,  $n=6$ ,  $p<0.02$ ).

The weather was cold and rainy in two days before observation (23-24 July), but in the week of observation the weather conditions were sunny and there was a slow rise in temperature.

On the first visit (25 July), there were several dozen of bumble-bees (*Bombus* spp.) on the ground directly beneath the burrow, far more than the usual number of items accidentally dropped during feeding. We observed the nest every day for a week, from 14.00-17.00 h. After each observation period we collected the surplus items.

### 3. Results. Quantity, size and composition of surplus food delivered to nest

On the first day of observation both fresh and old prey items were found beneath the nest (Tab. 1). These could be distinguished because the fresh items were whole, but damaged on their thorax, were sometimes still alive, and were sometimes found in the tunnel burrow. On the other hand, all old prey were dead and some of them were partly covered in sand because of the impact of rain drops on the ground while others

had much damaged exoskeletons. However, some of these old items were whole. The number of prey declined during the week (Tab. 1). By far the most common items were *Bombus terrestris* which accounted for 75.9% ( $n=79$ ) of items on the first day. From the fourth day onwards only that species was found (Tab. 1). Most *Bombus* spp. were small (1.5-2 cm in length, 65.4%,  $n=104$ ), and only a few were between 2-3 cm (19.2%) or over 3 cm (3-3.5cm, 15.4%).

Our observations were timed to correspond with the previously recorded peak feeding time of Bee-eaters in Hungary (Fintha 1968). The adults delivered prey to the nest at a rate of 50-60 visits/h at the beginning of the week, but at 40-50 visits/h at the end of the week. The visiting rate also decreased slowly within every observation period (Tab. 2). Only adults flew into the study burrow, but they were unmarked, therefore we did not know whether there was a helper among them.

### 4. Discussion

The following explanation can be suggested for this odd behaviour:

Day hour	1	2	3	4	5	6	7
14-15	60	61	56	49	51	45	48
15-16	51	60	52	50	46	41	42
16-17	55	48	48	46	41	39	43

Tab. 2. The number of visits per hour by adult Bee-eaters. Two ways ANOVA (day:  $F=12.61$ ,  $df=6$ ,  $p<0.001$ ; hour:  $F=23.99$ ,  $df=1$ ,  $p<0.001$ ).

HYPOTHESIS 1: Some or all of the nestlings perished during the two cold rainy days preceding the start of observations. There was a delay before the parents detected this, after which the amount of surplus food delivered to the nest decreased rapidly.

HYPOTHESIS 2: One (or more) failed breeder(s) from the surrounding Bee-eater colonies joined our breeding pair as helper(s), so the provisioning rate of the nestlings increased. The arriving helper was initially frightened of entering the burrow, so it dropped the prey delivered. Later the parents and helper(s) detected the unnecessarily high provisioning rate and delivered less food, so the surplus prey decreased rapidly.

HYPOTHESIS 3: In spite of the rainy and cold weather preceding the first day of observation, the foraging adults of the nest-hole studied discovered a large nest of bumble-bees (*Bombus* spp.) near the burrow, and plundered it over a week. The bumble-bees became much easier to catch during the cold rainy weather before the observations because they were colder so flew more slowly and were less able to evade the Bee-eaters. Later, as the abundant prey source was exhausted, and/or the adults detected the uneaten surplus food they delivered food at a lower rate.

HYPOTHESIS 4: Due to the bad weather the nestlings were provisioned almost exclusively with bumble-bees. The venom of bumble-bees might affect the

young adversely, so that the nestlings did not consume all the prey items which were not devenomed, killed and prepared suitably for them by the adults.

HYPOTHESIS 5: A predator (e.g., a snake, weasel) had been seen in or nearby the nest and the adults were frightened of entering the burrow and dropped the prey items delivered below the burrow entrance.

It is difficult to decide unequivocally between these hypotheses. In our opinion they are not mutually exclusive, in fact it is quite likely that two or more are acting at the same time.

HYPOTHESIS 1 is supported by the observation that young Bee-eaters may become lethargic during cold spells and food shortage (Valverde 1953). Chilled and moist young elicit no parental care, and may be pushed aside or even tossed out of the nest (Cramp 1985). Runts are usually left in nest, and the parents continue prey delivery uninterrupted after the death of some nestlings (Glutz & Bauer 1980).

Fintha (1968) noted that nest-holes are generally not dug less than 25-30 cm from the top of banks. Nests dug higher than this often leak, especially if the substrate above the burrow is sandy, leading to the death of nestlings (Fintha 1968). Nest-holes too near the top of banks may also be blocked by the growing roots of plants (e.g., *Medicago Eryngium campestre*), particularly after rain (Fintha 1968). The study nest was in sandy ground and 30 cm from the top of bank, so it may have leaked but we did not find root's mesh blocking the nest.

HYPOTHESIS 2 is possible because non-breeding Bee-eaters may attach themselves (either singly or several together) to breeding pairs as helpers (Lessells 1991). Helpers are tolerated at nest-holes and on territory perches, and help provision the young. They did not arrive until after the brood has hatched. It is not known if they

help the brood in any way other than feeding them (e.g., brooding). Helped broods receive more prey items and the breeding male, but not female, at helped nests delivers food at a lower rate than at unhelped nests. Helpers may start helping at any stage during the nesting period. The vast majority of helpers are male; male helpers comprise a slightly higher proportion of juveniles than occurs in the breeding population. Birds failing before early-mid June tend to re-nest (early-failed breeders), and those failing after this date to help (late-failed breeders) (Lessells & Krebs 1989).

Our observations were made in the last week of July, so it is likely that failed breeders were around. After the arrival of a helper, an initially surplus delivery of food might be compensated by decreased provisioning by the male.

HYPOTHESIS 3 is supported by the fact that Bee-eaters prefer Hymenoptera. Bumble-bees (*Bombus* spp.) are the most important prey for those living near clover fields and areas with many flowers. The diet often reflects variations in the insect fauna due to seasonal and geographical changes or to weather conditions and temporary and local exploitation of particular species are typical (Cramp 1985). The occurrence of *Bombus* in the diet may be higher during cold rainy weather when almost exclusively *Bombus* spp. fly in the fields (Fintha 1968). However hypothesis 3 would explain only the presence of *Bombus* spp. and not the other prey items.

HYPOTHESIS 4 seems likely, because large or venomous insects are difficult for inexperienced juvenile Bee-eaters to manage (the number of such prey items increases suddenly beneath perches after fledging). Birds show no further interest in prey which has been dropped onto ground (Koenig 1959, Ursprung 1979, Helbig 1982). Inexperienced young birds select large black and yellow insects in preference

to plain ones (Ursprung 1979, Cramp 1985). Considerable differences exist between nestling diet and that of the parents at the same time; the young are generally given larger items than the adults consume (Krebs & Avery 1985).

On the basis of the investigations made by Helbig (1982), most preys of Bee-eaters are over 10 mm long, with ca. 28% of them being 5-10 mm, ca. 51% 10-15 mm and ca. 18% 15-20 mm. Compared with this the surplus items delivered (Tab. 1) tend to be larger and perhaps more difficult to handle.

It is unlikely that prey dropped well down the burrow would manage to (regularly) crawl back to the burrow entrance, so most of the prey must have been dropped at the entrance. It is possible that the chicks were of an age when they sat in the burrow entrance, but we could not observe this during the time of observation. So it seems likely that the adults were dropping the prey without entering the burrow. In Bee-eater colonies adults do this if they are reluctant to enter the burrow for some reason, which might be because (Lessells pers. comm.): (a) they are a newly arrived helper, and are reluctant to enter the burrow; (b) the chicks do not make begging calls – when the adult arrives and calls at the nest entrance – because they are sated (Lessells et al. in press); (c) there is some danger (e.g., a snake near or in the nest).

Chicks reach a maximum weight several days before they leave the nest (Lessells & Avery 1989) and then lose weight before leaving the nest. At this time they feed, and prey can be often found below the nest entrance (Lessells pers. comm.).

## 5. Conclusions

The food provisioning rate of Bee-eaters is probably determined by three factors: (a) the food requirement of the nestlings

(FRN), (b) the sum of power of food delivery of adults (SPFDA) (parents and helpers) to the nest, and (c) the rate of prey capture (RPC) per bird. If FRN suddenly decreases – due to the death of some nestlings, for example (HYPOTHESIS 1) –, or SPFDA suddenly increases – e.g., due to the arrival of helpers (HYPOTHESIS 2) –, or RPC suddenly increases – due to weather conditions or the discovery of an abundant prey source (HYPOTHESIS 3) – then surplus food may be delivered to the nest for a while until the adults compensate for the change. In HYPOTHESIS 1, the decrease in FRN is compensated by a decrease in SPFDA, in HYPOTHESIS 2 the arrival of helpers is compensated by a decrease in provisioning rate by the breeding male, and in HYPOTHESIS 3 a temporary surplus is alleviated by the gradual exhaustion of the food source.

Recent studies have shown, that there is a trade off between reproductive effort such as feeding young and parental survival (Reid 1987, Nur 1988, Dijkstra et al. 1990). However, our observations suggests that the adjustment of prey delivery to the nest is not an instantaneous process, and that the adults need a few days to adjust their effort to the requirements of the nestlings.

**Acknowledgements.** We thank C. M. Lessells for her valuable remarks and comments considering some possible explanations underlying our observations, and for reading and correcting the manuscript. Thanks are due to E. Schmidt, P. Székely and L. Móczár for commenting on a previous version of the manuscript.

## Összefoglalás

**Egy gyurgyalagpár (*Merops apiaster*) fölös zsákmányhordása**

Egy gyurgyalagpár szokatlan viselkedéséről számolunk be, mely abban nyilvánult meg, hogy a

felnőtt madarak többlet táplálékot szállítottak a fészekhez. Az el nem fogyasztott fölösleges zsákmány a fészek bejáratí nyílásánál halmozódott fel. Beszámolunk a tápláléktöbblet faj és méret szerinti összetételeiről valamint mennyiségről az idő függvényében.

A gyurgyalagok viselkedésökológiájának alapján a következő elközelhető, egymást ki nem záró hipotéziseket állítottuk fel a zsákmány-felhalmozódásának magyarázatára: (1) a táplálékgény hirtelen lecsökkenése a fiókák egy részének a fészek beázása következtében való elpusztulása által, (2) a fészekbe hordott táplálék-mennyiség ugrásszerű növekedése segítő (helper) gyurgyalag(ok) érkezése és a fiókák etetésébe való bekapcsolódása miatt, (3) a felnőttek zsákmányszerzési hatékonyságának hirtelen növekedése a fészek közelében felfedezett gazdag táplálékforrásnak köszönhetően, (4) a fiókáknak a nagyszámú fullánkos, mérges poszméhtől való idegenkedése, mikor az időjárási körülmények következtében más táplálék nem állt rendelkezésre.

A zsákmánytöbbletnek a fészek környékén megfigyelt felhalmozódásából és időbeli csökkenéséből következtetni lehet a fészekhez való táplálékszállítási folyamat ütemére: a felnőtt gyurgyalagoknak néhány napra van szükségük, hogy a fiókák igényei szerinti mennyiségű táplálékot szállítsanak a fészekbe.

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*Received 1 April 1991, revised 10 June 1991, accepted 8 July 1991*

# Study of spring migration by weather radar in Eastern Hungary

T. Szép

Szép, T. 1992. Study of spring migration by weather radar in Eastern Hungary. — *Ornis Hung.* 2:17-24.



The main characteristics of spring migration were studied by meteorological radar in the Eastern part of the Carpathian Basin for 8 days in 1987. The radar is situated at Napkor, 200 km ENE from Budapest, and it can detect the birds in a 25-100 km range. The echoes were displayed on PPI and were recorded on 35 mm film by time exposure. During the study 6546 bird echoes were recorded on 413 pictures. The intensity of bird echoes was high at sunrise and early afternoon. In 25 km range, the intensity of the echoes was high at sunset because of intensive migration of passerine birds. The average direction was northeast (42°), and its daily value varied between 33°-59° during the study. The changing of the direction might come from the change in the composition of migrating species. Above some areas, the bird echoes were concentrated, and these concentrations showed a close relationship to some topographical elements.

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## 1. Introduction

The Carpathian Basin has an important role in the migration of Northern European, Northeastern European and North Asian birds. Old and recent observing, hunting, and ringing data show the importance of this area, especially of its eastern part (Haraszthy 1988). Data from direct observation of the migration by radar were not available until now in this region of Europe. These data can help to analyse more deeply the characteristics and dynamics of this behaviour (Eastwood 1967). In 1986, I started an investigation at Napkor Meteorological Radar Observatory to analyse how applicable that radar is for ornithological studies. The aim of this work is to describe some main characteristics of the spring migration based on radar data in Eastern Hungary.

## 2. Material and method

The weather radar station (OMSZ KEI) is situated at Napkor (47°58'N; 21° 54' E, 140 m ASL), and it is 200 km ENE from Budapest and 10 km E from Nyíregyháza which is the nearest town (Fig. 1). The MRL-5 type, Soviet made radar here is used for rainfall forecasting. I used a 10 cm wavelength with 1 microsecond pulse length, 500 kW peak power. The aerial diameter is 4.5 m and the radar beam is pencil shaped with a 1.5 beamwidth (Eastwood 1967). The radar sensitivity is -138.1 dBW.

The bird movements were detected by radar and displayed on the PPI (Plan Position Indicator) screen (range 25 km, 50 km and 100 km). The echoes were recorded on 35 mm film with a long time exposure. I used a 10 minute exposure time as described in

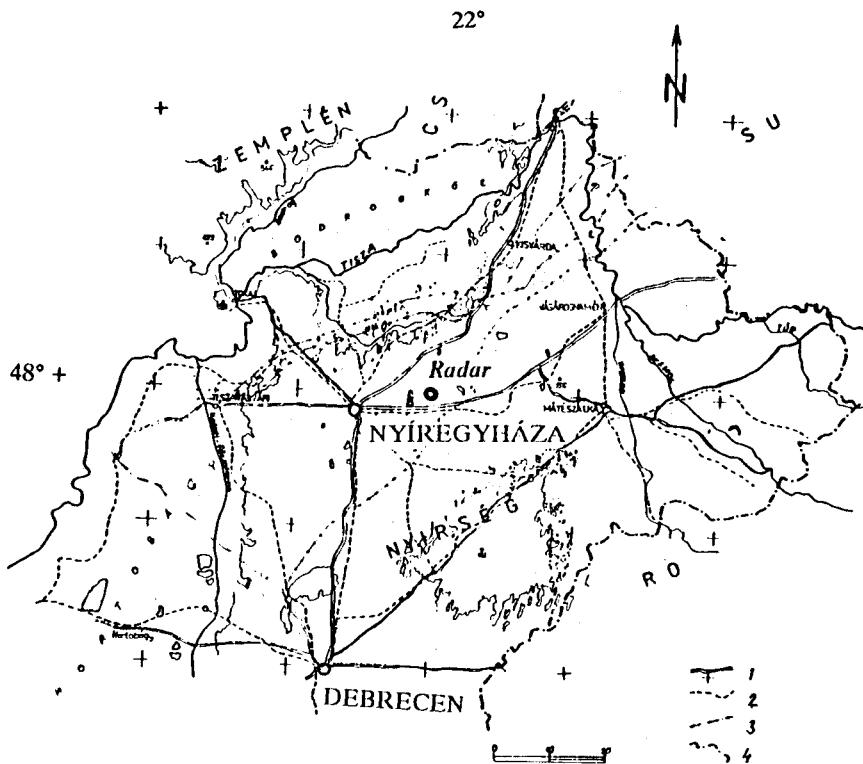


Fig. 1. Map of the study area (1: road; 2: railway line; 3: powerline; 4: state boundary).

Gauthreaux (1970). The pictures showed moving radar targets in all studied range except the nearest area around the radar station where the dense surface echoes hide

them (Fig. 2). I used different elevation angles at different ranges ( $3^\circ$  for 25 km,  $1^\circ$  for 50 km and  $0.3^\circ$  for 100 km), and in this way I studied the birds' movement at low alti-

Tab. 1. Number of bird echoes (n), observation time (t)[minute] and echoe intensity (n/t) at different range during the study.

Day	at 25 km			at 50 km			at 100 km		
	n	t	n/t	n	t	n/t	n	t	n/t
25.03	73	42	1.7	135	58	2.3	169	112	1.5
26.03	453	149	3.0	926	285	3.2	1284	464	2.8
27.03	45	34	1.3	162	76	2.1	172	66	2.6
29.03	176	132	1.3	24	15	1.6	0	142	0.0
05.04	210	62	3.4	214	193	1.1	60	134	0.4
06.04	289	121	2.4	335	340	1.0	113	171	0.7
07.04	323	103	3.1	252	242	1.0	77	127	0.6
08.04	559	230	2.4	429	420	1.0	66	131	0.5



Fig. 2. Time exposure of a PPI display showing heavy bird migration over Northeastern Hungary between 0537-0547 local time, GMT + 1, 25th March 1987. North is toward the top of the figure. Birds produce about 3-5 km long pale streaks, in this case toward the northeast. The angle of elevation of the radar beam is 1°, the range is 50 km and the revolution is 2/min. Tokaj hill and Zemplén mountains are situated at the northwest edge of the picture and the long line across the centre is a big 750 kW powerline (See the Fig. 1).

tude (100-2000 m). The average altitude of the echoes was between 400-800 m.

The data were collected in the spring of 1987 (25.03.1987 - 27.03.1987, 29.03.1987, 05.04.1987 - 08.04.1987), and as far as possible during all part of the day. The starting and ending positions and path of each moving radar target on the pictures were digitalized and used for measuring the direction and height of the flight. The characteristics of moving radar targets, low speed (30-100 km/h) and point like echo, differ from the echoes of surface, weather phenomenon or airplanes (Eastwood 1967). These targets were echoes of flying birds or bird flocks.

The numbers and species of birds taking part in the movements cannot be determined from the pictures.

I used the Nyíregyháza Meteorological Station data for measuring the wind parameters.

### 3. Results

During 8 days observation 6546 radar targets were identified as birds (64 hours observing time) on the 413 pictures (Fig. 3). Because the successive pictures may have

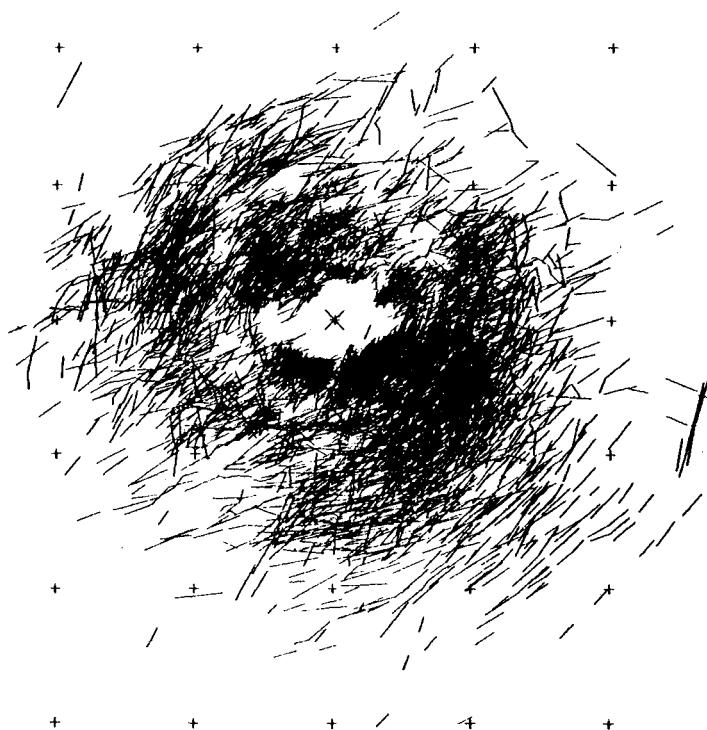


Fig. 3. Path of all bird echoes during the observation period in the study area. (Horizontal and vertical distance between the cross is 25 km.)

contained the same targets more than once, less separate targets were studied.

### 3.1. Daily distribution

In 26.03.1987, the continuous observation from 0504 to 2103 allowed me to analyse the daily distribution of the bird echoes in three different ranges (Fig. 4). As Fig. 4 shows, there was an intensive movement near sunrise which was followed by a smaller one at early afternoon (13-14 h local time, GMT+1). The distribution at the 25 km range differs from the other two (Fig. 4a). There is more intensive movement after sunset in this range than at the 50 km or the 100 km range. This difference can also be seen in the other day's data. The sensitivity of the radar is larger at 25 km range, and

smaller echoes, such as of migrating passerines in small flocks (Gauthreaux 1970, Williams et al. 1977), are more visible on the PPI screen and on the pictures. On the night of 07.04 there was a large movement in the 25 km range, and next morning around the radar station many Nightingales (*Luscinia megarhynchos*) and Lesser whitethroats (*Sylvia curruca*) started to sing. It is possible that intensive passerine migration in different directions explains the differences observed at night.

### 3.2. Direction

Comparison of the mean flying direction values at different ranges (Fig. 5) indicates slight difference between the 25 km, the 50 and 100 km range data. The mean direction

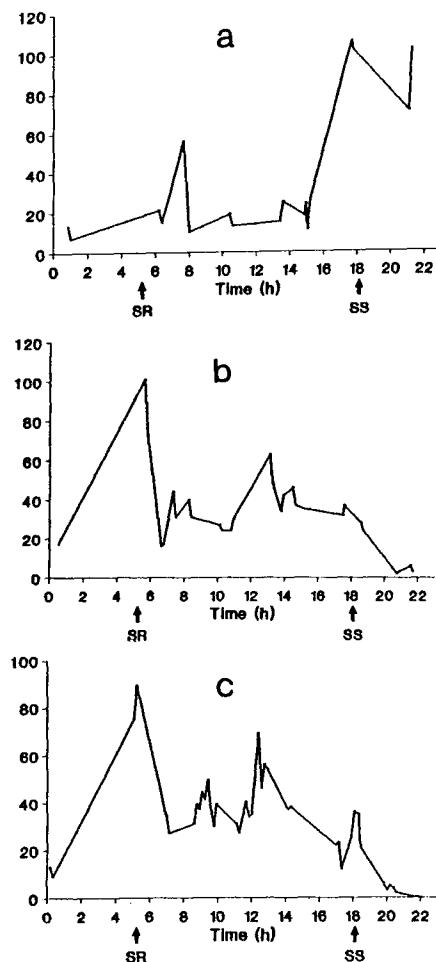


Fig. 4. Daily distribution of radar targets in 26.03.1987.

a. Number of targets at the 25 km range,  
 b. Number of targets at the 50 km range,  
 c. Number of targets at the 100 km range.  
 (SR: sunrise, SS: sunset.) Local time (GMT+1).

at 25 km range is closer to the north ( $38^\circ$ ) than that of the other ranges ( $46^\circ$  at 50 km and  $42^\circ$  at 100 km). The average direction for all ranges is  $42^\circ$ , NE (Fig. 5d).

When I compared the mean direction using all echo data during six days, there were differences in the daily directions (Fig. 6). The directions on 27.03., 05.04. and 06.04. are closer to east (51, 59, 51) than the aver-

age (Fig. 6b,c,d). The reason for these deviations may be the strong W, SW, and N wind at 27.03., but this is not too likely since on 07.04. and 08.04. there were the same strong winds, but the mean direction of these two days is different from the above mentioned three days' mean direction (Fig. 6e,f). In these two days, the decreasing mean direction coincided with increasing intensity of the small passerine migration, as the increasing echoes at 25 km range indicate (Tab. 1). The differences may come from the changing species composition of migrating birds.

### 3.3. Migration over the studied area

When all echoes are drawn on the map of the studied area (Fig. 3) we can see whether there were preferred areas during the migration. The diverse topographic features explain some significant deviations among the areas. In the more elevated areas e.g., Nyírség Southeastern part of the study area, the birds flew at a higher altitude and their echoes were more visible than echoes from lower areas like Hortobágy where the birds often flew at lower altitudes and are blocked from the view of the radar.

The echoes were concentrated above some particular areas e.g., along the Debrecen-Mátészalka railway line, the echoes were very concentrated and created a thick line (Fig. 1,3). This observation suggests that the birds may follow topographical features while migrating through this area (Bruderer 1978, 1982).

## 4. Discussion

This investigation was the first direct observation of bird migration by radar in the Carpathian Basin. The time exposure method (Gauthreaux 1970) provided appropriate data to reveal some main characteristics of the spring migration over this

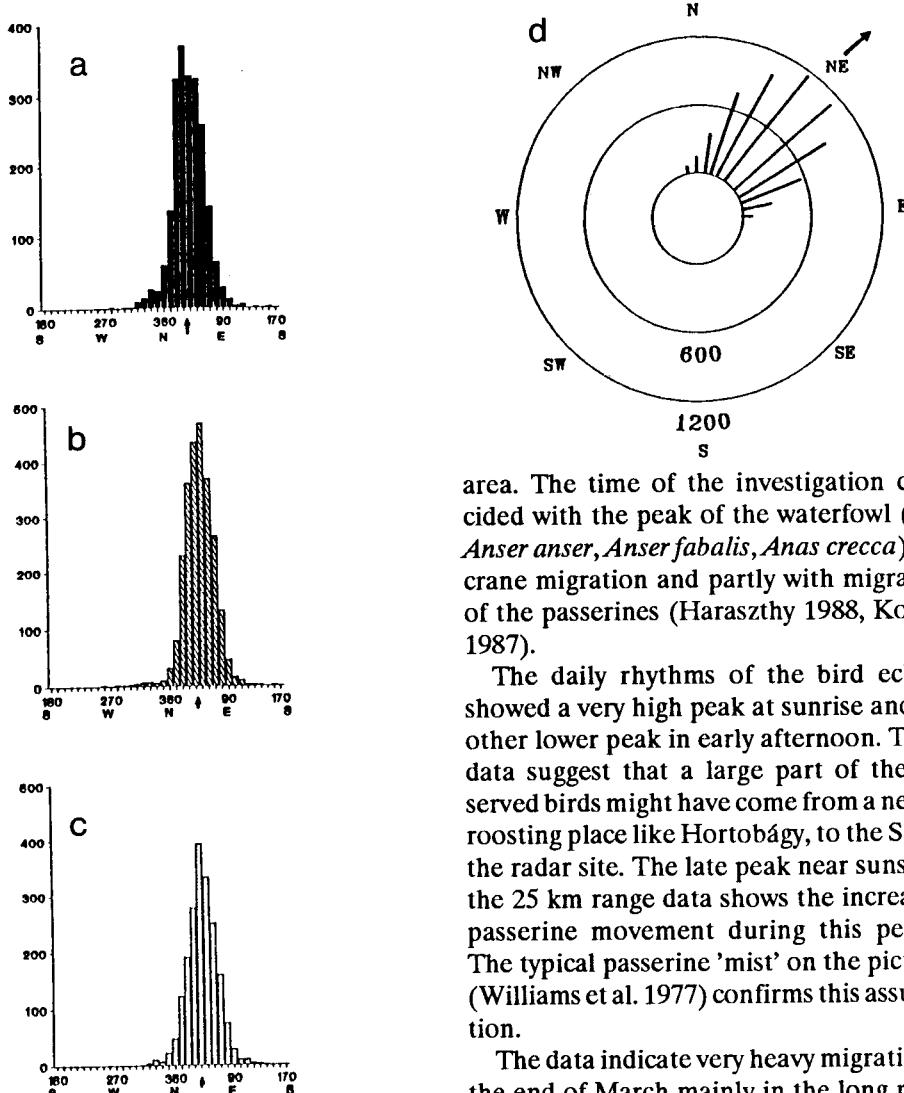


Fig. 5. Distribution of the direction of radar targets at different ranges. (Arrows shows the mean directions.)

- a. Directions at the 25 km range ( $n=2128$ ; mean= $38^\circ$ ),
- b. Directions at the 50 km range ( $n=2477$ ; mean= $46^\circ$ ),
- c. Directions at the 100 km range ( $n=1941$ ; mean= $42^\circ$ ),
- d. Directions at all ranges ( $n=6546$ ; mean= $42^\circ$ ). The diameters of circles shows the number of targets at different directions.

area. The time of the investigation coincided with the peak of the waterfowl (e.g., *Anser anser*, *Anser fabalis*, *Anas crecca*) and crane migration and partly with migration of the passerines (Haraszthy 1988, Kovács 1987).

The daily rhythms of the bird echoes showed a very high peak at sunrise and another lower peak in early afternoon. These data suggest that a large part of the observed birds might have come from a nearby roosting place like Hortobágy, to the SW of the radar site. The late peak near sunset in the 25 km range data shows the increasing passerine movement during this period. The typical passerine 'mist' on the pictures (Williams et al. 1977) confirms this assumption.

The data indicate very heavy migration at the end of March mainly in the long range observations. These presumably were echoes of migrating waterfowl flocks. At the end of the observation period (07.04.-08.04.), the composition of migrating birds changed. The increased number of fine passerine echoes on the short range pictures shows that the main passerine migration had started.

The observed average NE ( $42^\circ$ ) direction is closer to N than Bruderer (1971) found in Switzerland ( $60^\circ$ ), the nearest

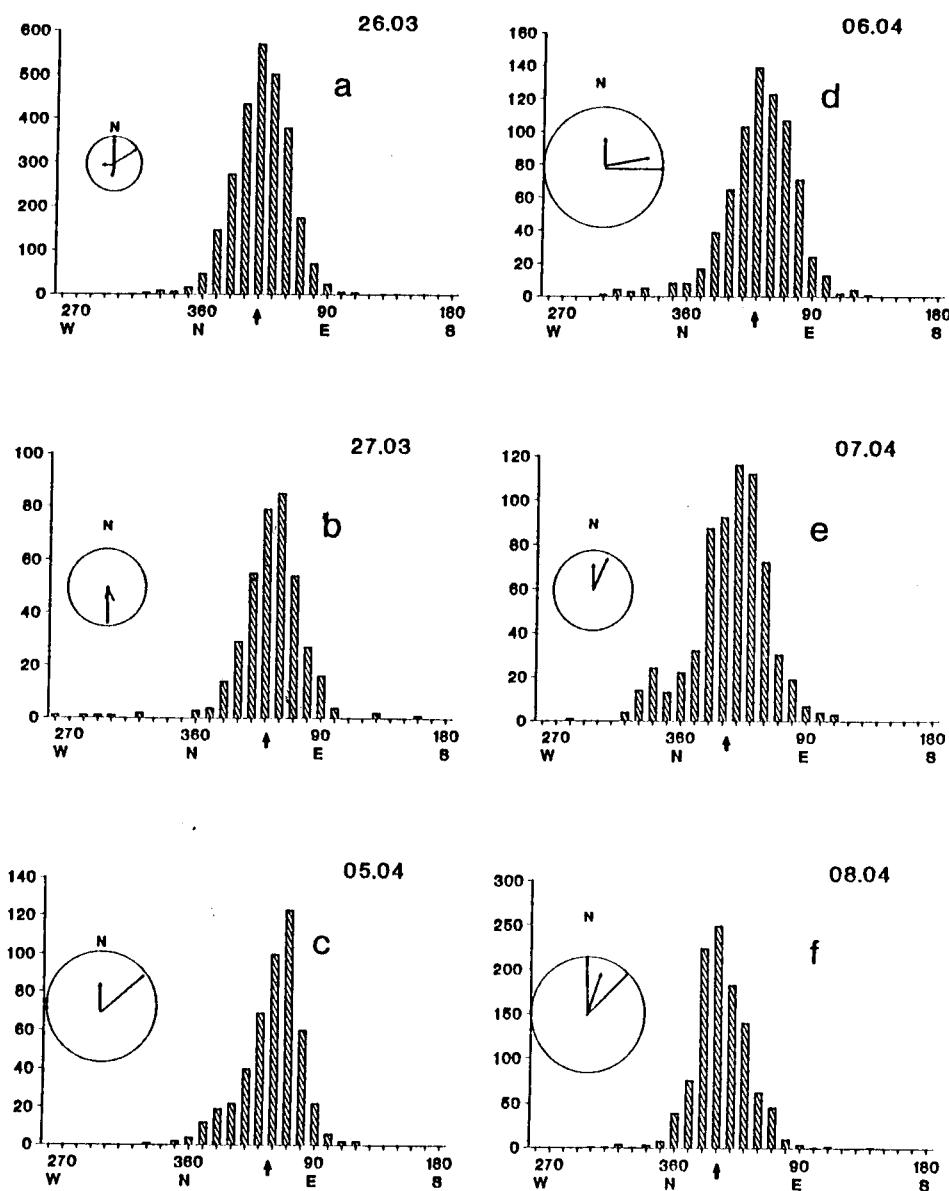


Fig. 6. Distribution of directions of radar targets on different days. The diameter of the circle with arrows show the average wind speed and direction during the observations.

- Direction at 26.03 ( $n=2663$ ; mean= $41^\circ$ )
- Direction at 27.03 ( $n=379$ ; mean= $53^\circ$ )
- Direction at 05.04 ( $n=484$ ; mean= $59^\circ$ )
- Direction at 06.04 ( $n=737$ ; mean= $51^\circ$ )
- Direction at 07.04 ( $n=652$ ; mean= $35^\circ$ )
- Direction at 08.04 ( $n=1064$ ; mean= $33^\circ$ )

place of another recent radar study. The daily average direction varied between 33°-59° and the reason may be the changing composition of migrating species. The increased passerine migration might cause the decreasing average direction during the late days. The data also show some preferred migration paths.

The meteorological radar at Napkor is appropriate to study of bird migration at one of the most important areas in Central Europe. Long-term radar investigations with development of equipments and methods, combined with simultaneous field observations would help to explore other important characteristics of the migration in the eastern part of the Carpathian Basin. Studying distribution of bird flocks in the migration season, analysing the number, direction and distribution of different groups of species would be very important for scientific and nature conservational reasons as well.

**Acknowledgements.** I wish to thank the Central Weather Forecasting Institute of the Meteorological Office (OMSZ KEI), Ferenc Dombai, Ferenc Tóth and the staff of the Napkor station, for use of the radar and assistance in many aspects of my work. I am indebted to the two reviewers kindly commented on earlier versions of this paper, to Kevin Anderson and Erzsébet Pappné Timkó for the provided assistance to the manuscript and to the Hungarian Ornithological Society providing the necessary material.

## Összefoglalás

### A tavaszi vonulás vizsgálata meteorológiai radar segítségével Kelet-Magyarországon

A Kárpát-medence keleti részén folyó tavaszi madárvonulás radarornitológiai módszerrel vizsgált főbb jellemzőit mutatja be a cikk. 1987-ben 8 napon keresztül, a Napkor Radarmeteorológiai Obszervatórium berendezéseivel 25-100 km-es körzetben vizsgáltam a madarak jeleit.

Madárjeleket a képernyőről (PPI) készített hosszú expozíciós idejű felvételek segítségével rögzítettem. A vizsgálat során készített 413 képről 6546 madárjelet azonosítottam és használtam fel az elemzésekhez. A madárjelek intenzitása a napfelkelte és a koradélutáni időszakban volt a legerősebb. 25 km-es körzetben a naplemente körüli időszakban is erőteljes mozgás mutatkozott, amelynek feltételezhető oka a kistestű énekesmadarak intenzív esti vonulása. Az átlagos irány 42° (ÉK) volt, mely 33° és 59° közötti értékeket vett fel a vizsgált napok során. A napi átlagos irányokban mutatkozó változások okai főként a vonuló madarak faji összetelében mutatkozó változások lehetnek. A vizsgált körzetben a madárjelek néhány terület felett igen sűrűn helyezkednek el, amely a Debrecen-Mátészalka közötti út és vasút esetében felveti, hogy a vonuló madarak bonyos topográfiai elemeket követnek.

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*Received 8 August 1991, revised 10 December 1991, accepted 5 January 1992*

# Különböző erdőtipusok madárközösségeinek vizsgálata a Szigetközben

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Waliczky, Z. 1992. Structure of avian communities in the forests of Szigetköz, Hungary. - *Ornis Hung.* 2: 25-31. (In Hungarian with English abstract.)

Bird density estimations were carried out in the Szigetköz in 1990. Three forest habitats were studied: natural willow-woodland, semi-natural oak forests, and poplar-plantations. The cluster analysis showed that these habitats clearly segregated from each other. The willow-woodland had the most diverse bird community and we also found the highest number of species there. The poplar plantations were the poorest habitat measured by diversity and number of species. From a nature conservationist's point of view the potential of willow- and oak forests to harbour forest avifaunas is very high. However, especially the willow-woodland is seriously threatened by the enormous dam-construction efforts in the area and the converting of natural habitats into more economical poplarwood. The highest importance of the poplar forests is that they give home to a significant portion of the Hungarian Icterine Warbler (*Hippolais icterina*) population.



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## 1. Bevezetés

Különböző élőhelyek összehasonlítása az egyik fontos módszere a madárközösségek ökológiának (Wiens 1989), és feltehetően az is marad még egy ideig, mert ezek a "természetes kísérletek" viszonylag könnyen elvégezhetők és a segítségükkel betekintést nyerhetünk közösségszervező folyamatokba. Ökológiaileg egymáshoz közel álló fajok szegregálódása élőhelyek szerint, hasonló igényű fajok csoportosítása, élőhelyek minősítése természetvédelmi szempontból, fajkicerélődések élőhely gradiensek mentén néhány olyan jellemző terület, ahol az ilyenfajta összehasonlítások nélkülözhetetlenek.

Hazánkban az erdei madárközösségek ökológiai vizsgálatai főként a természet-

szerű erdőtársulásokkal foglalkoztak (bükkös: Moskát 1985, 1988a, 1988b, Moskát és Székely 1989; tölgyes: Moskát 1985, 1988a, Moskát et al. 1988), kevés a kifejezetten mesterséges erdők madárközösségeivel foglalkozó munka (Legány 1979). Teljesen hiányoznak azonban az olyan vizsgálatok, amelyek egy adott területen a természetközeli (természeteszerű) és a mesterséges erdők madárközösségeit hasonlítják össze, holott az ilyen vizsgálatok természetvédelmi szempontból is fontosak.

Ezen dolgozat a Szigetköz három legjelentősebb erdőtípusának: a természeteshez közelálló fűzligetek és tölgyesek, valamint az ültetvényszerű nemesnyárasok madárközösségeinek összehasonlítását adja, faj- és egyedszámbecslő vizsgálatok alapján.

1. Táblázat. A három élőhely madárközösségeinek fajszáma (S), rarefakcióval számolt fajszáma (Sr), Shannon-féle diverzitása (H), a mintánkénti átlagos fajszáma (Sm), összdenzitás (egyedszám/10 ha) (D) és a mintavételi terület nagysága (ha) (A).

Table 1. Number of species (S), number of species counted by the rarefaction method (Sr), Shannon's diversity (H), mean number of species /sites (Sm), total density (individuals/10 ha) (D) and size of the study sites (ha) (A).

Előhely/Habitat	S	Sr	H	Sm	D	A
Füzes/Willow	30	30	3.15	20.67	97.66	9.42
Tölgy/Oak	36	26.10	3.09	17.43	85.53	21.98
Nyár/Poplar	27	23.15	2.90	17.00	88.11	18.84

## 2. Vizsgálati terület és módszerek

A vizsgálati területek a Szigetközben (ÉNy-Magyarország) fekszenek, Doborgazsziget és Feketeerdő községek határában. Mindkét terület ártéri erdőket foglal magában, az első (Doborgazsziget) az Öreg-Duna, a második (Feketeerdő) a Mosoni-Duna öntésterületén. Tengerszint feletti magasság 110-127m. Éves középhőmérséklet 9.5-10.0 °C, csapadék 550-600 mm (Göcsei 1979).

A felvételzést 1990 tavaszán végeztük három erdőtípusban. A fűz ligeterdők (*Salicetum albae-fragilis*) nyílt, ligetes

2. Táblázat. A különböző élőhelyek hasonlósága a Sörensen index alapján. A felső félmátrix a fajszámok, az alsó az egyedszámok alapján számolt értékeket mutatja.

Table 2. Similarity of the habitats measured by the Sörensen index. The upper half of the triangle was calculated from number of species, and the lower half from number of individuals.

	Füzes Willow	Tölgy. Oak	Nyáras Poplar
Füzes/Willow	1.00	0.48	0.70
Tölgyes/Oak	0.37	1.00	0.63
Nyáras/Poplar	0.50	0.66	1.00

élőhelye kisebb erdőfoltokkal a természetes állapothoz legközelebb álló típus. A második vizsgált erdőtípus, az ültetett kocsányostölgyesek (*Quercetum roboris*) természeteszerű, idős erdők, az ősi tölgy-kőris-szil ligeterdőket (*Querceto-Ulmetum hungaricum*) idéző szerkezettel. Végül a harmadik erdőtípus a Szigetközben legelterjedtebb nemesnyárasok (főleg *Populus canadensis*, *Populus euramericana* klónok), melyek egy teljesen mesterséges állapotnak felelnek meg.

Mindhárom erdőtípusban igen magas a cserjeszint borítása. A fő cserjefajok: veresgyűrűs som (*Cornus sanguineus*), csíkos kecskerágó (*Euonymus europaeus*), kányabangita (*Viburnum opulus*), fekete bodza (*Sambucus nigra*).

A felvételzéseket a módosított I.P.A. módszerrel végeztük (Moskát 1986). Ennek lényege, hogy ugyanazonon a pontokon két létszámbecslést kell végrehajtani, a fészkelési időszak első és második felében egyet-egyet (Magyarországon április második felében és május második felében). A felvételek ideje egy-egy ponton 10 perc, a becslés hatósugara 100 m. A két időben kapott egyedszámbecslések közül a nagyobbik alapján kell számolni a relativ denzitást.

A kapott faj- és egyedszámok alapján minden egyik élőhelyre diverzitást számol-

3. Táblázat. A három habitatban kimutatott madárfajok és a párok száma. (A: füzes, B: nyáras, C: tölgyes).

Table 3. Number of pairs of bird species in three habitats. (A: willow forest, B: poplar plantation, C: oak forest)

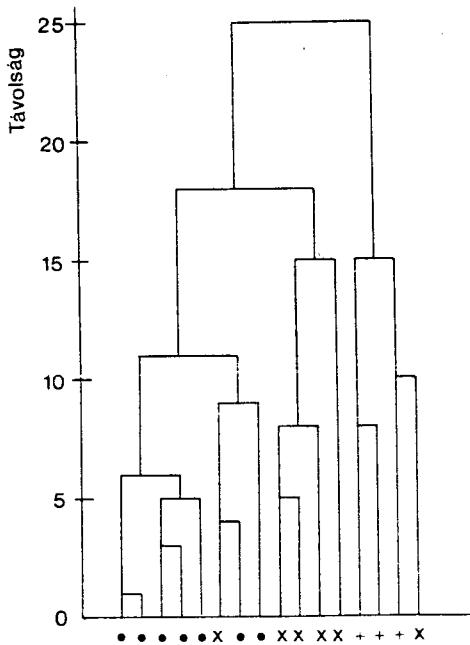
Madárfaj/Bird species	A	B	C	Madárfaj/Bird species	A	B	C
<i>Streptopelia turtur</i>	3	2	6	<i>Erihacus rubecula</i>	3	10	14
<i>Columba palumbus</i>	-	-	1	<i>Luscinia megachrynos</i>	-	-	1
<i>Cuculus canorus</i>	1	-	2	<i>Turdus merula</i>	6	6	8
<i>Picus viridis</i>	-	-	2	<i>Turdus philomelos</i>	6	9	6
<i>Dryocopus martius</i>	-	-	1	<i>Remiz pendulinus</i>	3	3	-
<i>Dendrocopos major</i>	1	6	7	<i>Aegithalos caudatus</i>	-	1	1
<i>Dendrocopos medius</i>	-	-	3	<i>Parus major</i>	2	4	13
<i>Dendrocopos minor</i>	-	-	2	<i>Parus caeruleus</i>	3	4	10
<i>Jynx torquilla</i>	-	-	1	<i>Parus palustris</i>	-	-	4
<i>Prunella modularis</i>	4	5	1	<i>Parus montanus</i>	1	-	-
<i>Troglodytes troglodytes</i>	1	7	-	<i>Sitta europea</i>	-	4	8
<i>Locustella fluviatilis</i>	3	3	-	<i>Certhia brachydactyla</i>	-	-	1
<i>Acrocephalus arundinaceus</i>	3	-	-	<i>Certhia familiaris</i>	-	2	2
<i>Acrocephalus schoenobaenus</i>	2	-	-	<i>Emberiza citrinella</i>	1	-	2
<i>Acrocephalus scirpaceus</i>	2	-	-	<i>Fringilla coelebs</i>	3	25	16
<i>Acrocephalus palustris</i>	7	2	-	<i>Carduelis carduelis</i>	1	-	-
<i>Hippolais icterina</i>	-	7	-	<i>Carduelis chloris</i>	7	1	2
<i>Sylvia atricapilla</i>	10	26	24	<i>Carduelis cannabina</i>	2	-	-
<i>Sylvia nisoria</i>	2	-	-	<i>Serinus serinus</i>	-	-	1
<i>Sylvia borin</i>	-	-	1	<i>Coccothraustes coccothraustes</i>	1	1	-
<i>Sylvia communis</i>	1	-	-	<i>Passer montanus</i>	1	4	1
<i>Phylloscopus collybita</i>	7	13	15	<i>Sturnus vulgaris</i>	-	8	17
<i>Phylloscopus trochilus</i>	-	-	1	<i>Oriolus oriolus</i>	4	6	2
<i>Phylloscopus sibilatrix</i>	-	1	3	<i>Garrulus glandarius</i>	1	1	-
<i>Muscicapa striata</i>	-	5	5	<i>Corvus corone cornix</i>	-	-	1
<i>Ficedula albicollis</i>	-	-	3				

tunk, az ismert Shannon-Weaner képlet alapján:

$$H = -\sum p_i \ln p_i,$$

ahol  $p_i$ : i - edik faj egyedszáma a mintában.

Mivel a diverzitás számításának módszere érzékeny a minta elemszámára (Heck et al. 1975, Moskát 1987), így az ún. rarefaction-görbék segítségével is kiszámoltuk az egyes élőhelyeken a fajszámokat a legkisebb mintaelemszámú élőhelyhez (füzes)



1. ábra. A mintavételi pontok cluster analízisének dendrogramja faj- és egyedszámok alapján. (+: füzes, ●: tölgyes, x: nyárasok).

Fig. 1. Dendrogram of the sample sites clustered by number of species and number of individuals (+: willow, ●: oak, x: poplar plantations).

viszonyítva. Ezen számításokhoz Ludwig & Reynolds (1988) RAREFRAC programját alkalmaztam.

Az egyes madárközösségek közötti hasonlóságot Sørensen-indexsel számítottuk:

$$\text{fajokra: } C = 2j / (a + b),$$

ahol a,b: teljes fajszám az a és a b mintában; j: a két minta közös fajainak száma;

$$\text{egyedszámokra: } C = 2j_N / (a_N + b_N),$$

itt  $a_N, b_N$ : összes egyed az a és a b mintában;  $j_N$ : minden mintában szereplő fajok kisebbik egyedszáma.

Ezeken kívül az egyes közösségekre a kapott denzitásadatok alapján cluster-analízist is végeztem, az SPSS/PC+ programcsomag segítségével (Norusis 1986). Ehhez a számításhoz csak azokat a fajokat vettet figyelembe, amelyeknek összegyedszáma legalább 4 volt, így 23 faj került be ebbe az analízisbe.

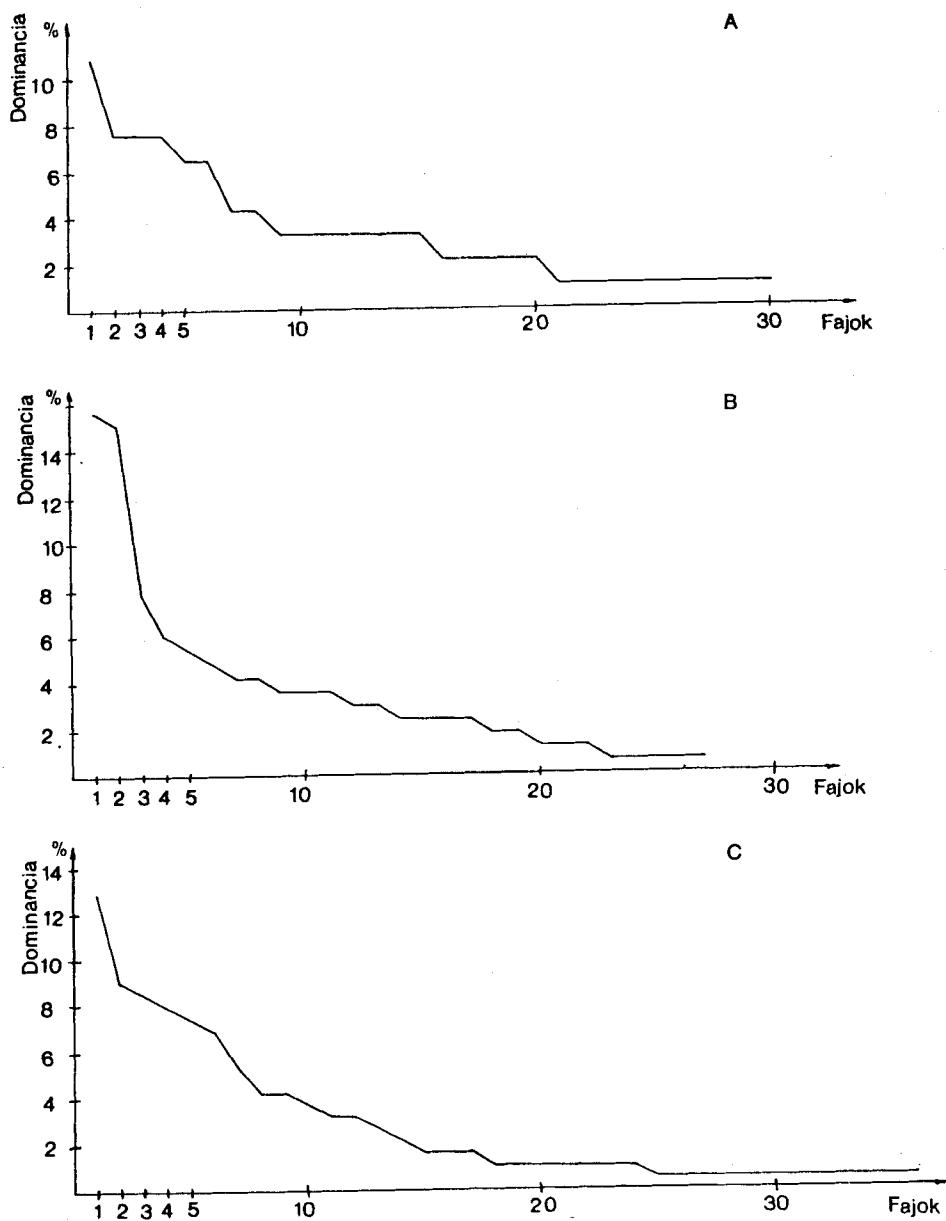
### 3. Eredmények és értékelésük

A cluster-analízis (1. ábra) szerint legmagasabb szintű a füzesek elkülönülése a többi mintától, majd a nyárasok és tölgyesek elkülönülése következik be. Mindössze két nyáras pont lett "rossz" helyre besorolva (1. ábra). Ennek oka az lehet, hogy a füzek aránya minden ponton kb. 10%, tehát nem teljesen homogén élőhelyekről van szó.

A diverzitás, rarefaction, és mintavételei pontonkénti fajszám értékek megegyező képet mutatnak. Ennek alapján a legmagasabb értékeket a füzesek, a legalacsonyabbakat pedig mindenütt a nyárasok madártársulásai adják (1. táblázat). A 10 ha-os egyedszám értékek is a füzesek esetében a legmagasabbak, de itt a nyárasokban mért értékek kissé magasabbak a tölgyesek hasonló értékeinekél (1. táblázat; a különbség szignifikáns  $p < 0.05$  szinten).

Dominancia-görbék. A füzes és tölgyes madárközösségek dominancia-görbéi nagyon hasonlóak, kiegyenlítettek, lapos lefutásúak (2. ábra). A nyáras madárközösség dominancia-görbéje kezdetben meredekebben esik, majd hasonlóan lapos, mint a másik két élőhelyé.

A cluster-analízis jelen esetben felderítő jellegű: képet ad arról, hogy az élőhelyeken belül, vagy azok között nagyobb a variancia. Az első esetben nem sok értelme van az élőhelyeket átlagolni, ehelyett minden mintát külön egysékként kell kezelni. A második esetben - mint jelen cikkben is - jogos



2. Ábra. A három élőhelyen az összes egyedszámból számított dominanciagörbék. (a: füzes, b: nyáras, c: tölgyes).

Fig. 2. Dominance curves based on number of individuals. (a: willow forest, b: poplar plantation, c: oak forest).

külön nyáras, tölgyes, stb. madárközösségekről beszélni, és az egyes élőhelyeken felvett mintákat összevonni és átlagolni.

Bár több szerző szerint az ún. rarefaction-módszer különböző elemszámú minták esetén többet mond és pontosabb a diverzitást számító képleteknél (összefoglalást lásd: Moskát 1987, Wiens 1989), az általunk a két módszerrel kapott eredmények megegyeznek. Ezek szerint a fajokban leggazdagabb közösség a füzeseké, legszegényebb a nemesnyárasoké. Ugyanezt erősítik a mintavételekenkénti átlagos fajszám indexek is. Ennek magyarázata két, egymást nem feltétlenül kizáró úton lehetséges.

Az egyik magyarázat, hogy a füzesek a Szigetköz legősibb, a természetes állapot-hoz legközelebb álló erdőtípus testesítik meg, így azok a szukcessziós klimax fázis összes sajátosságát mutatják. Ilyenek a magas denzitás, egyedszám, kiegyenlitettség, biomassza, sokoldalú trofikus relációk, stb. (Id. Helle 1984, Glowacynski & Weiner 1983, May 1982, Odum 1969). A másik lehetőség, hogy a magasabb faj- és egyedszám a vegetáció heterogenitásának a következménye. A füzesek a legnyíltabb élőhelyek a három közül és ezzel együtt a vegetáció szerkezeti összetettsége is a legmagasabb: nádasok, sűrű cserjések és zárt erdőfoltok változatos összetételeben jelennek meg. Ez a foltosság önmagában is növeli a faj- és egyedszámot (Wiens 1989), ehhez járul még a különböző szerkezetű foltok között fellépő szegélyhatás is, ami ugyanilyen irányú változást okoz (Lay 1938, Johnston 1947, Andeson et al. 1977, McElveen 1979).

Vegetációs szempontból a legegyszerűbb szerkezetűek a nemesnyárasok: egyfajú, egykorú egyedek alkotják ezeket az erdőállományokat. Ez a fiziognómiai jelleg ezen erdőtípus mesterséges jellegéből fakad, ami a madárközösség viszonylagos szégyénységét magyarázza. Az, hogy nincsenek még nagyobb különbösségek a nyárasok és a másik

két élőhely madárközösségei között, azzal hozható összefüggésbe, hogy a tápanyagokban gazdag öntéstalaj miatt ezen erdők gyepszintje és cserjeszintje sűrű.

A dominancia-görbék alapján is érzékelhető a különbözők a nyárasok és a másik két élőhely között. A nyárasok esetében két generalista faj, a barátposzta és az erdei pinty dominanciája kifejezett a többi faj felett, ezt jelzi a görbe kezdeti, meredeken eső szakasza (2. ábra). A szukcesszióra vonatkozó elméletek szerint (Odum 1969) a bolygatott, fiatal élőhelyekre jellemző néhány generalista faj numerikus dominanciája, a klimax állapotokra ezzel szemben az egyenletes forrásfelosztás és ezzel együtt kiegyenlitett dominancia-görbék jellemzők (Odum 1969, Whittaker 1965), amint ez a füzesek és tölgyesek esetében látható.

Hasonlóság szempontjából a nyárasok gyakorlatilag a tölgyes és füzes élőhely között állnak. Ha megnézzük a fajok eloszlását az élőhelyek között (appendix), azt látjuk, hogy minden egy faj van, amely az eredmények alapján kizárolag a nyárasokban fordul elő, ez pedig a kerti geze (*Hippolais icterina*). A kerti geze habitatszlekciós mechanizmusát elemző cikkben (Waliczky et al. 1991) kimutattuk, hogy a kerti gezének magas fákra és jelentős cserjeszintre egyaránt szüksége van a terület foglaláshoz. Ezekben kívül valószínűleg a korona alakja is szerepet játszik, mert a tölgyesekből a geze teljesen hiányzik. Így elmondhajuk, hogy a nyárasok elsődleges madárvédelmi szerepe a Szigetközben a hazai viszonyok között nagylétszámú kerti geze populáció fenntartása.

A Szigetközben a nemesnyárasok madárközösségeik elemzéséből levezetett értékhez képest aránytalanul nagy területet foglalnak el, míg a jóval értékesebb és együttesen gyakorlatilag a teljes erdei madárközösséget magukban foglaló füzesek és tölgyesek elterjedése jóval kisebb

és szétszórtabb. Elsősorban a nyílt fűzerek létét veszélyeztetik a Bős-Nagymarosi erőmű kiépítéséhez létesülő új, mesterséges folyómedrek, medencék és egyéb építési munkálatok. Ezek folytán a Szigetköz madarakban leggazdagabb élőhelyei semmisülnek meg, vagy legalábbis területileg csökkennek és feldarabolódnak. Ezért fokozottan hangsúlyos ezen élőhelyeknek teljes védelem alá helyezése.

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Érkezett 1990. november 2-án, átdolgozva 1991. február 10-én, elfogadva 1991. március 13-án.

# The effects of the patchiness and the nest location on mean flight distance: a model

Z. Barta

Barta, Z. 1992. The effects of the patchiness and the nest location on mean flight distance: a model. – *Ornis Hung.* 2:37-44.

One of the advantages of colonial breeding may be the enhanced foraging efficiency through the location of colony. In a patchy environment a colonial breeder may experience a shorter distance between the nest and an average food patch than an average dispersed breeder. How are this distance influenced by nest location, and varying patchiness? To develop a model of a predator moving by random walk in a patchy foraging area I found that: (i) the nest location in a bounded area influenced sufficiently the mean flight distance and (ii) the growing patchiness increases this distance.



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## 1. Introduction

Although colonial nesting may have disadvantages, many bird species breed in colonies throughout the world, (Lack 1968). A cost of this behaviour may be high infection rate by ectoparasites (Brown & Brown 1986) or increasing competition for food, for nest materials and for mates (Hoogland & Sherman 1976, Möller 1988).

Coloniality may have some advantages as well. One type of the gains is anti-predator behaviour such as mobbing or early detection of predator (Kenward 1978, Bertram 1980, Brown & Brown 1987). The other main advantage of coloniality may be the increased foraging efficiency (Brown 1988). One of the ways of the efficiency increasing may be the effect of colony location on the mean flight distance from the nest to a food patch as Horn (1968) has argued. He assumed that average individuals who breed in dispersed location over the

foraging area could experience an increased mean patch distance in a patchy environment than those breed in a single location, in a colony. On the basis of this model we should predict that the colony must be situated in the centre of the bounded foraging area. Wittenberger & Dollinger (1984) however, showed out that the acentric location of a colony do not influence the benefit of a colonial breeder over the disperse breeder up to 60% of acentricity. All Horn (1968), Wittenberger & Dollinger (1984) assumed that the birds know about the location of food and they use all food patches in equal proportion, although the birds do not behave in this way. How do the search and the location of nest influence the mean flight distance? What is the effects of the different degree of patchiness on this distance?

In this paper I try to answer to these questions to develop a model of foraging area and of a search behaviour in this area.

Tab. 1. Parameters of the models

**Parameters:** Meaning

$AF$ :	amount of food in a patch
$dN,i$ :	distance between N (nest) and $i$ th squares
$E(FP)$ :	number of food patch on the area
$F$ :	amount of food on the area
$fN,i$ :	probability that random walker arrives first from $N$ to $i$ th square at $k$ time unit
$n$ :	total number of squares
$p_i$ :	probability that $i$ th square becomes food patch
$P_i$ :	probability that the bird finds a food patch in $i$ th time unit
$P(food)$ :	probability that a square becomes food patch on a homogeneous area
$P_i(to\ i)$ :	probability that the bird gets at least once from $N$ to $i$ th square
$Rf$ :	ratio of food patches
$t$ :	maximum searching time
$TF$ :	average distance of food patch in time units
$TS$ :	average searching time

## 2. The model

### 2.1. The model of the foraging area

The foraging area is considered as a two-dimensional surface divided into a grid of equal-sized squares. For each square  $i$ ,  $p_i$  is the probability that square contains food (see the list of parameters in Tab. 1). There is at least one square which has  $p_i > 0$  in the foraging area.

A main feature of the area is the number of food patches [ $E(FP)$ ] which is equal to the expected value of the number of food patches on the area.

$$E(FP) = \frac{\sum_{k=0}^n Pr(x=k) k}{\sum_{k=0}^n Pr(x=k)} \quad (1)$$

where  $n$  is the total number of squares and  $Pr(x=k)$  is the probability that there are  $k$  food patches on the area.

$$Pr(x=k) = \sum_{i=0}^n \left[ \prod_{i=1}^k p_i \prod_{i=1}^{n-k} (1-p_i) \right] \quad (2)$$

and the indices in the parentheses run so that all  $k$ th-class combination of  $n$  are arisen.

The area is homogeneous when

$$p_i=p_j=P(food) \quad \text{for all } i \text{ and } j, \quad (3)$$

namely there are no differences among the squares. In this case  $E(FP)$  will equal to the mean of binomial distribution:

$$E(FP) = n P(food) \quad (4)$$

If we divide the number of food patches by the total number of squares we get the ratio of food patches ( $Rf$ ).

$$Rf = \frac{E(FP)}{n} \quad 1 \geq Rf > 0 \quad (5)$$

If the ratio of food patches is great ( $Rf \approx 1$ ), then the food is evenly distributed. On the other hand its small value ( $Rf << 1$ ) shows us that the food is clumped.

A food patch contains the following amount of food ( $AF$ ) in average:

$$AF = \frac{F}{Rf n} \quad (6)$$

where  $F$  is the total amount of food on the area.

### 2.2. Random foraging of single predator

In this case the predator has no information about the location of food, so its foraging path is a random walk. No previous events influence the next step of the predator. Since the bird has no memory the process can be represented by a Markov chain. To define the process we

have to give its matrix of transition probability which contains the probability of moving from one square to another. A normal element of this matrix is the following:

$$P_{ij} = \begin{cases} 0.25(1-p_i) & \text{if } i\text{th and } j\text{th} \\ & \text{squares are} \\ & \text{neighbouring} \\ p_i & \text{if } i=j \\ 0 & \text{otherwise} \end{cases} \quad (7)$$

On the basis of this model the bird remains the  $i$ th square if it has found a food patch there, otherwise it moves to each of the neighbouring squares with an equal probability. The process was assumed to be reflection. From this matrix we can determine the probability of  $f_{N,i}^k$  which gives us the chance a bird would be first in  $i$ th square at  $k$ th time unit if it was in  $N$  (nest) square when  $k$  equalled to 0 (for details see Karlin & Taylor 1975).

To sum  $f_{N,i}^k$  up by  $k$  we can calculate the probability that the bird gets at least once from  $N$  to  $i$ th square.

$$P_i(\text{to } i) = \sum_{k=0}^t f_{N,i}^k \quad (8)$$

where  $t$  is the maximum time of search, for example one day.

The average distance of food patch ( $t_F$ ) is an important feature of the movement of a what Orians & Pearson (1979) call 'central place' forager. We assume that it is equal to the means of distance of each square weighted by  $P_i(\text{to } i)$  and  $p_i$ . (The distances are in time unit.)

$$t_F = \frac{\sum_{i=1}^n P_i(\text{to } i) p_i d^t N_i}{\sum_{i=1}^n P_i(\text{to } i) p_i} \quad (9)$$

For homogeneous area:

$$t_F' = \frac{\sum_{i=1}^n P_i(\text{to } i) d^t N_i}{\sum_{i=1}^n P_i(\text{to } i)} \quad (10)$$

where  $d^t N_i$  is the distance of  $i$ th square from  $N$  in time unit.

A significant parameter of predator's foraging is also the average time of food finding (or searching time  $t_S$ ). Let this time equal to the mean of time of random steps at the end of which the bird finds a food patch. But it is not certain that a bird finds food in under  $t$  time units, so we must weight this mean by the inverse of probability that the bird find at least one food patch in  $t$  time unit.

$$t_S = \frac{\sum_{j=0}^t P_j \prod_{i=0}^{j-1} (1-P_i)}{\sum_{j=0}^t P_j \prod_{i=0}^{j-1} (1-P_i)} \frac{1}{1 - \prod_{i=0}^t (1-P_i)} \quad (11)$$

where  $P_i$  is the probability that the bird finds a food patch in  $i$ th time unit.

The expression of  $P_j \prod_{i=0}^{j-1} (1-P_i)$  gives the probability that the bird first finds food in time unit  $j$ .

Let  $P_j$  equal the mean of probability of  $p_i$  weighted by probability of the first visit.

$$P_j = \frac{\sum_{i=1}^n f_{N,i}^j p_i}{\sum_{i=1}^n f_{N,i}^j} \quad j \geq 1 \quad (12)$$

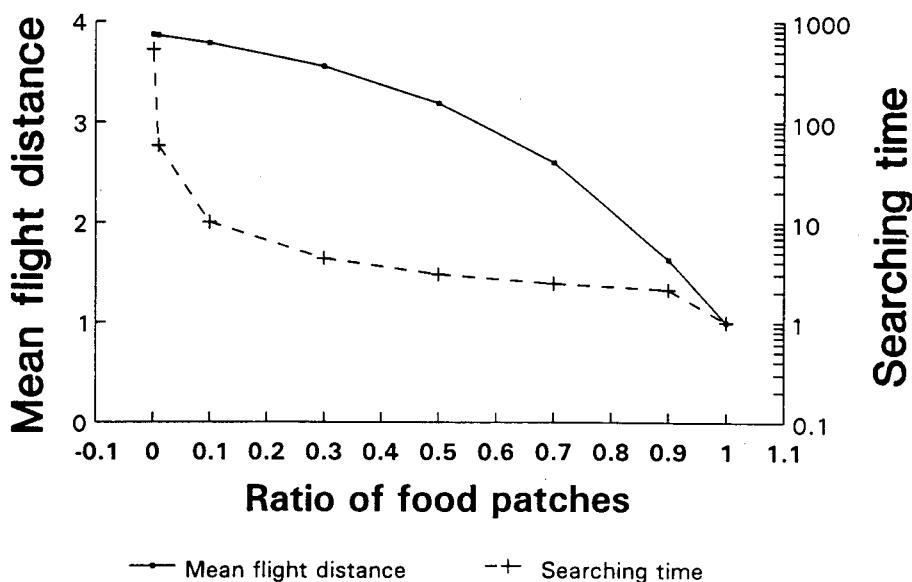


Fig. 1. The average distance of food patch from the nest and searching time, when ratio of food patches was manipulated from  $1-10^{-6}$  (evenly distributed) to 0.001 (clumped). Area size was 9 x 9 squares and the nest was in the centre of the area. The maximum searching time was 30 units.

where  $f_{N,i}^j$  is determined from a transition probability matrix of a same-sized area which has no square with  $p_i > 0$ .

For an homogeneous area equations (11) and (12) become the following:

$$\bar{P}_j = P(\text{food}) \quad \text{for all } j \quad (13)$$

and

$$t_s = \frac{\sum_{j=0}^t j \bar{P}_j (1-\bar{P}_j)^{j-1}}{\sum_{j=0}^t \bar{P}_j (1-\bar{P}_j)^{j-1}} \frac{1}{1 - (1-\bar{P}_j)^t} \quad (14)$$

### 3. Results

On the basis of the model, I determined the parameters of random walk on a homogeneous area sized 9 x 9 squares under different ratios of food patches (Fig.

1.). The maximum searching time was 30 units.

When the ratio of food patches is decreased the average distance of food patch from the nest ( $t_F$ ) is increased (Fig. 1.). When the food is evenly distributed the simulated bird used the squares near the nest (Fig. 2a). On the other hand when food is clumped it exploits more frequently the farther parts of the area (Fig. 2b). The searching time ( $t_s$ ) is also increased strongly (Fig. 1).

To study the effects of nesting place on the predator's movement, I changed the location of the nest – as showed by Fig. 3. – on a homogeneous area where the distribution of food was clumped ( $R_f = 0.001$ ) and the maximum searching time was 30 units. The distance of an average food patch from the nest ( $t_F$ ) was first decreased then increased when the nest was moved from the centre of the area to the edge (Tab. 2). The distance

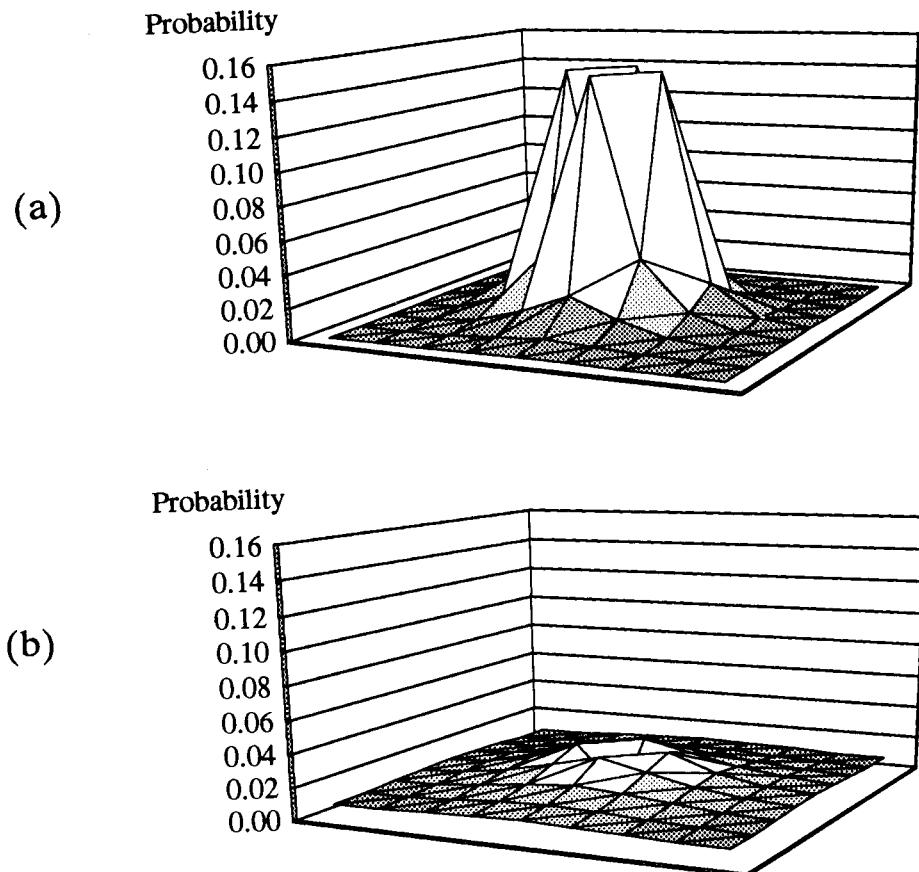


Fig. 2. Probabilities of at least once getting. The basis of figures is the area, and the surface represents the probabilities. The nest is in the centre of the area. (a) Food is evenly distributed, ratio of food patches equals to 0.9; (b) Food is very clumped, ratio of food patches is 0.001.

was the smallest when the nest was in the middle position, although the unweighted mean of distance of squares ( $d^l N_{i,j} / n$ ) was greater than in the case of the nest in the centre (Fig. 4a and 4b). It may be that the bird used the closer squares more frequently because of the nearness of edge of the area. When the nest was on the edge, the unweighted mean of distance of squares (see above) was greatly increased and the bird could

not use many near squares because of the location of nest, so the average distance of food patch ( $t_F$ ) was increased too (Fig. 4c).

Furthermore I investigated the movement of a predator on an heterogeneous area. On this area all squares had a  $p_i = 0.001$  except of one which had a  $p_i = 0.8$ , so there is a stationary food patch in the area. This stationary patch was further from the nest. The maximum

Tab. 2. The average distance of food patch and the unweighted mean distance of squares from the nest, when the nest was placed in the centre, in a middle position and on the edge. (See also Fig. 3.). Area size was 9 x 9 squares and the food was clumped ( $R_f=0.001$ ). The maximum searching time was 30 units.

Place of the nest	Distance of food patch from the nest	Unweighted distance of squares from the nest
centre	3.865	360
middle	3.715	396
edge	3.992	504

searching time was 30 and the nest was in the centre of the area. The searching time ( $t_s$ ) decreased strongly compared to its value on a homogeneous area where all squares had a  $p_i = 0.001$  (Tab. 3). On the other hand the average distance of food patches ( $t_F$ ) was increased. The ratio of food patches ( $R_f$ ) on this area was also greater than on the similar homogeneous area.

#### 4. Discussion

To improve a model of foraging bird in a patchy environment in this paper I investigated the effects of patchiness and nest location on the mean flight distance in a bounded foraging area.

With decreasing patchiness the mean flight distance increased from which we may conclude that birds living in a

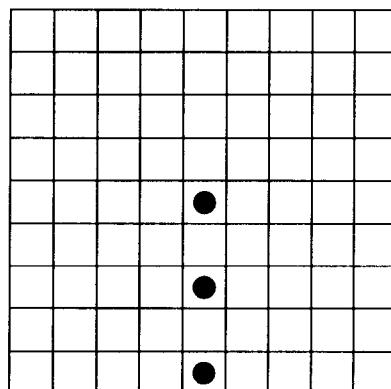


Fig. 3. The nest site in three investigated cases, the dots represent the nests. In baseline case, the nest is in the centre.

patchy environment may collect and carry to their nest more food than those living in an even environment. On this basis we may expect that species foraging on clumped food has relatively larger bill or stomach compared to a relative species at evenly distributed food.

The location of nest influences strongly the mean patch-nest distance. Surprisingly a nest placed close but not on the edge of the area is the best for a breeder from the viewpoint of mean flight distance. This result may explain why the colonies are not located in the centre of the foraging area (Wittenberger & Hunt 1985). The insufficiency of my model is that it does not account the competition for food so it cannot

Tab. 3. The effects of a stable food patch of heterogeneous area on the predator's movement compared a homogeneous area. All squares have  $p_i=0.001$  except of one which has  $p_i=0.8$  in the heterogeneous area. On the other hand in the homogeneous area all squares have  $p_i=0.001$ . Both area size were 9 x 9 squares and the nest was in the centre of the both area. The maximum searching time was 30 units.

Area	Distance of food patch from nest	Searching time	Ratio of food patchess
heterogenous	4.832	68.749	0.0109
homogenous	3.865	521.662	0.0010

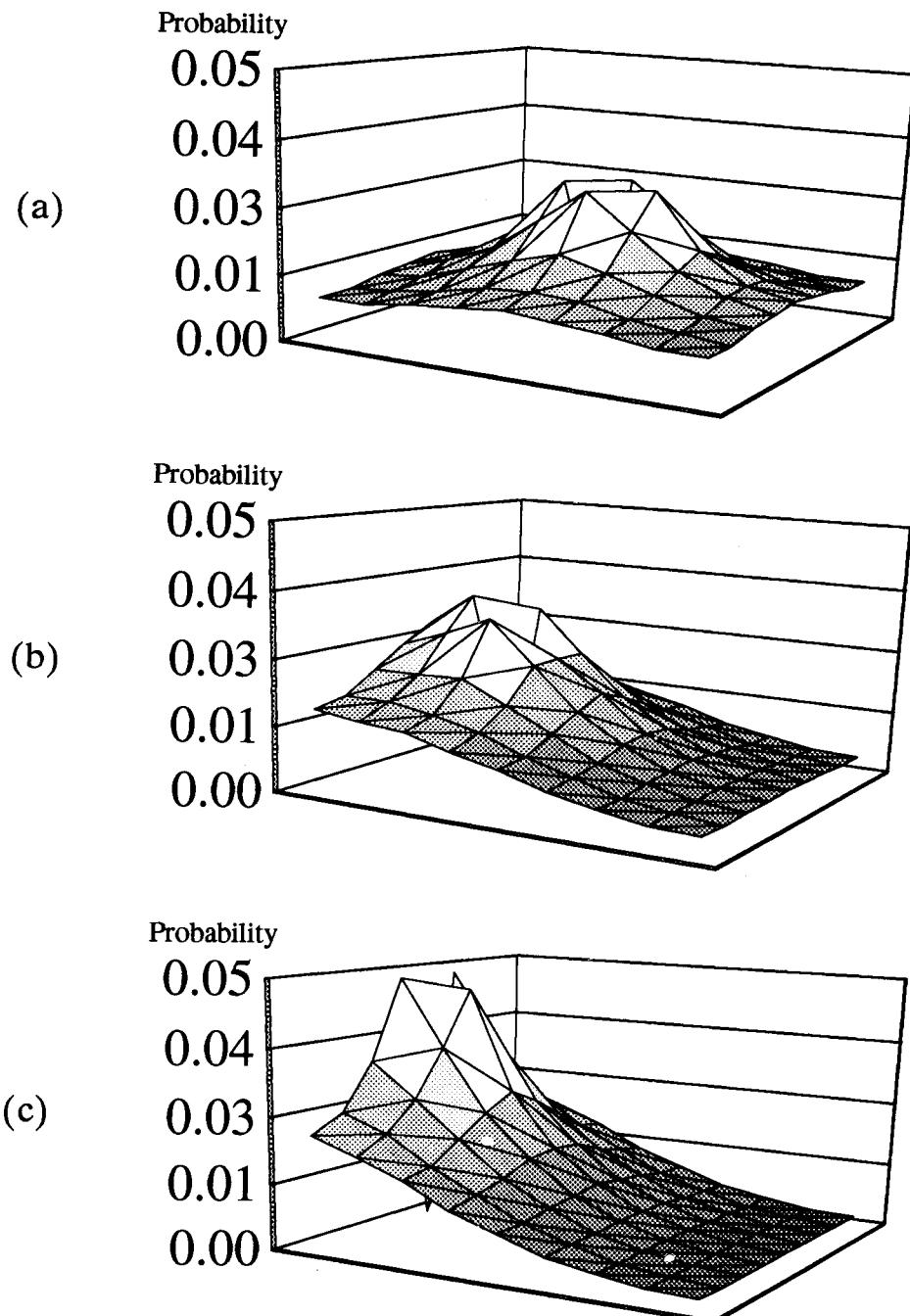


Fig. 4. Probabilities of at least once getting when the nest place was changed. The basis of figures is the area, and the surface represents the probabilities. The food was clumped,  $R_f=0.001$ . The nest was (a) in the centre, (b) middle and (c) on the edge of the area.

compare the solitary and colonial breeding.

The long search time in a patchy environment predicted by the model may show the importance of information transfer at a central place in such environment (Ward & Zahavi 1973).

In an heterogenous area the nest is expected to be placed near the most stationarious patch, otherwise the mean distance in this area increase considerably.

*Acknowledgements.* I am grateful to Alaisder Houston, Erzsébet Pásztor, Tamás Székely and Tibor Szép for helpful comments on this paper and I would like to thank Zoltán Varga for facilities.

## Összefoglalás

### A táplálék foltosságának és a fészek elhelyezkedésének hatása az átlagos repülési távolságra: egy model

A telepes fészkkelének egyik oka lehet, hogy a madaraknak az időben és téren változó helyzetű táplálékfoltok miatt rövidebb távot kell megtenniük a fészek és egy átlagos táplálékfolt között, mintha a területen szétszórva fészkelnének. Mitől függ ezen távolság? Hogyan befolyásolja nagyságát a fészek területen belüli helyzete, a táplálék "csonósságának" (aggregáltságának) foka? A kérdésekre a választ egy modell kifejlesztéssel próbálom megadni. A modell egy véletlen bolyongással kereső predátor mozgását írja le egy négyzethálón, ahol a táplálék eloszlása a csomóstól az egyenletesig változtatható.

A kapott eredmények: A fészek és a folt közötti távolság a táplálék csomósodásával egyre hosszabbá válik. Egy körülhatárolt területen a fészek helyzete jelentősen befolyásolja a táv hosszát. A modell alapján a kissé excentrikus fészekelhelyezés az optimális.

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Received 2 February 1992, revised 5 August 1992, accepted 20 September 1992

# Bird-vegetation relationships along ecological gradients: ordination and plexus analysis

C. Moskát and Z. Waliczky

Moskát, C. and Waliczky, Z. 1992. Bird-vegetation relationships along ecological gradients: ordination and plexus analysis. – *Ornis Hung.* 2: 45-60.

Breeding birds were counted and vegetation structure was recorded along two series of forest succession, in beech forest (*Aconito-Fagetum*) and oak forest (*Quercetum petraeae-cerris*) in Central-Europe. Bird-vegetation relationships were analyzed by two multivariate techniques: canonical correspondence analysis (CCA) and multivariate plexus analysis (MPA). The two methods revealed different aspects of bird-vegetation relationships. CCA demonstrated the dynamical aspect of changes in community structure. In both habitats it revealed two gradients which are important in bird-vegetation relationships. The first axis was interpreted as the successional gradient and the second axis as the closeness-openness gradient. Results of MPA revealed the association structure between individual bird species and vegetation components. Multiple regression analysis showed that MPA is sensitive to the detection of both the linear and the non-linear features of bird-vegetation relationships. CCA and MPA gave some new insights into bird-vegetation relationships across the forest succession. They are not alternatives of each other, they revealed different aspects of the relationships.



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## 1. Introduction

Many studies have shown strong associations between vegetation physiognomy and avian community structure (e.g., MacArthur & MacArthur 1961, MacArthur et al. 1966, Cody 1974, Willson 1974, Rotenberry & Wiens 1980, James & Wamer 1982), although floristical composition of vegetation may also be relevant (e.g., Tomoff 1974, Wiens & Rotenberry 1981, Rotenberry 1985, Moskát 1988). Although multivariate statistical analyses are frequently applied in these studies (see review in Wiens 1989), the analysis of bird-vegetation relationships suffers from methodological problems (Moskát 1991).

The [site x birds x vegetation] -type data matrices cannot be analyzed directly by standard ordination techniques. Methodological problems increase when the ecological data relate to long ecological gradients, such as in a successional sere (Gauch 1982).

The present paper demonstrates the usefulness of two new techniques, which can be recommended for such type of analyses, namely the canonical correspondence analysis (CCA) (ter Braak 1986, 1987a), and the multivariate plexus technique (MPA) (Whittaker 1987, Moskát 1991). The application of these multivariate statistical methods gives more insight into bird-vegetation relationships.

## 2. Study area, successional categories

The study was conducted in two successional seres of Central-European deciduous forests in Hungary. In 1985 an area of managed beech forests (*Aconito-Fagetum*) was studied in the Bükk Mountains (Bükk National Park, 48°06'N, 20°35'E). The area is situated about 600-750 m a.s.l. Six stages of forest regeneration were distinguished:

- B1: Clear-cut area (0-1 years old).
- B2: Younger shrubby phase (2-5 years old).
- B3: Older shrubby phase (5-10 years old).
- B4: Young forest (brushwood) (10-20 years old).
- B5: Preclimax stage (50-60 years old).
- B6: Climax stage (90-110 years old).

See more details of habitat description in Moskát & Székely (1989).

A sere of oak forest (*Quercetum-petraeae cerris*) was studied in the Buda Hills, near the capital Budapest (47°35'N, 18°90'E) in 1988. Oak forests occupy lower zones in Central-Europe than the beech forests. This study area is situated about 240-450 m a.s.l. Six stages of forest regeneration were also distinguished:

- O1: Younger shrubby phase (<20 years old).
  - O2: Older shrubby phase (21-40 years old).
  - O3: Young forest (brushwood) (41-60 years old).
  - O4: Middle-aged forest (61-80 years old).
  - O5: Preclimax stage (81-100 years old).
  - O6: Climax stage (100 years old).
- See more details on vegetation physiognomy and floristical composition in Waliczky (1991).

Different stages of growth were not equally available in the two seres. Young stages of growth were much more strongly represented in the beech than the oak sere.

## 3. Methods

### 3.1. Bird censuses

A double-visit fixed radius point count technique was applied (Moskát 1987) for counting woodpeckers, pigeons, and passerine bird species. This technique is a variant of the French IPA technique (Blondel et al. 1981). In early mornings birds were counted for 10 minutes on circles with 100 m radius around each site, while the census-taker was standing at the centre of the sampling circle. The first counts were carried out in April, the second in May for both seres. The greater value of the two counts was chosen as a representative value, as in the IPA technique. Relative density of breeding pairs was calculated by relating the number of singing males and/or observed pairs to the area of the sampling circle. The results can be regarded as abundance indices for the sites. The accuracy of this technique was over 70%, as tested against the territory mapping method in a climax beech forest (Moskát 1987).

In the beech forest sere 83 sites were located; 9, 13, 11, 11, 16, and 23 in the six successional stages denoted by B1 to B6, respectively. In the oak forest sere 92 sites were selected; 9, 13, 24, 23, 9, and 14 in the six stages abbreviated by O1 to O6. A sampling circle at a site covered about 3.14 ha, so sampling areas varied between 28.26 ha and 75.36 ha in stages. For this reason the rarefaction method (Heck et al. 1975, James & Rathbun 1981) was required for the comparison

of bird communities between stages.

### 3.2. Vegetation measurements

Vegetation physiognomy data were collected on 20–25 points within the circles used for bird counts. The average of these measurements was used to represent a site. The basic variables were chosen after James & Shugart (1970), and they were estimated visually.

The vegetation variables measured were grass cover (%), bush cover (%), canopy cover (%), average tree height (m), average bush height (m), average minimal stem distance (m), average minimal bush distance (m), number of tree species, dominance of the most dominant tree species, beech or oak (%), average diameter at breast height (cm).

### 3.3. Statistical analyses

#### 3.3.1. Canonical correspondence analysis

Canonical correspondence analysis (CCA) is a statistical method to relate community composition to known variation in the environment (ter Braak 1986). This technique combines the algorithm of correspondence analysis on [species x site] data, and a weighted multiple regression analysis on environmental data. We applied CCA to reveal bird-habitat relationships relating the [bird abundance x site] data matrix to the [vegetation physiognomy x site] matrix. We carried out CCA by the computer program CANOCO (ter Braak 1987b).

#### 3.3.2. Multivariate plexus analysis

The plexus technique is useful to produce a graph representation of plant species associations according to their

ecological similarities (Whittaker 1967, McIntosh 1978). Matthews (1978) tried to combine this technique with numerical ordinations, drawing a plexus graph on an ordination diagram obtained by non-metric multidimensional scaling, based on species correlations. Whittaker replaced the correlation coefficient by the more robust rank correlation, and analyzed detrended correspondence analysis (DCA) components of vegetation together with environmental variables (Whittaker 1987). Whittaker's plexus analysis identifies the vegetation-environment complex in four stages: (1) DCA for vegetation variables, (2) rank correlation for vegetation components and environmental variables, (3) ordination of rank correlations by non-metric multidimensional scaling, (4) drawing the plexus graph on the ordination diagram. This technique seems to be suitable for the analysis of complex ecological data ('multiway data matrices'), and can be generalized into the multivariate plexus concept (Moskát 1991). We can substitute DCA in Whittaker's version of the method by any other eigenvector ordination technique (e.g., principal component analysis, principal coordinate analysis, correspondence analysis), so it is possible to choose the best technique for the statistical features of the data set.

We derived vegetation components by correspondence analysis (CA, also called 'reciprocal averaging') (Hill 1973). We selected only the first two components for the subsequent steps, because the interpretation of results is more difficult at higher dimensions (Gauch 1982). For correspondence analysis the computer program CANOCO was applied (ter Braak 1987b).

Vegetation components and bird spe-

Tab. 1. Number of species (S), expected number of species on 28 ha, counted by the rarefaction method (R), and densities (D) (pairs/10 ha).

Category	S	R	D
<b>Beech sere</b>			
B1	12	12.00	14.51
B2	19	17.77	33.32
B3	19	17.86	32.43
B4	19	17.53	26.35
B5	23	20.63	35.63
B6	29	26.04	50.68
<b>Oak sere</b>			
O1	20	20.00	46.35
O2	24	21.27	45.32
O3	29	21.67	59.31
O4	28	24.11	70.61
O5	24	24.00	61.92
O6	25	22.51	63.24

cies abundance values were pooled into a common data matrix, then Kendall's rank correlation coefficients ( $\tau$ ) were computed between all of the elements. For computation of Kendall's tau the program package SPSS/PC+ was applied (Norusis 1986). Following the transformation of the rank correlations ( $\tau$ ) into the  $(1 - \text{abs}(\tau))$  dissimilarities, non-metric multidimensional scaling (NM-MDS) was applied. It was carried out according to the suggestions by Orlóci and Kenkel (1985), applying their computer program MDS.

### 3.3.3. Multiple regression analysis

Multivariate plexus analysis is a suitable technique to detect both the linear and the non-linear relationships between individual bird species and vegetation

components. For detecting the relationships in detail we applied stepwise linear regression analysis, using the program package SPSS/PC+ (Norusis 1986). Following Meents et al. (1983) the correspondence analysis component scores for the first and the second components were transformed by squaring and cubing. We ran the program on the set of the original linear and the transformed polynomial CA components as the independent variables, and on the abundance of individual bird species as the dependent variable.

### 3.3.4. Cluster analysis

We classified bird community data derived from both of the seres by agglomerative cluster analysis. The analysis was performed by the group average technique from similarities calculated according to the Czekanowski's formula. The computer program NCLAS2 was applied from the program package SYNTAX-III (Podani 1988).

## 4. Results

### 4.1. General characteristics of the bird communities

Overall, 40 woodpecker, pigeon, and passerine bird species were recorded in the beech sere, and 40 species in the oak sere. Species richness and density increased with successional stages in the beech sere, whereas the pattern was slightly different in the oak sere where it showed peak at about the fourth stage (Tab. 1). The Tree Pipit (*Anthus trivialis*), the Greenfinch (*Carduelis chloris*), and the Yellowhammer (*Emberiza citrinella*) were the most abundant species (>10%) in the B1 stage, the Barred Warbler (*Sylvia nisoria*) and the Yellow-

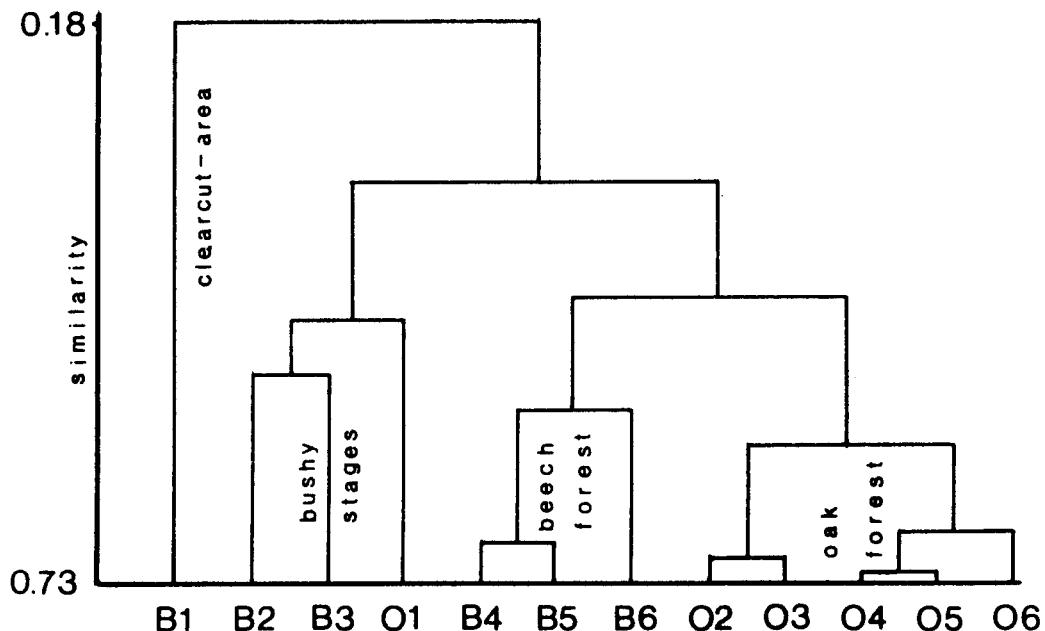


Fig. 1. Dendrogram of bird communities with respect to seral stages in a beech and oak sere, derived by agglomerative cluster analysis (Czekanowski's index, group average fusion strategy).

hammer in stage B2. In all of the other four stages of the beech sere the Robin (*Erithacus rubecula*) and the Chaffinch (*Fringilla coelebs*) were the most dominant species, while in stage B3 the following three species also showed dominance value greater than 10%: Blackbird (*Turdus merula*), Blackcap (*Sylvia atricapilla*), and Chiffchaff (*Phylloscopus collybita*). The oak sere can be characterized by the following species: Blackcap, Chiffchaff, and Nightingale (*Luscinia megarhynchos*) in the O1 stage, Chaffinch and Yellowhammer in the O2 stage, Yellowhammer, Blackcap, and Chaffinch in the O3 stage, Chaffinch in the O4 stage, Great Tit (*Parus major*) and Nuthatch (*Sitta europaea*) in the stage O5, Starling (*Sturnus vulgaris*) and Great Tit (*Parus major*) in the stage O6.

Generally, the bird communities in the young stages were very similar in the two seres, but less so between the mature and the climax stands (Fig. 1). A more detailed discussion of bird community structures of these seres can be found in Moskát & Székely (1989), and in Waliczky (1991).

#### 4.2. Ordination of the bird-vegetation data by canonical correspondence analysis

Fig. 2 shows the ordination diagram of the beech forest sere. We interpreted the first axis as the successional gradient, and the second axis was identified as a closeness-openness gradient. This interpretation was supported by the correlation values between these axes and the vegetation variables, and by the values

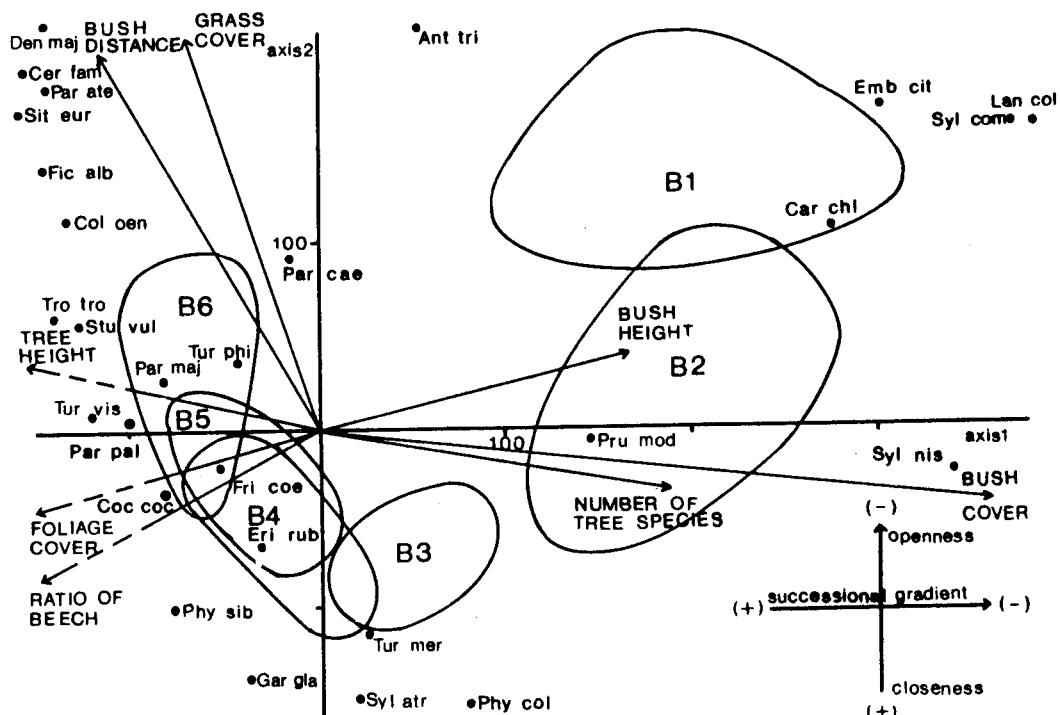


Fig. 2. Bird distribution in a successional sere of beech forests: CCA ordination diagram with bird species (.) and site scores (only contour-line of site points are presented).

of standardized regression/canonical coefficients and interset correlations.

In order to make the interpretation of the ordination diagram easier, we did not draw the exact positions of individual site scores. Only the contour lines for the clouds of the points for each of the seral stages were drawn. Positions of the seral stages on the ordination diagram show a sequence from stage B1 to B6. Variability of stages B1 and B2 is much greater than that of the older stages. Stages from B3 to B6 show a partial overlap with their neighbours representing the continuity of stages. Contour maps of the stages are positioned on an arch, indicating the well-known arch effect (Hill & Gauch 1980), which reveals important non-linear characteristics of the data set (Warten-

berg et al. 1987). In the case of the beech forest sere, the arch effect has drawn attention to a slight relationship between the two ends of the sere. Open patches within the climax stage make possible territory establishment for the Tree Pipit. The Yellowhammer is also known to be a similar species in habitat selection along a beech forest sere (Moskát & Székely 1989), but its density is much greater in the youngest stage than in the old one, therefore CCA placed it far from the Tree Pipit.

Positions of the bird species on the ordination diagram with respect to the contour maps of the stages reveal the association between individual species and successional stages. CCA placed habitat specialists for the young stages (e.g., Red-backed Shrike *Lanius collurio*, and

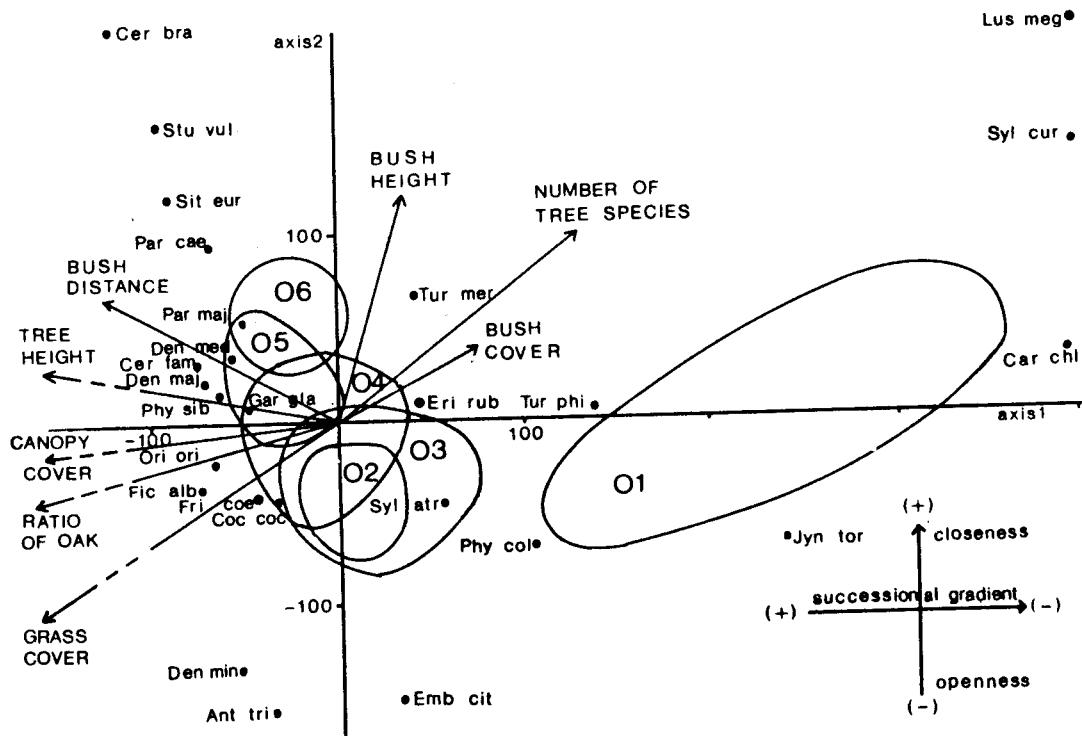


Fig. 3. Bird distribution in a successional sere of oak forests: CCA ordination diagram with bird species (.) and site scores (only contour-line of site points are presented).

Whitethroat (*Sylvia communis*) on the upper right corner of the diagram. In the inner parts of the sere there are habitat generalist species (e.g., Blackcap, Robin, Blackbird), and there are older stage specialists around the older stages (e.g., Mistle Thrush *Turdus viscivorus*, Great Tit). Some climax specialist species (Stock Dove *Columba oenas*, Great Spotted Woodpecker *Dendrocopos major*, Collared Flycatcher *Ficedula albicollis*, Nuthatch, Tree Creeper *Certhia familiaris*) are placed to the upper left corner of the diagram. The Coal Tit (*Parus ater*) was also put into this group. Although this species can be found in pine and coniferous forest stands at great variability in age in Central-Europe, in the beech sere it is restricted to the climax stage.

In CCA vegetation variables are presented by arrows, where close angle with any of the axes show close relation between the variable and the axis. The length of the arrows represents the relative importance of the vegetation variable among the vegetation characteristics.

Arrows of the vegetation variables 'bush height', 'bush cover' and 'number of tree species' show close relation to the right side of the first ordination axis ('successional gradient'). In the beech forest sere bushes are represented only in the young stages, they are nearly absent from the older ones. The number of tree and bush species in the older stages is low. The variables 'tree height' and 'foliage cover' show close relation to the other side of the first ordination axis, representing the main physiognomical

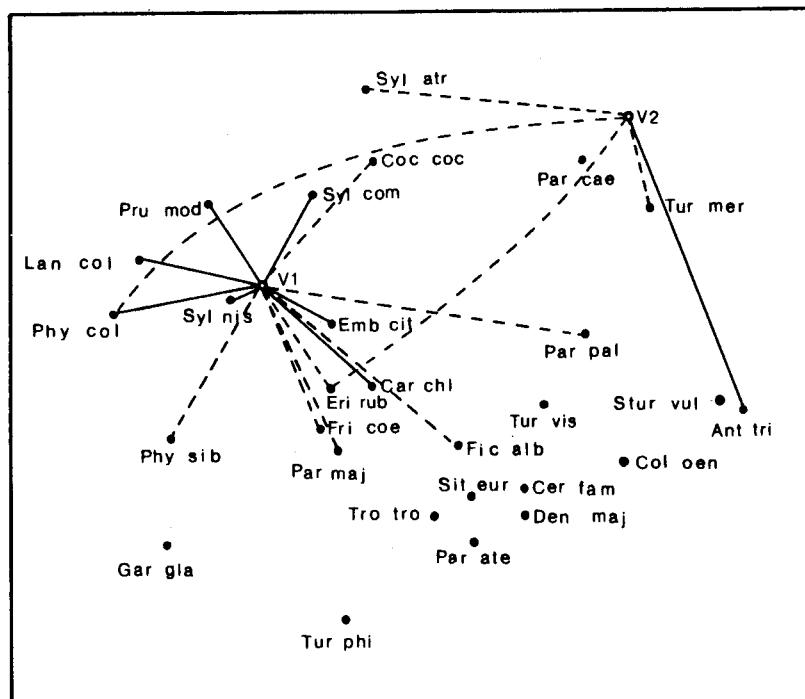


Fig. 4. Relationships between bird species and vegetation components in a successional sere of beech forests: plexus diagram with bird species (.) and vegetation components (V1, V2). (Only highly significant relationships are shown ( $P < 0.01$ ); straight line represents a positive (+) relationship, broken line means a negative (-) relationship; V1+: shrub character, V1-: old forest character/scarce shrub layer, V2+: openness, V2-: closeness).

characteristics of the older stages. The position of the variable 'percent of beech trees' along the left part of the successional gradient agrees with the floristical simplicity of the older stages. The vegetation variables 'grass cover' and 'bush distance' show relations with the second axis, which was identified as a closeness-openness gradient. Tree Pipit is positioned to the upper end of this axis, showing a close association with openness. Open areas are typical in the 'B1' stage, moreover small open patches can be found in the 'B6' stage. Stages in the middle of the sere, such as the 'brushwood' - like young forest are very closed, therefore they were placed to the

lower part of this axis.

The ordination diagram of the oak sere (Fig. 3) revealed a very similar pattern to the beech one. Axis 1 is the successional gradient, axis 2 is the openness-closeness gradient, but the interpretation of the second axis is not as clear as in the case of the beech sere. Seral stages take place on an arch from stage 'O1' to 'O6'. There is a little difference in the structural characteristics between the stages of the oak and beech vegetation seres. The beech sere starts from the clear-cut area, while the oak one begins from the small bush stage, therefore stage 'B2' in the beech sere is approximately equal in structure to

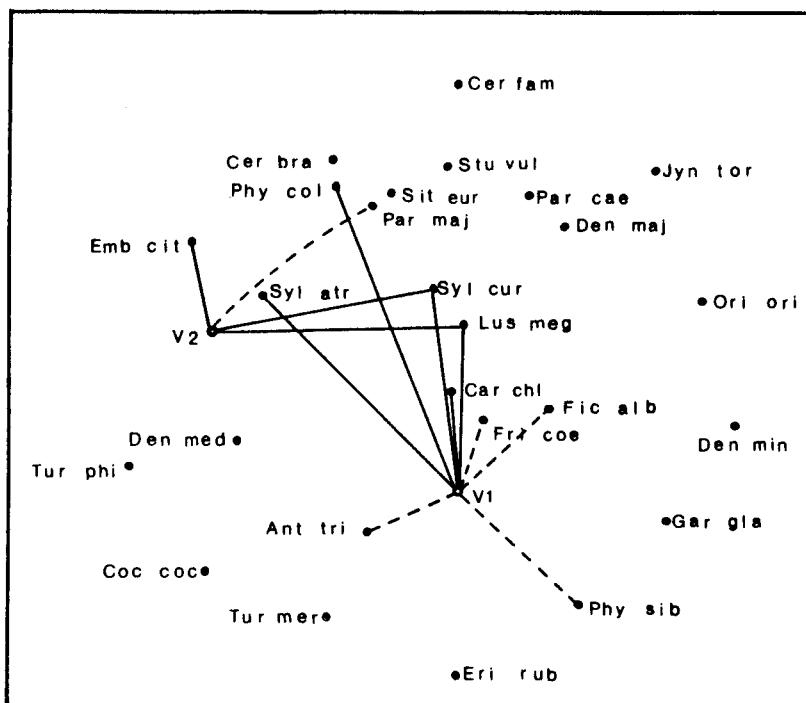


Fig. 5. Relationships between bird species and vegetation components in a successional sere of oak forests: plexus diagram with bird species (.) and vegetation components (V1,V2). (Only highly significant relationships are shown ( $p < 0.01$ ); straight line represents a positive (+) relationship, broken line a negative (-) relationship; V1+: shrub character, V1-: old forest character/scare shrub layer, V2+: openness, V2-: closeness).

stage 'O1' in the oak sere. Stages 'O2' and 'O3' in the oak sere did not separate from each other in this analysis. In both of the seres variability of the older stages is much less than that of the young stages.

Many species (e.g., Blackcap and Chaffinch) are placed around the middle of the sere on the diagram. Although the signs of the second axes on Fig. 2 and Fig. 3 are opposite, the axes represent nearly the same closeness-openness gradients for both of the seres. Along axis 2 on Fig. 3 species preferring openness (Tree Pipit and Yellowhammer) and closeness (Robin, Blackbird) are well separated. Species preferring the older

stages are at the left side of axis 1. The Nuthatch, the Short-toed Tree Creeper (*Certhia brachydactyla*), and the Starling prefer old, closed stands.

Vegetation variables represented by arrows on the diagram show only a slightly different pattern from the beech sere. The variables 'bush height', 'bush cover' and 'number of species' show relations with both of the axes. 'Tree height', 'foliage cover' and 'percent of oak trees' are positioned to the left side of axis 1, which means a considerable role of these characters at the older stages. 'Grass cover' and 'bush distance' have only minor importance according to this analysis.

Tab. 2. Significant bird-vegetation relationships in the beech sere, according to Kendall's rank correlation and stepwise multiple regression. (Non-linearity was tested by using  $x^2$  and  $x^3$  transformations in the regression models.) (V1 and V2 are the vegetation components derived by correspondence analysis; significance levels: +/-:  $p < 0.1$ , +/--:  $p < 0.05$ , ++/---:  $p < 0.01$ ).

Bird species	Kendall's tau ( $\tau$ )		Stepwise multiple regression					
	$V_1$	$V_2$	$V_1$	$V_2$	$V_1^2$	$V_2^2$	$V_1^3$	$V_2^3$
<i>Columba oenas</i>		-						
<i>Dendrocopos major</i>								
<i>Garrulus glandarius</i>			--					
<i>Parus palustris</i>	---			---				
<i>Parus ater</i>								
<i>Parus caeruleus</i>	-	++						
<i>Parus major</i>	---			---				
<i>Sitta europaea</i>	--	+	---					
<i>Certhia familiaris</i>								
<i>Troglodytes troglodytes</i>	--		---					
<i>Erithacus rubecula</i>	---	---	---	---				---
<i>Turdus merula</i>		---		---				
<i>Turdus philomelos</i>								
<i>Turdus viscivorus</i>	--							
<i>Sylvia nisoria</i>	+++	--	+++	--	+++			
<i>Sylvia atricapilla</i>		---		---				
<i>Sylvia communis</i>	+++	++	+++					
<i>Phylloscopus collybita</i>	+++	---	+++	---	---	--		
<i>Phylloscopus sibilatrix</i>	---		---					
<i>Ficedula albicollis</i>	---		---					
<i>Prunella modularis</i>	+++		+++					
<i>Anthus trivialis</i>		+++		+++				
<i>Lanius collurio</i>	+++						+++	
<i>Sturnus vulgaris</i>	--							
<i>Fringilla coelebs</i>	---		---				+++	
<i>Carduelis chloris</i>	+++		+++				+++	
<i>Coccothraustes coccothraustes</i>	---		---					
<i>Emberiza citrinella</i>	+++	+	+++	++				

Tab. 3. Significant bird-vegetation relationships in the oak sere, according to Kendall's rank correlation and stepwise multiple regression. (Non-linearity was tested by using  $x^2$  and  $x^3$  transformations in the regression models.) (V1 and V2 are the vegetation components derived by correspondence analysis; significance levels: +/-:  $p < 0.1$ , +/--:  $p < 0.05$ , ++/---:  $p < 0.01$ ).

Bird species	Kendall's tau ( $\tau$ )		Stepwise multiple regression					
	$V_1$	$V_2$	$V_1$	$V_2$	$V_1^2$	$V_2^2$	$V_1^3$	$V_2^3$
<i>Jynx torquilla</i>	++			--			+++	
<i>Dendrocopos major</i>	-	-			---			
<i>Dendrocopos medius</i>	-	-						
<i>Dendrocopos minor</i>								
<i>Oriolus oriolus</i>								
<i>Garrulus glandarius</i>	--	-						
<i>Parus caeruleus</i>			--		---			
<i>Parus major</i>			---		---			
<i>Sitta europaea</i>			-				---	
<i>Certhia brachydactyla</i>								
<i>Certhia familiaris</i>			++					
<i>Erythacus rubecula</i>	++	--						
<i>Luscinia megachrynos</i>	+++	+++			+++	+++	+++	
<i>Turdus merula</i>	++		++					
<i>Turdus philomelos</i>							++	
<i>Sylvia atricapilla</i>	+++	++	+++					
<i>Sylvia curruca</i>	+++	+++				+++	+++	
<i>Phylloscopus collybita</i>	+++	+	+++			---		+++
<i>Phylloscopus sibilatrix</i>	---						---	
<i>Ficedula albicollis</i>	---		---					
<i>Anthus trivialis</i>	---	++	---	+++				
<i>Sturnus vulgaris</i>		-	++		---			
<i>Fringilla coelebs</i>	---		---					
<i>Carduelis chloris</i>	+++	++			+++			+++
<i>Coccothraustes coccothraustes</i>	--							
<i>Emberiza citrinella</i>	-	+++		+++		---		

#### 4.3. Ordination of the bird-vegetation data by multivariate plexus analysis

MPA reveals both the positive and negative associations between individual bird species and vegetation components (Moskát 1991). The most important vegetation components (V1 and V2) were selected for further analysis of the CA results. In both of the seres the first component was identified as bush character with '+' sign, and on the other side of the axis ('-') as old forest character. The second vegetation component reflects to openness with '+' sign, and to closeness with '-' sign. These meanings of the components are similar to the interpretation of the CCA axes (see above). Tab. 2 and Tab. 3 exhibit the values of Kendall's rank correlation coefficients, measured between the vegetation components and individual bird species.

The plexus diagram for the beech sere is shown on Fig. 4. It revealed strong positive correlations between V1 and 7 bird species (Whitethroat, Chiffchaff, Dunnock *Prunella modularis*, Red-backed Shrike, Greenfinch, Yellowhammer, Barred Warbler *Sylvia nisoria*). All of them prefer bushy habitats, the earlier stages of the sere. The Yellowhammer prefers clearcut areas as well as short bushy stages, therefore it shows a very close '+' association with V1, which is the positive part of the successional gradient (axis 1). Close negative associations were found between V1 and 5 bird species (Great Tit, Wood Warbler *Phylloscopus sibilatrix*, Collared Flycatcher, Chaffinch, Hawfinch *Coccothraustes coccothraustes*). Each of them prefer old stages with tall trees. Preference of the Tree Pipit for open habitats is confirmed by its close '+' association with V2. The Blackcap, the Chiffchaff, and

the Robin showed an affinity to close habitats according to their close '-' association with V2.

The plexus diagram for the oak sere indicates strong positive associations between the successional variable (V1) and 5 bird species (Fig. 5). The Nightingale, the Blackcap, the Lesser Whitethroat, the Chiffchaff, and the Greenfinch belong to this group, whereas 4 species (Wood Warbler, Tree Pipit, Collared Flycatcher, and Chaffinch) show negative relationships with V1. Three bird species show association with V2, which means the openness ('+') and closeness ('-') gradient. Whereas the Yellowhammer is placed near to V2, the Nightingale, and the Lesser Whitethroat have significant relations with V1 too, so they are placed at about half way between V1 and V2. The Great Tit is the only species, which shows great '-' association with V2, hence it prefers closed habitats.

Although plexus analysis is sensitive to both the linear and nonlinear cases of relationships between individual bird species and vegetation components we needed a further analysis by stepwise multiple regression to reveal the linear or nonlinear characteristics. We tested nonlinearity by using  $x^2$  and  $x^3$  transformations in the regression models (see above). In Tab. 2 and Tab. 3 we represent the significant relationships between birds and vegetation. In the beech sere 18 out of the 28 bird species exhibit linear relationships with at least one of the two vegetation components. These numbers in the oak sere are 9 and 26, respectively. About 55% of the linear relationships are negative. Six bird species showed nonlinear relationships with vegetation components in the beech sere, and 13 in the oak one. Taking into

account the most significant results ('+++ and '---'), there is a great agreement between them and the values of Kendall's rank correlation.

## 5. Discussion

### 5.1. Habitat selection of birds along forest successional gradients

If the gradient studied is long enough to contain habitats with rather sharply different physiognomic structure, as in our case, either CCA or plexus diagram can reveal broad affinities of bird species to certain characteristics of those habitats. In both seres CCA sharply distinguishes between the open grassy or brushy stages and the other, more closed forest stands. The initial phases are more diffusely distributed and heterogenous in themselves, whereas the older phases overlap widely. This indicates that the successional changes in bird communities are not gradual between the open brushwood and closed forest stages but that there is a sudden break in species habitat distribution: species with close affinities to trees (mainly hole-nesters) appear, while the densities of many shrub-nesting species fall to zero.

In the CCA space of the two successional seres the majority of species common to both forests show a very similar position according to the two axes. This suggests that, although the sample plots of the two seres differ greatly in species composition and densities, the structure of these forest types is similar and the individual habitat selection of common forest birds is much the same.

The plexus diagrams emphasize these general patterns. Interestingly, almost all of the species showing (+) and (-)

connection with the first or the second vegetation components are open-nesting species (exceptions are Great Tit and Collared Flycatcher). This is partly explained by the fact that species selecting brushy or open habitats are exclusively open-nesters. For woodpeckers the diameter at breast height is the most important factor in their habitat selection.

Our findings that the brushy phases differed much from closed stages in forest successions agrees with the hypothesis of Blondel & Farré (1988) and Blondel et al. (1988). They examined bird communities along forest successions from different geographical locations in Europe and found that there were sharp differences among communities of open and shrubby habitats but in a mature forest the phases converged on each other. They explained this pattern as a consequence of different speciation rates in homogeneous forest tracts and more patchily distributed open habitats in the Pleistocene. However, the early phases of several successional seres examined by them differed not only in location but in floristic composition as well, which has an impact on bird community structure (Rotenberry & Wiens 1980). Moreover, the physiognomical structure of vegetation was considered to be similar on the basis of vegetation height (in all four sites) and number of vegetational layers (in the two mediterranean sites only) alone, which is a rather poor measure of vegetational stratification in itself. On the other hand, oak forests are structurally similar all over Europe. Generally, initial phases differed relevantly, but the old forest avifauna tended to be similar. We consider the theory of Blondel & Farré (1988) and Blondel et al. (1988) to be relevant in explaining the overall simi-

larity of forest avifaunas throughout Europe. Speciation processes among birds inhabiting primarily broad-leaved forests (e.g., tits, woodpeckers) might have taken place largely within the biogeographical boundaries of Europe or, more broadly, in the Western Palearctic. On the other hand, birds of open and semi-open habitats in Europe might have evolved outside this region, especially in Africa (e.g., warblers, wheatears). This is, from our point of view, why the basic forest-dwelling species pool from which the actual community develops is so similar in different locations in Europe. For the bird communities of the second-growth habitats recent history, differential dispersal ability of species and chance effects may be more important.

## 5.2. Linear and nonlinear relationships

Investigations of nonlinear relationships between birds and vegetation are very scarce. Meents et al. (1983) analyzed relationships between birds and vegetation in the lower Colorado River valley, and found that about one-third of the cases showed a significant curvilinear response when there was no linear response at all. Best & Stauffer (1986) revealed nonlinear relationships between vertical vegetation density and habitat suitability indices for birds in riparian habitats of Iowa. They stated that commonly used statistical procedures in ecology were based upon assumption of linearity, but such relationships may be the exception rather than the rule. Our results also call attention to the importance of nonlinear features, besides the linear ones.

Technically, nonparametric statistical methods (e.g., Kendall's rank correlation) are robust and powerful tools for

the detection of linear and nonlinear relationships together, but we need further analysis to reveal the characteristics of these relationships in detail. Following Meents et al. (1983) we squared and cubed variables to detect nonlinear features, but other type of nonlinearity may also occur.

## 5.3. CCA or MPA ?

Whereas multivariate plexus analysis revealed negative and positive associations between vegetation components and bird species abundances, canonical correspondence analysis placed sample sites and bird species into a common coordinate system. Although CCA suffers from linear distortion, it demonstrates the process of succession. MPA is the more robust procedure, because it uses non-metric multidimensional scaling for the main ordination, and it reveals both the linear and the nonlinear relationships as well.

Both CCA and MPA proved to be very helpful in understanding relationships between birds and vegetation components. These methods are not alternatives to each other, but reveal different aspects of bird-habitat relationships along a successional gradient. MPA showed close associations between elements, whereas CCA demonstrated the changes of community composition during the successional process.

*Acknowledgements.* Fieldwork of the study was carried out within the framework of the 'Succession Project', an OKKFT programme of the Hungarian Natural History Museum. Data analysis was partly supported by the grant OTKA I/2 (grant no. 740/88) to C.M. Some of the analyses were made during the stay of C.M. at the Zoological Department of Colorado State University, Fort Collins, sponsored by the MTA-Soros Foundation. We are grateful to J. A. Wiens and J. Podani for their helpful comments on the manu-

script and to T. Székely for measuring the vegetation variables in the beech sere.

## Összefoglalás

### Madárközösségek- és vegetáció-szerkezet kapcsolata ökológiai grádiens mentén: ordináció és plexus analízis

Bükös és tölgyes másodlagos szukcessziós sorozatában mértünk 10 vegetáció-szerkezeti változót és a madárfajok denzitásértékeit. A madárközösségek- és vegetáció-szerkezet összefüggéseit sokváltozós analízisekkel elemeztük: a kanonikus korreszpondencia analízzsel (CCA: ter Braak 1986) és a sokváltozós plexus analízzsel (MPA: Whittaker 1987, Moskát 1991). Utóbbi nem-metrikus skálázáson alapuló többletpcsős módszer, melynél az egyes lépések az adattípushoz és a problémához viszonylag szabadon választhatók ("multivariate plexus concept", Moskát 1991). Módszertanilag minden két eljárás rendkívül érdekes, mert megoldási lehetőséget kínál a [mintavételi hely x vegetációs komponensek x madárdenzitások]-tipusú adatmátrixok közvetlen elemzhetőségének problémájára.

A két sokváltozós ordinációs eljárás a madárközösségek- és vegetáció-szerkezet kapcsolatok különböző oldalát tárta fel. A CCA a szukcesszió során bekövetkező közösségi-szerkezeti változások dinamikus jellegét hangsúlyozta. Az első ordinációs tengelyt a szukcessziós grádiens-ként azonosítottuk, míg a második tengelyt egy nyitottsági–zárttági grádiensnek. Az MPA a vegetációs komponensek és a madárfajok közötti kapcsolatok finomabb részleteit tárta fel. A vegetációs komponensek speciális transzformációja után végrehajtott sokváltozós regresszióanalízzsel kimutattuk, hogy az MPA egyaránt érzékeny a lineáris és a nem-lineáris kapcsolatokra. A CCA és az MPA új oldalát tárták fel a madárközösségek- és vegetáció-szerkezet összefüggéseknek. A két eljárás nem tekinthető egymással alternatív módszernek, mivel az összefüggések más-más jellegét emelik ki.

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*Received 15 September 1992, revised 14 November 1992, accepted 30 November 1992*

# A bíbic (*Vanellus vanellus*) szaporodásbiológiai vizsgálata szikespusztai élőhelyen

Liker András

Liker, A. 1992. Breeding biology of Lapwing (*Vanellus vanellus*) in alkaline grassland. – *Ornis Hung.* 2: 61-66. (In Hungarian, abstract in English.)

Breeding biology of Lapwings was studied in a Hungarian alkaline grassland in 1990 and 1991. 22-25 pairs of Lapwings bred on the study site (70 ha) in both years and the breeding density was 0.31-0.36 pairs per ha. Vegetation cover ranged from 20% to 100% and the height of plants was typically 5-12 cm around the nests. Clutch size was  $3.8 \pm 0.5$  (mean  $\pm$  SD), egg size was  $45.4 \pm 1.3$  x  $32.7 \pm 0.8$  mm. Egg size was smaller than those of West European populations, and similar to the size of East and South-East European populations. Lapwings bred in higher densities in pasture (0.57 and 0.78 nest per ha) than in hayfield (0.19 and 0.35 nest per ha). Hatching success was 51.5% and 55.6% in 1990 and 1991, respectively. The most frequent reason of failure was predation, particularly by birds (Magpie *Pica pica*, Black-headed Gull *Larus ridibundus*, Marsh Harrier *Circus aeruginosus*) although mammals e.g. small mammals, straying dogs also took a heavy toll.



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## 1. Bevezetés

A hetvenes évektől kezdve jelentősen megnőtt a partimadarakon (*Charadrii* alrend) végzett vizsgálatok száma (Hale 1980), egyre több – elsősorban nyugat-európai és skandináv országban indított – program foglalkozik a partimadarak fészkelésének ökológiai és etológiai kérdéseivel. A kutatások egyik ága természetvédelmi szempontból vizsgálja a partimadarakat (pl. Beintema 1983, Galbraith 1988, Baines 1990), míg a vizsgálatok másik csoportja párzási és utódnevelési viselkedésükre irányul (pl. Lessells 1984, Seather et al. 1986). Habár e két kutatási terület módszerei és céljai alapvetően különböznek, a fészkelésbiológiai ismeretek mindenkorra fontosak.

Magyarországon tizenhárom parti-

madárfaj fészkel rendszeresen (Haraszthy 1984), hazai populációik költésbiológiájáról azonban csak elszórt adataink vannak (Sterbetz 1962, Mödlinger 1979, Székely 1991). A csoport leggyakoribb képviselője a bíbic (*Vanellus vanellus*), ma is jelentős állománya él az Alföldön. Ennek ellenére fészkelésökölgiáját csak Molnár (1986) vizsgálta, aki a fészkelő bíbicek környezeti igényéről közölt ismereteket. Vizsgálatom célja az volt, hogy további adatokat gyűjtsek a bíbicek fészkelésbiológiájáról.

## 2. Vizsgálati terület

Szegedtől 15 km-re, a Fehérvári északi szélén elhelyezkedő Székely (Sándorfalvi rét) kb. 70 hektáros részén végeztem a vizsgálatot. A terület fele már-

**1. Táblázat. A fészkelési időszak jellemzői**  
**Table 1. Characteristics of breeding season (month.day)**

Év/Year	Érkezés/Arrival	Első teljes fészek/ First complete nest	Első kelés/ First hatch	Utolsó kelés/ Last hatch
1990	02.20	04.05	04.25	07.05
1991	02.27	03.27	04.21	06.26

cius–áprilisban vízállásos, később kiszáradó szoloncsák szikes legelő, másik fele nedvesebb, mélyebben fekvő szikes kaszáló. A száraz legelő magasabb részeit soványcsenkesz (*Festuca pseudovina*) borítja, míg az erősen szikesedő alacsonyabb szint domináns növényei a sziki mézpázsit (*Puccinellia limosa*), a báránypáréj (*Camphorosma annua*) és a pozsgás zsálsa (*Lepidium crassifolium*). A kaszáló növényzete főként homogén mézpázsit gyepből áll. Mindkét területen kiterjedt vakszikkes foltok találhatók. A környéken levő számos tanya és az utak közelisége miatt egyes időszakokban erős az emberi zavarás. A legelőterület egy részét fészkelési időszak alatt is legeltetik (nem védett rész), míg a másikon a legeltetés áprilistól júniusig szünetel (védett rész). A nedvesebb rét kaszálását nyár közepén, júliusban végezik.

### 3. Módszerek

1990-ben és 1991-ben március utolsó hetétől kezdve kerestem a bíbicfészkeket. A fészek egy és öt méteres körzetében becsültem a növényzet százalékos borítását, valamint centiméteres pontossággal mértem a fészek körüli növényzet magasságát 5-5 ponton. Lemértem a tojások hosszát és szélességét. A talált fészekkaljak sorsát négy-hatnaponkénti ellenőrzésekkel

követtem, pusztulás esetén a tojásma-radványok és egyéb nyomok alapján próbáltam meghatározni a pusztulás okát. A vizsgálatot július első hetében fejeztem be.

A dolgozatban az eredmények közlésére átlag±szórás formát használok. A statisztikai analíziseket SPSS-PC programcsomaggal végeztem.

### 4. Eredmények

#### 4.1. Fészkelő állomány

A Székáljon minden évben 22-25 pár bíbic költött. A költőpárok denzitása 0.31-0.36 pár/hektár, a fészekkaljak denzitása 1990-ben 0.47, 1991-ben 0.45 fészek/hektár volt.

#### 4.2. Fészkelési időszak

A bíbicek minden évben február második felében érkeztek vissza a telelésből, 1991-ben a területet ekkor még részben hó borította. A hímek territóriumfoglalása március harmadik hetére fejeződött be. A fészkelés kezdete március utolsó napjaira esett, a legkorábbi teljes fészekaljat 1991. március 27-én találtam. Mindkét évben 18-20 pár április 10 előtt lerakta első fészekalját. A pót-költések miatt a költési időszak július elejéig elhúzódott. A kotlás időtartama  $>25.0 \pm 1.0$  nap volt (N=5).

Az első költések fészekaljai rendsze-

2. Táblázat. A fészek körüli növényzet borítása és magassága (átlag $\pm$ szórás, () = mintanagyság, Mann–Whitney U–teszt: \* = P<0.03, NS = nem szignifikáns)

Table 2. Cover of vegetation and height of plants around the nests (mean $\pm$ SD, () = sample size, Mann–Whitney U test between variables of 1 m and 5 m: \* = P<0.03, NS = not significant)

	1990	1991	Összes/All
Borítás 1 m-en belül (%) / Vegetation cover within 1 m (%)	68.3 $\pm$ 25.6 (31) NS	67.2 $\pm$ 29.8 (27) NS	67.8 $\pm$ 27.4 (58) NS
Borítás 5 m-en belül (%) / Vegetation cover within 5 m (%)	68.4 $\pm$ 27.2 (29)	64.0 $\pm$ 27.9 (26)	66.3 $\pm$ 27.4 (55)
Magasság 1 m-en belül (cm) / Height of plants within 1 m (cm)	8.1 $\pm$ 4.1 (29) NS	9.2 $\pm$ 8.6 (27) *	8.7 $\pm$ 6.6 (56) *
Magasság 5 m-en belül (cm) / Height of plants within 5 m (cm)	10.4 $\pm$ 5.4 (29)	11.0 $\pm$ 9.9 (27)	10.7 $\pm$ 7.8 (56)

rint április utolsó és május első napjaiban keltek ki. A legkorábbi kelési dátum 1991. április 21., a legkésőbbi 1990. július 5. volt (1. Táblázat).

#### 4.3. A fészkek környezetének növényzete

A fészkek környezetében a növényzet borítása széles tartományban változott. Néhány esetben csaknem kopár, 20%-os borítottságú helyen is költöttek békísek (N=3), más fészkekkel viszont sűrű, 100%-os borítottságú gyepben találtam (N=15). Az egy méteres és az öt méteres körzet borítása között nem volt szignifikáns eltérés (Mann–Whitney U–teszt, 1990: U = 415.5, P>0.8, 1991: U = 319, P>0.5, a két év együtt: U = 1468, P>0.5)(2. Táblázat).

A fészkekkel általában alacsony, 5–12 cm-es növényzet vette körül, a fészek körüli növényzet magassága csak egyes május végi és júniusi fészkeknél haladta meg a 25 cm-t (N=3). Öt méteres körzetben a növényzet magasabb volt mint egy méteren belül, bár a különbség 1990-ben nem volt szignifikáns (Mann–Whitney U–teszt, 1990: U=319,5,

P=0.11, 1991: U=235, P < 0.03, a két év együtt: U = 1185, P<0.03)(2. Táblázat).

#### 4.4. A fészekkalják jellemzői

A fészkek 83.6%-a 4 tojásos volt, kisebb gyakorisággal előfordultak 2 tojásos (3.3%), 3 tojásos (11.5%) és 5 tojásos (1.6%) fészkek is (1. Ábra). A fészekkaljméret 3.80 $\pm$ 5 tojás (N=61), a tojások mérete 45.4 $\pm$ 1.3 x 32.7 $\pm$ 0.8 mm (N=174) volt (3. Táblázat). A legkisebb tojás mérete: 42.4 x 28.5 mm, a legnagyobbé: 48.2 x 34.6 mm.

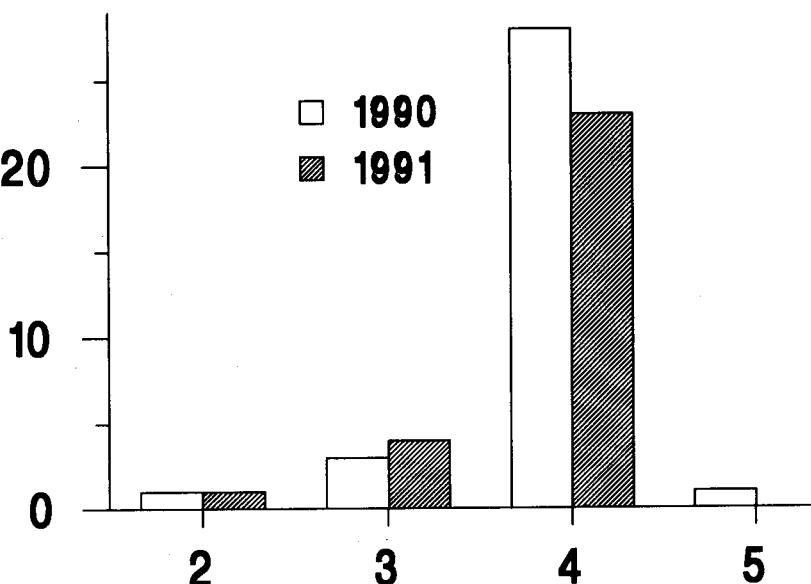
3. Táblázat. Tojásméretek (átlag $\pm$ szórás, () = mintanagyság) (mm)

Table 3. Size of eggs (mean $\pm$ SD, () = sample size) (mm)

	1990	1991	Összes/All
Hossz / Length	44.9 $\pm$ 1.1 (74)	45.8 $\pm$ 1.3 (100)	45.4 $\pm$ 1.3 (174)
Szélesség/ Breadth	32.5 $\pm$ 0.8 (74)	32.8 $\pm$ 0.8 (100)	32.7 $\pm$ 0.8 (147)

1. Ábra. Bébic fészkeljméretek eloszlása.

Fig. 1. Frequency distribution of clutch size (number of nests)



#### 4.5. Kelési sikér

A költéseknek csaknem fele minden évben elpusztult a kotlás során, a kelési sikér 1990-ben 51.5 %, 1991-ben 55.6 % volt (4. táblázat). A fészkaljak pusztulását főként madarak (szarka *Pica pica*, dankasirály *Larus ridibundus*, barna rétihéja *Circus aeruginosus*) és emlősök (kisemlősök, kóbor kutyák) predációja okozta. Három fészket birkák tapostak szét, másik hármat talajvíz öntött el. Egy fészkenél a tojó eltűnése után a hím nem folytatta a kotlástart. A fészkek egy részénél a pusztulás pontos okát nem lehetett megállapítani, néhány valószínűleg tojásgyűjtés miatt hiúsult meg.

#### 4.6. A legelő és a kaszáló összehasonlítása

A két élőhelytípusban különbözött a fészkek denzitása: a legelőn 1990-ben 0.78, 1991-ben 0.57 fészek/hektár, a kaszálón 1990-ben 0.19, 1991-ben 0.35 fészek/hektár volt. Az első terület foglalások minden évben a legelőn történtek. Az első teljes fészkalj találásának dátuma a legelőn: 1990-ben

április 5, 1991-ben március 27, a kaszálón: 1990-ben április 5, 1991-ben április 6 volt.

Nem volt szignifikáns különbség a legelő és a kaszáló között a fészkek körüljövőzet borításában sem egy méteren belül (legelő:  $71.2 \pm 27.8\%$ , kaszáló:  $59.1 \pm 25.3\%$ , Mann-Whitney U-teszt:  $U=243$ ,  $P>0.1$ ) sem öt méteren belül (legelő:  $67.2 \pm 29.4\%$ , kaszáló:  $64.4 \pm 22.5\%$ ,  $U=282$ ,  $P>0.5$ ). A növényzet magassága ugyancsak nem különbözött egy méteren belül (legelő:  $8.9 \pm 7.7$  cm, kaszáló:  $8.1 \pm 2.6$  cm,  $U=254.5$ ,  $P>0.2$ ) és öt méteren belül (legelő:  $10.7 \pm 8.9$  cm, kaszáló:  $10.8 \pm 4.2$  cm,  $U=238.5$ ,  $P>0.1$ ). Nem volt szignifikáns eltérés a két élőhelyen talált fészkaljak méretében, a tojások hosszában és szélességében (fészkaljméret: legelő:  $3.9 \pm 0.5$  tojás, kaszáló:  $3.8 \pm 0.6$  tojás,  $U=367.5$ ,  $P>0.6$ ; tojáshossz: legelő:  $45.3 \pm 1.2$  mm, kaszáló:  $45.7 \pm 1.6$  mm,  $U=208.5$ ,  $P>0.4$ ; tojásszélesség:  $32.7 \pm 0.8$  mm, kaszáló:  $32.50.9$  mm,  $U=197.5$ ,  $P>0.3$ ).

A fészkek kelési sikere a legelőn 1990-ben 42.3%, 1991-ben 76.4%, a kaszálón 1990-ben 85.7 %, 1991-ben 20.0 % volt.

## 4. Táblázat. A fészakaljak sorsa (százalékosan).

Table 4. Fate of clutches (%).

Év/ Year	A pusztulás oka/ Failure due to					Kelt/ Hatched	N
	predáció/ predation	taposás/ trampling	elöntés/ flooding	elhagyás/ desertion	ismeretlen/ unknown		
1990	21.2	9.1	0	0	18.2	51.5	33
1991	22.2	0	11.1	3.7	7.4	55.6	27
Összes/All	21.7	5	5	1.7	13.3	53.3	60

## 5. Értékelés

A fészek körüli növényzet borítása és magassága közel esik más külföldi illetve hazai vizsgálatok eredményeihez: dél-alföldi szikeseken az átlagos borítás 66.5%, a fészek melletti átlagos növényzetmagasság 10.4 cm, a fészeket öt méteres körzetében mért átlagos növényzetmagasság 15.5 cm volt (Mol-

nár 1986); Hollandiában 6-15 cm-es, Németországban 5-16 cm-es növényzetmagasságot mértek (Glutz et al. 1975). Az egy és öt méteren belül mért magasság közti különbség az élőhely alacsony növényzetű foltjainak preferenciáját mutatja.

A fészkaljméret hasonló más populációk fészkaljméretéhez (Angliaban és Németország egyaránt 3.85 tojás, Cramp & Simmons 1983). A 45.4 x

## 5. Táblázat. A bsbic kelési sikere néhány európai vizsgálatban (\* =intenzív mezőgazdasági művelésű élőhely)

Table 5. Hatching success of Lapwings in some European populations (\* = improved habitat)

Szerző / Author	Vizsgálat éve/Year of study	Előhely / Habitat	Kelési sikeres / Hatching success (%)
Matter (1982)	1977	szántó (arable)*	39
Kooiker (1987)	1980-85	legelő (pasture)	81
		szántó (arable)*	55
Galbraith (1938)	1984-86	legelő (pasture)	34
		szántó (arable)*	28
Baines (1990)	1985-97	legelő (pasture)	51
		legelő (pasture)*	19
		kaszáló (hayfield)*	26
		szántó (arable)*	64
Jelen vizsgálat/ This study	1990-91	legelő (pasture)	55
		kaszáló (hayfield)	47

32.7 mm-es tojásméret kisebb a nyugat-európai populációkból származó méreteknél: pl. Anglia: 47.0 x 33.7 mm (Makatsch 1974), Hollandia: 46.9 x 33.3 mm, Németország: 46.6 x 33.2 mm (Glutz et al. 1975). Azonban hasonlóan kis tojásméreteket mértek Kelet-Európában: 45.3 x 32.8 mm, valamint Dél-Kelet-Európában: 45.7 x 32.8 mm (Makatsch 1974, pontos helymegjelölés nélkül).

A földön fészkelő partimadarak fészkepusztulása jelentős, ennek mértéke azonban élőhelyenként eltérő. Jelen vizsgálatban a kelési siker 50-55% volt, ami más vizsgálatok eredményeivel összehasonlítva viszonylag magas kelési siker (5. Táblázat). Ez az eredmény összhangban van azzal, hogy a bőbicek költési sikere a természetes állapotú legelőkön általában nagyobb, mint a mezőgazdasági művelés alatt álló területeken (bár a művelési módtól függően nagyok a különbségek), ahol a gázdálkodással összefüggő munkák miatt (Matter 1982, Kooiker 1987, Galbraith 1988) vagy a fokozott predációs veszély következtében (Baines 1990) jelentősen nagyobb lehet a fészkek pusztulása.

A nagyobb fészekdenzitás azt mutatta, hogy a bőbicek fészkelőhelyenként előnyben részesítették a legelőterületet (0.57-0.78 fészek/hektár) a kaszálóval szemben (0.19-0.35 fészek/hektár), szintén erre utalt, hogy az első territórium-foglalások minden évben a legelőn történtek. Mivel a két terület között a vizsgált paraméterekben nem volt különbség, a preferencia okának kidirítéséhez további adatok szükségesek.

**Köszönetnyilvánítás.** Köszönöm Dr. Székely Tamás, Kosznai Norbert és Krnács György munkához nyújtott segítségét. A vizsgálatot a KVM támogatta.

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Érkezett: 1992. május 10-én, átdolgozva 1992. november 5-én, elfogadva 1992. december 10-én.

# **Fészkelő nádi madárfajok alliancia vizsgálata\***

**Molnár Gyula**

Molnár, G. 1992. Data on alliances in breeding of some marshland-nesting birds. – *Ornis Hung.* 2: 67-70. (In Hungarian with English abstract.)



I studied alliance of breeding birds between 1982-1990 in three different marshes of Hungary. I found several co-nestings, that is, when a small bird nested under the nest of a large bird (usually a heron). From the total 803 heron nests there were only 42 cases, when a nest of a small bird was found under the big nest. There were great differences between the observed number of co-nestings in the three study areas (37, 5, 0, respectively), which can be attributed to the differences in the vegetation structure. Thus one reason for co-nesting may be the provision of well-hidden nesting place. Another explanation may be the alliance, that is an increase of vigilance.

G. Molnár, Szeged, Pinty u. 11/5., H-6726, Hungary.

## **1. Bevezetés**

Gémtelepeken végzett vizsgálataim során néhány olyan esetet regisztráltam, amikor egy nagyobb testű gémfélé fészke alatt egy kisebb testű vizimadár fészket. Az irodalomban csak néhány utalást találtam ilyen esetekre, Warga (1959) a Kis-Balatonról írt le egy nagykócsag (*Egretta alba*) fészke alatti guvat (*Rallus aquaticus*) fészkelést, Bankovics (1979) a Kis-réten egy nagykócsag-törpegém (*Ixobrychus minutus*) -vizityúk (*Gallinula chloropus*) együttfészkelést. Ezért a továbbiakban nagy figyelmet fordítottam az együttfészkelések vizsgálatára. Célom a jelenség leírása, valamint a lehetséges magyarázatok vizsgálata volt.

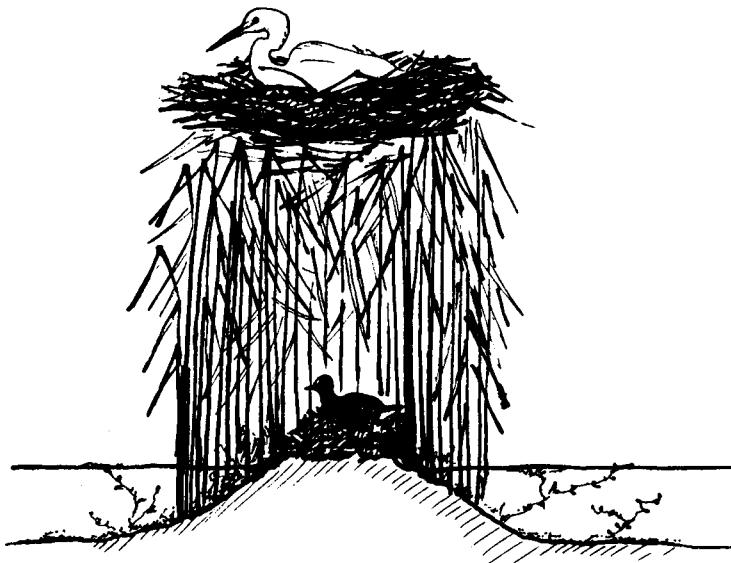
## **2. Vizsgálati terület és módszerek**

A vizsgálatokat 1982 és 1990 között

végztem három területen: (1) a Tiszaalpár melletti Nagy-tavon és Sulymos-mocsáron ( $46^{\circ}45' E$ ,  $20^{\circ}00' K$ ); (2) a Tamási melletti Pacsmagi-tavakon ( $46^{\circ}38' E$ ,  $18^{\circ}15' K$ ); és (3) az Ócsai Tájvédelmi Körzet nádasáiban ( $47^{\circ}15' E$ ,  $19^{\circ}15' K$ ).

A gémtelepek ellenőrzésekor átvizsgáltam a fészkek alatti területet. Ezenkívül a gémtelepek könyékén megtalált vizimadár fészkeket is feljegyeztettem, figyelembe véve a becsült terület-nagyságot is. Együttfészkelés esetén (1. Ábra) rajzon rögzítettem a fészkek elhelyezkedését, és mérőléccel a következő adatokat vettem fel: a nagy és a kis fészek átmérője; a nagy fészek magassága a vízfelszíntől; a vízmélység a kis fészknél és távolabb; a kis fészek a nagy fészek tengelyében fekszik-e, illetve ha nem, mekkora az eltérés (1. Táblázat). Feljegyeztem a költés stádiumát: friss fészek tojások nélkül; tojásos fészek; fiókás fészek; a fiókák által már elhagyott fészek; valamilyen zavarás miatt otthagyott fészek.

\* Előadta a szerző a Magyar Madártani és Természetvédelmi Egyesület III. Tudományos Ülésén, Szombathelyen (1991. március 1-3.).



1. Ábra. Együttfészkeléses riasztási közösség (alliancia) vázlata.  
Fig. 1. Co-nesting for alliance.

### 3. Eredmények és értékelésük

A vizsgálat kilenc éve alatt összesen 42 együttfészkelést találtam: Pacsmagon 37, Tiszaalpáron 5, és Ócsán 0. A felmért fészkek biometriai adatait a 1. Táblázat mutatja. A nagy és a kis fészkek madárfajait és gyakoriságukat a 2. Táblázat ismerteti. Az együttfészkelések gyakoriságát a 3. Táblázat tünteti fel.

Az együttfészkelések gyakorisága alacsony fokú. A regisztrált 42 eset minden össze 5.23%-a az összes fészkekhez viszonyítva (803 gémtelepi fészkek).

A legtöbb együttfészkelés egy gémtelepen 1984-ben a Pacsmagi-tavakon volt (15), de az összes itt költő gémfélé (120 pár) fészke számához viszonyítva ez is csak 12.5%. A 42 együttfészkelésből 27 esetben (64.3%) minden fészkek lakott volt, és 4 esetben (9.52%) minden kettő üres volt. A gémtelepeken talált 42 együttfészkelés mellett a telepek 15

m-es körzetében 18, míg távolabb 6 kistestű nádi madár fészke került elő.

Három esetben a becsült területre vonatkoztatott együttfészkelést és külön fészkelést is megállapítottuk: (1) 3 ha-os területen 6 együtt, és 1 külön fészkelés; (2) 17.5 ha-on 7 együtt, és 4 külön fészkelés; (3) 2 ha-on 2 együtt, és 2 külön fészkelés volt.

A gémtelepeken, főleg ha az külön foltokba szerveződött, a páros fészkeket a telepfoltok szélén találtam. Ha a gémtelep egy-egy foltja rekettye fűz (*Salix cinerea*) bokrára épült, a vizek és a törpe gém fészkei sok esetben a fűzbokrok szélén, a bokor és a nád találkozásánál épültek. Warga (1951) is többször talált törpegém fészkeket gémtelepek szélén.

Az együttfészkelés gyakorisága eltér a három vizsgálati terület között. Ennek oka valószínűleg a növényzet szerkezetében keresendő. Pacsmagon a sás

## 1. Táblázat. Az együttfészkelés fészek-paramétereinek átlagértékei.

Table 1. Data on the nests of the species breeding in alliance

	átlag/ average	szélső érté- kek/range
nagy fészek átmérője / diameter of the big nest	97.6	45-140
kis fészek átmérője / diameter of the small nest	26.7	16-50
nagy fészek vízfelszíntől számított magassága / height of the big nest	90.2	60-150
kis fészek peremének magassága a vízfelszíntől / height of the small nest	27.2	
víz mélysége a nagy fészek mellett / depth of water at the big nest	63.2	22-100
víz mélysége a kis fészek mellett / depth of water at the small nest	13.7	5-20
kis fészek központi függőleges tengelyének eltérése a nagy fészek tengelyétől / deviation of vertical axis of the small nest from that of the big nest	24.1	1-48

és a nád csomókból kiindulva, ferdén szétterülve nő, felső harmadukban levélzetük ritka, így nem nyújtanak kellő védelmet, illetve rejtőzködési lehetőséget. Tiszaalpáron magas, párhuzamosan növő nádszálak dominálnak, Ócsán viszont alacsony, de igen sűrű a sás és a nád. Az első esetben tehát a fajok által igényelt fedettség hiánya miatt keresik a gémfélék fészkei által nyújtott védőtetőt. Tiszaalpáron már bizonyos fokú fedettséget találnak, Ócsán pedig az igen sűrű növényzetben bárhol védelmet találhatnak.

Az átlagos vízmélység (63.15 cm)

feltehetően azt jelzi, hogy ez jelenti a biztonságot a nagytestű fészelők számára. A fészek alatt a nád és a sás felfejlődő zsombékjai miatt a víz mélysége csekély, átlagosan 13.7 cm, ami megkönnyíti a kistestű fajok fészeképítését, valamint a fészekre történő feljutást és eltávozást. A kis fészek három esetben lőgött ki annyira a nagy fészek alól, hogy a gémi fiókák sűrű üritése miatt a vizityúk elhagyta a fészkét. A tojások és a fészek környéke gémürülékkel volt borítva.

A vizityúk a fészkét minden takarásban építi, valamiféle védőtető alá.

## 2. Táblázat. A nagy és a kis fészek előfordulási gyakorisága a különböző fajoknál.

Table 2. Number and frequency of big and small nests of the co-nesting bird species.

Nagy fészket rakó fajok / Species with big nest			Kis fészket rakó fajok / Species with small nest		
	n	%	n	%	
<i>Egretta garzetta</i>	2	4.8	<i>Ixobrychus minutus</i>	4	9.5
<i>Egretta alba</i>	23	54.8	<i>Anas platyrhynchos</i>	14	33.3
<i>Ardea cinerea</i>	14	33.3	<i>Aythia niroca</i>	2	4.8
<i>Nycticorax nycticorax</i>	2	4.8	<i>Rallus aquaticus</i>	1	2.4
<i>Circus aeruginosus</i>	1	2.4	<i>Gallinula chloropus</i>	19	45.2
			<i>Pica pica</i>	2	4.8

3. Táblázat. Az együttfészkelések esetszáma és százalékos megoszlása.

Table 3. Number and frequency of occurrences of alliance.

	n	%
<i>Egretta alba</i> – <i>Gallinula chloropus</i>	12	28.6
<i>Egretta alba</i> – <i>Anas platyrhynchos</i>	6	14.3
<i>Ardea cinerea</i> – <i>Anas platyrhynchos</i>	6	14.3
<i>Ardea cinerea</i> – <i>Gallinula chloropus</i>	5	11.9
<i>Egretta alba</i> – <i>Ixobrychus minutus</i>	2	4.8
<i>Egretta alba</i> – <i>Aythya niroca</i>	2	4.8
<i>Ardea cinerea</i> – <i>Pica pica</i>	2	4.8
<i>Ardea cinerea</i> – <i>Ixobrychus minutus</i>	1	2.4
<i>Egretta garzetta</i> – <i>Gallinula chloropus</i>	1	2.4
<i>Egretta alba</i> – <i>Rallus aquaticus</i>	1	2.4
<i>Nycticorax nycticorax</i> – <i>Gallinula chloropus</i>	1	2.4
<i>Nycticorax nycticorax</i> – <i>Anas platyrhynchos</i>	1	2.4
<i>Circus aeruginosus</i> – <i>Anas platyrhynchos</i>	1	2.4
<i>Egretta garzetta</i> – <i>Ixobrychus minutus</i> – <i>Gallinula chloropus</i>	1	2.4

Schenk (1906a) hasonló megállapítást tesz a guvat fészkelésével kapcsolatban. Saját megfigyeléseim, valamint Schenk (1906b) szerint más nádban fészkelő fajok, például az énekesek (*Acrocephalus scirpaceus*, *Panurus biarmicus*, *Lusciniola melanopogon*) is előszeretettel rakja a fészket valamilyen természetes védőtető, rendszerint megdölt sás- vagy nádköteg alá. A kistestű fajok számára a nagy fészek védelmet nyújt, bár egy esetben egy vihar mind a szürkegém, mind az alatta fészkelő vizitűk költését elpusztította.

**Köszönetnyilvánítás.** Hálás köszönetemet fejezem ki Molnár Zoltánnak és Tajti Lászlónak az adatok gyűjtésében való aktív részvételükért. Az

ábra megrajzolásáért Újhelyi Pétert illeti köszönöt.

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## Short communications – Rövid közlemények

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### Sand Martin (*Riparia riparia*) with suspended or continued moult

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Of eighteen adult Sand Martins, which were trapped at Istria (cost of the Black Sea, in Romania) between August 30th–September 5th 1991, 6 individuals were found with suspended or continued moult.

The moult sequences (Ginn & Melville 1983) were:

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1	0 0 0 0 0 0 0 5 5	0 0 0 0 0 0	0 5 0	0 0 0 0 0 0
2	0 0 0 0 0 0 0 4 5	0 0 0 0 0 0	0 0 0	0 5 0 0 0 0
3	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0	0 5 0	0 0 0 0 0 0
4	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0	0 5 0	0 0 0 0 0 0
5	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0	0 5 0	0 0 0 0 0 0
6	0 0 0 0 0 2 5 5 5	0 0 0 0 0 0	0 5 0	0 0 0 0 0 0

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Three of six had new feathers among primaries, two had growing ones. No specimen with moulted secondaries were found, five of six had one new tertial fully developed, but only had a new one among the rectrites.

Usually the moults were symmetrical,

except the 6th of the primary (left wing score 17, right wing score 15) and the rectrites of second bird (no renewed feather in left tail). In the UK adults start primary moult before migration. The active moult may continue during the early stages of migration, but probably suspended later, and is finished during winter (Mead 1975, Ginn & Melville 1983).

At Istria we caught much more moulting birds, and one of them was in more advanced stage. It is possible that the moult of the eastern european population differs from the western one.

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Received 5 March 1992, revised 10 September 1992, accepted 25 September 1992.